GENOTYPIC RESPONSE OF SOUTH AFRICAN WHEAT CULTIVARS TO PHOTOPERIOD, VERNALIZATION AND ADAPTATION

BY

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DECLARATION

I declare that the thesis attached herewith for the degree *Magister Scientiae Agriculturae* at the University of the Free State, handed in by myself, is my own work and has not previously been handed in for obtaining a degree at another university/faculty. I hereby relinquish my author's rights in favour of the University of the Free State.

Olaf Müller

31 May 2004

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DEDICATION

I am dedicating this work to the Lord who gave me the ability to complete this task and to my mother and father who raised me with dedication and love. This work is also dedicated to my wife who stood by me with encouragement, care and sacrifice.

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CHAPTER 1

1. INTRODUCTION

Wheat is considered to be the number one grain crop directly consumed by humans world wide. The unique dough characteristics and relative high protein content of bread wheat contribute to the wide acceptance and consumption by the end-user. In South Africa the estimated national wheat crop is 2.1 million metric tons and is grown in the followings three main production areas of South Africa: i) Summer rainfall rainfed regions, ii) summer rainfall irrigated regions, and iii) the winter rainfall rainfed regions.

The summer rainfall, rainfed regions are represented by the Free State province, which on its turn is subdivided into three distinct regions. These regions are the Western Free State, the Central Free State and the Eastern Free State. The Western Free State is characterised by variable rainfall and high temperatures during the summer months. The Central Free State has higher rainfall than the Western Free State, but yield is subjected to variable rainfall during the spring and early summer months. The Eastern Free State is characterised as a region with lower mean temperatures and a higher, more reliable rainfall. Winter, intermediate and in some areas even spring wheats are planted in all the Free State regions.

The irrigation wheat producing regions fall in the summer rainfall region and comprise of two sub-regions: the warmer and cooler irrigation regions. The warmer irrigation areas are, as the name suggests, areas with warmer winter temperatures and also lower yields than in the cooler irrigation region. The cooler irrigation region has low (even vernalising) winter temperatures and yields are often higher than those in the warmer irrigation regions. Wheat production is mainly restricted to spring wheats.

The Winter Rainfall Regions are typical Mediterranean and are subdivided into the Swartland, higher yields and better soil types, the Rûens, and South Western Districts, lower yields and marginal soils. Grain yield is very dependant on rainfall during the winter months, especially early rains to

ensure early planting. Since the winter temperatures are not low enough for proper vernalization and the growing season do not allow for long growing periods, only spring wheat cultivars are planted in the winter rainfall region.

Taking into account the wide array of climatic conditions under which bread wheat is produced in South Africa, and the variable rainfall patterns, it is essential that wheat breeders understand the germplasm that they are working with. It is generally accepted that vernalization requirement and photoperiodic response are the major characters that influence phasic development, and thus adaptation, in bread wheat. Breeders all over the world are using these characters in their breeding programs to seek for the ultimate adapted wheat cultivar.

Although breeders in other countries are also using vernalization and photoperiod genes to select for adaptation, a very low frequency of these introductions into South African programs are adapted well enough for release. The response of genotypes to vernalization and photoperiod, and their interactions with the environment are sometimes unknown to the breeder. Adding the complexity of yield stability to this unknown, further complicates the breeder's task to breed for an adaptive stable bread wheat variety.

The objectives of this study were thus to:

(i) assess some of the most popular bread wheat cultivars on their response to vernalization,

(ii) assess some of the most popular bread wheat cultivars in terms of their response to photoperiod,

(iii) investigate the relation between vernalization, photoperiod and yield stability in 30 South African bread wheat cultivars.

CHAPTER 2

2. LITERATURE STUDY

A brief history

The geographic centre of origin of wheat is the south western region of Asia, where it has been grown for more than 10,000 years (Poehlman and Sleper, 1995). The genetic origin of wheat, according to Poehlman and Sleper (1995), lies in the combination of closely related species to form a polyploid series. Wheat falls under the genus *Triticum*, and the species of *Triticum* are grouped into three ploidy classes: diploid (2n = 2x = 14), tetraploid (2n = 4x = 28) and hexaploid (2n = 6x = 42). Of these species only two are of commercial importance: the hexaploid species, *T. aestivum,* also known as bread wheat; and the tetraploid species, *T. turgidum*, the durum wheat used in pasta making.

Tetraploid wheat, or *T. turgidum* (AABB) constitutes of the diploid species, *T. monococcum* (AA), and an unknown parent containing the BB genomes. *T. aestivum* (with the AABBDD genomes), or bread wheat, is an alloploid that evolved from combining the AABB genomes of *T. turgidum* with the DD genomes of the diploid species of *Triticum tauschii* (*Aegilops squarrosa*). The D genome introduced genes that control the intrinsic baking qualities of *T. aestivum* that are not found in other *Triticum* species (Poehlman and Sleper, 1995).

The 42 chromosome pairs over the three genomes (AABBDD) are divided into seven homoeologous groups. Each homoeologous group contains three partially homologous chromosome pairs, one chromosome pair from each of the AA, BB, and DD genomes. The group number and genome originates from the chromosome and therefore identify each chromosome. Poehlman and Sleper (1995), summarizes that the three chromosomes

within the ABD homoeologous group often contain common loci for a particular character.

Kimber and Sears (1987) also conclude that the way in which the wheat group evolved is clear, and is characterised by a group of diploid species. The diploids diverged from a common ancestor bearing seven chromosomes (gametic number), and tetraploid species resulted from the hybridization between diploids and the consequent doubling of chromosomes. Further hybrid forming between the tetraploids and other diploids evolved, after chromosome doubling, into the hexaploid species.

It is commonly known that the cultivated wheats constitute a series of polyploid species ranging from diploids, as the primary ancestors, to hexaploid. Kimber and Sears (1987) stated that hexaploid wheat evolved from the initial cross between two diploids to form a tetraploid whereto a third diploid was added to finally have the genomic constitution of AABBDD.

Importance of wheat

According to Briggle and Curtis (1987), wheat is the top ranked cereal food grain consumed directly by humans, and its production leads all other crops, including rice, maize and potatoes. It is therefore also true that more land is devoted worldwide to the production of wheat than to any other commercial crop. Poehlman and Sleper (1995) supported this finding by stating that wheat is the world's leading cereal grain and most important food crop. The importance of wheat is derived from the properties of wheat gluten that stretches with the expansion of fermenting dough, but hold together when heated to produce a loaf of bread. Wheat is also used as feed grain, but the quantities vary with relation to wheat and maize prices.

Wheat adaptation

Common wheat (*Triticum aestivum* L. em. Thell.) has the broadest adaptation of all cereal crops and it is cultivated across environments ranging from 60^0 North to 40^0 South. Wheat is a cool-season crop although it flourishes in many different agro climatic zones but it is also known, however, that wheat can also be grown under environmental conditions beyond those prevailing in these limits (Kimber and Sears, 1987).

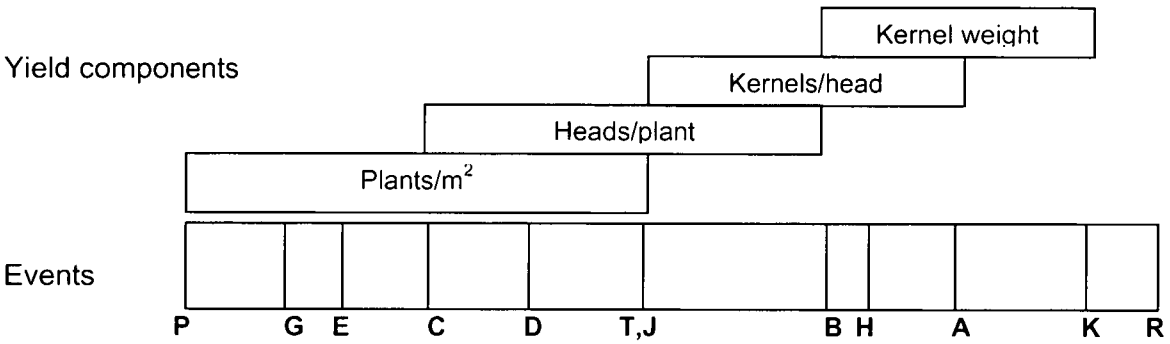
The ability of wheat to produce grain in different regions is controlled by vernalization, temperature, and photoperiod. This is also the reason why wheat is produced throughout the major agro-climatic areas of the world (Mosaad *et al*, 1995). Hexaploid wheat has the largest cultivated area among crop plants due to its adaptability to different agro-climatic conditions. According to Ortiz-Ferrara *et al* (1998), a large part of this adaptability depends on the variation in vernalization and photoperiod requirements.

Košner and Žurková (1996) stated that the genetic control of growth and developmental phases of wheat is complex, determined by vernalization and photoperiodic reactions, and by earliness *per se* genes. Environmental conditions govern the life cycle of wheat through its developmental phases e.g. tillering, stem extension, heading, flowering and physiological maturity. Thus, genes controlling the reaction of the wheat plant to environmental conditions also condition the growth habit of wheat. Using this knowledge, the breeder can alter the life cycle of wheat by selecting plants that can grow, flower and mature in a diverse array of agro-climatic conditions during the periods of the year most favourable to grain production.

Worland *et al* (1998) confirms that the life cycle of wheat is controlled by three sets of genes, e.g. vernalization, photoperiod and earliness *per se*. Two of these sets: vernalization and photoperiod acts in response to the

environmental stimuli, whilst the third set of genes, earliness *per se*, acts independently of the environment. These three sets of genes determine the number of vegetative and floral primordia being initiated or their rate of development after initiation. Photoperiod and temperature are also two major environmental determinants of plant phenology, adaptation and yield (Yan and Wallace, 1998).

To be successful in selecting genotypes that are adapted in a wide or narrow sense, it is important to fully understand the developmental phases and their influence on yield. Total yield can be defined as the sum of the contributions made by each yield component; plants/m^2, heads/plant, kernels/head, and kernel weight. The contribution of each yield component is influenced by interactions between developmental events and environmental factors. The yield components with the developmental events are illustrated in Figure 2.1.



P = Planting
G = Germination
E = Emergence
C = Tillering begins
D = Double ridge
T = Terminal spikelet
J = Jointing
B = Boot begins
H = Heading begins
A = Anthesis
K = Grain fill ends
R = Ripe, Harvest ripe

Figure 2.1 Developmental events related to yield components for wheat (modified from Klepper *et al*, 1998)

Plants/m^2, the first yield component, is the result of planting density, and survival rate from planting to spring. Tillering and tiller abortion determine the second yield component (heads/plant), whilst the third yield component, kernels/head, is the result of the length of spikelet and floret development duration, and pollination success. Kernel fill, the fourth and last component, is ultimately a function of the processes prior and immediately after anthesis, and the rate and duration of kernel fill (Klepper *et al*, 1998). The challenge to the plant breeder therefore is to select a genotype that completes all phases of development within the window of optimum environmental conditions by using the control measures available through vernalization requirement, photoperiodic response, and earliness *per se*.

The varietal variation in heading time and its constituent of these previously mentioned three characters result in the wide adaptability of bread wheat (Kato and Yokoyama, 1992). Poehlman and Sleper (1995) attribute adaptation of wheat cultivars to different environments to the general relatedness of physiological characteristics to vernalization requirement, cold tolerance, and photoperiodic response.

The timing of the reproductive cycle in wheat is an important determinant of yield. Schipper (1996) considers the yield of wheat and other cereal crops to be the result of the number of ears per plant, number of spikelets per ear, number of kernels per spikelet and kernel weight. Thus, for any given grain crop to produce and reproduce it has to flower, which makes this period the most important phase of all developmental phases. It is therefore important when breeding wheat to be adapted to a specific environment, that the life cycle of the wheat plant is adjusted so it flowers and matures at the most expedient time. The development of delicate floral primordia should occur during a period when damage from adverse conditions is unlikely and flowering is followed by a sufficient period of favourable conditions to permit grain filling and development (Worland, 1996).

Miura and Worland (1994) ascribes part of the wide adaptability of wheat to the exploitation of genes that control ear-emergence time. The most important genes to control ear emergence time are the genes for vernalization and photoperiodic responses, which are associated with the geographical origins of different wheat varieties (Hunt, 1979).

Stefany (1993) reports that wheat is grown around the world in environments which vary widely in amount and seasonal distribution of rainfall, as well as temperatures and temperature ranges experienced during the growing season. Adaptation is therefore often dependant on the crop reaching anthesis at an optimal time with respect to environmental limitations. Again it is stated that vernalization requirement and response to photoperiod are the two major mechanisms through which the development rate in wheat is controlled. Stelmakh (1981) suggests that the *Vrn* genes contribute up to 70 – 75% of differences in the total length of the wheat cycle.

Adaptation of wheat to diverse agro-climatic conditions can thus be summarised as the result of its genetic response to the two major environmental stimuli: temperature (vernalization) and photoperiod. These are under genetic control and therefore available to the wheat breeder to manipulate the life cycle of the wheat plant to best fit the environment it is intended for.

Wheat adaptation is the result of a complex interaction between the genetic background of varieties and how these varieties interact with environmental factors. Halloran (1975) concluded that the processes determining the timing of flowering and development (i.e., vernalization, photoperiod responses, and those influenced by growth temperature) can therefore be considered as highly significant to wheat's adaptation and yield. Appleton and Haggar (1985) added to that by stating that an understanding of adaptation allows better targeting of germplasm to specific environments, reduces the risks of crop failure, and allows better targeting of inputs to ensure maximum production. It is clear then that a

better understanding of the genetic control of flowering, as expressed by vernalization requirements and photoperiodic response, will guide breeders in targeting crosses of different types and improve understanding of regional adaptation requirements (Ortiz Ferrara *et al*, 1998). Photoperiod and vernalization are thus usually considered to account for almost all, if not all of the differences between cultivars in development rate (Slafer, 1996).

Vernalization requirement and response in wheat

Pugsley (1970) classified wheat on its genomic constitution of at least three dominant genes. He concluded that any one of these genes is able to suppress the expression of the winter growth habit. In a later study Pugsley (1972) confirmed these results and added that winter wheat cultivars carry the recessive alleles at all of the above-mentioned three loci. Pugsley, in consultation with Dr R. A. McIntosh (Pugsley, 1972) designated the genes governing spring habit as *Vrn1*, *Vrn2*, and *Vrn3*.

In many plants temperature has a profound influence on the initiation and development of reproductive structures. Lysenko (1928, as cited by Chouard, 1960) used the term vernalization to refer to the phenomenon in wheat where the duration of the vegetative phase is reduced by exposure to low temperatures. Purvis (1961) defined vernalization as the promotion of flowering by previous exposure of a plant to low temperatures in the range of 0 to 15°C. Flood and Halloran (1986) see vernalization as a physiological process of widespread occurrence where its adaptive value essentially appears to be the delay of initiation of floral development. When the word vernalization is directly translated from Latin to English it results in "springisation" (Crofts, 1989). This implies that a plant is converted from a winter growth habit to a spring growth habit. Crofts (1989) suggests four definitions for a winter wheat: 1) Winter wheat is a wheat sown before winter; 2) Winter wheat is a wheat possessing a strong vernalization response compared to an intermediate type which has some

response to vernalization and a spring type which does not respond; 3) Winter wheat is a wheat which has a long vegetative period, prostrate growth and freezing resistance beyond that found in wheat with an intermediate habit or spring habit; 4) Winter wheat has only recessive alleles at all *Vrn* loci. For the purpose of this study, only definitions two and three are valid, whilst definition four is assumed for the so-called strong winter types.

Hexaploid wheat is a polyploid that originated from two major evolutionary events as stated earlier. Polyploids lend themselves to the loss or increase of chromosome dosage due to the genetic duplication that occurs in polyploids. This is also known as aneuploidy. The ability of hexaploid wheat to tolerate the loss of a chromosome has enabled the substitution of single chromosomes from donor varieties for their homologues in a recipient variety (Sears, 1953). Law *et al* (1976) used aneuploid and inter-varietal chromosome substitution lines to locate the position of genes controlling the spring-winter growth habit of bread wheat. They concluded that *Vrn1* is located on the long arm of chromosome 5A and *Vrn3* is located on the long arm of chromosome 5D. The specific use of Vrn3 combined with a gene(s) conferring insensitivity to photoperiod is encouraged by the Plant Breeding and Genetics Institute in Odessa, Ukraine, to develop spring wheat cultivars with improved adaptation to environments prone to late drought and heat stress (Stelmakh, 1993). Law (1966) assigned an additional locus, *Vrn5*, to the short arm of chromosome 7B. From the literature cited, *Vrn1* and *Vrn3* are viewed as the most important genes controlling vernalization requirement.

There are numerous responses to vernalization treatment differing within and between species. In winter and facultative or intermediate wheat types the response to vernalization is delayed, meaning that it will only flower after being exposed to a minimum period of cold and not during the cold treatment itself. The flowering response to vernalization is dependent on the temperature and the duration of the vernalization period. Slafer and Rawson (1994) found that there is considerable genotypic variation in the

response to vernalization that can show itself differentially in the durations of both pre- and post double ridge stage. They further concluded that the effects of vernalization are commonly greater on the earlier phase than on the later phases.

It is to be expected that an array of genotypes will produce a range of different responses to varying vernalization periods. Flood and Halloran (1984a) vernalised 16 Australian spring wheats and four near-isogenic lines of Triple Dirk's (differing for vernalization response) for periods of 4, 6 and 8 weeks. They found no difference in days to ear emergence between the 4, 6 and 8 weeks vernalization treatments among Triple Dirk (two dominant alleles on *Vrn 1* and *Vrn 2*), Triple Dirk D (a dominant allele on *Vrn 1* only), and Triple Dirk B (a dominant allele on *Vrn 2*), and with the Triple Dirk C (complete recessive on *vrn 1*, *vrn 2* and *vrn 3*) there was no difference between the 6 and 8 weeks treatment. According to their data this indicates that the requirement for the vernalization genes, *vrn 1* and *vrn 2* is met with 4 weeks of cold when genes occur singly and by 6 to 8 weeks when they are combined.

Wang *et al* (1995) used two winter wheat cultivars that were adapted to Michigan, USA, namely Pioneer 2548 and Augusta, to evaluate the length of vernalization period required and the response of plant age to vernalization. In their study all plants in all treatments, including the unvernalised controls headed and flowered. According to their data all vernalization treatments equal or longer than 14 days reduced final leaf number relative to the unvernalised control in one or more age treatments. They found that the number of days of vernalization required reaching insensitivity to further cold treatments changes with plant age, expressed as leaf stage, as well as with genotype. This is illustrated in the response of genotypes to vernalization where leaf tip stages (LTS) 0 to 1 reached no plateau in response to vernalization after 70 days, whereas LTS 2 to 7 reached a plateau from days 49 to 35.

Using four Triple Dirk isogenic lines Flood and Halloran (1984a) set up a 0, 2, 4, 6, 8, and 10 weeks vernalization treatment trial. Seeds were imbibed and sown into a soil mixture after which they were vernalised at 3°C. They also found no response for the *Vrn 1* genotypes when vernalised for 4 weeks or less. The *vrn 1* genotypes, however, showed a significant difference in ear emergence when vernalised for 4 weeks and less, i.e. the longer the duration of vernalization, the shorter the days to ear emergence. These genotypes exhibited a cumulative response on vernalization treatment up to 4 weeks, but vernalization periods greater than 6 weeks did not significantly alter the number of days to ear emergence. They came to the conclusion that after floral initiation, genes for vernalization response have no further effect on floral development.

In their investigation of the relationship between cold resistance and heading traits, Fujita *et al* (1992) subjected 30 genotypes to 9 (0, 10, 20, 30, 40, 50, 60, 70, and 80 days) vernalization periods. They found clear differences in vernalization requirement between spring and winter wheat cultivars, ranging from 20 to 40 days in spring wheat cultivars and from 50 to 80 days in winter wheat cultivars. To differentiate between winter and spring wheat cultivars they used a 24-hour photoperiod at 20°C with no vernalization treatment. Spring wheat cultivars were defined as those whose flag leaf unfolded within 90 days after planting. Vernalization requirement was expressed as the minimum duration of low-temperature treatment necessary to reach full vernalization, and was evaluated by comparing the days from the first leaf unfolding to the flag leaf unfolding.

Much has been said on the length of vernalization treatment and the response of genotypes to this vernalization period. As mentioned above some so-called winter genotypes were fully vernalised, or reached a state of vernalization insensitivity in as little as 4 to 6 weeks (Flood and Halloran, 1984a). Fujita *et al* (1992) reported wheats that were only saturated for vernalization after 80 days. Gotoh (1976) reported that 8 weeks cold treatment should saturate virtually all wheats, but results obtained by Košner and Pánková (1996) suggested that 8 weeks vernalization is not

entirely sufficient for all the allelic combinations. From the literature cited it is thus concluded that there are vast differences between winter genotypes in their reaction to the length of the vernalization period, and therefore the definitions of winter types for different regions.

In setting the vernalization period it is also important to choose the correct temperature at which vernalization is induced. If interactions between temperature and genotypic constitutions exist, surely there should then also be an optimum temperature and an optimum period of vernalization. According to Flood and Halloran (1986) winter types bear all major vernalization genes in the recessive state and these genotypes are found in habitats where the daily mean temperatures are between 2-4^{0}C for at least seven continuous weeks. They further state that genotypes that are adapted in warmer areas show a replacement of the recessive alleles with the dominant form and thereby reducing the cold requirements for flowering.

Briggs (1999) used a vernalization temperature of 0.5^{0}C for six weeks in the dark to evaluate the response of Canadian and other spring wheat cultivars for days to heading, days to maturity and days from heading to maturity. He found that only 40% of the genotypes, for days to heading, showed significant ($P<0.20$) response to vernalization. He concluded that although the vernalization protocol he used is only one of many that could have been used to determine genotypic responses, it is a protocol that had a significant effect on many of the genotypes used. In another study of flowering time Dubcovsky *et al* (1998) used parents of the *T. monococcum* mapping populations and *T. aestivum* varieties Sonora 64 (spring type) and Klein Rendidor (winter type) and vernalised these for six weeks with an 8-hour photoperiod at 10^{0}C. The vernalised and unvernalised plants were grown under short and long day conditions. Some unvernalised plants failed to reach ear emergence even under long day conditions. Large differences were also found between vernalised plants under long and short days.

Ortiz-Ferrara *et al* (1995) examined two techniques for screening wheat genotypes for their response to photoperiod and vernalization and to compare them to field screening. They vernalised seedlings at 1 to 2^0 C for six weeks and confirmed the sensitivity of wheat development to vernalization. In a study on the response of Mediterranean wheats to photoperiod and vernalization and its implication for adaptation, Ortiz-Ferrara *et al* (1998) again used 1 to 2^0C for six weeks as vernalization treatment. Midmore *et al* (1982) used a pre-treated vernalization treatment of 1 to 2^0C for four weeks in the dark to vernalise spring wheat to evaluate phasic development and spike size of wheat in tropical environments. They concluded significant difference between genotypes when vernalised *versus* not vernalised. On the other hand Mosaad *et al* (1995) investigated the effect of vernalization on the total number of leaves and the rate of leaf emergence in spring and winter wheat genotypes. They also used a vernalization temperature of 1 to 2^0C for six weeks and found that vernalised winter wheat plants stopped tillering at flowering, while nonvernalised winter wheat plants continued to produce leaves and tillers until the trial was terminated. In another study Wang *et al* (1995) also used final leaf number and a series of vernalization periods to derive a generalised conceptual model for wheat vernalization. Their vernalization treatment consisted of 5^0C during the light period and 2^0C during the dark period. Stelmakh (1993) in his investigation of the genetic effects of *Vrn* genes on heading date and agronomic traits in bread wheat used 2^0C as well, but he applied continuous light for the total length of the fifty day photoperiod.

Flood and Halloran (1984a), in their study of basic development rate in spring wheat, used 3^0C at three different vernalization periods under 12 hour light and found that the vernalization requirement of genotypes with *vrn 1* and *vrn 2* is satisfied by four weeks of cold when in single dose and 6 to 8 weeks when combined. In another study done by Flood and Halloran (1984b), they again used 3^0C to investigate the nature and duration of gene action for vernalization response in wheat. Fujita *et al* (1992) followed the same vernalization temperature scenario and used 3^0C over 8

treatment periods to evaluate the physiological traits influencing heading date in wheat.

Cahalan and Law (1979) used 4^0C in the dark for three weeks followed by a two-week period at 8^0C with 8 hours light to vernalise the genotypes in their study. They found significant differences in period to ear emergence between genotypes when using these temperature settings. Griffiths *et al* (1985) treated germinated grains with a temperature of 4^0C over six weeks to evaluate the effects of vernalization on the growth of the wheat shoot apex. Studying the related concepts of the basic vegetative period in wheat, Slafer *et al* (1995a) vernalised imbibed seed of four wheat varieties at a temperature of 4^0C for 50 days. Miura and Worland (1994) used 4^0C as vernalization temperature as well in their quest to identify homoeologous group-3 chromosomes that carry genes for vernalization. In reporting of and implicating *Vrn* and *Ppd* genes with response to salt stress, Taeb *et al* (1992) used a 4^0C temperature treatment on four-day-old seedlings to neutralise the effect of vernalization requirement. A vernalization temperature range of 4 to 5^0C was used by Rawson and Zajac (1993) to determine if the rate of development, expressed in thermal time, slowed at high temperatures. They concluded that cold treatment resulted in earlier ear emergence.

Pugsley (1970), one of the pioneers in defining the genetic mechanism of vernalization in wheat, used 5^0C as vernalization temperature for his genetic analyses of the spring-winter habit of growth in wheat. Penrose *et al* (1991) measured the degree of winter habit, and its relationship to other developmental controls by vernalising seedlings in the dark for seven weeks. Stefany (1993) used a vernalising temperature of 6^0C over six weeks in darkness to evaluate the response of a diverse set of genotypes to vernalization.

Researchers use low temperature treatments to evaluate or investigate adaptation related traits such as vernalization requirement, photoperiod sensitivity, and intrinsic earliness. Cold treatment is used to neutralise the

vernalization requirement of winter wheats and from the literature cited it is clear that a wide array of vernalization temperatures were used and is still being used. Rawson *et al* (1998) concluded in their study on the effect of seedling temperature and its duration on development of wheat cultivars differing in vernalization response that cold treatment of 4^0C will always lead to flowering. Their study did, however, point out that optimum vernalising temperatures might differ between genotypes.

Photoperiod requirement and response in wheat

Photoperiod, like vernalization, is a mechanism controlling flowering time in bread wheat and therefore plays an important role in adaptation. The importance of photoperiodic response is found in the influence it has on the duration and the course of fundamental growth, including leaf and floral initiation, and developmental phases. Yield is indirectly affected by the direct influence of photoperiod on the photoperiodic response of a genotype. Although bread wheat is classified as a natural long day plant, the modern commercial varieties respond differently to photoperiod duration. This gives wide adaptability throughout the world (Košner and Žurková, 1996). Most of the wheat grown in the world is grown in environments where the early part of the vegetative phase is completed under short photoperiods, although considerable and increasing areas of wheat are grown in sub-tropical Asia. This necessitates the understanding of phenological response to moderate photoperiods (Slafer and Rawson, 1995b).

Photoperiod requirement can be described as the sensitivity of a genotype to day length and it affects the rate of development in many crops. Photoperiod sensitive genotypes typically require long days to initiate floral primordia. According to Gotoh (1979) radiation becomes photoperiod effective at dawn, or when the sun is 6^0 below the horizon. Wang and Engel (1998) categorise plants into four major groups: short day plants, long day plants, day neutral plants, and one dual photoperiod response, the short-long day plants. According to them the development rate

decreases under non-optimal day length. The threshold between optimal and non-optimal day lengths can be defined as the maximum optimal photoperiod for short day (photoperiod insensitive) plants or alternatively it is the minimum optimal photoperiod for long day (photoperiod sensitive) plants. Leaves perceive the photoperiod stimulus from where a signal is transmitted to the apex (Evans, 1987). The plants can consequently not respond to photoperiod before it has emerged from the soil. It is assumed that wheat do not have a juvenile phase to go through before responding to photoperiodic stimuli (Slafer and Rawson, 1994). The plants therefore have the potential to respond to photoperiod throughout their life cycle, from emergence to maturity. Stefany (1993), however, concluded in his study on vernalization requirement and response to day length that there is indeed a phase when genotypes are insensitive to day length, and when development is vegetative. After this phase initiation of floral primordia is induced and progress towards flowering is affected by day length. He further concluded that the juvenile phase in spring wheat is shorter than in facultative and winter wheats. Fedorov (1995) states in his study that the type of development and duration of the vegetative phase are determined by the reaction of plants to light at the initial period of life, rather than by vernalization. He concludes that there are only two photoperiodic reactions: a strong expression in non-vernalised plants and a weak expression in vernalised plants. In contrast to this conclusion Slafer and Rawson (1995b) found vernalising temperatures as well as photoperiod can change the period of crop growth as well as the relative duration of each phase in plant development. Worland (1996) states that photoperiod genes are sensitive to the length of day and photoperiod sensitive varieties therefore require a period of long days to initiate the production of floral primordia. When photoperiod sensitive genes are combined with vernalization sensitive genes, floral initiation will be delayed, even if the vernalization requirement of such genotypes is met during winter. This delay will be present until the photoperiod requirement of the genotype is satisfied.

Welsh *et al* (1973) and Law *et al* (1978) concluded from their studies, that insensitivity to photoperiod is controlled by three dominant orthologous *Ppd* genes located on the group-2 chromosomes. From research done by Keim *et al* (1973), Pirasteh and Welsh (1975), and Law *et al* (1978) it is evident that *Ppd1* is located on chromosome 2D, *Ppd2* on chromosome 2B and *Ppd3* on chromosome 2A. A study with aneuploids done by Miura and Worland (1994) implicated chromosome 3D with an additional *Ppd* locus and also found allelic variation on chromosomes 3A and 3B in substitution lines. These results were not conclusive in determining if the responses found were due to genes for day length response. As in the case of vernalization, Pugsley (1970, 1972) stated that insensitivity to photoperiod duration is dominant over sensitivity to day length, with individual dominant alleles expressing different responses to day length. Federov (1995) claimed methodological mistakes in data processing and analyses of the so-called Lysenko and Pugsley followers. He used three photoperiod treatments, natural, 12-hour, and continuous illumination to evaluate the response of the offspring of crosses made between varieties differing in their type of development. The F1 progeny (winter x spring cross) was six days earlier than the spring type parent under natural light and 30 days under 12-hour photoperiod. Crosses between different genotypes resulted in different responses to photoperiod. He therefore concluded that no predominance in terms of reaction to light, type of development, or duration of vegetative period was observed. Welsh *et al* (1973) concluded that *Ppd1* is epistatic to the other alleles. In his study on the influence of flowering time genes on environmental adaptability in European wheats, Worland (1996) ranked the potency of the group-2 photoperiod genes for insensitivity in the order *Ppd1>Ppd2>Ppd3*, meaning *Ppd1* as the least and *Ppd3* the most sensitive to photoperiod duration.

The primary effect of *Ppd1* is to accelerate the time to heading, with the degree of acceleration dependant on environmental conditions (Worland *et al*,1998). Worland (1996) indicated that *Ppd1* exhibited significant pleiotropic effects on a large number of agronomic characters. *Ppd1* shortens the plant's life cycle and thereby reduces vegetative and floral

primordia, which then produces a shorter plant with smaller ears and fewer tillers. According to Worland (1996) the reduction in height caused by pleiotropic effects of *Ppd1* is always greater than the reduction in plant height caused by the dwarfing gene *Rht8*. *Ppd1* more than compensates for the reduction in spikelet numbers through significant increases in grains per spike in the first and second florets as well as a large increase in the number of grains setting in the central florets of each spikelet.

Islam-Faridi *et al* (1996) investigated the response of Chinese Spring (CS) euploid, the three monosomics of groups 2 and 6, and the short- and long-arm ditelosomics of chromosome 6B. Group-2 monosomics returned expected results where major differences were found for chromosome 2B and presumably reflected the previous known location of *Ppd2* on this chromosome. This experiment resulted in a delay in ear emergence under short days when the dosage of *Ppd2* is reduced. A different behaviour was found in the monosomics of group-6 chromosomes with respect to the potency of expression of the response to photoperiod. It is noted that the loss of both doses of the gene carried on chromosome 6 may be required to express a response due to the possibility that the gene(s) for day length insensitivity on the long-arm of 6B may be hemizygous effective. The opposite may also be true; that the gene(s) responsible for day length sensitivity show a degree of hemizygous ineffectiveness and is therefore only expressed when the gene dosage is reduced by one. Some evidence was also found of related day length sensitive genes on chromosomes 6A or 6D.

Levy and Peterson (1972) found that photoperiod plays an important role in the transition of the shoot apex from producing leaf primordia to producing spikelet primordia. Various studies were carried out on the rate of leaf appearance in response to photoperiod (Cao and Moss, 1989), but it did not address the effect of photoperiod on leaf dimensions or leaf area components (Pararajasingham and Hunt, 1996). Pararajasingham and Hunt (1996) undertook a study to evaluate the effects of photoperiod on various leaf area components. They subjected eight wheat cultivars to

four photoperiod regimes (8, 12, 16, and 20-hour day length) to measure length and width of the main stem leaves when these leaves were fully expanded. Only one spring wheat cultivar responded in enhancing leaf rate appearance under 20-hour photoperiod, while the rest showed no effect. The final number of leaves formed under 8 and 12-hour photoperiods was higher than the final leaf number under 16 and 20-hour photoperiod. When the apex changes from the vegetative to the reproductive phase, all leaf primordia and some spikelet primordia have been initiated and thus the longer the vegetative phase, the more leaf primordia are initiated and hence the higher final leaf number will be. If shorter photoperiods lead to a lengthening in the vegetative period it explains why the final leaf number in spring wheats is higher under shorter photoperiods. Leaf length of spring wheat cultivars grew progressively shorter as photoperiod was extended. This is attributed to the competitive demands following a change in the reproductive condition of the plant.

In defining the response of bread wheat genotypes to photoperiodic duration it is necessary to evaluate the response of these genotypes under varying day lengths. Stefany (1993) used three photoperiod treatments to evaluate the response to day length in 8 different genotypes. He controlled day length with black sheeting when shorter photoperiods were required and used halogen lamps to extend the photoperiod. All genotypes responded to day length in reaching the double ridge phase more quickly the longer the photoperiod and he therefore concluded that a day length insensitive genotype does not exist. More variation was found between genotypes in the control treatment and less genotypic variance in the extended photoperiod treatment. Midmore *et al* (1982) studied the phasic development and spike size of wheat in tropical environments and used growth cabinets to quantify the sensitivity of 37 genotypes to photoperiod. Using two photoperiods, 10 hours and 14 hours, they found that the longer photoperiod led to the earliest flowering. Genotypes were considered sensitive to photoperiod if the delay in flowering was more than 16 days. From the results the genotypes were divided into five groups: insensitive to photoperiod, sensitive to photoperiod, sensitive to

vernalization, sensitive to vernalization and photoperiod, and very sensitive to photoperiod (delay in flowering more than 51 days).

Mosaad *et al* (1995) studied the phyllochron response to vernalization and photoperiod using three photoperiods: 8, 12 and 16-hours. They found that the number of leaves at anthesis on the main stem decreased as the length of photoperiod increased. There was no significant reduction in leaf number between the 12 and 16-hour treatments, indicating that these genotypes were not very sensitive to day length. Flag-leaf size also decreased with increasing photoperiods. They concluded that both vernalization and photoperiod control phenology, but for simplicity and consistency it should be advantageous if selection of spring wheat adapted to the tropics were controlled through the mechanism of photoperiod.

The effects of higher temperatures, photoperiod and seed vernalization on development in two spring wheat varieties were evaluated by Rawson and Zajac (1993). Their results indicate that ear emergence occurred progressively earlier with longer photoperiods regardless of temperature or seed vernalization treatment. The leaf number at ear emergence was higher in shorter photoperiods than those in longer photoperiods. Penrose *et al* (1991) acknowledges the fact that short photoperiods delay floral development in wheat sensitive to day length, but states that short photoperiods may promote floral initiation in winter wheat. In a study using 9, and 18-hour day length they found that photoperiod sensitive spring wheat attained ear emergence before all winter wheats in summer sowings, but later than all except winter wheat sensitive to photoperiod, in winter sowings and concluded that wheat differed significantly in response to photoperiod. Evans (1987) suggests that floral initiation is not responsive to photoperiods exceeding 18 hours.

Ortiz-Ferrara *et al* (1995) investigated two techniques to screen wheat genotypes for their response to photoperiod and vernalization and to compare these to field screening. The photoperiodic response of twenty genotypes was evaluated under 8, 12, and 16-hour photoperiods. The

genotypes were classified as either photoperiod sensitive or insensitive. Genotypes were classified as photoperiod sensitive if the delay in anthesis was more than 16 days. They found a significant decrease in days to anthesis with an increasing light duration. Ortiz-Ferrara *et al* (1998) again investigated photoperiod and vernalization response of wheats and the implications for adaptation, but this time specifically for Mediterranean wheats from the west Asia and north Africa (WANA) regions. Three photoperiods, 8,12, and 16-hour light duration were used for 49 genotypes (19 old cultivars and 30 improved cultivars) under two vernalization treatments. As in their previous study, days to anthesis decreased significantly with increasing light duration. The 49 genotypes were divided into four groups based on the main effects of photoperiod and vernalization. All except one of the genotypes that were classified as insensitive to vernalization and photoperiod were improved cultivars, indicating that the majority of the modern adapted wheats in low latitudes of WANA have been selected for insensitivity to both vernalization and photoperiod. Thirteen genotypes were sensitive for vernalising temperatures, but insensitive to photoperiod duration. Again the majority of these genotypes (11 from 13) were modern cultivars. Ortiz-Ferrara *et al* (1998) suggest that low sensitivity to photoperiod is a characteristic of new high yielding wheat cultivars, sown in latitudes below 40^0 north and south. These are areas where spring wheats are often adapted. They claim that screening for day length sensitivity can be done in a greenhouse under 12 and 16-hour day lengths.

Other studies done on the distribution of varieties carrying genes for insensitivity to photoperiod also indicate that specific genotypic constitution of improved varieties is better adapted at certain latitudes. Hunt (1979) suggested that the northern latitude countries (Canada, UK, and France) are better suited for genotypes highly sensitive for photoperiod, whilst those grown at more southern latitudes (Italy and Yugoslavia) were highly insensitive to photoperiod. Again the older varieties or landraces in the southern parts of Europe were more sensitive to photoperiod than the more modern varieties. Worland *et al* (1998) found a clear division

between northern and southern Europe in terms of photoperiod sensitivity. They concluded that all tested southern European wheat varieties were highly insensitive and northern European varieties selected in the UK or Germany were highly sensitive to photoperiod. Until recently wheat cultivars in the central and southern wheat belt of New South Wales (Australia) relied upon photoperiod sensitivity to delay crop development to avoid frost damage during anthesis in early spring (Martin, 1981). Photoperiod insensitive winter wheats have been introduced to south-central New South Wales and Penrose and Martin (1997) compared the effects of winter habit and photoperiod sensitivity in delaying ear emergence in wheat. Their findings show that photoperiod and temperature determine the development of photoperiod insensitive spring wheats. Ear emergence was more accurately predicted for photoperiod insensitive winter wheats than for facultative or spring wheats with mild sensitivity to photoperiod. Winter wheats also had a wider sowing window than photoperiod sensitive spring wheats.

Investigating the effects of high temperature and photoperiod on floral development Rawson and Richards (1993) used four photoperiod regimes: 9, 11, 13, and 15-hour photoperiods and two temperature treatments: 33,3/20^{0}C and 20/12^{0}C maximum/minimum temperature, to evaluate the response of six Triple Dirk isolines. From their research, they found that all isolines headed earlier when photoperiod increased even in isolines classified as photoperiod insensitive. Little overall effect of temperature on the response to photoperiod was observed, but lines did, however, differ in their individual responses to temperature. Double ridges appeared later under shortened photoperiods and final number of spikelet primordia increased, although the rate at which spikelet primordia appeared decreased with shortening photoperiods. These simple patterns were absent under high temperature regimes. In conclusion they suggested that the degree of interaction between temperature and photoperiod for genotypes can be characterised by growing plants under 8, and 15-hour photoperiods at two contrasting temperatures.

According to Slafer and Rawson (1995b) the interactions found between photoperiod and temperature may not be of practical consequence in areas where crops are exposed to phenological delaying factors of short photoperiod and vernalising temperatures. These interactions could, however, be significant in areas where one factor is delaying development and the other is accelerating development. They therefore used 6 photoperiod treatments; 9, 12, 15, 17, and 21-hour light duration, and two temperature regime treatments: 16 /12 and $21/17^0$ maximum/minimum values. The photoperiod treatments resulted in all genotypes to respond to photoperiod by heading earlier. All genotypes also reached heading significantly earlier at higher temperature under all photoperiods. In their study they found that all the interactions between photoperiod and temperature were highly significant. When comparing photoperiod x temperature interactions under the extreme photoperiod regimes, Slafer and Rawson (1995b) found that the response to temperature was not the same at different photoperiods and it varied amongst genotypes. This also resulted in different optimum temperatures under different photoperiod regimes for each genotype. Again they found, as previous authors did, that the interaction between photoperiod and genotype is highly significant. Some genotypes displayed a qualitative response under short photoperiods, but a quantitative response under longer photoperiods, whilst other had a quantitative response throughout. Heading time of all genotypes was affected by photoperiod, temperature, and by photoperiod x temperature interactions, however, only final leaf number was affected by photoperiod. It was thus concluded by the authors that photoperiod and temperature affect development in wheat through different mechanisms. According to them, increasing photoperiod reduces the number of leaf primordia initiated, and therefore leads to a reduced time to heading. Increasing temperature, on the other hand, accelerates the rate of leaf initiation as well as the rate of development. They also found that the optimum photoperiod for final leaf number was much shorter than the optimum photoperiod for time to heading. Importantly this difference suggests that the effect of photoperiod on time to heading is completely independent from that on final leaf number and the correlation between

these two traits is not causal, or alternatively that photoperiod affects the rate of development and leaf number in a dependant fashion to the stage when final leaf number is fixed, such as terminal spikelet appearance from where photoperiod only affects development.

Yan and Wallace (1998) put a challenge to the usual assumptions that appropriate photoperiod is required to induce flowering. They cited Summerfield *et al* (1993) and quoted: "Genes conferring photoperiod sensitivity can cause delays in flowering but cannot promote flowering". This in other words means that the development of plants happens autonomously and photoperiod sensitivity or the response to photoperiod only delays this autonomous process. In conclusion they state that this photoperiod gene action can only delay development in proportion to the point where light duration is beyond the critical photoperiod and above a base temperature.

Intrinsic earliness

Much has been said on the influence of the group-2 and group-5 chromosomes on adaptability of wheat under a wide range of agro-climatic conditions. These chromosomes carry genes for photoperiod response and vernalization requirement in wheat. It is also well documented that in addition to these genes another set of genes play an important role in wheat adaptation (Keim *et al*, 1973; Same, 1973; Halloran 1975). If all requirements for vernalization and photoperiod are fully satisfied, there is still variation between genotypes in time to heading, flowering and physiological maturity (Slafer and Rawson, 1995a). Thus there are still developmental differences among genotypes once the delaying mechanisms of vernalization and photoperiod have been nullified by low temperatures and long photoperiods respectively. In most cases this phenomenon of variation in flowering time has been given a name or different names. Ford *et al* (1981) referred to it as "earliness", while Takahashi and Yasuda (1971) called it "earliness in the narrow sense". Other authors named it "earliness *per se*" (Hoogendoorn, 1985), "minimum

vegetative period" (Yasuda, 1981), "basic vegetative period" (Major, 1980), "flowering tendency" (Wallace, 1985), "intrinsic earliness" (Masle *et al*, 1989), "base maturity" (Koester *et al*, 1993), and "basic development rate" (Flood *et al*, 1984b). Slafer and Rawson (1995a) listed some theories surrounding earliness *per se* as:

- Each phase in the development of a plant has a set minimum time duration that is an absolute value for a specific genotype regardless of other conditions.
- When using thermal time as measurement of earliness *per se*, the minimum period is not influenced by temperature.
- The minimum period concerned is only relative to a certain identified stage, which serves as a marker for flowering such as floral initiation, heading, or anthesis.
- Earliness *per se* is measurable as a rate, which is the result of continuous change.

Slafer (1996) summarised and described intrinsic earliness as: "A major, intrinsic factor influencing the length of the vegetative phase (i.e. the time to floral initiation) independently of any effects of photoperiod and vernalization. i.e. it is responsible for any difference in time to ear emergence among genotypes under above-optimum photoperiod and vernalization conditions, when the responses to photoperiod and vernalization are saturated".

Evidence of the existence of a so-called "third-factor" influencing the rate of genotypic differences in terms of phenological development was gathered by Flood and Halloran (1984b). They referred to this factor as "basic development rate" and suggested that these gene(s) control the rate of development in the absence of vernalization and photoperiod responses. A vernalization period of 8 weeks at 3^0C was used to evaluate the differences in basic development rate of 21 spring wheats. Differences, although not large, in this development rate lead the authors to believe that it may be important for adaptability and thus yield in wheat. According to them the possibility of interactions between basic

development rate and temperature, and photoperiod and temperature does exist, and that these interactions have a much stronger influence on time to ear emergence in normal (field conditions) sowings. After further investigation they found no association within genotypes to vernalization response, and had no data to support any conclusion on photoperiod and basic development rate interactions. From their data they could also not determine whether the basic development rate increases or decreases the rate of development in a genotype and if the different phases of development were influence differently relative to other genotypes. In the chromosome substitution study (7B of Thatcher with that of CS) the increase in basic development rate and decrease in vernalization response indicated that chromosome 7B carries genes that influences both vernalization and basic development rate. This is considered to have important implications for plant breeders since it proved to be a qualitative character.

Slafer and Rawson (1995b) conducted a study to investigate whether diverse genotypes differed in the duration between sowing time and anthesis, if measured in thermal time, and if the response of genotypes remains the same under six temperature regimes. They extended their study to determine whether the rankings in terms of earliness of these genotypes change under different temperature treatments. If ranking changed under various temperature conditions they aimed to identify the stage(s) of development in which this occurs. Four wheat varieties were grown under 18-hour light duration and six (10, 13, 16, 19, 22, and 25^0C) temperature treatments. All varieties were vernalised at 4^0C for 50 days. They found that the earlier genotype was always earlier than the latest genotype and was thus intrinsically earlier, although the basic vegetative period for each genotype was not absolute, and varied across temperature treatments. It is thus clear that if a basic vegetative period exists, that period is affected by temperature. The presumption that thermal time can be used to remove temperature effects did not contribute to assign a value of intrinsic earliness in this study. From this the authors concluded that intrinsic should not be linked to earliness, because of the

complex interaction between temperature and development. The same argument is valid for basic development, as it is a function of development and temperature interaction. It should however be noted that relative constant rankings were found for these genotypes under 10, 13, and 16^0C treatments, and they finally conclude that breeding for intrinsic earliness should be done under temperature regimes where that genotype is to be grown. In another study Slafer and Rawson (1995b) investigated photoperiod and temperature interactions in contrasting wheat genotypes, but from this study they were also able to examine the theory of intrinsic earliness. Subjecting three genotypes to 4^0C for 60 days satisfied their vernalization requirement, the authors recorded differences in heading time under 21-hour photoperiod. They did indeed find differences between genotypes, but in contradiction with the theory of intrinsic earliness, they also found varying results under different absolute and relative temperatures. This indicated that what previously had been perceived as intrinsic earliness, or a static genotypic trait is mainly a result of genotypic and temperature interaction. In conclusion they suggest that intrinsic earliness is merely a descriptor of differences in sensitivity between genotypes and that intrinsic earliness values cannot be extrapolated from one temperature to another.

Miura and Worland (1994) on the other hand reported on the effects of ear emergence of the group-3 aneuploid and substitution lines under different vernalization and photoperiod regimes. When they reduced the dosage of chromosome 3A in CS it resulted in earlier heading and *vice versa*; increasing the dosage of chromosome 3A delayed ear emergence. The differences in ear emergence were insignificant or at most marginally significant, indicating that the differences observed in heading time could not be attributed to either vernalization, or photoperiodic response. Similarly the monosomic plants produced significantly fewer primordia than the tetrasomic and euploid plants, which is indicative of fewer primordia produced and thus earlier ear emergence. Evidence from these results led to the conclusion that the hemizygous CS chromosome 3A can be linked to earliness and also a reduction in the number of spikelets

induced. If, however the dosage of 3A is increased it incurs delayed ear emergence and increased leaves and spikelets. This is in accordance with Zemetra *et al* (1986) reporting that ear-emergence time is the result of major genes carried by chromosome 3A and 3D.

Kato and Yokoyama (1992) consider vernalization requirement, photoperiodic response and narrow-sense earliness as intrinsic characters of each landrace. They evaluated 158 landraces gathered from various countries under two photoperiods (12 and 24-hour), and two vernalization treatments (40 and 70 days). The countries were divided into central (Georgia, Armenia, Turkey, Iran), eastern (Afghanistan, Nepal, Bhutan), western (Turkey, Italy, Greece) and southern (Egypt, Iraq, Ethiopia) regions. Narrow-sense earliness was measured as the days from sprouting to flag-leaf unfolding under a 24-hour photoperiod. They concluded that landraces from the central region fell in the medium to late maturity classes while the frequency of early maturity landraces was higher in the other regions, especially in the eastern region.

Slafer (1996) reviewed literature, summarised the understanding of the assumptions made regarding earliness *per se*, and re-analysed data from several studies to evaluate to what extent the theory and its assumptions hold true across an array of temperature conditions. In his evaluation process, he described earliness *per se* and then fitted research results to the different descriptors he summarised for this concept. He found that:

- Genes responsible for intrinsic earliness are independent from those governing response to photoperiod and vernalization, although these genes could be present in any combination with those.
- Genotypes not only differ for intrinsic earliness with regard to length of the vegetative period, but also with regard to the length of the reproductive phases.
- Differences in intrinsic earliness amongst genotypes are indeed affected by temperature and there is no quantitative value for a

genotype for intrinsic earliness. Even when viewed as a qualitative trait the rankings for earliness changed under different temperature regimes.

Wheat phasic development

From the literature cited it is clear that most authors agree that there are three groups or sets of genes controlling the way in which the wheat plant develops. Ortiz-Ferrara *et al* (1998) confirms this in stating that vernalization, photoperiod and temperature are the major traits conferring earliness in wheat and are thus significant to the adaptation of wheat. Flood and Halloran (1984a) added basic development rate or earliness *per se* to vernalization and photoperiodic response to complete the three groups. These genes affect the rate of development in wheat and thus adaptation. Development in wheat has been described as "stage development of plants" (Lysenko, 1936; as cited by Fedorov, 1995), "phasic development" (Midmor *et al*, 1982), "phenological development" (Slafer and Rawson, 1995b), and "phenological events" (Klepper *et al*, 1998). All of these refer to the development of the wheat plant to be in identifiable stages or phases. These development stages and the prevailing environmental conditions are important and attribute significantly to adaptation and hence, yield.

CHAPTER 3

3. ASSESSMENT OF SOUTH AFRICAN BREAD WHEATS FOR VERNALIZATION REQUIREMENT

3.1 Introduction

Bread wheat (*Triticum aestivum* L. em. Thell.) is grown over a wide array of environmental conditions and has, according to Briggle and Curtis (1987), the broadest adaptation of all cereal crops. Wheat is considered to be a cool season crop, but it thrives under a wide spectrum of agro-climatic conditions. Production of wheat is not only limited to the traditional latitudes between 30 and 60^0N and 27 and 40^0S, but extend beyond these limits. Wheat is grown in areas from within the artic circle to areas close to the equator (Briggle and Curtis, 1987). It is thus clear that wheat, through evolution, developed to adapt to certain environmental conditions, including different temperature regimes.

The growth type, or developmental pattern, of wheat is controlled by a set of cold requirement or vernalization genes. The spring type or low vernalization requirement genotype has dominance over the winter or high vernalization requirement genotype. Variation in reaction to vernalization is higher in winter types than in spring types (Pugsley, 1970).

Three major genes, *viz Vrn1*, *Vrn2*, and *Vrn3*, govern the genetic sensitivity of wheat to low temperatures. These genes are located on the long arms of chromosome 5A, 5B, and 5D respectively. Allelic variation of the *Vrn1* locus on chromosome 5AL is considered to be primarily responsible for the different reactions of spring and winter wheat to low temperatures (Pugsley, 1972; Law *et al*, 1976). Crofts (1989) concluded that the difference between a spring wheat and winter wheat should be described with a genetic definition, where a winter wheat has only recessive alleles (*vrn*) at all *Vrn* loci, and spring type

wheats have the dominant *Vrn1* allele. Semi-winter wheat lacks *Vrn1*, but possesses at least one other dominant *Vrn* allele.

Knowledge of the characteristics that influence the developmental pattern of wheat enables the breeder to select and breed individuals, with a specific genetic constitution, that are adapted to specific environmental conditions. This is especially true in South Africa, where wheat is cultivated under a wide array of agro-climatic conditions, ranging from irrigation to low rainfall, dryland conditions. South Africa can be divided into two major wheat-producing areas: 1) the winter rainfall region, and 2) the summer rainfall region. The summer rainfall region is sub-divided into irrigation and dryland production areas.

The aim of this study was to:

1. Classify and group the most important South African wheat cultivars in terms of their response to vernalization requirement, and
2. To determine the variation in response to vernalization treatment within each group.

3.2 Materials and methods

3.2.1 Cultivars

Thirty South African bread wheat cultivars, including spring, intermediate (facultative), and winter wheats were characterised on their response to vernalization treatments. The cultivars were selected to represent cultivars cultivated in the major wheat production areas of South Africa.

The cultivars used are summarised in Table 3.1

Table 3.1 Thirty South African bread wheat cultivars evaluated for their response to different vernalization treatments

Entry	Cultivar	Company	Growth Habit
1	KARIEGA	Small Grain Institute	Spring
2	MARICO	Small Grain Institute	Spring
3	INIA	Small Grain Institute	Spring
4	PALMIET	Small Grain Institute	Spring
5	STEENBRAS	Small Grain Institute	Spring
6	BAVIAANS	Small Grain Institute	Spring
7	SST822	Monsanto	Spring
8	SST876	Monsanto	Spring
9	SST57	Monsanto	Spring
10	SST65	Monsanto	Spring
11	SST88	Monsanto	Spring
12	LIMPOPO	Small Grain Institute	Intermediate
13	SST124	Monsanto	Intermediate
14	GARIEP	Small Grain Institute	Intermediate
15	ELANDS	Small Grain Institute	Intermediate
16	CALEDON	Small Grain Institute	Intermediate
17	SST363	Monsanto	Intermediate
18	SST367	Monsanto	Winter
19	TUGELA-DN	Small Grain Institute	Intermediate
20	BETTA-DN	Small Grain Institute	Winter
21	PAN3211	Pannar	Intermediate
22	PAN3235	Pannar	Intermediate
23	PAN3349	Pannar	Intermediate
24	PAN3377	Pannar	Winter
25	MOLEN	Small Grain Institute	Winter
26	HUGENOOT	Small Grain Institute	Winter
27	SST936	Monsanto	Winter
28	SST983	Monsanto	Intermediate
29	SST966	Monsanto	Winter
30	SST399	Monsanto	Winter

3.2.2 Vernalization treatment

All 30 cultivars were subjected to eight cold treatment regimes, including a control treatment that was not exposed to low temperatures. Treatment descriptions are listed in Table 3.2 below.

Table 3.2 Vernalization treatment descriptions

Treatment	Description
1	Control – No cold treatment
2	1 Week Vernalization treatment
3	2 Weeks Vernalization treatment
4	3 Weeks Vernalization treatment
5	4 Weeks Vernalization treatment
6	5 Weeks Vernalization treatment
7	6 Weeks Vernalization treatment
8	7 Weeks Vernalization treatment

Eight replicates of five seeds per treatment per replicate were planted in seedling trays filled with seedling soil. Each tray consisted of 98 individual removable seedling wells with a 30 x 30 x 80mm well dimension. A constant seeding depth was obtained by filling each individual well of the seedling tray to 1 cm from the top of the well before planting. After five seeds per cultivar per replicate were placed in the well, it was filled with seedling soil. The entries were randomised before planting according to a factorial experimental design as used by the Agrobase (1999) computer software.

Treatment eight was planted first, as it had the longest cold treatment with the others following in descending chronological order to ensure that all treatments (after vernalization) were transplanted in the field on the same day. Each treatment was planted one week prior to the commencement of vernalization, and was germinated at room temperature under natural light. Seedlings reached the two-leaf stage before the trays were transferred to a cold room.

Seedlings were vernalised at a 3^0C (+/-1^0C) temperature and under a 10-hour light, 14-hour dark photoperiod regime. Fujita *et al* (1992) also used this cold treatment temperature to evaluate the relationship between cold resistance, heading traits and ear primordia development in wheat. Flood and Halloran (1986) stated that winter cultivars are found in habitats where the mean temperature varies between 2 – 4^0C. Cool fluorescent tube lights were used for artificial illumination. All trays were moved at two-day intervals to ensure a uniform environment. The seedlings were watered daily to maintain adequate water supply. After vernalization was completed, the seedlings, including the control treatment, were still at the two-leaf stage. Briggle and Curtis (1987) confirmed this by stating that the minimum temperature for growth is about 3 to 4^0C.

3.2.3 Field planting

The field in which the vernalised and unvernalised seedlings were to be transplanted was chisel ploughed three weeks prior to planting. Final seedbed preparation and fertiliser incorporation were done with a rotavator five days prior to transplanting. A fertiliser mixture N:P:K [3:2:1 (25) + 0.5 Zn] was applied at a rate of 300 kg.ha^{-1}. The field was watered to field capacity with an overhead sprinkling system before transplanting started.

The seedlings were planted as a hill plot, meaning that the five seedlings per plot were not separated, but planted in the same hole. Holes were made with a hoe 50 cm from one another within a row. An inter-row spacing of 50 cm was used. Each treatment was planted as a block. To minimise the effect of high temperatures during transplanting, all seedling trays were watered extensively before transportation to the field. After transplantation the field was watered to field capacity again.

3.2.4 Trial maintenance

The trial was covered with bird netting to prevent birds and rodents to enter and damage the hill plots. Irrigation was applied regularly to ensure that no drought stress occurred during the trial period. An additional 50 kg nitrogen (N) per hectare was applied at flag leaf stage in the form of LAN(28%). Metasystox R

(active ingredient – 250 g/l oxydemeton-methyl) was used to control Russian wheat aphids (*Diuraphis noxia*) during the trial period. This pesticide is an emulsifiable concentrate and was applied at a rate of 500 ml/ha using a knapsack sprayer. Two applications were given before heading. Weeding was done by hand.

3.2.5 Characters measured

Data on the following traits were gathered:

- Days to heading: The days calculated from transplanting in the field to the date when 50% of the hill plot headed. Heading is recorded when half of the ear is visible outside the boot.
- Days to flowering: The days calculated from transplanting in the field to the date when 50% of the hill plot flowered. Flowering is recorded when anthers are visible on half of the ear.
- Days to physiological maturity: The days calculated from transplanting in the field to the date when 50% of the hill plot reached physiological maturity. Physiological maturity is recorded when the peduncle has lost all chlorophyll with only the nodes still green.
- Days from heading to flowering: Calculated by subtracting days to heading from days to flowering.
- Days from heading to physiological maturity: Calculated by subtracting days to heading from days to physiological maturity.

3.2.6 Statistical analysis

Statistical analyses were done on the data sets using cluster analysis to group the cultivars and analysis of variance to determine the variance within each group. Two computer software programmes: NCSS (2000) for cluster analysis and AGROBASE (1999) for ANOVA were used to calculate statistical analyses.

3.2.6.1 Cluster analysis

Cluster analysis encompasses a number of different classification algorithms. This analysis is used to organise observed data into meaningful structures. Tree or hierarchal clustering method, the method used in this study, uses

dissimilarities or distances between observations when forming the clusters. Starting off, each object is in a class by itself after which the threshold is lowered to declare two or more objects to be members of the same cluster. This continuous process results in linking more objects together and aggregate larger and larger clusters of increasing dissimilar elements. In the final step all objects are joined together.

The chosen type distance in the study is a Euclidean distance and is the geometric distance in the multidimensional space. The Euclidean distance was calculated as follows:

$$\text{Distance}(x, y) = \{ \sum_i (x_i - y_i)^2 \}^{1/2}$$

When several objects have been linked together it is important to determine the distances between the new clusters. To accomplish this, a linkage or amalgamation rule is needed to link clusters together that are sufficiently similar. In this study the unweighted pair-group average method was used. In this method, the distance between two clusters are determined by the average distance between all pairs of objects in the two clusters.

3.2.6.2 Analysis of variance

Analysis of variance is an arithmetic technique by which total variation presented in a set of data is partitioned into different components. The general purpose of analysis of variance is to test for significant differences between means. A factorial design was used to calculate the analysis of variance in the data set using AGROBASE (1999). Significant differences between cultivar means were separated using a least significant difference (LSD) at $P \leq 0,05$.

3.3 Results and Discussions

3.3.1 Cluster analysis

Using actual values, the clustering of South African bread wheat cultivars was determined for days to flowering and days to physiological maturity, over all

vernalization temperature regimes, and is presented as a dendrogram in Figure 3.1.

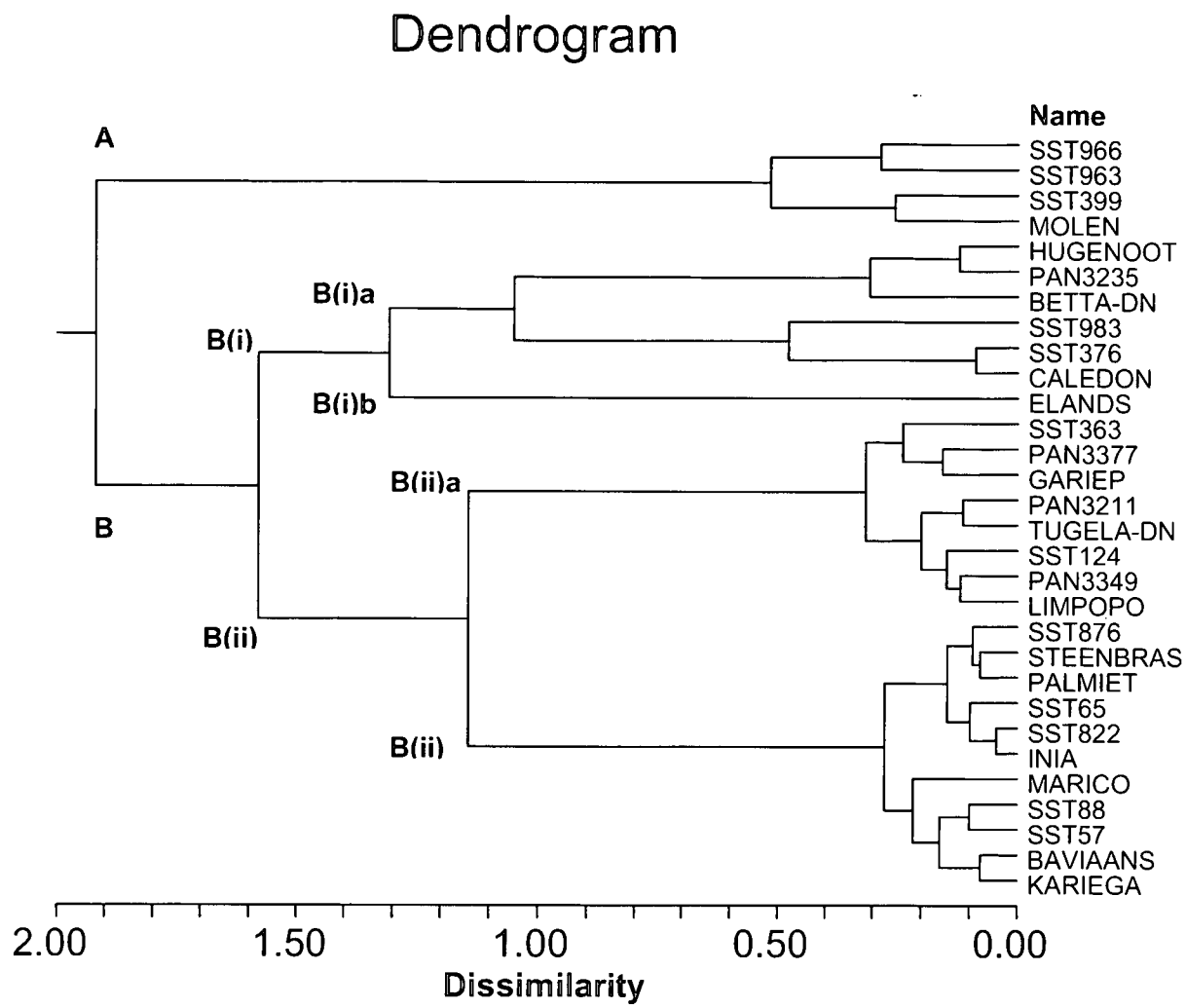


Figure 3.1 Cluster analyses for 30 wheat cultivars over all vernalising temperature regimes

Cophenetic Correlation = 0.960451
Delta(0.5) = 0.104508
Delta(1.0) = 0.125027

The highest level of dissimilarity between the cultivars is illustrated by clusters A and B in Figure 3.1. At this point the cultivars were distinctly grouped into two clusters, suggesting large phenotypic differences. Cluster A constituted of four cultivars: SST399, SST966, SST936, and Molen with a typical long vernalization requirement. These four cultivars can be classified as strong vernalization requirement cultivars or true winter wheats.

Cluster B further divided into B(i) and B(ii) and separated the cultivars that required more than 0, but less than six weeks vernalization from those that required no vernalization to initiate the reproduction phase. B(i) included Caledon, SST367, SST983, Betta-DN, PAN3235, Hugenoot, and Elands. It was notable that B(i) divided into clusters B(i)a and B(i)b, while Elands clustered on its own on B(i)b. This phenomenon will be discussed later in the chapter. On the B(i)a cluster Hugenoot, PAN3235, and Betta-DN clustered together with a minor distance from SST983, SST376, and Caledon. B(ii) represented all the cultivars with no vernalization requirement to initiate the reproductive phase.

Finally the B(ii) cluster, with no minimum vernalization requirement, divided into B(ii)a and B(ii)b. SST363, PAN3377, and Gariep clustered closely to PAN3211, Tugela-DN, SST124, PAN3349, and Limpopo on the B(ii)a cluster, while SST876, Steenbras, Palmiet, SST65, SST822, and Inia clustered closely with Marico, SST88, SST57, Baviaans, and Kariega on B(ii)b.

From Figure 3.1 it is clear that the cultivars were divided into four main clusters indicating four different growth habit types. The first cluster (denominated as A) included all the cultivars with a very strong vernalization requirement, while the cultivars in cluster B(i) also required vernalization, but less than those in cluster A. Clusters B(ii)a and B(ii)b represent all the cultivars with no minimum vernalization requirement, but the dissimilarity between these two groups of cultivars was large enough to warrant separate clusters. The minimum vernalization requirement for each of the cultivars is summarised in Table 3.3.

Table 3.3 Minimum vernalization requirement in weeks for 30 wheat cultivars

0 Weeks	2 Weeks	3 Weeks	4 Weeks	6 Weeks
KARIEGA	ELANDS	BETTA-DN	CALEDON	MOLEN
MARICO		PAN3235	SST367	SST936
INIA		HUGENOOT	SST983	SST966
PALMIET				SST399
STEENBRAS				
BAVIAANS				
SST822				
SST876				
SST57				
SST65				
SST88				
LIMPOPO				
SST124				
GARIEP				
SST363				
TUGELA-DN				
PAN3211				
PAN3349				
PAN3377				

The groupings in Table 3.3 concur largely with the results obtained from the cluster analysis in Figure 3.3 in so far the main clusters were concerned. B(ii) in Figure 3.1 was thus represented by 0 Weeks in Table 3.3, while B(i) was represented by 2 Weeks, 3 Weeks, and 4 Weeks. Cluster A was represented by six Weeks in Table 3.3. These figures indicate the minimum required duration of exposure to vernalising temperatures for cultivars before the reproductive phase is initiated.

From the above results it is clear that cultivars could be divided into groups, and that these groups were determined on the grounds that vernalization was either

a prerequisite for phasic development or was not. This is illustrated in Figure 3.2.

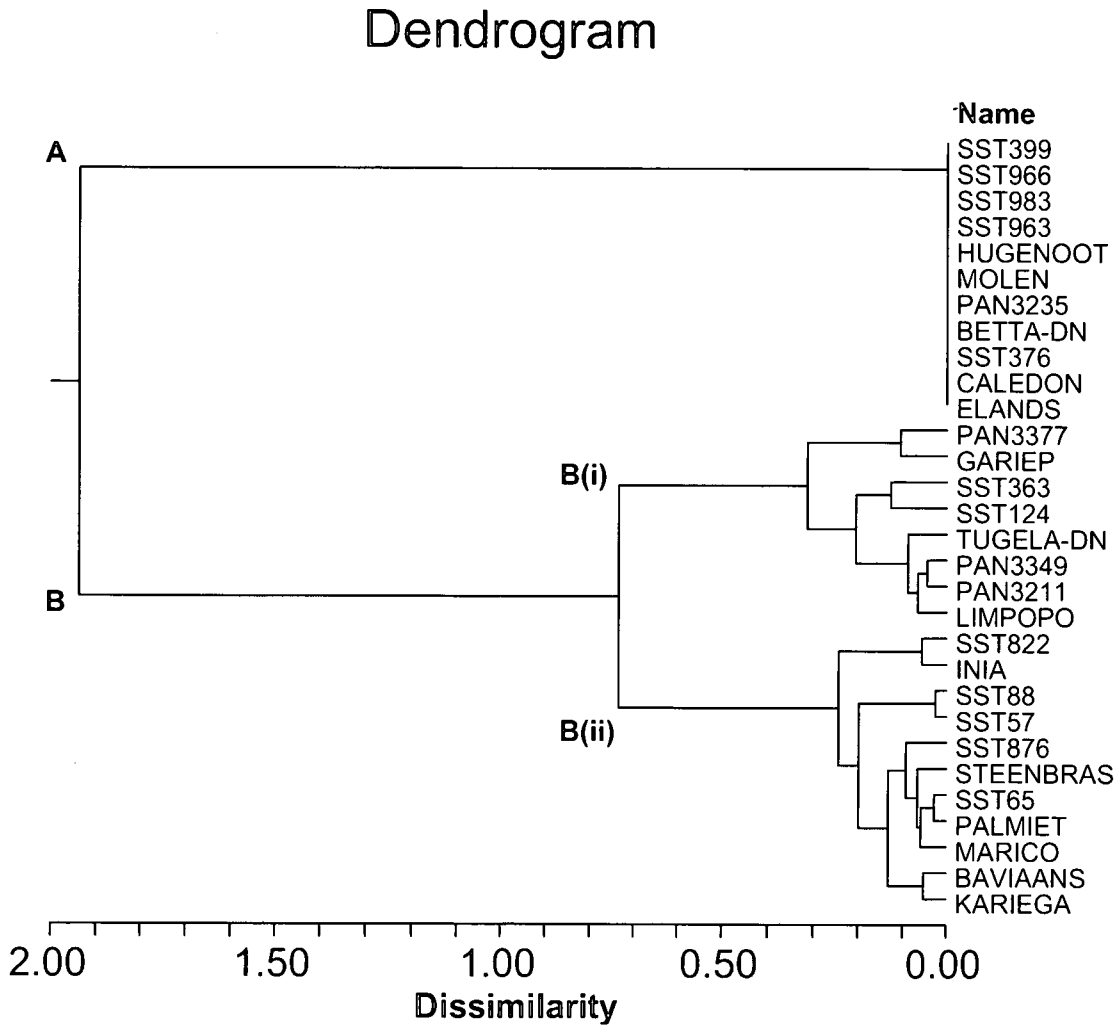


Figure 3.2 Cluster analyses of 30 wheat cultivars under a zero week vernalization treatment

Cophenetic Correlation = 0.946134
Delta(0.5) = 0.190064
Delta(1.0) = 0.203280

Simplistically viewed, clusters A and B in Figure 3.2 represent cultivars with a minimum vernalization requirement, and with no vernalization requirement respectively. Cluster A consolidated all the cultivars that were traditionally considered to be winter wheats and included SST399, SST966, SST936, Hugenoot, Molen, PAN3235, Betta-DN, SST367, and Caledon. Elands and SST983 were usually classified as intermediate wheat cultivars. Cluster B on

the other hand encompassed intermediate (facultative) and spring wheats with the exception of PAN3377. PAN3377 in this case contravened the common belief that a winter growth habit, under natural conditions, is indicative of the vernalization requirement of a cultivar. It is clear from this dendrogram that vernalization requirement is not always a prerequisite to express a phenotypic winter growth habit.

The further division of B into B(i) and B(ii) emphasised the variance that existed between cultivars even within an apparent clear cluster. Although B(i) represented cultivars with no minimum vernalization requirement, these cultivars were different from those on cluster B(ii), even if the relative low dissimilarity level, as indicated in Figure 3.2, was considered. The number of days to flowering suggested that two groups could be identified within the cultivars that clustered on cluster B. Although all these cultivars reached anthesis without any vernalization they cannot be classified in the same group. The first group, and thus those cultivars that required fewer days to realise anthesis was classified as spring wheat, while intermediate cultivars were situated somewhere between winter and spring wheat. The intermediate cultivars: Gariep, SST363, SST124, Tugela-DN, PAN3349, PAN3211, and Limpopo clustered on B(i) and the spring wheat cultivars: SST822, Inia, SST88, SST57, SST876, Steenbras, SST65, Palmiet, Marico, Baviaans, and Kariega clustered on B(ii).

Figure 3.3 illustrates the dissimilarity between cultivars that clustered as similar in Figure 3.2 above.

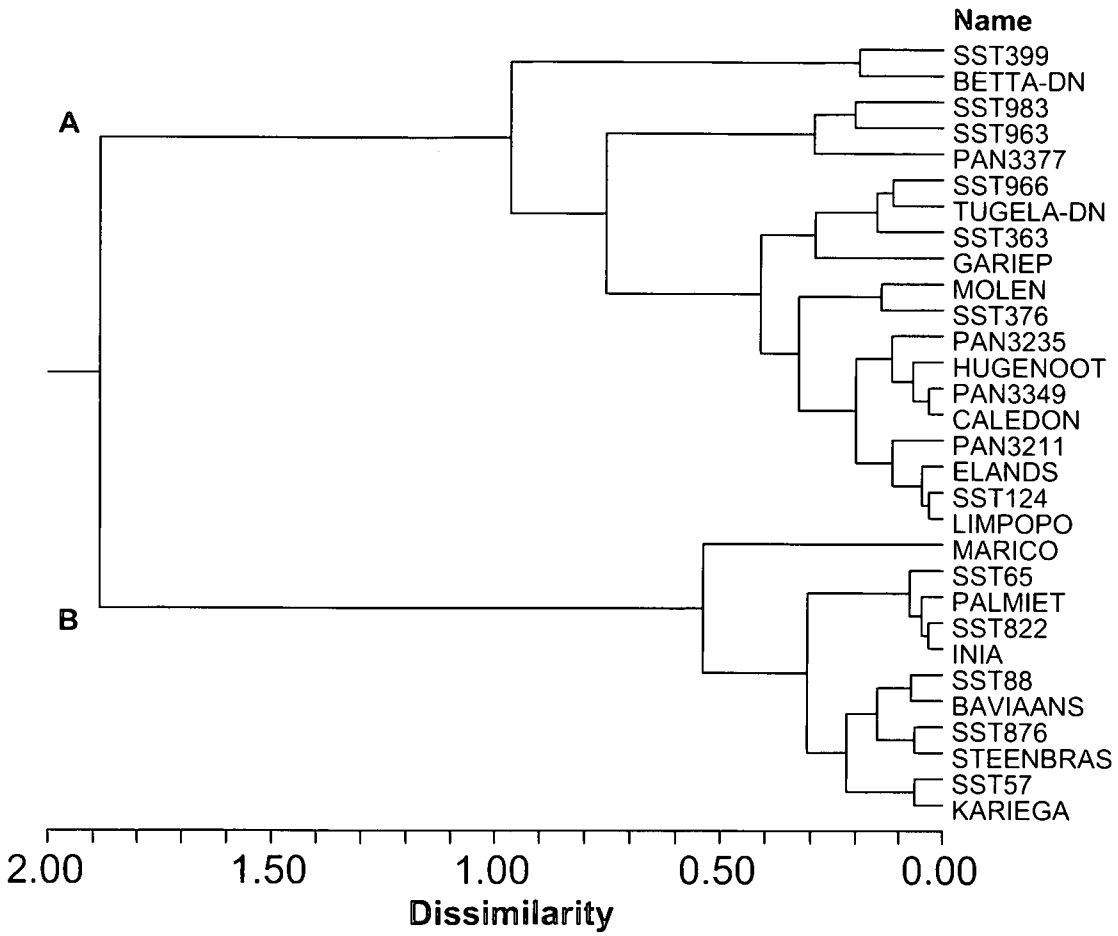


Figure 3.3 Cluster analyses of 30 wheat cultivars under a seven week vernalization treatment

Cophenetic Correlation = 0.898037
Delta(0.5) = 0.214058
Delta(1.0) = 0.262511

The dissimilarity found between cultivars in Figure 3.3 was the result of the genotypic reaction to vernalization, even in cases where no minimum vernalization was required. Again two clear clusters: A and B could be identified, with A representing cultivars sensitive to seven weeks vernalization, and B less sensitive to seven weeks vernalization. Sensitivity to vernalization, however, does not imply vernalization requirement *per se* and cultivars with no apparent vernalization requirement such as Tugela-DN and SST363 were clustering with cultivars exhibiting a strong vernalization requirement such as SST966. The typical spring wheat cultivars: Marico, SST65, Palmiet, SST822,

Inia, SST88, Baviaans SST876, Steenbras, SST57, and Kariega still grouped together, although different similarity scenarios were observed. Marico was a clear example of this. In Figure 3.2, where no vernalization was applied, Marico clustered closely with Steenbras, SST65, and Palmiet. In Figure 3.3, however, under seven weeks vernalization Marico was a cluster on its own and reacted differently to vernalization than Steenbras, SST65, and Palmiet. Cluster analyses on single treatments represented only the reaction of cultivars to specific vernalization treatments and are not recommended as base for identifying broad groups to which cultivars can be apportioned to.

Due to contributing confusion brought about by cluster analysis on single treatments, it is advisable to use only the results from the combined analysis to classify cultivars into similarity groups. Cultivars were previously classified as winter, intermediate, or spring wheat and this was also used as base for this study as indicated in Table 3.1. The results from the cluster analysis in Figure 3.1, however, portray a fourth and distinct group that required more vernalization than other winter wheats. This group included SST399, SST966, SST936, and Molen. To summarise, it is thus suggested that an additional group, true winter wheat, is added to the existing 3 groups: Winter, intermediate and spring wheat. Classification should be based on true winter wheat, winter wheat, intermediate wheat, and spring wheat.

3.3.2 Analysis of variance

The results obtained from the cluster analysis can now be used to group the cultivars in terms of similar vernalization requirement for analyses of variance. Since some cultivars did not reach anthesis if their vernalization requirements have not been met, it would be almost impossible to calculate standard analyses of variance on the data. To be able to detect variance between cultivars it is necessary to calculate analysis of variance within each cluster. Table 3.4 summarises the cultivars into four groups as suggested in the previous paragraph.

Table 3.4 Classification of 30 wheat cultivars in terms of similarity groups

True winter wheat	Winter wheat	Intermediate wheat	Spring wheat
SST399	Hugenoot	SST363	SST876
SST966	PAN3235	PAN3377	Steenbras
SST936	Betta-DN	Gariep	Palmiet
Molen	SST983	PAN3349	SST65
	Caledon	Tugela-DN	SST822
	SST367	SST124	Inia
	Elands*	PAN3211	Marico
		Limpopo	SST88
			SST57
			Baviaans
			Kariega

* Elands clusters somewhere between winter and intermediate wheat, and because Elands requires some minimum vernalization period it will be considered as a winter wheat to simplify discussion.

3.3.2.1 True winter wheats

SST399, SST966, SST936, and Molen were considered true winter wheats and required a minimum of six weeks vernalization before the reproductive phase is initiated. The cluster analysis, as presented in Figure 3.1, showed that there was some dissimilarity between cultivars within the true winter wheat cluster. It was clear that SST966 and SST936, both hybrid wheats, clustered closer to one another than to SST399 and Molen, which are pure breeding cultivars. When analysing the true winter wheat cluster as a separate entity, certain differences between cultivars were significant. The results of the analyses of variance for the measure characteristics are given in Table 3.5.

Table 3.5 Analysis of variance for reproductive characteristics in true winter wheat cultivars

Source	df	DTF	DTPM	DFTPM
Replications	7	134.48	520.44	518.66
Cultivars	3	1736.42**	13010.06**	5312.42**
Treatments	1	199.52*	2475.06**	1269.14**
Cultivar x treatment	3	123.55	433.06	289.05
Residual	49	1803.64	3877.81	3453.27
Total	63	3997.61	20316.44	10842.48
LSD for cultivar at 0.01		5.16	7.56	7.14
LSD for cultivar at 0.05		3.60	5.27	4.98

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

3.3.2.1.1 Days to flowering (DTF)

The number of days to flowering for each cultivar for eight different vernalization treatments is presented in Figure 3.4. These cultivars responded to vernalization only after six weeks cold treatment. Significant differences were found between cultivars for the six weeks and seven weeks vernalization treatments. SST399 reached anthesis over the longest period, with Molen the second longest period followed by SST966 and SST936.

Differences between treatments were also observed where a significant reduction (7.5 days) in days to flowering was recorded for SST966. No significant differences between treatments for the other three hybrids included in the cluster were observed. Molen had the second largest reduction (3.6 days) in days to anthesis, followed by SST936 (2.5 days). SST399 expressed no reduction in days to flowering between the six and seven weeks vernalization treatments.

There was no significant difference for cultivar x vernalization interaction.

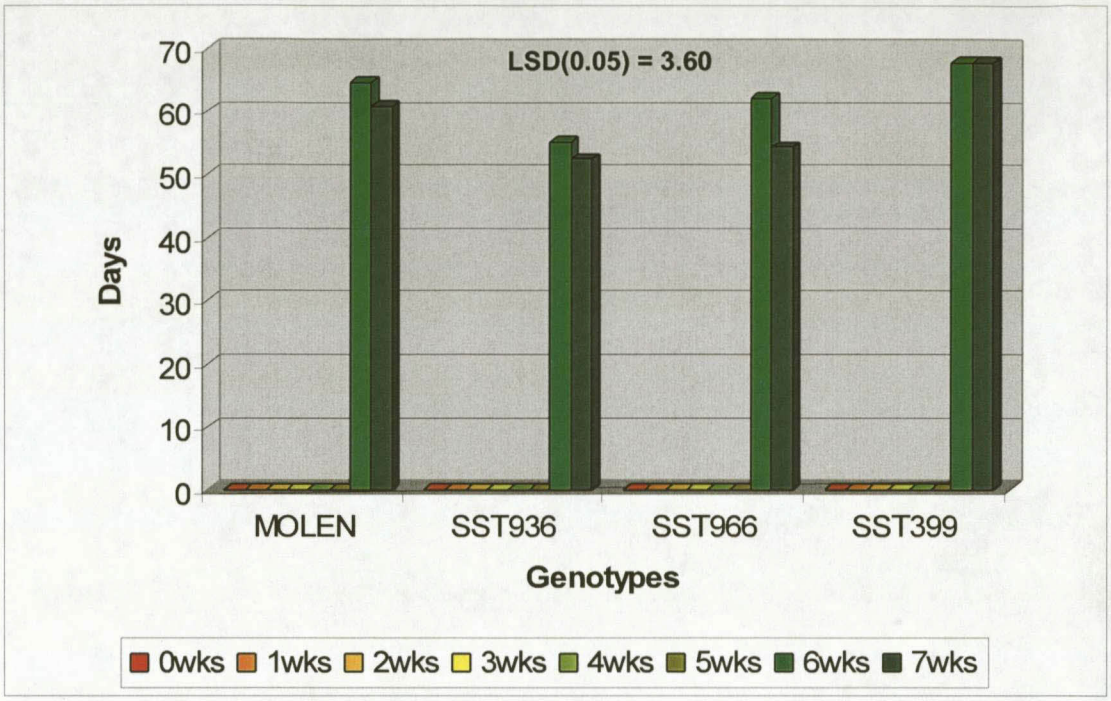


Figure 3.4 Days to flowering of true winter wheat cultivars for eight vernalization treatments

3.3.2.1.2 Days to physiological maturity (DTPM)

Figure 3.5 summarises the number of days for each cultivar to reach physiological maturity over the eight vernalization treatments. Physiological maturity was again only reached for six and seven weeks vernalization. From Table 3.5 it was deduced that the four cultivars in the true winter wheat cluster differed significantly in terms of days to physiological maturity. SST936 was the earliest to reach physiological maturity, followed by SST966, Molen, and lastly SST399.

Significant differences for treatments were also found. The largest response was observed in SST966 (19.2 days), with SST936 (14.9 days) the second highest and SST399 (10.4 days) third. Molen responded to a much lesser extent than the other three cultivars with a reduction in days to physiological maturity of only 5.3 days.

No significant differences were found for cultivar x vernalization interaction.

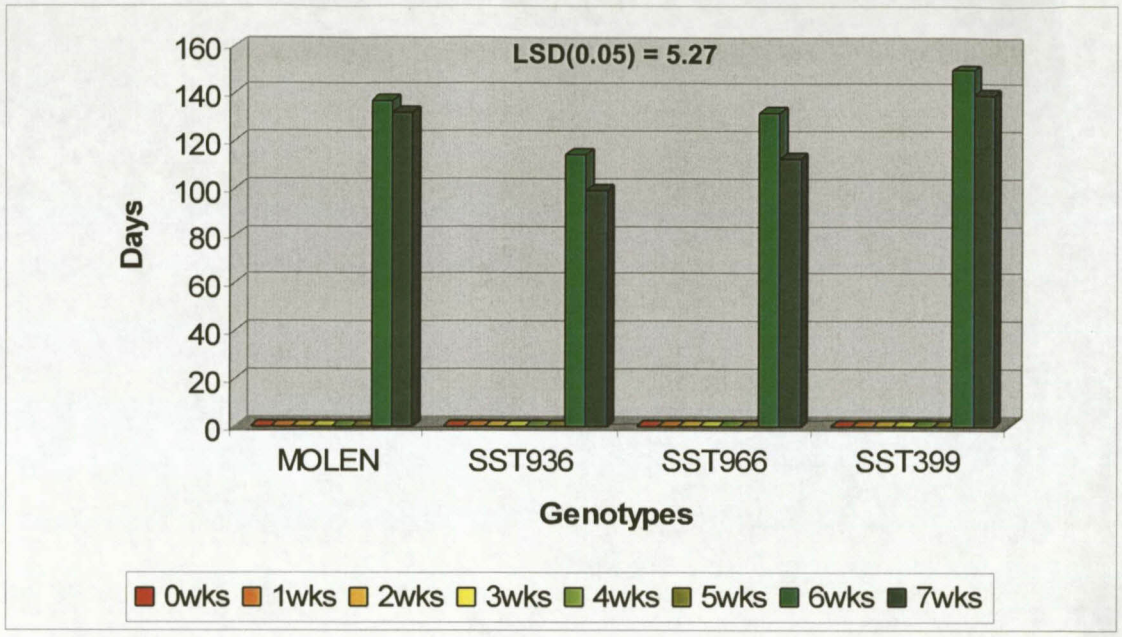


Figure 3.5 Days to physiological maturity of true winter wheat cultivars for eight vernalization treatments

3.3.2.1.3 Days from flowering to physiological maturity (DFTPM)

The days from flowering to physiological maturity for each cultivar under the eight vernalization treatments are presented in Figure 3.6. The shortest average period from anthesis to physiological maturity was observed for SST936 (52.7 days), followed by SST966 (63.9 days), Molen (71.6 days) and SST399 (76.9 days).

Significant differences were also noted between treatments. All cultivars expressed a reduction in the period needed to reach physiological maturity after anthesis. SST936 and SST966 (12.1 days and 11.5 days respectively) reached physiological maturity the earliest after anthesis, followed by SST399 (10.4 days) and Molen (1.6 days).

There were no significant differences for cultivar x vernalization interaction.

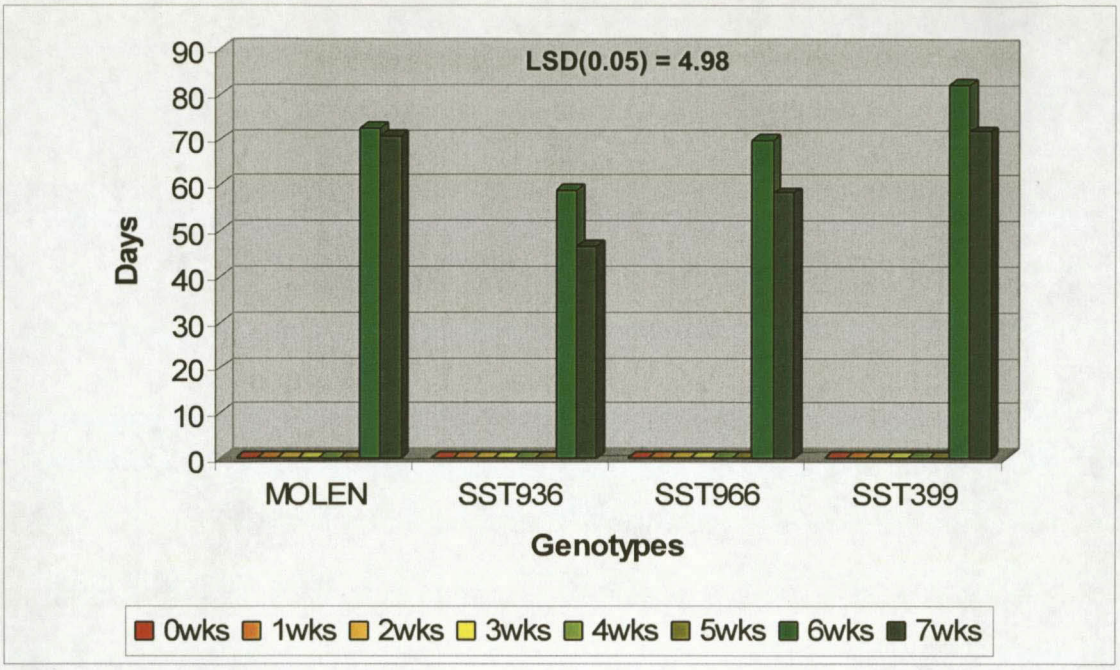


Figure 3.6 Days from flowering to physiological maturity of true winter wheat cultivars for eight vernalization treatments

Discussion

Significant differences were observed between all the cultivars for all characters measured. SST399 ranked as the cultivar with the longest period to reach anthesis, the longest period from flowering to maturity, and therefore also the longest period to reach physiological maturity under any of the responsive vernalization treatments. SST399 expressed no reduction in days to flowering between six and seven weeks cold treatments, but a reduction in the period from flowering to physiological maturity was observed. This cultivar ranked third, in response to vernalization, for the reduction in number of days to reach physiological maturity.

The cultivar that ranked second for the longest period to flowering, days from flowering to physiological maturity, and days to physiological maturity was Molen. Molen reacted positively to the vernalization treatments for all the measured characteristics, but it is noteworthy to mention that Molen had the lowest response to vernalization in terms of reduction in the number of days between anthesis and physiological maturity and subsequently the reduction in number of days to reach physiological maturity.

Both the hybrids (SST966 and SST936) responded strongly to vernalization treatment. These two cultivars ranked third and fourth respectively for the number of days to reach anthesis and physiological maturity. The number of days to flowering of SST966 was significantly reduced by increasing the vernalization treatment from six to seven weeks. SST966 also ranked first for the highest reduction in days to reach physiological maturity. SST936 ranked first for the highest reduction in days from flowering to physiological maturity.

The four cultivars that clustered together as true winter wheat were ranked for days to flowering, days to physiological maturity and days from flowering to physiological maturity, and the longest vernalization period in ascending order was: SST399, Molen, SST966, and SST936. The response of the cultivars to vernalization can be defined as the reduction in days to flowering, days to physiological maturity, and days from flowering to physiological maturity. The ranking, in descending order, for the cultivars in terms of sensitivity to vernalization expressed in 1.) reduction of number of days to anthesis was: SST966, Molen, SST936, and SST399, 2.) reduction in number of days to physiological maturity was: SST966, SST399, SST936, and Molen, and 3.) reduction in number of days from flowering to physiological maturity was: SST936, SST966, SST399, and Molen. It is clear, however, that more vernalization treatments are required to accurately measure the sensitivity of true winter cultivars to vernalization treatment, but from the current data it is deduced that all the cultivars were highly sensitive to vernalization.

3.3.2.2 Winter wheat

Winter and true winter wheat were separated on basis of their minimum vernalization requirement. In the cluster analysis Hugenoot, PAN3235, Betta-DN, SST983, Caledon, and SST367 grouped together as cultivars requiring less than six weeks, but more than three weeks vernalization. Elands required at least two weeks vernalization and, although clustering on its own, could be included in the above mentioned group. Thus winter wheats require at least some period of vernalization, but less than true winter wheats.

The dendrogram as presented in Figure 3.1 suggests that three groups can be identified within the winter wheat cluster. The first group was: Hugenoot, PAN3235 and Betta-DN, the second group was: SST983, SST367 and Caledon, while the third group consisted only of Elands. Analyses of variance were done within the winter wheats to determine difference within the group. The results from the analyses of variance are summarised in Table 3.6 and Table 3.7.

Table 3.6 Analysis of variance for reproductive characteristics in winter wheat cultivars for eight vernalization treatments

Source	df	DTF	DTPM	DFTPM
Replications	7	168.99	329.04	388.67
Cultivars	6	27335.76**	106401.09**	26975.93**
Treatments	7	324724.35**	1469894.14**	414878.03**
Cultivar x treatment	42	107489.56**	393545.48**	91877.29**
Residual	385	11006.26	27046.96	20207.08
Total	447	470724.92	1997216.71	554326.99
LSD for cultivar at 0.01		3.47	3.60	5.27
LSD for cultivar at 0.05		2.21	3.46	2.99

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

Table 3.7 Analysis of variance for reproductive characteristics in winter wheat cultivars for four to six weeks vernalization treatments

Source	df	DTF	DTPM	DFTPM
Replications	7	312.78	286.57	907.10
Cultivars	6	1560.53**	9454.93**	4445.61**
Treatments	3	1101.23**	8910.32**	4024.23**
Cultivar x treatment	18	662.87**	5681.43**	3181.68**
Residual	189	7027.34	23888.68	16682.02
Total	223	10664.75	48221.93	29241.64
LSD for cultivar at 0.01		3.58	6.59	5.51
LSD for cultivar at 0.05		2.52	4.65	3.88

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

3.3.2.2.1 Days to flowering (DTF)

The number of days to flowering for the winter wheats is presented in Figures 3.7. and 3.8. All the cultivars that were grouped into the winter wheat cluster needed a minimum period of vernalization to initiate the reproductive phase, although the minimum period differed between cultivars. As mentioned previously, three groups or categories were identifiable within the winter wheat cluster and the minimum vernalization period differed for each category. Elands was the only winter wheat that required only two weeks to initiate flowering, while Betta-DN, PAN3235, and Hugenoot required a minimum of three weeks vernalization, and Caledon, SST367, and SST983 required four weeks vernalization to progress to the reproductive phase.

Elands ranked first for the longest period to flowering and was significantly later than PAN3235, Hugenoot, and Betta-DN, as well as the third group of Caledon, SST367, and SST983. No significant differences were found between PAN3235, Hugenoot, and Betta-DN, but these 3 cultivars differed significantly from Caledon, SST367, and SST983. Caledon and SST367, ranked 5th and 6th respectively, differed significantly from SST983, but not from each other.

SST983 had a significant shorter period to flowering than any other cultivar and was ranked last.

If the zero to three weeks vernalization treatments were dropped from the analyses of variance, the significant differences between cultivars were reduced, but not negated. The data from this modified analysis of variance suggested a different scenario than the complete analysis. Betta-DN ranked first with the longest period to anthesis, but the period to anthesis was not significantly longer than that for PAN3253, Hugenoot, Caledon, Elands, and SST367 at the 0.01 significance level. SST983 had the shortest period in reaching anthesis and it was significant shorter than all the other cultivars in the winter wheat cluster at the 0.01 significance level. Both Elands and SST367 had significant shorter periods to anthesis than Betta-DN, PAN3235, Hugenoot, and Caledon at the 0.05 significance level.

Significant differences between treatments were also observed, with a general trend of reduced number of days to physiological maturity in response to longer vernalization treatments. Although some cultivars i.e. SST367, Betta-DN, PAN3235, and Hugenoot had slight increases in the number of days to physiological maturity at the highest vernalization treatment, the net result was still a decrease in number of days to physiological maturity.

Significant differences were observed between cultivar x treatment interactions and this could mainly be ascribed to the large response of Elands, PAN3235, and Hugenoot to the initial vernalization. Elands had the largest response to vernalization with a 19 day reduction in days to physiological maturity after four weeks vernalization, followed by Hugenoot with 13 days and PAN3235 with 10 days. When vernalization treatments one to four were removed from the analysis, no significant differences were observed for cultivar x vernalization treatment interactions.

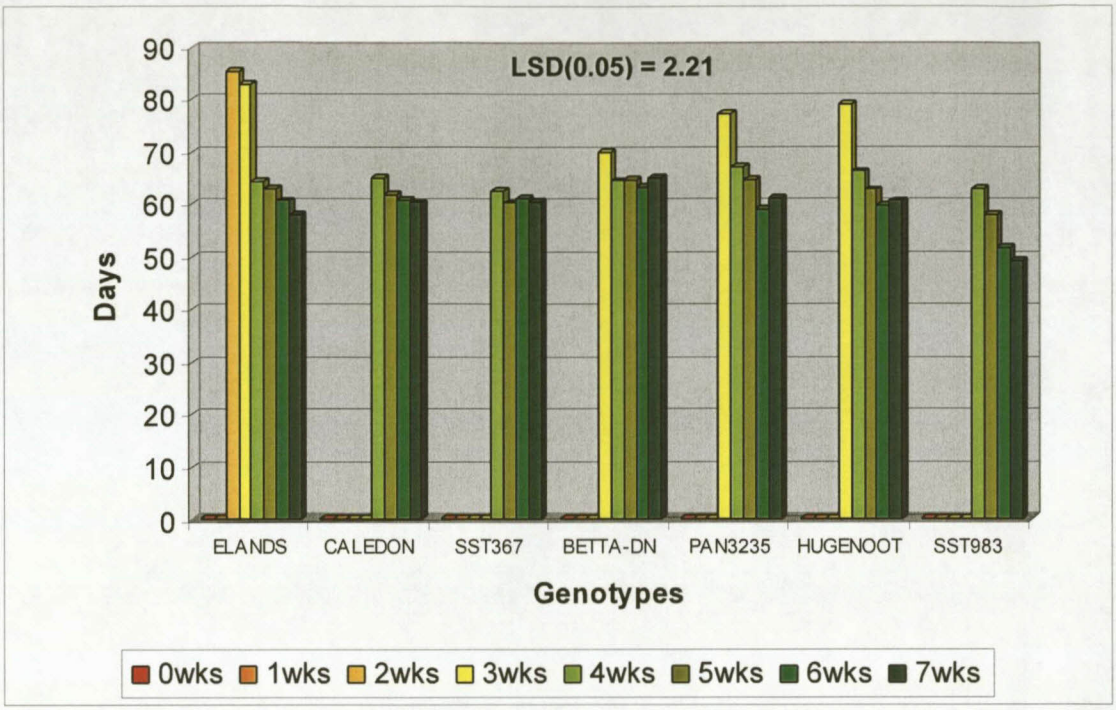


Figure 3.7 Days to flowering of winter wheat cultivars for all eight vernalization treatments

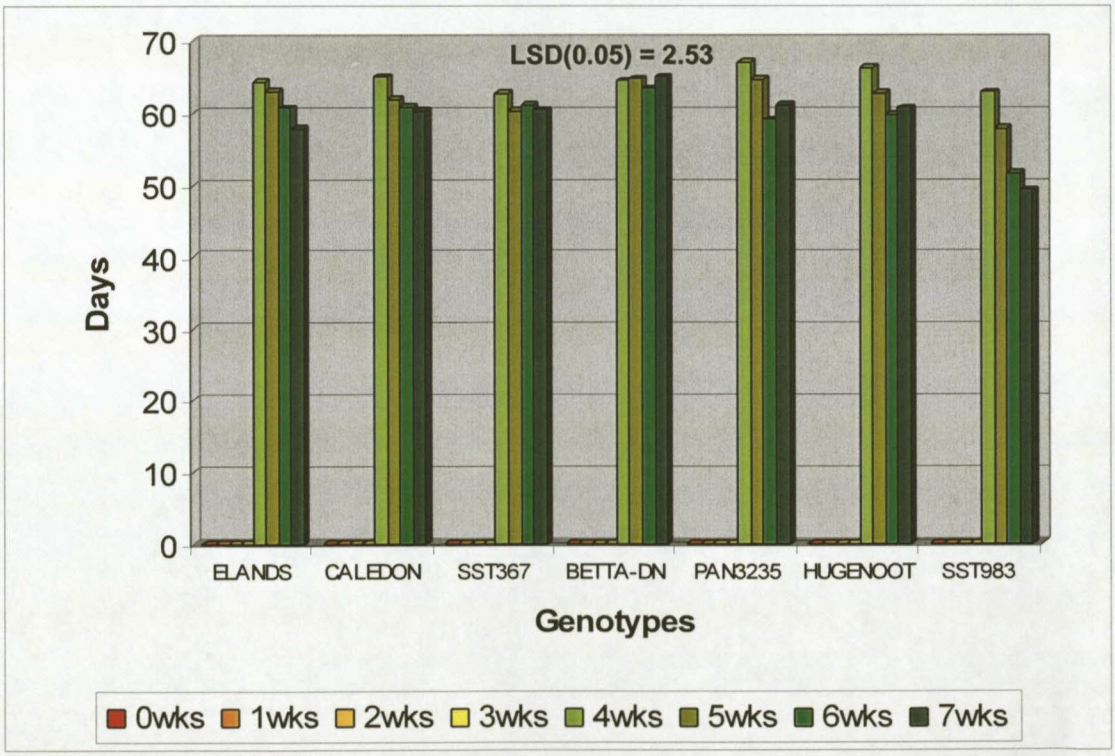


Figure 3.8 Days to flowering of winter wheat cultivars for four to seven weeks vernalization treatments

3.3.2.2.2 Days to physiological maturity (DTPM)

Figure 3.9 and Figure 3.10 summarise the days to physiological maturity for the seven winter wheats. Elands had a significantly longer period to physiological maturity than any other cultivar in the winter wheat cluster at the 0.05 significance level. Betta-DN ranked second with a significantly longer period to physiological maturity than all cultivars, except Elands. No significant differences were observed between PAN3235 and Hugenoot, but both had significantly longer periods to physiological maturity than SST367, Caledon, and SST983. SST983 ranked last, differing significantly from all cultivars except Caledon. A significant difference between Caledon and SST983 was observed, but only at the 0.05 significance level.

When dropping vernalization treatments one to four from the analysis of variance, Betta-DN took significantly longer to reach physiological maturity than all other cultivars at both the 0.01 and 0.05 significance levels. No significant differences were observed between PAN3235, SST367, Elands, Hugenoot, and Caledon at the 0.01 significance level, and no significant differences were observed between PAN3235, SST367, and Elands at the 0.05 significance level. At the 0.05 significance level, PAN3235 had a significantly longer period to physiological maturity than Hugenoot and Caledon. SST983 had the shortest period to physiological maturity at all significance levels.

Significant differences were present between vernalization treatments, with the longest treatment (seven weeks vernalization) resulting in the shortest period between flowering and physiological maturity. Significant differences were found between cultivar x vernalization interaction. Vernalization treatments five to eight resulted in relatively low total reductions in days to physiological maturity for Caledon (10 days), SST367 (5 days), and Betta-DN (4 days). On the other hand, Elands, PAN3235, Hugenoot, and SST983 responded with larger total reductions in days to physiological maturity. Elands reduced total days to physiological maturity by 19 days, PAN3235 by 25 days, Hugenoot by 13 days, and SST983 by 38 days for vernalization treatments five to eight.

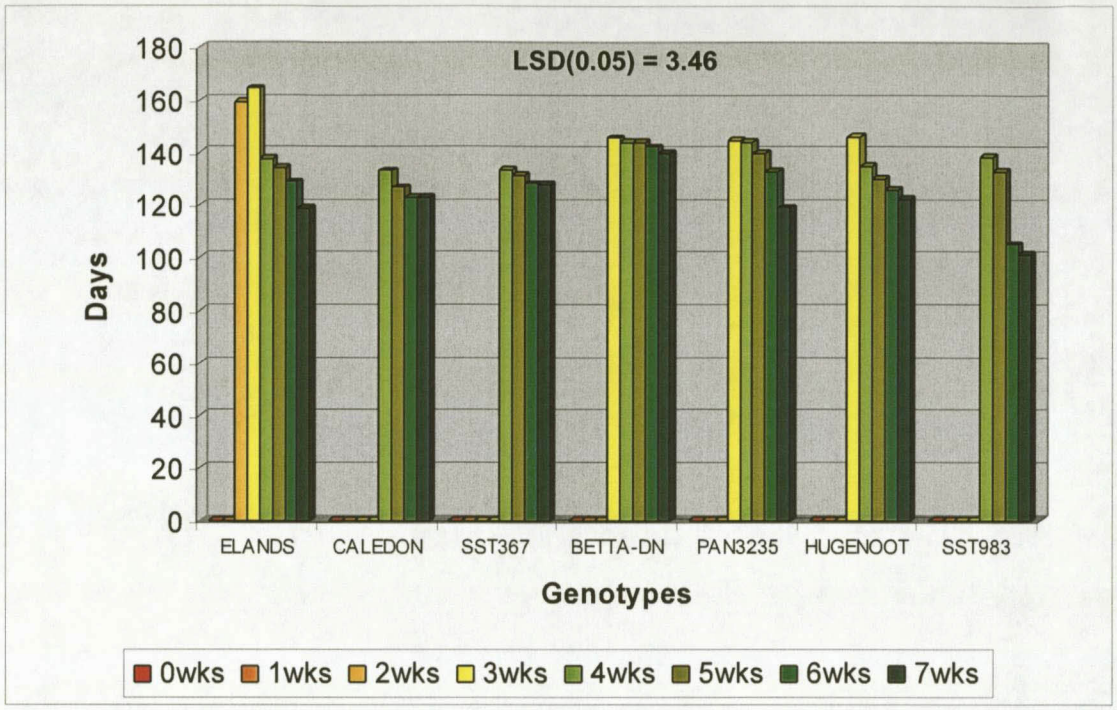


Figure 3.9 Days to physiological maturity of winter wheat cultivars for all eight vernalization treatments

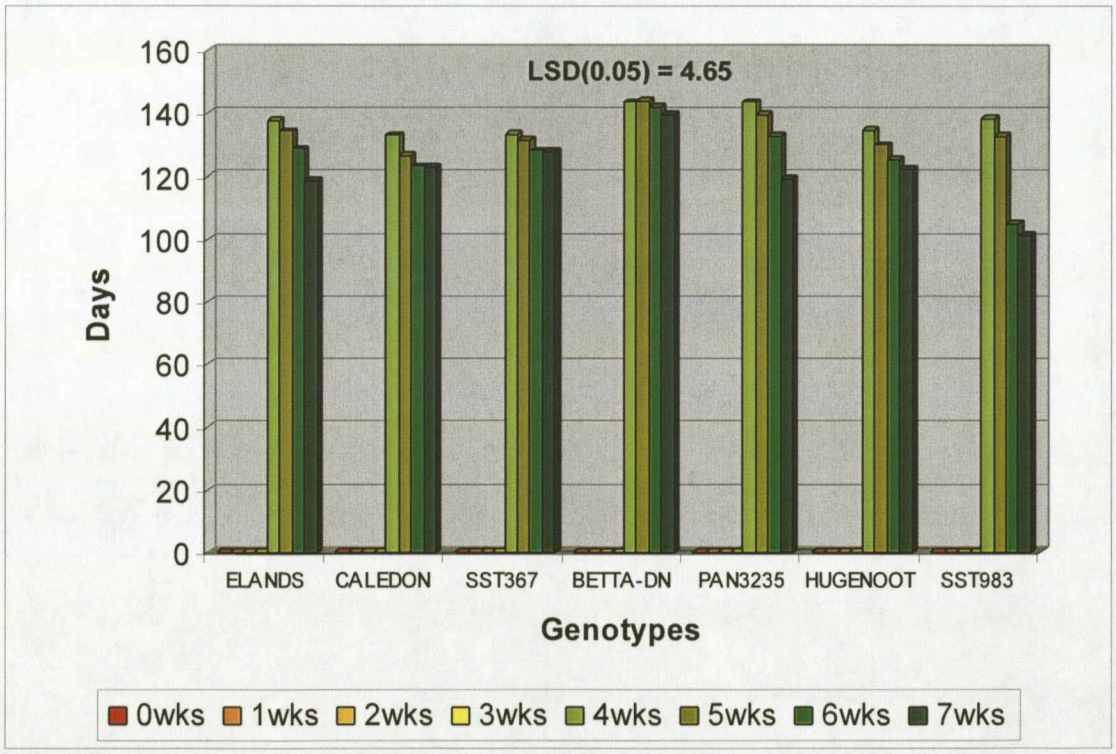


Figure 3.10 Days to physiological maturity of winter wheat cultivars for four to seven weeks vernalization treatments

3.3.2.2.3 Days from flowering to physiological maturity (DFTPM)

The number of days from flowering to physiological maturity for the winter wheats is presented in Figure 3.11 and Figure 3.12. Elands had a significantly longer period from flowering to physiological maturity than all other cultivars in the winter wheat cluster. Betta-DN ranked second with a significantly longer period between flowering and physiological maturity than the remaining hybrids in the cluster. SST983 yielded the shortest period and this period was significantly shorter than all the hybrids except Caledon in the cluster.

Excluding the first four vernalization treatments from the analysis, resulted in different rankings for days from flowering to physiological maturity. Betta-DN was ranked as the cultivar with the longest period between flowering and physiological maturity and was significantly different from all cultivars in this cluster. PAN3235, SST367, and Elands did not differ significantly from each other, as did Hugenoot, Caledon, and SST983. SST983 had the shortest period between flowering and days to physiological maturity which was significantly shorter than Elands, SST367, PAN3235, and Betta-DN.

The days from flowering to physiological maturity differed significantly between treatments with the seven week vernalization treatment resulting in the lowest number of days to flowering, and the four weeks treatment with the highest number of days from flowering to physiological maturity.

The reaction of cultivars to vernalization differed significantly between cultivars and treatments, indicating cultivar x vernalization treatment interaction. Elands (eight days) and PAN3235 (16 days) had large reductions in days from heading to flowering at seven weeks vernalization, while six weeks vernalization reduced the period between flowering and physiological maturity of SST983 by 22 days. The reduction in the days from flowering to physiological maturity varied between zero to four days per treatment for the other cultivars.

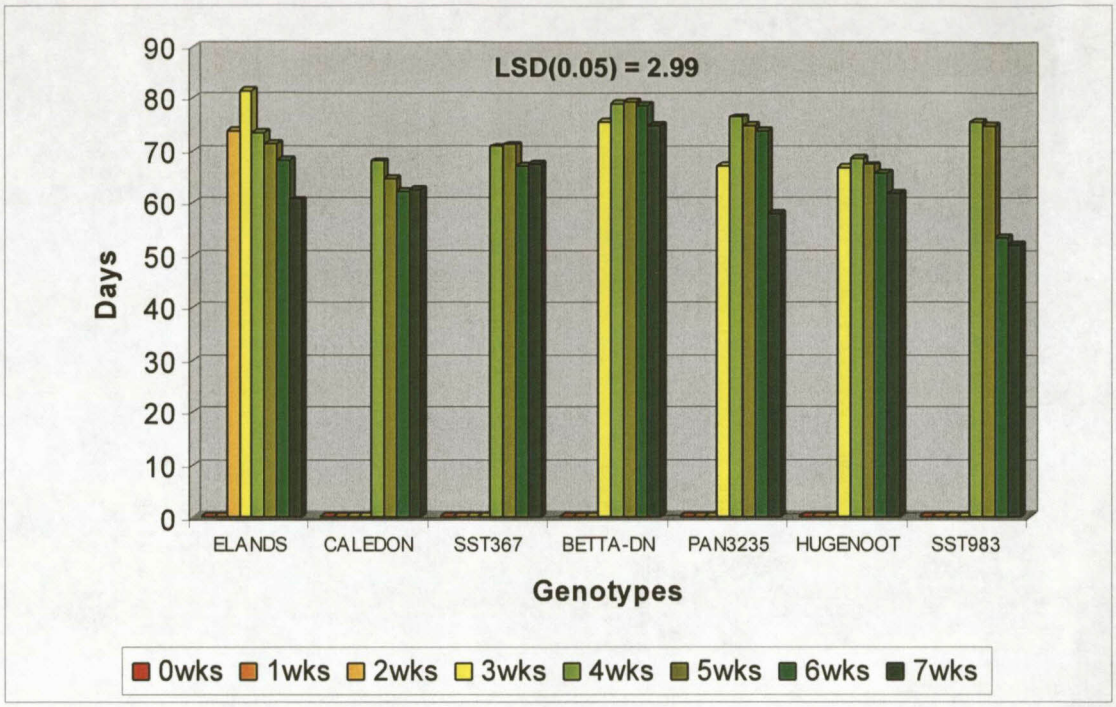


Figure 3.11 Days from flowering to physiological maturity of winter wheat cultivars for eight vernalization treatments

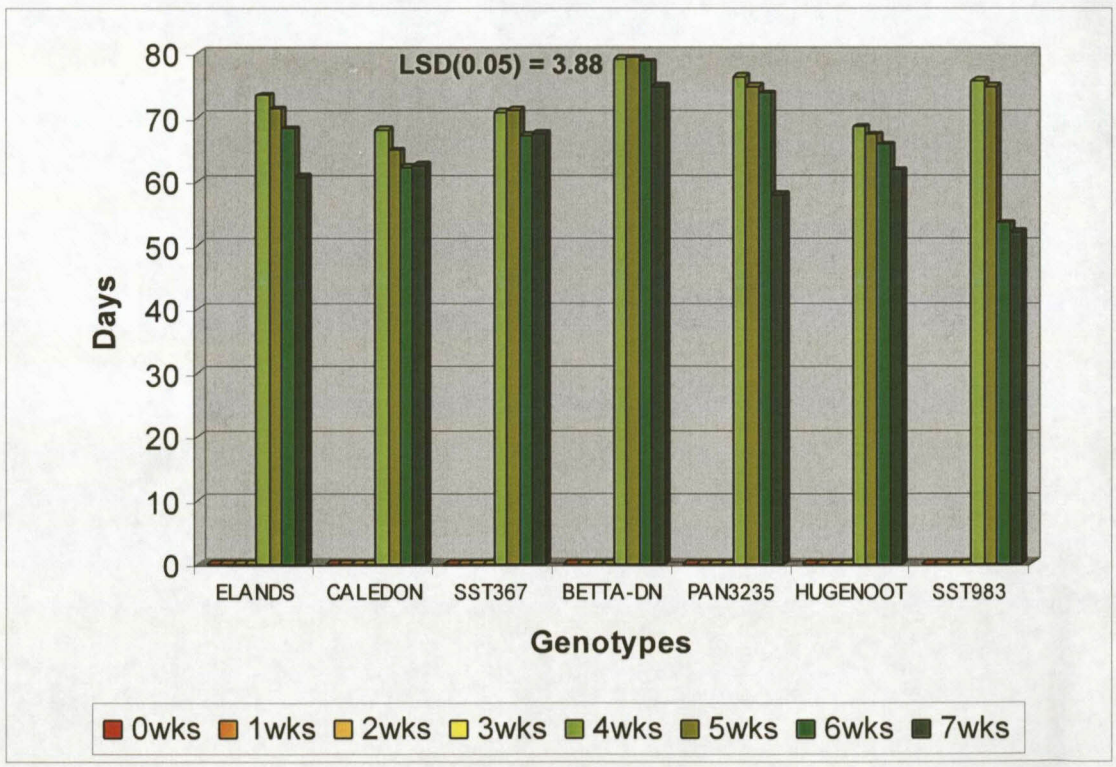


Figure 3.12 Days from flowering to physiological maturity of winter wheat cultivars for four to seven weeks vernalization treatments

Discussion

The major difference between winter wheat and true winter wheat was the amount of vernalization required to initiate the reproductive phase. All cultivars that require some period, but less than six weeks vernalization were grouped into the winter wheat cluster. These cultivars also differed significantly from one another for days to flowering, days to physiological maturity, and days from flowering to physiological maturity, within the same group. Within the winter wheat group, three sub groups of vernalization requirement were identified: for at least two weeks, three weeks, and four weeks vernalization requirement.

Elands was ranked as the cultivar with the longest periods for all measured characteristics. This ranking is somewhat skewed by the differences in required vernalization duration between the cultivars. After only two weeks of vernalization, the vernalization threshold for Elands is reached, although the duration in reaching anthesis and maturity was still considered long. It is only after four weeks cold treatment that Elands responded greatly to vernalization. The reduction in days needed to reach anthesis between the three week vernalization treatment and the four weeks vernalization treatment was 19 days for days to flowering and 27 days for days to maturity. It was clear that Elands required a shorter period of cold treatment than all other cultivars in this cluster to progress to the reproductive phase. However, as shown previously, Elands clustered on its own and was only included in this cluster because of its vernalization requirement.

After four weeks of cold treatment Elands, Caledon, PAN3235, and Hugenoot responded very similar to vernalization in reducing the number of days needed to reach the two (days to flowering and days to maturity) stages in wheat development. In general a moderate incremental reduction in duration of the different phases was observed for these cultivars. On the other hand two cultivars could be singled out with a very low response to vernalization treatments. Betta-DN and SST367 showed little reduction in days to flowering and days to physiological maturity. Betta-DN needed a shorter period than SST367 to initiate the reproductive phase, but after three weeks the response to vernalization was very low. It can thus be deduced from the data presented that

Betta-DN and SST367 had very stable responses to vernalization, and could be considered as relatively insensitive to vernalization once the threshold for cold requirement has been bridged.

The reaction of SST983 at different cold treatment levels reflected true sensitivity to vernalization. The number of days to reach anthesis was reduced from 63 days under a four week vernalization scenario, to 49 days when vernalised for seven weeks. The reduction in days to physiological maturity resulted in 38 days. Elands, PAN3235, and SST983 had the largest reduction in days from flowering to physiological maturity indicating a shorter grain filling period under longer periods of cold treatment.

3.3.2.3 Intermediate and spring wheats

From the cluster analyses presented previously, spring and intermediate wheats could be classed as cultivars with no minimum vernalization period requirement and, therefore, justified the means to discuss these two groups together. The dendrogram as presented in Figure 3.2, however, discriminates between two groups within the class of cultivars with no minimum vernalization requirement. Since all the cultivars required no vernalization, the length of their period to flowering and physiological maturity was used as discriminating character to sub divide these cultivars into two separate clusters. PAN3377, Gariep, SST363, SST124, Tugela-DN, PAN3349, PAN3211, and Limpopo were clustering together and were considered as intermediate wheats. Spring wheats, including: SST822, Inia, SST88, SST57, Steenbras, SST876, SST65, Palmiet, Marico, Baviaans, and Kariega had a shorter period to flowering and physiological maturity than intermediate wheats and this is evident from Figure 3.13 to Figure 3.15. The analyses of variance within the group consolidating cultivars with no vernalization requirement are summarised in Table 3.8.

Table 3.8 Analysis of variance for reproductive characteristics in intermediate and spring wheat cultivars with no vernalization requirement

Source	df	DTF	DTPM	DFTPM
Replications	7	37.16	294.12	212.27
Cultivars	18	131753.92**	561624.79**	162586.70**
Treatments	7	10267.24**	36983.51**	8765.75**
Cultivar x treatment	126	3677.91**	14317.38**	7366.57**
Residual	1057	6720.22	52627.51	40630.98
Total	1215	152456.44	665847.31	219562.26
LSD for cultivar at 0.01		1.04	2.91	2.55
LSD for cultivar at 0.05		0.73	2.05	1.80

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

3.3.2.3.1 Days to flowering (DTF)

Figure 3.13 clearly distinguishes between spring and intermediate wheat cultivars. Significant differences were observed between the cultivars classed as intermediate wheat. Limpopo had a significantly longer period to reach anthesis than any other intermediate cultivar, while SST363 was significantly shorter than all intermediate cultivars. No significant difference was found between PAN3211 and SST124, or between SST124 and Tugela-DN. All the intermediate wheat cultivars were significantly longer growing than any of the spring wheat cultivars. In the spring wheat cluster, SST88 and Marico had a significantly longer period to flowering than all other spring wheat cultivars. SST57 ranked third on length of the period to reach flowering, followed by SST876 and Steenbras that were significantly earlier. Palmiet, Baviaans, Kariega, and SST65 did not differ significantly from one another, but differed significantly from all other cultivars. Finally, Inia and SST822 had a significantly shorter period to reach anthesis than all other cultivars.

Differences between treatments were also highly significant, with zero days vernalization treatment resulting in the longest period needed to reach anthesis, while all cultivars reached anthesis earlier under a seven week vernalization

regime. Again, although some cultivars showed small increases in the number of days to reach the flowering stage under certain vernalization regimes, the general trend in reduction of the period to anthesis was positively related to vernalization treatment.

Significant differences were also observed between cultivar x vernalization treatment interactions. In the intermediate class from zero to 7 weeks vernalization treatment Limpopo (14 days), Tugela-DN (12 days), PAN3211 (12 days), and PAN3349 (10 days) had the largest response in reducing the period needed to reach anthesis, while Gariep (3 days) showed little response. Some of the spring cultivars responded in a relatively similar way to vernalization as did the intermediate cultivars. SST57 (14 days), SST88 (13 days), SST65 (12 days), Steenbras (11 days), and Palmiet (10 days) showed high responses to vernalization, while Kariega (2 days) and Baviaans (4 days) responded weakly under different vernalization treatments.

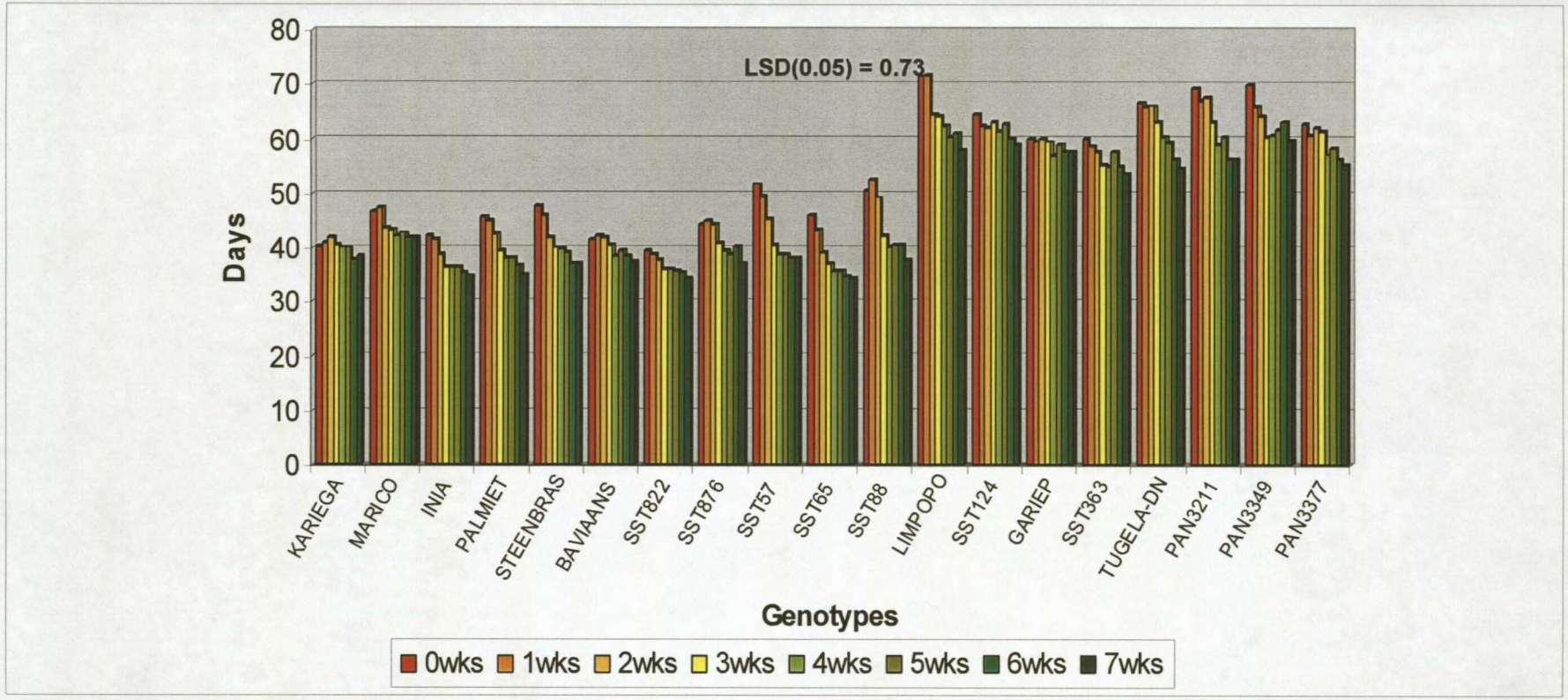


Figure 3.13 Days to flowering for intermediate and spring wheat cultivars with no vernalization requirement under eight vernalization treatments

3.3.2.3.2 Days to physiological maturity (DTPM)

Figure 3.14 illustrates the number of days to physiological maturity for all cultivars with no minimum vernalization requirement. Tugela-DN, in the intermediate cultivar class, needed a significantly longer period to reach physiological maturity than all other intermediate cultivars. No significant differences were found between PAN3211, Limpopo, and PAN3349, but these three cultivars were significantly later in reaching physiological maturity than the remaining four intermediate cultivars. Significant differences were found between SST124 and SST363, and between these two cultivars and Gariep and PAN3377. No significant differences were observed between Gariep and PAN337, but these two cultivars were significantly earlier in reaching physiological maturity than all other cultivars in the intermediate class.

Marico had a significantly longer period to reach physiological maturity than all other spring wheat cultivars except SST57. SST57 and Kariega did not differ significantly from one another. No significant differences in elapsed time to physiological maturity were found between Kariega, SST88, and Baviaans, or between Palmiet, SST876, Steenbras, and SST65. Inia and SST822 were significantly earlier in reaching physiological maturity, but no significant difference was found between Inia and SST822.

Significant differences were observed between vernalization treatments and the zero week treatment reached physiological maturity significantly later than the seven weeks vernalization treatment. This is clearly indicated in Figure 3.14 where the number of days needed to reach physiological maturity was reduced when the vernalization period was extended. In the intermediate wheat cultivar group, the total reduction in number of days to physiological maturity was reduced with 16 days, while only a seven days reduction in number of days to physiological maturity was observed in the spring wheat cultivar group.

Highly significant differences were also found for cultivar x vernalization treatment interactions. PAN3211 (28 days), Tugela-DN (27 days), and Limpopo (23 days) had the strongest response in reducing the number of days to physiological maturity from the minimum to the maximum length of vernalization

treatment. Gariep (6 days) had the lowest response to vernalization treatment. In the spring wheat class SST65 (25 days), SST88 (23 days), and Palmiet (22 days) showed the largest reduction in reaching physiological maturity, while SST822 (9 days), Kariega (10 days), and Marico (10 days) had a relatively poorer response to vernalization treatment.

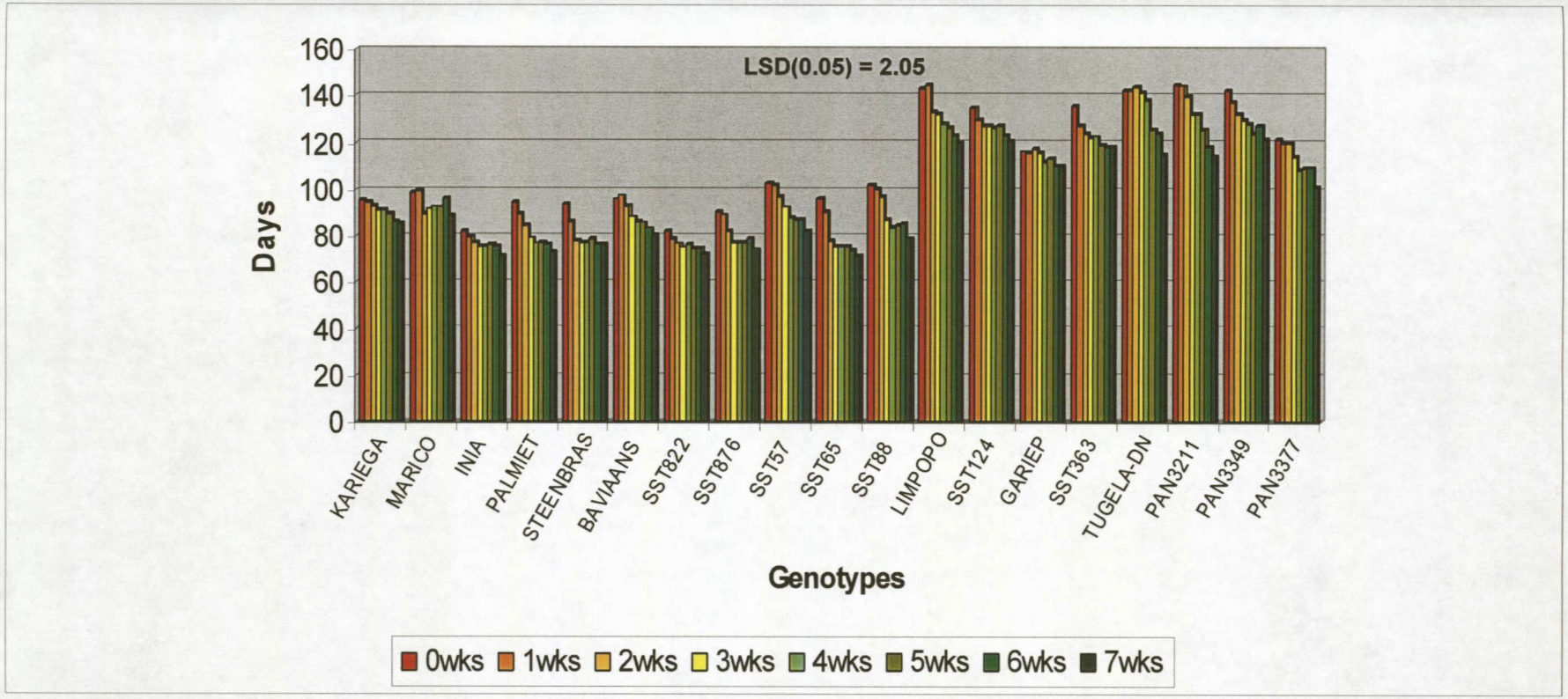


Figure 3.14 Days to physiological maturity for intermediate and spring wheat cultivars with no vernalization requirement under eight vernalization treatments

3.3.2.3.3 Days from flowering to physiological maturity (DFTPM)

The number of days for cultivars with no minimum vernalization requirement to reach physiological maturity after anthesis is summarised in Figure 3.15. Tugela-DN had a significantly longer period between anthesis and physiological maturity than any other intermediate wheat cultivar. PAN3211 differed significantly from SST124, Gariep, and PAN3377, whilst no significant differences were observed between PAN3349, Limpopo, SST363, and SST124. Gariep and PAN3377 did not differ significantly from one another, but were significantly earlier than all other intermediate cultivars in reaching physiological maturity after flowering.

Kariega, Marico, SST57, and Baviaans had the shortest period between flowering and physiological maturity and differed significantly from all other cultivars in the spring wheat class, but not from one another. No significant differences were observed between Palmiet, SST65, SST822, and SST876, or between SST822, SST876, Steenbras, and Inia. Inia had significantly the shortest period of all spring cultivars excluding Steenbras, SST876, and SST822 from flowering to physiological maturity.

Significant differences were found between vernalization treatments. Cultivars with the longest vernalization treatment had the shortest grain filling period, while cultivars with the shortest vernalization period had the longest grain filling period. Certain cultivars in both the intermediate and spring wheat cultivars responded variably to different vernalization treatments, but the general trend remained inversely related to the length of the vernalization treatment.

Highly significant differences were also found between cultivar x vernalization treatment interactions. From zero weeks vernalization to seven weeks vernalization PAN3211 (16 days), Tugela-DN (15 days), PAN3377 (13 days), and SST363 (13 days) responded strongly to vernalization, while Gariep (4 days) had a very weak response. In the spring wheat class SST65 (16 days) had the largest reduction in the period between flowering and physiological maturity, with Marico (5 days), Inia (4 days), and SST822 (4 days) responding to a much lesser extent to vernalization.

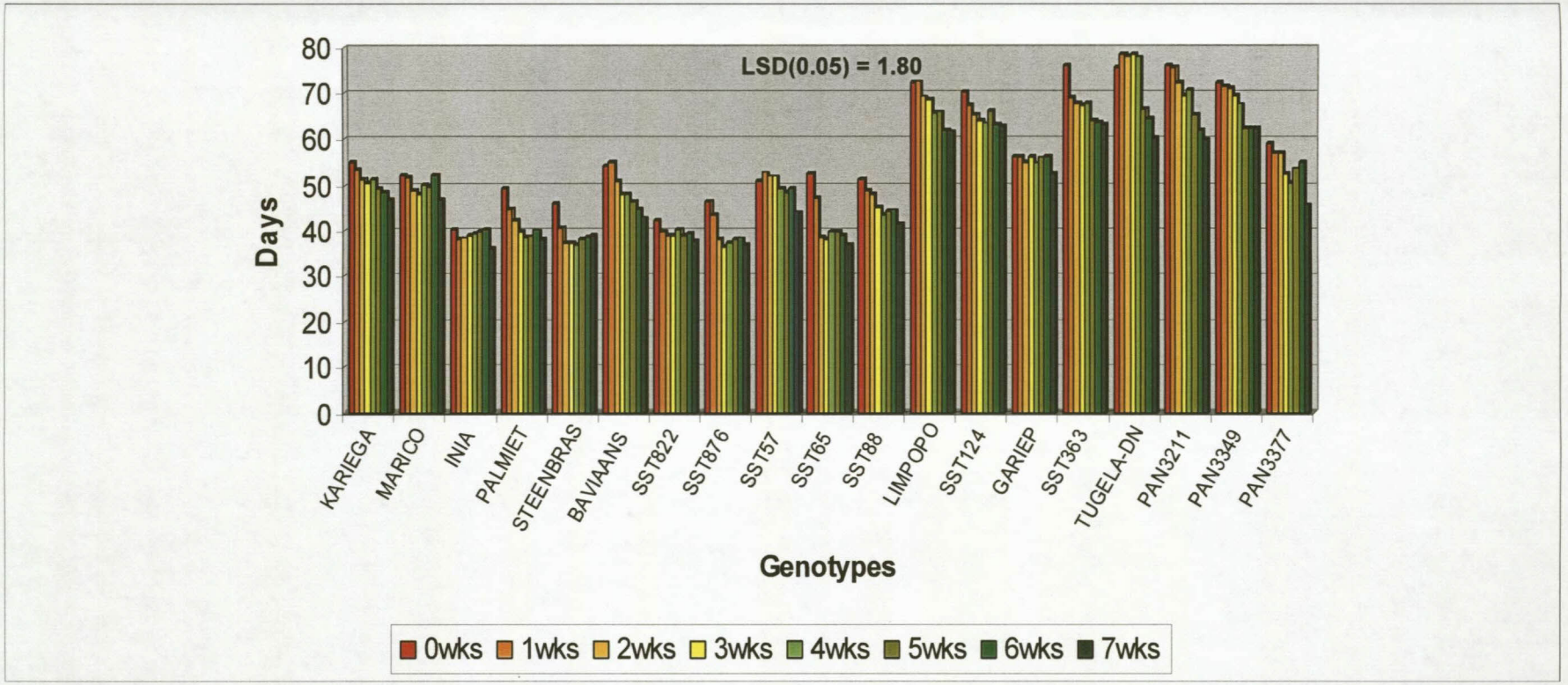


Figure 3.15 Days from flowering to physiological maturity for intermediate and spring wheat cultivars with no vernalization requirement under eight vernalization treatments

Discussion

The one factor that discriminated between winter (whether true winter, or winter) and intermediate wheat, and between winter and spring wheat was minimum vernalization requirement. From the data presented it is clear that vernalising temperatures, as described earlier in this chapter, is not a prerequisite for intermediate and spring wheat to progress to the reproductive phase. The difference between intermediate and spring wheat, however, is found in the length of the critical growth stages of the cultivars. Although no vernalization is required, intermediate wheat cultivars have significantly longer growth periods than spring wheat.

The response of intermediate wheat cultivars is variable and range from large to almost no response. Limpopo initially responded largely after two weeks vernalization by decreasing the number of days to flowering with seven days. This suggested that two weeks vernalization was the critical period for reduction in days to flowering. Limpopo responded similarly for the characters: days to physiological maturity and days from flowering to physiological maturity. PAN3349 also responded in a similar way, but the critical vernalization period was three weeks for earlier flowering. The response of PAN3349 to vernalization in terms of days to physiological maturity and days from flowering to physiological maturity followed a stepwise reduction pattern over all vernalization treatments.

Tugela-DN and PAN3211 had similar responses to vernalization treatment and both reduced the number of days to flowering gradually over the eight treatments. The difference between these two cultivars was found in their response to vernalization in terms of the period to physiological maturity and the period between flowering and physiological maturity. Tugela-DN uniquely had a low response to vernalization for both days to physiological maturity and days from flowering to physiological maturity over four weeks of vernalization treatment. This indicated that Tugela-DN has a more stable grain filling phase when subjected to low temperatures for four weeks. After five weeks vernalization, however, Tugela-DN responded strongly to low temperatures by

reducing the grain filling period with 11 days. PAN3211 gradually reduced the days to physiological maturity with longer vernalization treatments.

SST124, Gariep, and SST363 revealed low responses to vernalization treatments for days to flowering. The response of Gariep to vernalization suggested low sensitivity to low temperature treatments. This was illustrated in the negligible reduction of three days in days to flowering and four days in days from flowering to physiological maturity over the eight vernalization treatments. SST124 and SST363 initially responded with high sensitivity to vernalization, but after one week cold treatment, the response decreased to a reduction of five days for SST124 and six days for SST363 in days from flowering to physiological maturity over the remaining six vernalization treatments.

The majority of the spring wheat cultivars, except Kariega, Baviaans, and SST822, responded with high sensitivity to two weeks vernalization treatment by reducing the number of days needed to reach anthesis. Kariega, Baviaans and SST822 on the other hand were insensitive to cold treatment in terms of days to flowering. SST65, SST88, and SST57 could be considered as the most sensitive of the spring wheat cultivars to cold treatment. These cultivars reduced the number of days to flowering by 12, 13, and 14 days respectively, where the largest percentage reduction was obtained after three weeks cold treatment. The reduction in number of days to physiological maturity was also the largest for these three cultivars. Palmiet responded in a similar fashion with a moderate reduction in days to flowering and a large reduction of 22 days in days to physiological maturity.

The number of days to physiological maturity recorded for SST822 (10 days) and Inia (11 days) was the lowest for all spring wheat cultivars. The same response was observed for the grain filling period with a reduction in the grain filling period for SST822 of two days and for Inia four days. In the previous paragraph SST822 also had a low response to vernalization in terms of days to flowering, suggesting this spring cultivar to be insensitive to cold treatment. Inia responded initially to vernalization treatment, but this response reached a

plateau after two weeks vernalization. Thus, Inia could also be classified as a vernalization insensitive spring wheat cultivar.

Interestingly, Kariega and Baviaans showed little response in reducing the number of days to flowering, but both these cultivars, however, reduced the number of days from flowering to physiological maturity with 10 days and 15 days respectively when vernalised. In this case, these two spring wheat cultivars can be classed as sensitive to vernalization in terms of number of days needed to reach physiological maturity.

3.4 Conclusions and recommendation

The ability to correctly classify wheat cultivars according to their responses to vernalization is important in deciding where and when to plant specific cultivars, i.e. directing cultivars for targeted environments. Understanding the reaction of cultivars in terms of reaching critical growth phases when subjected to low temperatures is also useful when yield data is validated under given environmental conditions. The results obtained from this study suggest that South African bread wheat cultivars can be classed into the following distinct groups: 1) true winter, 2) winter, 3) intermediate, and 4) spring wheat cultivars.

Because of the complexity of vernalization response in wheat, the 30 wheat cultivars assessed in this study cannot be grouped into classes by merely using the sensitivity to vernalization treatments as only criterion. The variability in response of different cultivars to vernalization treatment and degree to which they respond contribute to the complexity of vernalization sensitivity. Clearly the majority of cultivars showed some sensitivity to vernalization by reducing the number of days to reach critical phenological stages. However, from this study Molen, SST936, SST966, and SST399 were classed as true winter wheat cultivars. The traditional winter wheat class covered Caledon, SST367, SST983, Betta-DN, PAN3235, and Hugenoot. Limpopo, SST124, Gariep, SST363, Tugela-DN, PAN3211, PAN3349, and PAN3377 were classed as intermediate wheat cultivars, while Kariega, Marico, Inia, Palmiet, Steenbras, Baviaans, SST822, SST876, SST57, SST65, and SST88 formed the spring wheat cultivar class as expected.

Tugela-DN, Baviaans, Kariega, and other cultivars responded differently in terms of days to flowering and days from flowering to physiological maturity although none of them required a minimum vernalization period. Tugela-DN exhibited a very stable grain filling period response to vernalization treatment and did not reduce its grain filling period significantly when subjected to longer vernalization periods. Elands reached its vernalization threshold after only two weeks vernalization, but still had a long duration in reaching physiological maturity. Gariep, an intermediate cultivar, and SST822 a spring cultivar, showed low to negligible responses to vernalization treatments for all observed phenological phases, but are classed differently due to their difference in growth period. Under field conditions PAN3377 has a prostrate growth habit that is typical of winter wheat cultivars. Yet, PAN3377 is classed as an intermediate wheat cultivar with no minimum vernalization requirement. This indicates that other characteristics like photoperiod or basic development rate could be responsible for its indifference response to vernalization.

From this study it is concluded and recommended that South African cultivars be classed as: 1) true winter, 2) winter, 3) intermediate and 3) spring wheat and that this classification should be based on minimum vernalization requirement as well as the length of the growth period. It is also suggested that yield trials, and trial layouts should be planned according to the different classes of wheat cultivars to obtain comparable results.

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CHAPTER 4

4. ASSESSMENT OF SOUTH AFRICAN BREAD WHEATS FOR PHOTOPERIOD RESPONSE

4.1 Introduction

Because wheat is grown under a wide range of agro-climatic conditions it has the largest cultivation area among crop plants (Ortiz-Ferrara *et al*, 1995). Wheat is, as indicated in the previous chapter, also adapted in areas with vastly different latitudes and therefore different lengths of day. Rawson and Zajac (1993) found that the number of days to ear emergence decreased progressively as the photoperiod lengthened. This occurred regardless of temperature or seed vernalization treatment. Wang and Engel (1998) concluded from their research that a second process is initiated after vernalization insensitivity is reached which can clearly involve photoperiod. Slafer and Rawson (1995a) stated that most of the world's wheat production is done in environments where the crop completes its vegetative growth under short photoperiods. However, with wheat being cultivated in sub-tropical Asia, understanding photoperiodic response in wheat has grown in importance. Worland (1996) concluded that all the southern European wheats were highly insensitive to day length, whereas cultivars bred in England and Germany were highly sensitive to day length. In France, the most wheat cultivars are insensitive to photoperiod, but cultivars adapted to areas north of Paris were found to be photoperiod sensitive. Although phenology or plant development is controlled by both vernalization and photoperiod, Mosaad *et al* (1995) reasoned that selection for photoperiodic response in spring wheat adapted to the tropics would be simpler and more consistent than selecting for vernalization requirement. Penrose and Martin (1997) found that ear emergence was more accurately predicted for photoperiod-insensitive winter wheats than for spring or facultative wheats with moderate sensitivity to photoperiod.

The response to intermediate and very short photoperiod change with cultivar (Slafer and Rawson, 1995a). They found that the least photoperiod sensitive cultivar had only one degree of sensitivity regardless of photoperiod, and thus responded in a qualitative way, while on the other extreme cultivars responded quantitatively to photoperiod.

Photoperiodic response along with vernalization requirement and earliness *per se* predominantly determine the developmental phases of bread wheat (Worland *et al*, 1998). Three sets of homoeologous chromosomes are primarily responsible for the complex genetic control of photoperiodic response. These genes are denominated as *Ppd1*, *Ppd2*, and *Ppd3* located on chromosomes 2D, 2B, and 2 A respectively. *Ppd1* is considered to be the least photoperiod sensitive followed by *Ppd2*, with *Ppd3* the least insensitive (Law *et al*, 1978). Worland (1996) found Ppd1 to exhibit a pleiotropic effect on the majority agronomic traits recorded. Miura and Worland (1994) implicated chromosome 3D as the site for an additional *Ppd* locus by using aneuploids in studying genetic control of photoperiod response in wheat.

The aim of this study was to:

1. Classify and group the most important South African wheat cultivars in terms of their response to photoperiod, and
2. To determine the variation in response to photoperiod treatment within each group.

4.2 Materials and methods

4.2.1 Cultivars

Thirty South African bread wheat cultivars, including spring, intermediate (facultative), and winter wheats were characterised on their response to photoperiod treatments. The cultivars were selected to represent cultivars cultivated in the major wheat production areas of South Africa. The cultivars used are summarised in Table 4.1

Table 4.1 Thirty South African bread wheat cultivars evaluated for their response to photoperiod treatments

Entry	Cultivar	Company	Growth Habit
1	KARIEGA	Small Grain Institute	Spring
2	MARICO	Small Grain Institute	Spring
3	INIA	Small Grain Institute	Spring
4	PALMIET	Small Grain Institute	Spring
5	STEENBRAS	Small Grain Institute	Spring
6	BAVIAANS	Small Grain Institute	Spring
7	SST822	Monsanto	Spring
8	SST876	Monsanto	Spring
9	SST57	Monsanto	Spring
10	SST65	Monsanto	Spring
11	SST88	Monsanto	Spring
12	LIMPOPO	Small Grain Institute	Intermediate
13	SST124	Monsanto	Intermediate
14	GARIEP	Small Grain Institute	Intermediate
15	ELANDS	Small Grain Institute	Intermediate
16	CALEDON	Small Grain Institute	Intermediate
17	SST363	Monsanto	Intermediate
18	SST367	Monsanto	Winter
19	TUGELA-DN	Small Grain Institute	Intermediate
20	BETTA-DN	Small Grain Institute	Winter
21	PAN3211	Pannar	Intermediate
22	PAN3235	Pannar	Intermediate
23	PAN3349	Pannar	Intermediate
24	PAN3377	Pannar	Winter
25	MOLEN	Small Grain Institute	Winter
26	HUGENOOT	Small Grain Institute	Winter
27	SST936	Monsanto	Winter
28	SST983	Monsanto	Intermediate
29	SST966	Monsanto	Winter
30	SST399	Monsanto	Winter

4.2.2 Photoperiodic treatments

Two, 2 litre pots per cultivar and ten seeds per pot were planted in a bark based growth medium. The seeds were germinated at room temperature for seven days, after which all the pots were moved into a cold room. All cultivars were vernalised at 3^0C (+/-1^0C) for 8 weeks under a 10 hour photoperiod regime. Cool fluorescent tube lights were used for artificial illumination. The pots were rotated at two-day intervals to minimise environmental variability. The seedlings were watered daily to maintain adequate water supply. The seedlings were at the two-leaf stage when vernalization treatment was completed.

The pots were transferred to three greenhouses with three different photoperiod regimes. The photoperiod treatments are listed in Table 4.2 below.

Table 4.2 Description of the photoperiod treatments

Treatment	Description
1	10 Hour natural light
2	14 Hour natural light
3	14 Hour natural light extended to 18 hours with artificial lighting

4.2.3 Glasshouse procedures

All treatments were carried out under lights even though the natural photoperiod was long enough to satisfy a 13.5 hour day length. This was done to reduce any temperature effects that could be induced where artificial light was used to lengthen the photoperiod treatment. Four 300 watt globes were installed one meter above canopy level to supply artificial lighting in each photoperiod treatment and these were controlled by electronic time switches. Pots in the 10 hour photoperiod treatment had to be moved in and out of a growth cabinet to ensure that the correct day length was applied. The glasshouse temperatures were set for 18^0C (+/-2^0C) and 24^0C (+/-2^0C) night day temperature regimes.

The pots were watered daily to guarantee adequate water supply and liquid fertiliser was given once a week in the form of a mixture of Supafeed (54 g), Maxi-Boost (22ml), Magnisol (22 g) dissolved in 2000 ml water.

4.2.4 Characters measured

Data on the following traits were gathered:

- Days to heading: The days calculated from transplanting in the field to the date when 50% of the hill plot headed. Heading is recorded when half of the ear is visible outside the boot.
- Days to flowering: The days calculated from transplanting in the field to the date when 50% of the hill plot flowered. Flowering is recorded when anthers are visible on half of the ear.
- Days to physiological maturity: The days calculated from transplanting in the field to the date when 50% of the hill plot reached physiological maturity. Physiological maturity is recorded when the peduncle has lost all chlorophyll with only the nodes still green.
- Days from heading to flowering: Calculated by subtracting days to heading from days to flowering.
- Days from heading to physiological maturity: Calculated by subtracting days to heading from days to physiological maturity.

4.2.5 Statistical analysis

Statistical analyses were done on the data sets using cluster analysis to group the cultivars and analysis of variance to determine the variance within each group. Two computer software programmes: NCSS (2000) for cluster analysis and AGROBASE (1999) for ANOVA were used to calculate statistical analyses.

4.2.6 Cluster analysis

Cluster analysis encompasses a number of different classification algorithms and. This analysis is used to organise observed data into meaningful

structures. Tree or hierarchal clustering method, the method used in this study, uses dissimilarities or distances between observations when forming the clusters. Starting off, each object is in a class by itself after which the threshold is lowered to declare two or more objects to be members of the same cluster. This continuous process results in linking more objects together and aggregate larger and larger clusters of increasing dissimilar elements. In the final step all objects are joined together.

The chosen type distance in the study is a Euclidean distance and is the geometric distance in the multidimensional space. Euclidean distance is calculated as follows:

$$\text{Distance}(x, y) = \{\sum_i (x_i - y_i)^2\}^{1/2}$$

When several objects have been linked together it is important to determine the distances between the new clusters. To accomplish this, a linkage or amalgamation rule is needed to link clusters together that are sufficiently similar. In this study the unweighted pair-group average method was used. In this method, the distance between two clusters are determined by the average distance between all pairs of objects in the two clusters.

4.2.7 Analysis of variance

Analysis of variance is an arithmetic technique by which total variation presented in a set of data is partitioned into different components. A factorial design was used to calculate the analysis variance in the data set using AGROBASE98. Significant differences between cultivar means were separated using a least significant difference (LSD) at $P \leq 0,05$.

4.3 Results and Discussions

4.3.1 Cluster analysis

Using actual values, the clustering of South African bread wheat cultivars was determined for days to flowering and days to physiological maturity, over all vernalization temperature regimes, and is presented as a dendrogram in Figure 4.1. Clusters A and B represent the highest point of dissimilarity and

discriminates between two clear groups. Cluster A constitutes of all the true winter, winter, and intermediate cultivars, excluding the hybrid wheats: SST966, SST936, and SST983. SST966 and SST936 were classified as true winter types, while SST983 was classified as a winter type in Chapter 3.

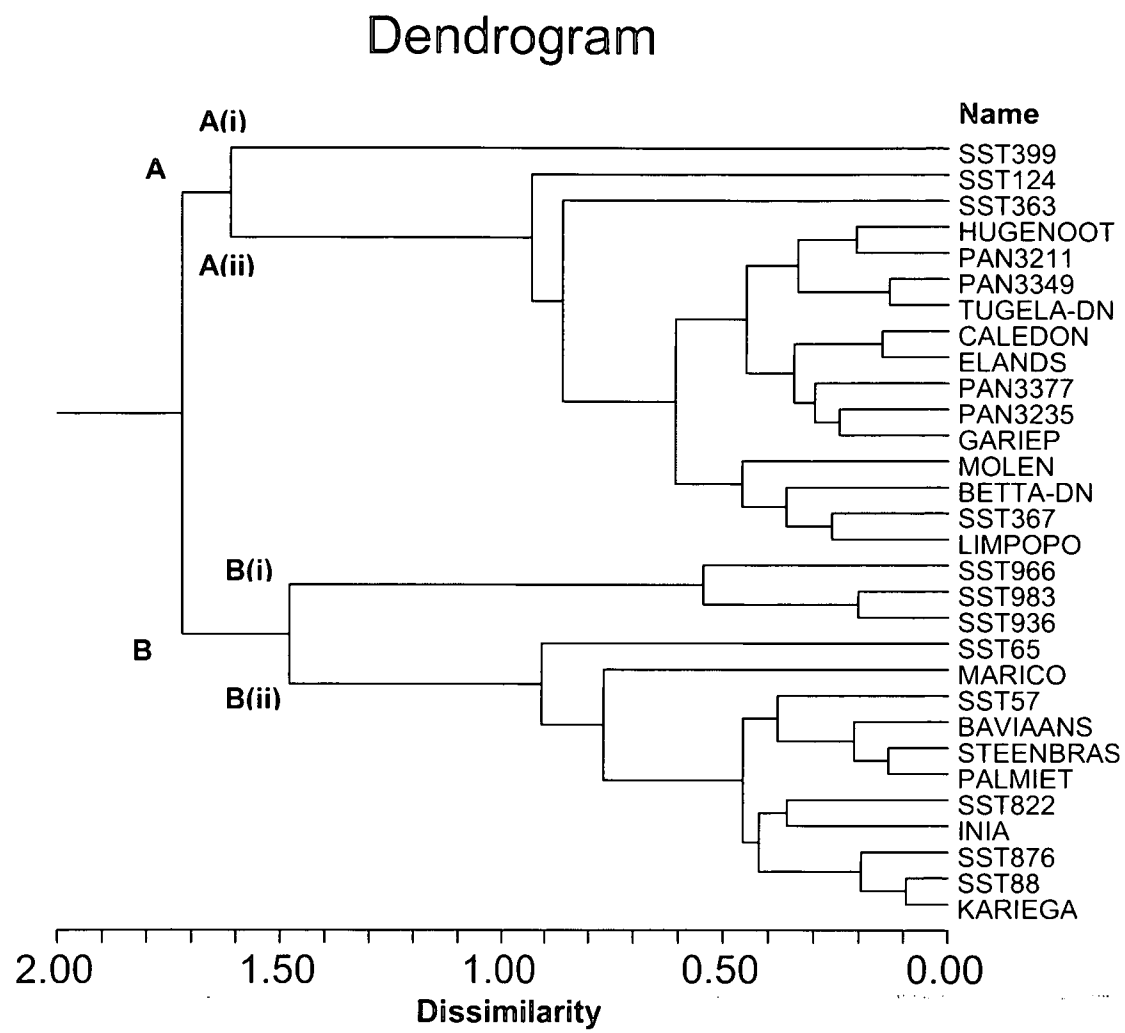

Figure 4.1 Cluster analysis of 30 wheat cultivars under three photoperiod treatments

Cophenetic Correlation = 0.893683
Delta(0.5) = 0.147791
Delta(1.0) = 0.202184

Cluster A further divides into sub-cluster A(i) and sub-cluster A(ii). Sub-cluster A(i) only constitutes of SST399, a typical long growth period true winter wheat. A(ii) includes true winter, winter, and intermediate cultivars with SST124 and SST363 clustering on their own within the larger cluster. Another three

smaller clusters are visible within the A(ii) cluster and although the level of dissimilarity at this point is very low, cultivars within the smaller cluster are more similar than to those in the other clusters. Hugenoot, PAN3211, PAN3349, and Tugela-DN cluster together, with Caledon, Elands, PAN3377, PAN3235, and Gariep differing slightly from them. The last of the three clusters consolidates Molen, Betta-DN, SST367 and Limpopo into one cluster.

The cultivars on cluster B are from extreme phenological constitution, and include spring, winter, and true winter cultivars. Cluster B subdivides into B(i) and B(ii) with B(i) representing the true winter (SST966 and SST936) and winter (SST983) cultivars. All the spring wheat cultivars are represented by sub-cluster B(ii) with four clear smaller clusters within the main spring wheat cluster. SST65 clusters on its own with Marico reacting similar. The third cluster constitutes SST57, Baviaans, Steenbras, and Palmiet, while SST822, Inia, SST876, SST88, and Kariega form the final cluster within B(ii). The level of dissimilarity between the spring wheat clusters is very low and all spring wheat cultivars should be seen as falling in one cluster.

From Figure 4.1 it is evident that, although more, smaller clusters are present within the main clusters, only four main clusters can be identified. The first cluster is SST399 on its own, followed by the remaining true winter, winter, and intermediate cultivars, but excluding the hybrid wheats. The third cluster represents all the hybrid wheats. The fourth and last main cluster includes all the spring wheat cultivars.

The unexpected clustering of winter or true winter cultivars with spring cultivars can be explained by Figure 4.2. Figure 4.2 represents the cluster analysis for all cultivars under a 10 hour photoperiod regime. In Figure 4.2 all the true winter, winter, and intermediate cultivars (excluding the hybrid wheat cultivars) cluster together on cluster A. Cluster A, therefore, represents all wheat cultivars that require more than 10 hours photoperiod to initiate the reproductive phase. The minimum photoperiod requirement for these cultivars is unknown and cannot be determined from the current study and the

same holds true for the cultivars that did initiate the reproductive phase at 10 hours daylight.

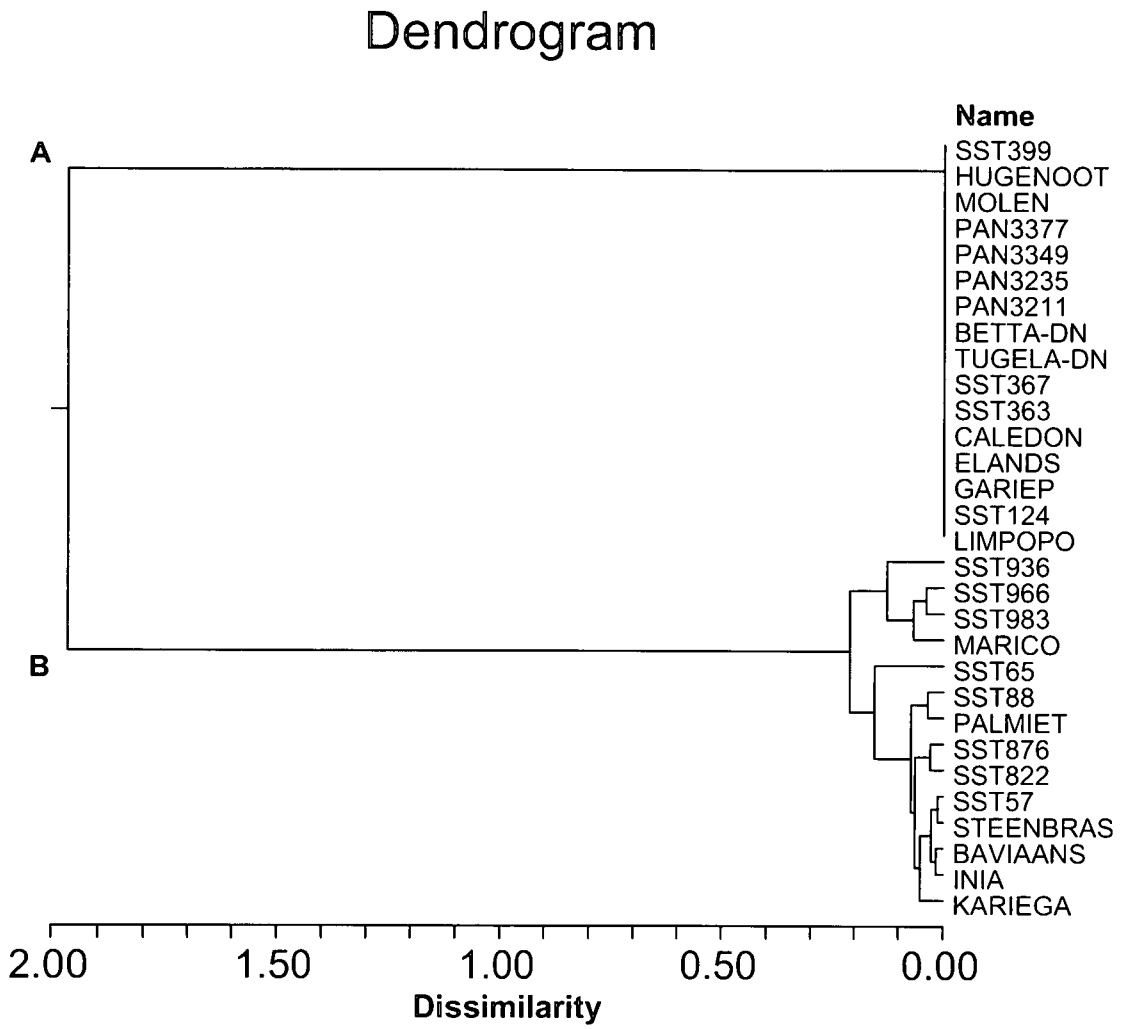

Figure 4.2 Cluster analyses of 30 wheat cultivars under a 10 hour photoperiod treatment

Cophenetic Correlation = 0.996361
Delta(0.5) = 0.050629
Delta(1.0) = 0.057822

Cluster B, in Figure 4.2, represents all the cultivars that flowered under a 10 hour day length and includes the hybrid wheat cultivars: SST966, SST936, SST938, and all the spring wheat cultivars: Marico, SST65, SST88, Palmiet, SST876, SST822, SST57, Steenbras, Baviaans, Inia, and Kariega. This explains the similar clustering habit of the hybrid wheat and spring wheat cultivars compared to the intermediate wheats. It is also interesting to note that Marico clusters with the hybrid cultivars when only the 10 hour

photoperiod is considered. This can be attributed to Marico's relative long growing period.

Figure 4.3 summarises the results from a cluster analysis for the response of 30 wheat cultivars to a 14 hour photoperiod treatment.

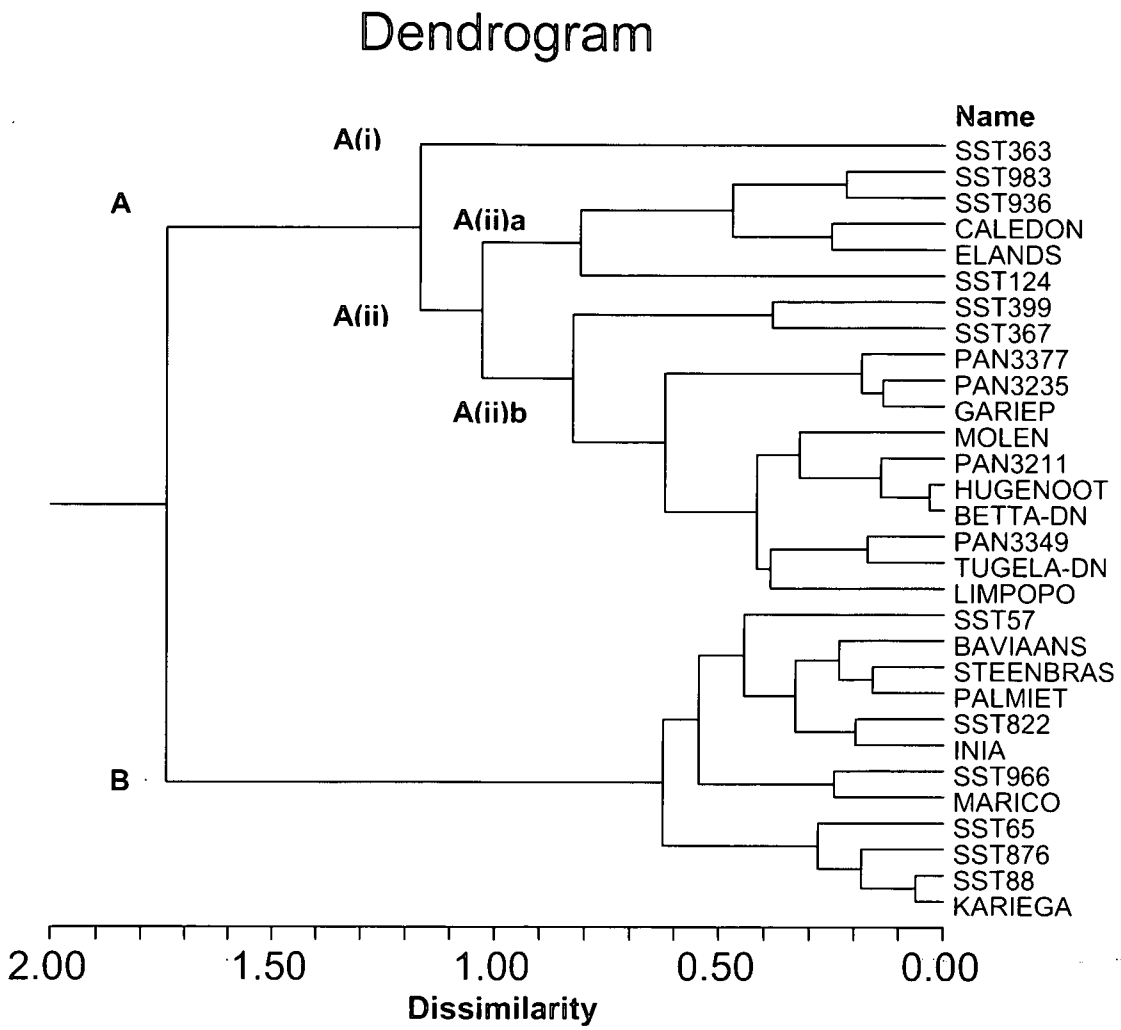

Figure 4.3 Cluster analyses of 30 wheat cultivars under a 14 hour photoperiod treatment

Cophenetic Correlation = 0.787954
Delta(0.5) = 0.256492
Delta(1.0) = 0.320412

Figure 4.3 represents how wheat cultivars relate to one another after their vernalization requirement has been satisfied and when they are subjected to a 14 hour day length. Cluster A represents all the true winter, winter, and intermediate cultivars, while cluster B represents all the spring wheat cultivars.

The clustering as presented in Figure 4.3 differs from the one in Figure 4.2 and this discrepancy is brought about by cultivar x photoperiod interaction.

Figure 4.4 illustrates the clustering of cultivars when both vernalization and photoperiod requirements (18 hours) are satisfied.

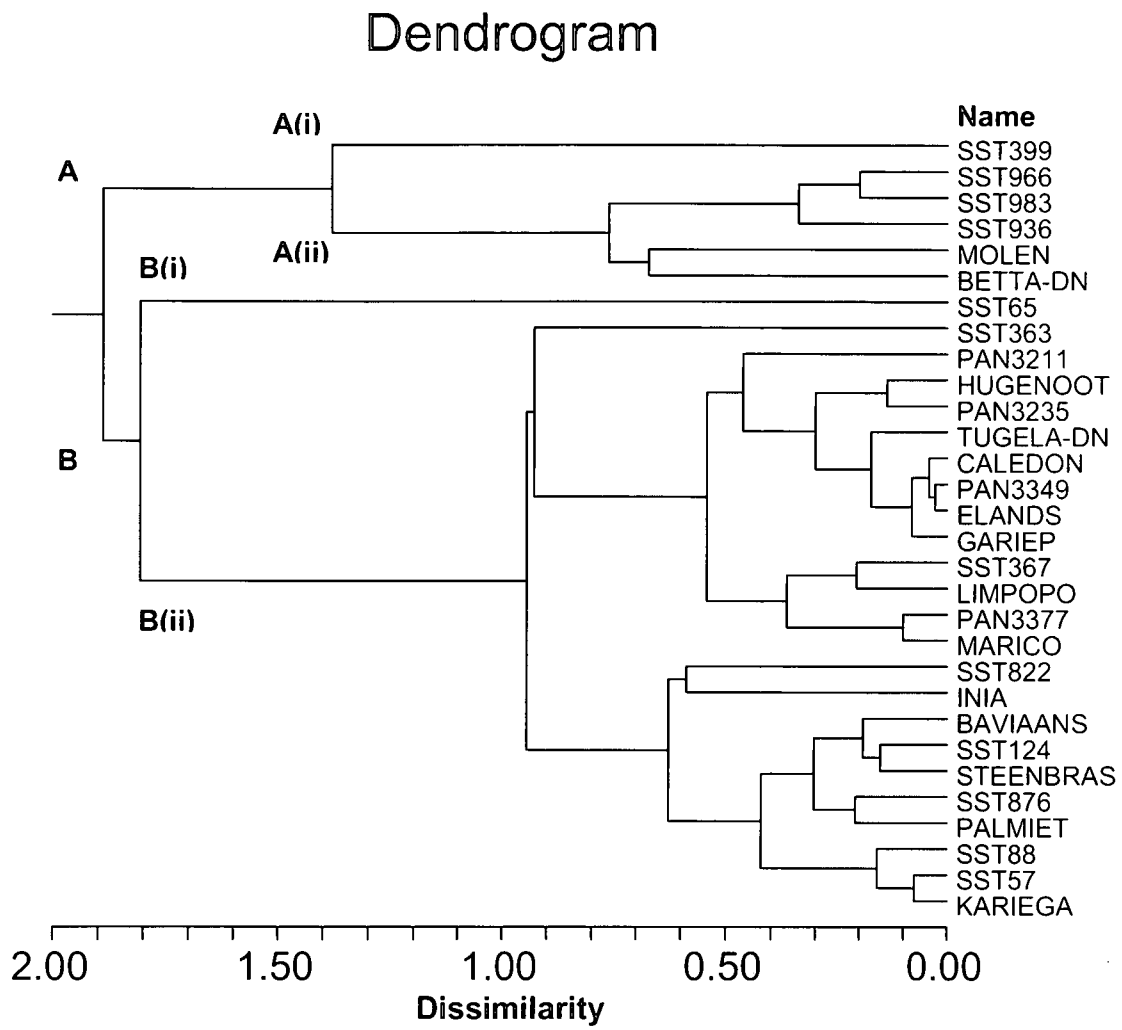

Figure 4.4 Cluster analyses of 30 cultivars under an 18 hour photoperiod treatment

Cophenetic Correlation = 0.758828
Delta(0.5) = 0.303927
Delta(1.0) = 0.396923

When the vernalization and photoperiod requirements of cultivars are satisfied, the only remaining trait, under a constant temperature regime, that can contribute to differences in flowering time between cultivars is intrinsic

earliness (Hoogendoorn, 1985). Evans (1987) reported that floral development is not responsive to photoperiods of longer than 18 hours and it could therefore be assumed that the photoperiod requirements for the cultivars in this study were saturated. In Chapter 3, the minimum vernalization requirement for the most vernalization sensitive cultivars was six weeks. In this study the cultivars were subjected to eight weeks vernalization treatment and should thus satisfy the vernalization requirements of all cultivars.

The Dendrogram in Figure 4.4 represents the clustering of cultivars in terms of intrinsic earliness, or basic development rate. This clustering is also different from the last two cluster analyses and this again emphasized the importance of correct interpretation of these analyses. To accurately classify the cultivars according to their response to photoperiod, it is necessary to combine all treatments and measured characters into one analysis as presented in Figure 4.1. The 30 cultivars used in this study are classified according to the results presented in Figure 4.1 and are summarised in Table 4.3.

4.3.2 Analysis of variance

Clustering the 30 wheat cultivars into similarity groups enables one to calculate analyses of variance for wheat cultivars with similar requirements for photoperiod. Analyses of variance are important to determine differences in the response of wheat cultivars within the same cluster due to cultivar, or cultivar x environment interaction.

Table 4.3 Classification of 30 wheat cultivars in terms of photoperiodic response

Group 1	Group 2	Group 3	Group 4
SST399	SST124	SST966	SST65
	SST363	SST936	MARICO
	HUGENOOT	SST983	SST57
	PAN3211		BAVIAANS
	PAN3349		STEENBRAS
	TUGELA-DN		PALMIET
	CALEDON		SST822
	ELANDS		INIA
	PAN3377		SST876
	PAN3235		SST88
	GARIEP		KARIEGA
	MOLEN		
	BETTA-DN		
	SST367		
	LIMPOPO		

4.3.2.1 Group 1

The only wheat cultivar that fell into this group was SST399. Clustering of SST399 into a group on its own illustrates the unique growth and development characteristics of this cultivar under different lengths of photoperiod. Although SST399 and the cultivars in Group 2 responded similarly to photoperiods longer than 10 hours it was the long growth period of SST399 that separated it from the Group 2 cultivars. Since only one cultivar is represented by Group 1, no analysis of variance is possible.

4.3.2.1.1 Days to flowering (DTF)

The number of days to flowering under three photoperiod treatments for SST399 is presented in Figure 4.5. No initiation of the reproductive phase occurred when SST399 was subjected to 10 hours photoperiod. Flowering was only reached when 14 hours daylight was applied. SST399 responded to

photoperiod treatment by reducing the number of days needed to reach anthesis with 31days from 14 to 18 hours day length.

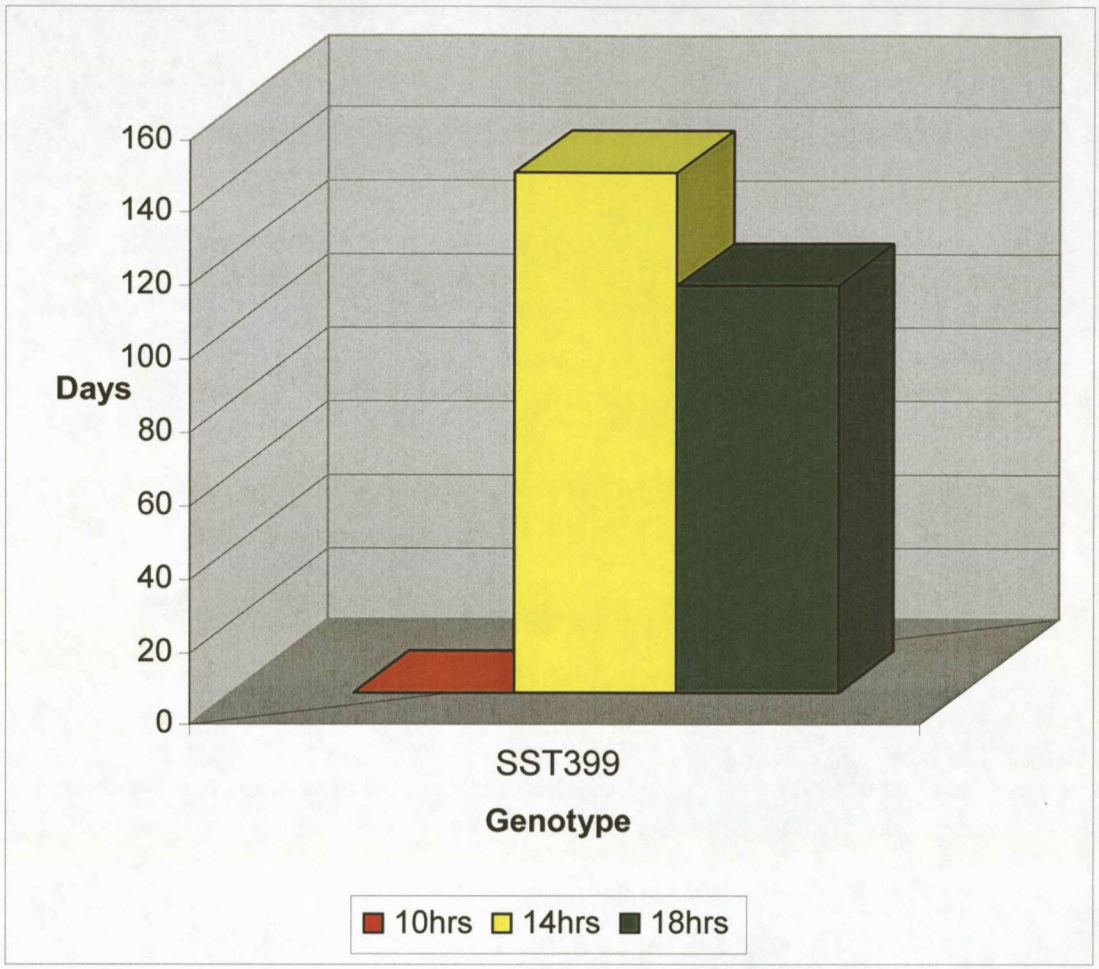

Figure 4.5 Days to flowering of the Group 1 wheat cultivar(s) for three photoperiod treatments

4.3.2.1.2 Days to physiological maturity (DTPM)

The days SST399 needed to reach physiological maturity is summarised in Figure 4.6. Since physiological maturity can only be reached if flowering occurs, no data is available for the 10 hour photoperiod treatment. A difference of only 15 days between the 14 and 18 hour photoperiods for SST399 was observed. Compared to the reduction in days to flowering, this reduction in days to physiological maturity is relatively low.

Figure 4.6 Days to physiological maturity of the Group 1 wheat cultivar(s) for three photoperiod treatments

4.3.2.1.3 Days from flowering to physiological maturity (DFTPM)

The days from flowering to physiological maturity (grain filling period) for SST399 is presented in Figure 4.7. The results obtained from this trial almost contravened logic by showing an increase in the number of days from flowering to physiological maturity. The grain filling period for SST399 under an 18 hour photoperiod was 54 days compared to 38 days under a 14 hour period. This amounted to an increase of 16 days when the photoperiod was extended from 14 to 18 hours.

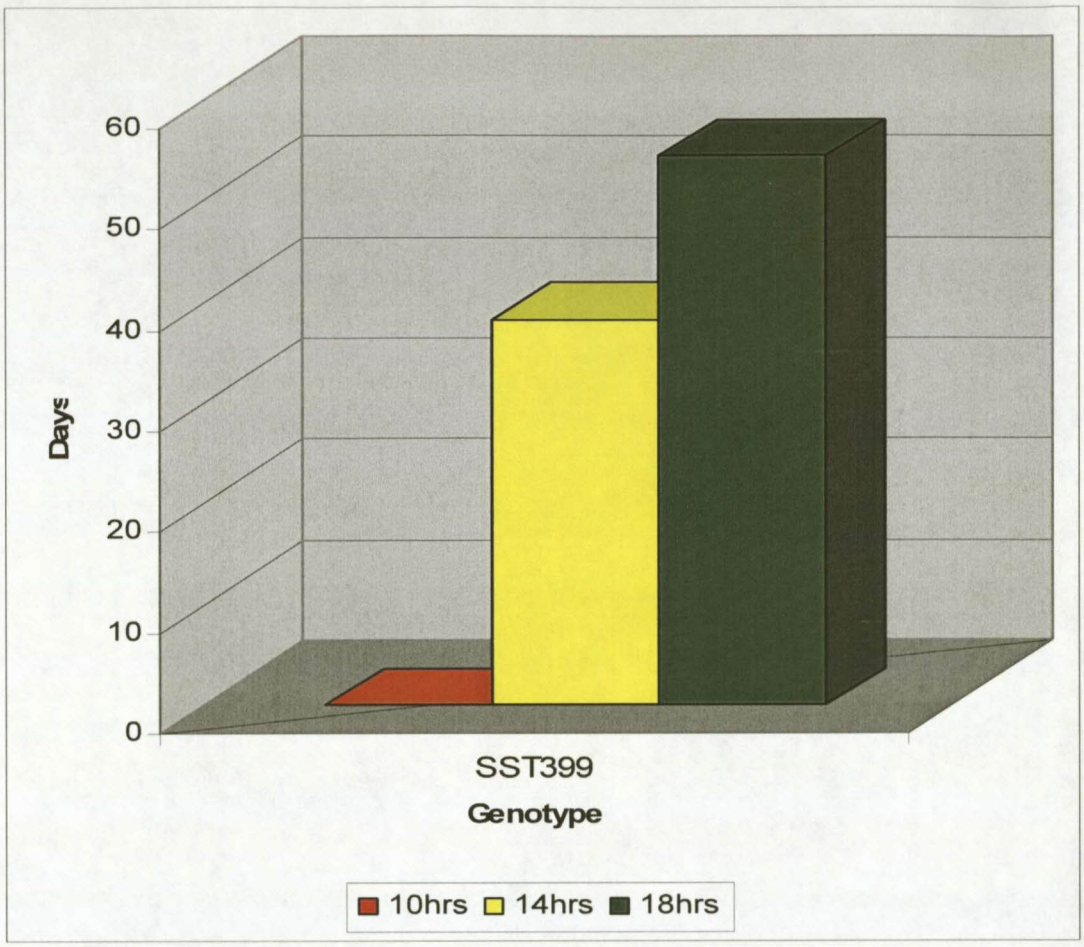

Figure 4.7 Days from flowering to physiological maturity of the Group 1 wheat cultivar(s) for three photoperiod treatments

Discussion

SST399 responded to photoperiod treatments by not flowering under a 10 hour photoperiod, but it flowered when subjected to 14 and 18 hours photoperiod. Although the minimum required photoperiod to initiate flowering cannot be determined from this study, it is clear that SST399 is sensitive to the length of photoperiod. This is illustrated by the response of SST399 in terms of number of days to flowering and physiological maturity. Both these numbers were reduced when a longer photoperiod was applied.

The grain filling period or period from flowering to physiological maturity increased with longer photoperiods. This phenomenon was the result of and was explained by a much lower reduction in days to physiological maturity (15 days) than in day to flowering (31 days).

4.3.2.2 Group 2

Cultivars in Groups 1 and 2 required more than 10 hours day light to initiate the reproductive phase. These two groups were separated on the basis of their growth length under 14 and 18 hour photoperiods. Group 1 had longer average periods (both photoperiod treatments) in reaching flowering (127 days) and physiological maturity (174 days) than Group 2 (120 and 163 days respectively).

From Figure 4.1 five smaller groups can be identified within the Group 2 cluster. SST124 and SST363 clustered on their own as two separate groups. The third group consisted of Hugenoot, PAN3211, PAN3349, and Tugela-DN. Caledon, Elands, PAN3377, PAN3235, and Gariep form the fourth group, while Molen, Betta-DN, SST367, and Limpopo were included in the fifth group. It is thus clear that differences between the cultivars in the Group 2 cluster do exist. Analyses of variance were therefore calculated to determine the magnitude of differences within Group 2. A summary of the results of analyses of variance is presented in Table 4.4.

Table 4.4 Analysis of variance for reproductive characteristics in the Group 2 photoperiod cluster wheat cultivars

Source	df	DTF	DTPM	DFTPM
Replications	9	473.88**	1133.47**	188.39**
Cultivars	14	1880.07**	2586.19**	3352.09**
Treatments	1	52245.60**	37163.07**	1289.61**
Cultivar x treatment	14	880.75**	679.48**	1490.09**
Residual	261	1114.62	1379.03	1332.21
Total	299	56594.92	42959.24	7652.39
LSD for cultivar at 0.01		1.67	1.70	1.67
LSD for cultivar at 0.05		1.08	1.20	1.18

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

4.3.2.2.1 Days to Flowering (DTF)

Figure 4.8 represents the response to photoperiod of the 15 wheat cultivars in the Group 2 cluster. All the cultivars included in this cluster needed more than a 10 hour photoperiod to flower. The cultivars differed significantly in their response to photoperiod treatment and significant differences were also observed for replications. Molen had the longest period to flowering and differed significantly from 11 cultivars, but not from Betta-DN, SST367, and Hugenoot. Betta-DN, SST367, and Hugenoot did not differ significantly from one another. Betta-DN and Hugenoot reached flowering significantly later than Gariep, PAN3349, Tugela-DN, Elands, Caledon, SST124, and SST363. Betta-DN was in addition also significantly later than Limpopo. PAN3377, PAN3235, PAN3211, and Limpopo did dot differ significantly from each other, but they flowered significantly later than Gariep, PAN3349, and Tugela-DN, who in turn reached anthesis significantly later than Elands, Caledon, and SST124. No significant differences were observed between Gariep, PAN3349, and Tugela-DN or between Elands, Caledon, and SST124. SST363 was significantly the earliest cultivar to reach the flowering stage.

Treatments differed significantly with an 18 hour photoperiod resulting in the shortest period from planting to anthesis and all cultivars under a 10 hour photoperiod failed to progress to the reproductive phase. The days to flowering was reduced from 132 days to 106 days under a 14 and 18 hour photoperiod treatment respectively.

Significant differences for cultivar x photoperiod were observed. The number of days to reach anthesis for SST367, Hugenoot, and PAN3211was reduced with 31, 30.8, and 30.1 days respectively. Betta-DN (29.3days) and PAN3235 (28.8 days) formed the group with the second largest reduction in number of days to anthesis. This group was followed by Gariep (27.6 days), PAN3349 (26.1 days), PAN3377 (27.3 days), and Molen (27.3 days) forming a third group. For SST124 and Limpopo the number of days was reduced by 25.3 and 25.2 days respectively from the 14 to the 18 hour photoperiod. Tugela-DN (23.8 days), Caledon (22.5 days), and Elands (22.4 days) responded

similarly to photoperiod. Lastly, SST363 had the lowest response, expressed in days to flowering, to photoperiod with a reduction of 18.4 days.

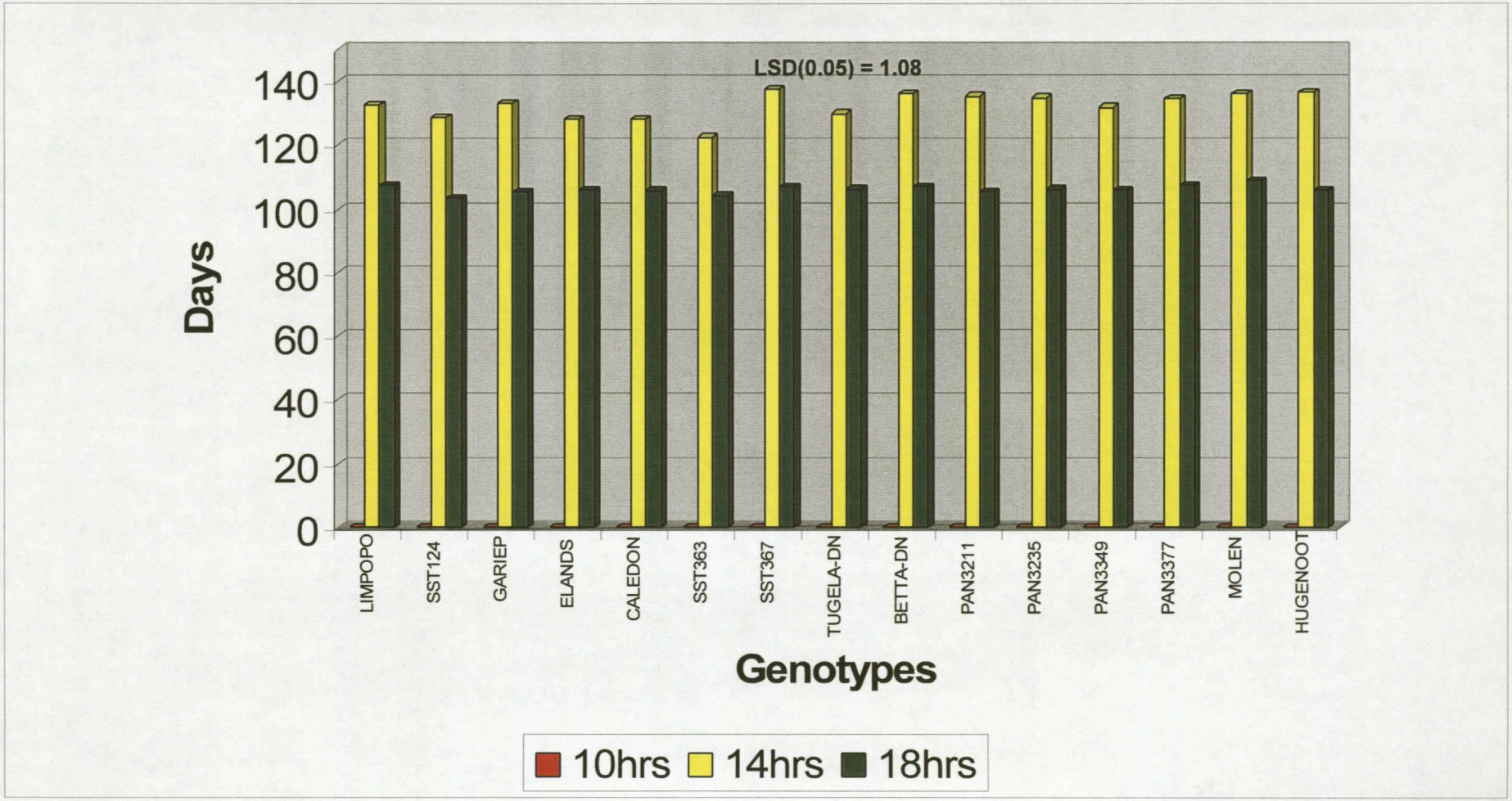

Figure 4.8 Days to flowering of the 15 Group 2 wheat cultivars for three photoperiod treatments

4.3.2.2.2 Days to physiological maturity (DTPM)

Figure 4.9 summarises the response of the 15 cultivars to photoperiod, expressed as the change in days to reach physiological maturity when subjected to different photoperiods. SST363 was ranked first with a significant longer period to reach physiological maturity than the 14 other cultivars. Betta-DN, SST367, Limpopo, and PAN3211 did not differ significantly from each other, but all four cultivars took significantly longer than all other cultivars, except SST363, in the group to reach physiological maturity. Molen and Hugenoot responded the same to photoperiod, but differed significantly in terms of a longer period to physiological maturity, from PAN3349, Tugela-DN, PAN3235, Gariep, PAN3377, Caledon, Elands, and SST124. PAN3349, Tugela-DN, and SST3235 did not differ significantly from each other, but were significantly later than Gariep, PAN3377, Caledon, Elands, and SST124, while Gariep, PAN3377, Caledon, and Elands did not differ significantly. SST124 had significantly the shortest period to physiological maturity.

As expected the two responsive photoperiod treatments were significantly different from one another in terms of period between planting and physiological maturity. The 18 hour photoperiod resulted in the shortest period to physiological maturity. The 15 wheat cultivars took 174 days to reach physiological maturity under a 14 hour photoperiod, whereas only 152 days were required for the same set of cultivars to reach physiological maturity under the 18 hour photoperiod.

All 15 wheat cultivars had a reduction in days to physiological maturity when the 14 hour photoperiod was extended to 18 hours. Significant differences were observed for cultivar x photoperiod interaction. SST124 had a reduction of only 15.7 days, followed by Betta-DN (19.4 days), PAN3235 (19.5 days), Elands (19.6 days), PAN3377 (19.8 days), and Molen (19.8 days). The reduction in days to physiological maturity for Caledon, and Gariep was 22 .0 days and 22.3 days respectively. Caledon and Gariep were followed by PAN3211 (24.0 days), SST363 (24.3 days), and Tugela-DN (24.9), while in both Hugenoot and Limpopo a reduction of 25.1 days was observed.

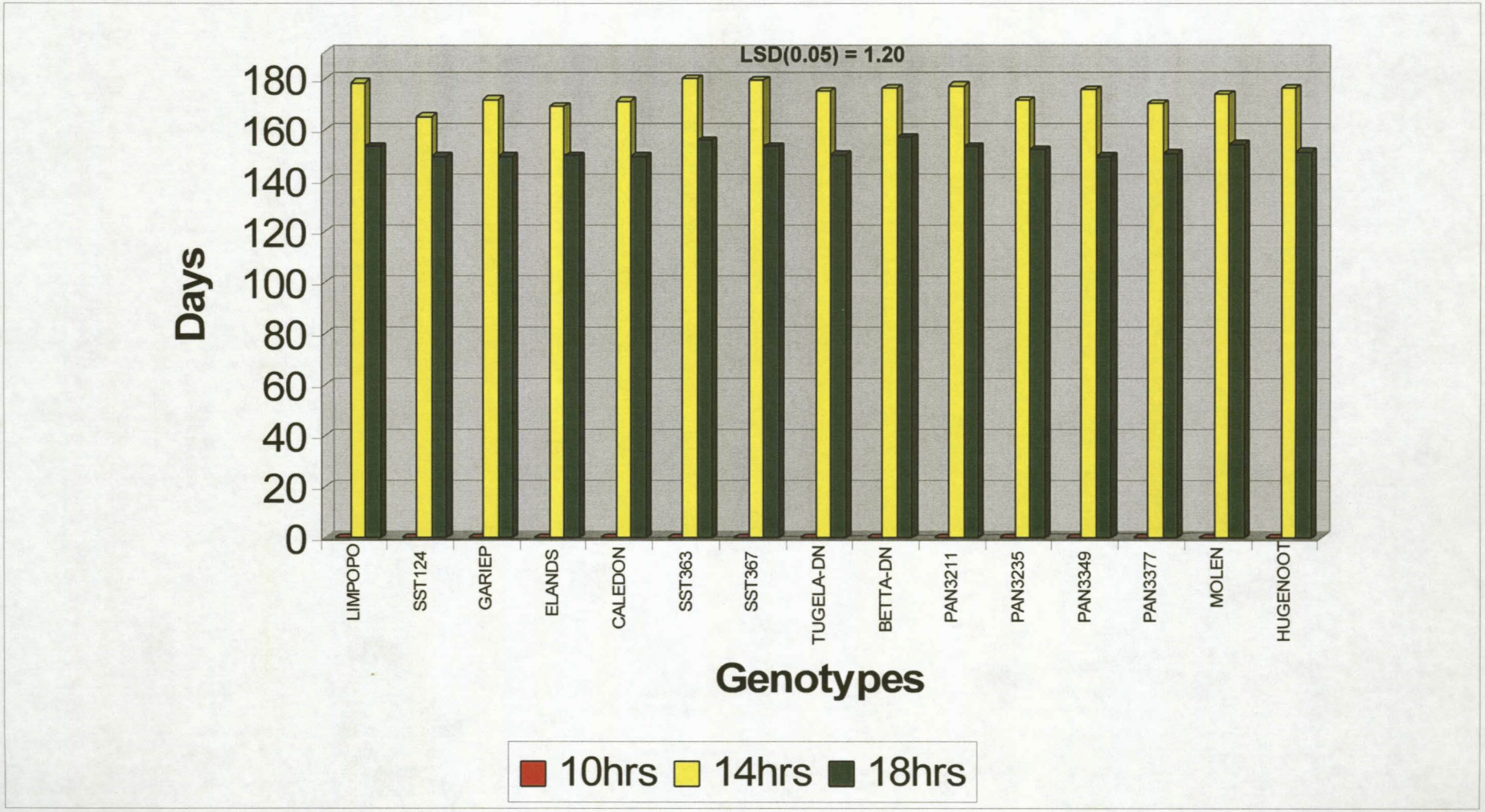

Figure 4.9 Days to physiological maturity of the 15 Group 2 wheat cultivars for three photoperiod treatments

The two cultivars with the longest period to physiological maturity were SST367 (24.3), and PAN3349 (26.4 days).

4.3.2.2.3 Days from flowering to physiological maturity (DFTPM)

Response in the grain filling period, expressed as the days from flowering to physiological maturity, for the 15 Group 2 wheat cultivars is presented in Figure 4.10. Significant differences were observed between the 15 cultivars, where SST363 had significantly the longest and PAN3377 significantly the shortest grain filling period for all cultivars. Limpopo was ranked second for grain filling period and was significant longer than all the cultivars, excluding SST363, in reaching physiological maturity after flowering. Betta-DN and PAN3211 had significantly longer periods from flowering to physiological maturity than all other cultivars, with the exception of SST363 and Limpopo. Tugela-DN, SST367, and PAN3349 responded similarly with no significant difference between them, but they were significantly later than Caledon, Hugenoot, Elands, Molen, Gariep, PAN3235, SST124, and PAN3377. No significant difference was found between Hugenoot and Elands, but both had a significantly longer grain filling period than SST124 and PAN3377. Molen, Gariep, PAN3235, and SST124 did not differ significantly from one another, but they required a significantly longer period to reach physiological maturity after flowering.

Significant differences were observed for treatments. In contrast to days to flowering and days to physiological maturity, the average grain filling period increased when subjected to the longer photoperiod. The Group 2 cultivars reached physiological maturity 45.7 days after flowering under an 18 hour photoperiod, while it took only 41.5 days under a 14 hour photoperiod. This phenomenon was observed for the majority of the 15 wheat cultivars.

Significant differences were also observed for cultivar x photoperiod interaction. From all the cultivars, only SST363 and Tugela-DN showed a decrease in the number of days from flowering to physiological maturity.

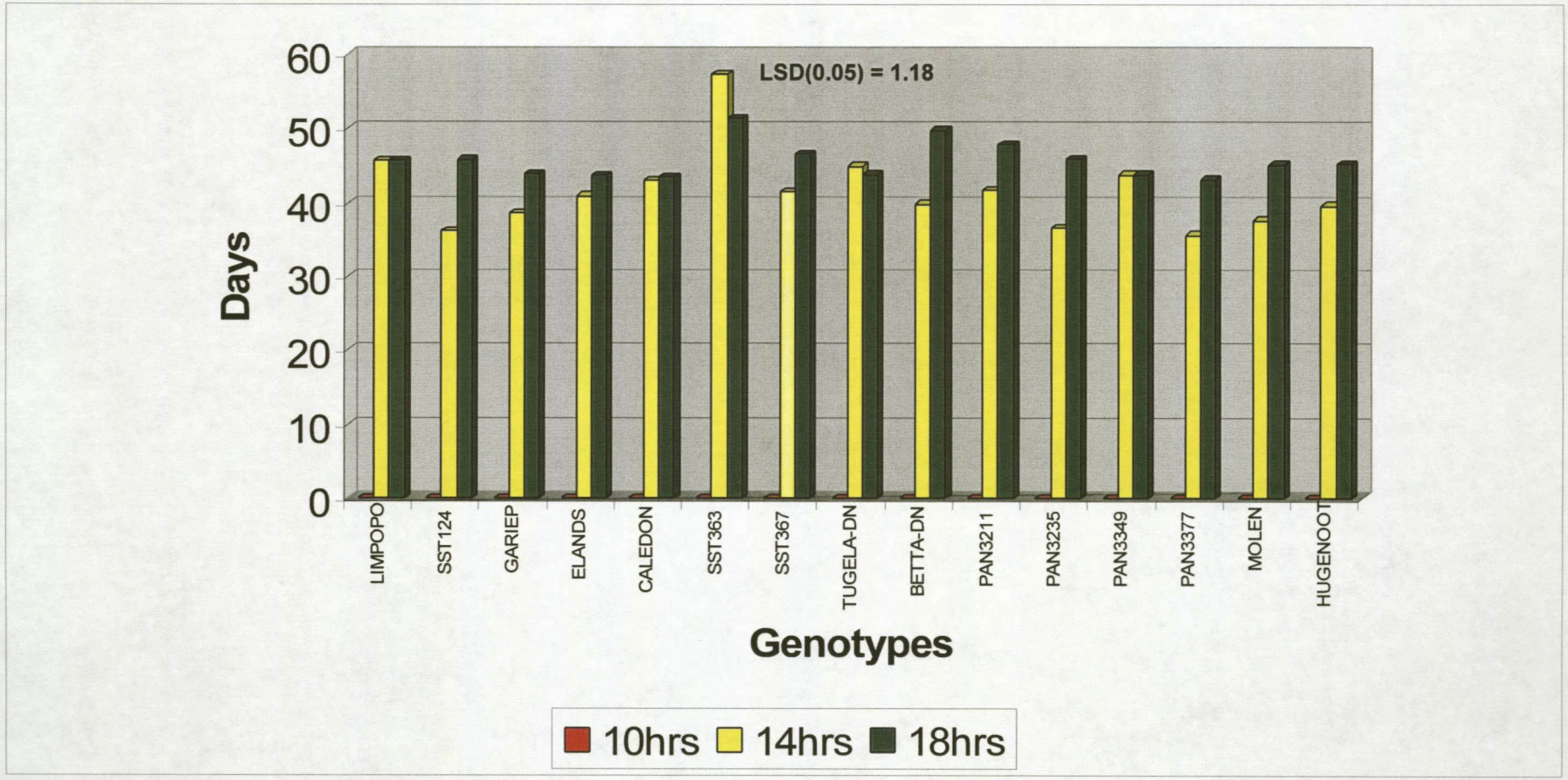

Figure 4.10 Days from flowering to physiological maturity of the 15 Group 2 wheat cultivars for three photoperiod treatment

Betta-DN (9.9 days), SST124 (9.6 days), and PAN3235 (9.3 days) had the largest increase in days from flowering to physiological maturity, followed by Molen (7.5 days) and PAN3377 (7.5 days). PAN3211 (6.1 days) responded similar to Molen and PAN3377 and to Hugenoot (5.6 days), Gariep (5.3 days), and SST367 (5.1). Elands had an increase of 2.8 days in the number of days from flowering to physiological maturity when the photoperiod was increased from 14 to 18 hours. Compared to Betta-DN this increase indicated a very low response. Four cultivars: Caledon, Limpopo, PAN3349, and Tugela-DN were insensitive to photoperiod variation between 14 and 18 hours. Caledon increased the number of grain filling days with 0.5 days, whereas both Limpopo and PAN3349 showed no change in the number of days. Tugela-DN, on the other hand responded with a slight decrease of 1.1 days in the grain filling period. SST363 was the only cultivar that clearly decreased the number of days from flowering to physiological maturity when subjected to a longer photoperiod. The reduction in the case of SST363 was 5.9 days.

Discussion

The Group 2 cultivars responded to photoperiod variation in a similar way as the Group 1 cultivars and only their growth length separated these two groups. All the cultivars in Group 2 were sensitive to photoperiod at least at a 10 hour photoperiod, because the reproductive phase was only initiated under the 14 and 18 hour photoperiod treatments.

All the cultivars responded to photoperiod with a reduction in number of days to flowering. It is thus deduced that all the cultivars in Group 2 were sensitive to photoperiod in terms of flowering time. SST363 had the shortest period to reach anthesis and reduced (from a 14 to an 18 hour photoperiod) the number of days needed to flower with the significantly lowest number. Molen had the longest average period between flowering and physiological maturity, and ranked only sixth in days to physiological maturity. Molen recorded the eleventh longest grain filling period. Hugenoot, Betta-DN, and SST367 did not differ significantly from Molen in terms of days to flowering, but only Hugenoot did not differ significantly from Molen in terms of days to physiological

maturity. Both Betta-DN and SST367 were significant longer in reaching physiological maturity.

All the cultivars showed sensitivity to photoperiod in terms of days to physiological maturity. This is illustrated by the reduction in days to reach physiological maturity. It is, however, expected to see a reduction in days to physiological maturity if a reduction in days to flowering was observed. Interesting, though, is the observation that the reduction in days to flowering (26.4 days) was higher than the reduction in days to physiological maturity (22.3 days). The ratio between the average reduction in days to flowering and days to physiological maturity is 1.6:1. No cultivar had a 1:1 or smaller ratio, and this indicated that the response to photoperiod for cultivars in Group 2 was more sensitive for days to flowering than for days to physiological maturity. SST363 flowered the earliest of all cultivars, but reached physiological maturity last. Betta-DN had the second longest grain filling period and did not differ significantly from SST363. The cultivar that reached physiological maturity the earliest was SST124. It was also significantly earlier than all the other cultivars in Group 2.

When a lower reduction in days to physiological maturity than for days to flowering was observed, it was clear that the possibility of an increase in the grain filling period could be expected. This was especially true for Betta-DN, SST124, and PAN3235 who all had more than nine days increase in their grain filling period. Other cultivars (Limpopo, Caledon, Tugela-DN, and PAN3349), however, had almost no change in the length of their grain filling periods when the 14 hour photoperiod was extended to 18 hours. SST363 showed a decrease in the period from flowering to physiological maturity. From this data it is clear that all the cultivars are sensitive to photoperiod even though some cultivars showed no change in grain filling period.

4.3.2.3 Group 3

All cultivars in Group 3 flowered under the three photoperiod treatments. This separated Group 3 from Groups I and 2 that did not reach anthesis under a 10 hour photoperiod treatment. Group 3 included only the hybrid wheats from

the true winter and winter wheat classes. Within Group 3 two smaller clusters could be identified. The first cluster was SST966 on its own and the second comprised of SST936 and SST983. An analysis of variance was calculated and the mean squares are summarised in Table 4.5.

Table 4.5 Analysis of variance for reproductive characteristics in the Group 3 photoperiod cluster wheat cultivars

Source	df	DTF	DTPM	DFTPM
Replications	9	549.344	584.944	43.878
Cultivars	2	152.600*	293.422**	93.956**
Treatments	2	23181.267**	13392.689**	1329.156**
Cultivar x treatment	4	416.733**	513.778*	250.444**
Residual	72	1846.956	2224.556	594.222
Total	89	26146.900	17009.389	2311.656
LSD for cultivar at 0.01		3.11	3.42	1.77
LSD for cultivar at 0.05		2.18	2.39	1.24

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

4.3.2.3.1 Days to flowering (DTF)

The number of days to flowering for each of the three cultivars in Group 3 is presented in Figure 4.11. From the data presented it is clear that all the cultivars in this cluster will initiate the reproductive phase if subjected to only a 10 hour photoperiod. A significant difference in the number of days needed to reach anthesis for the three cultivars was only observed at the 0.05 significance level. SST936 ranked first with the longest period to flowering, but it did not differ significantly from SST966. SST936 reached anthesis significantly later than SST983. SST983 ranked last, but did not differ significantly from the second ranking SST966.

Significant differences were observed between all the photoperiod treatments. The 10 hour photoperiod (148 days) resulted in the longest period to

flowering. As expected the 14 hour photoperiod treatment (122.9 days) ranked second with the 18 hour photoperiod (109.2 days) last.

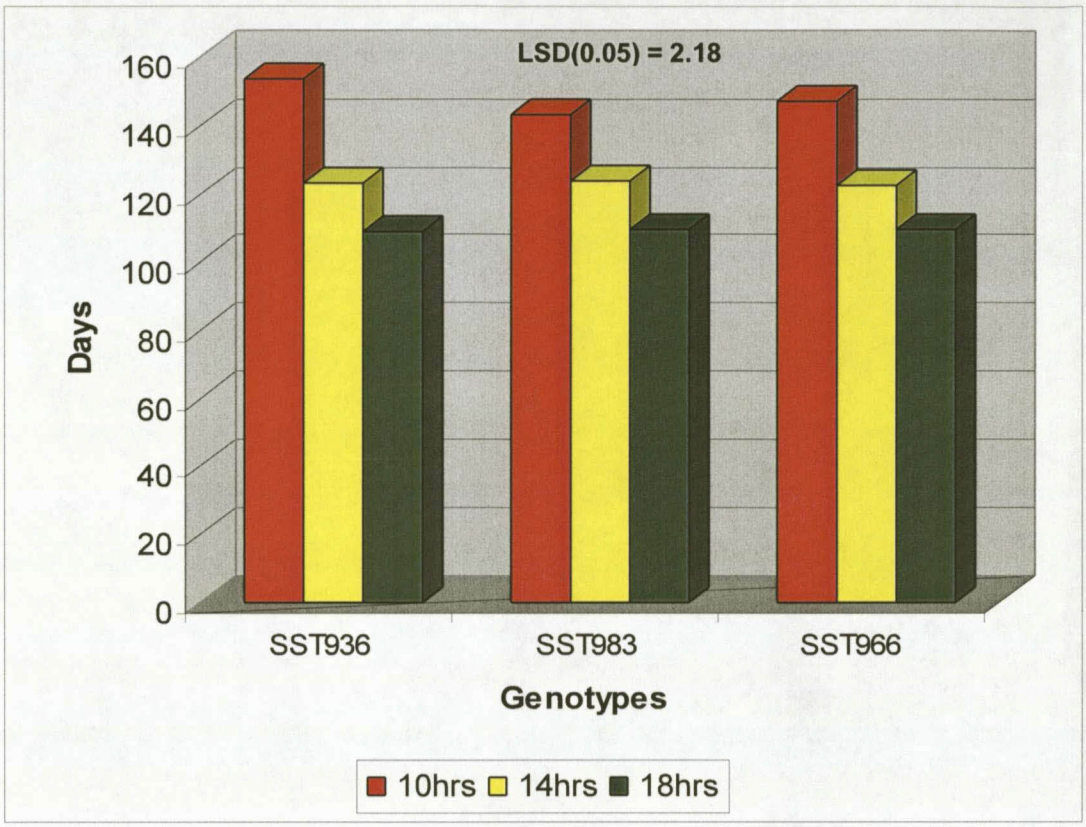

Figure 4.11 Days to flowering of the Group 3 wheat cultivars for three photoperiod treatments

The three cultivars differed significantly in their individual response to photoperiod. SST936 reduced the period to flowering with 30.7 days from a 10 to a 14 hour photoperiod and with 14.3 days when the 14 hour photoperiod is extended to 18 hours. SST966 followed a similar pattern with a reduction of 24.6 days and 12.7 days when the photoperiod was lengthened to 14 and 18 hours respectively. The response of SST983 was somewhat different than those of SST936 and SST966. SST983 had a much lower response to variation in photoperiod, with a 19.8 days reduction from a 10 to a 14 hour photoperiod and a 14.2 days reduction in days to flowering from a 14 to 18 hour photoperiod.

4.3.2.3.2 Days to physiological maturity (DTPM)

Figure 4.12 represents the response of the Group 3 wheat cultivars to photoperiod treatment.

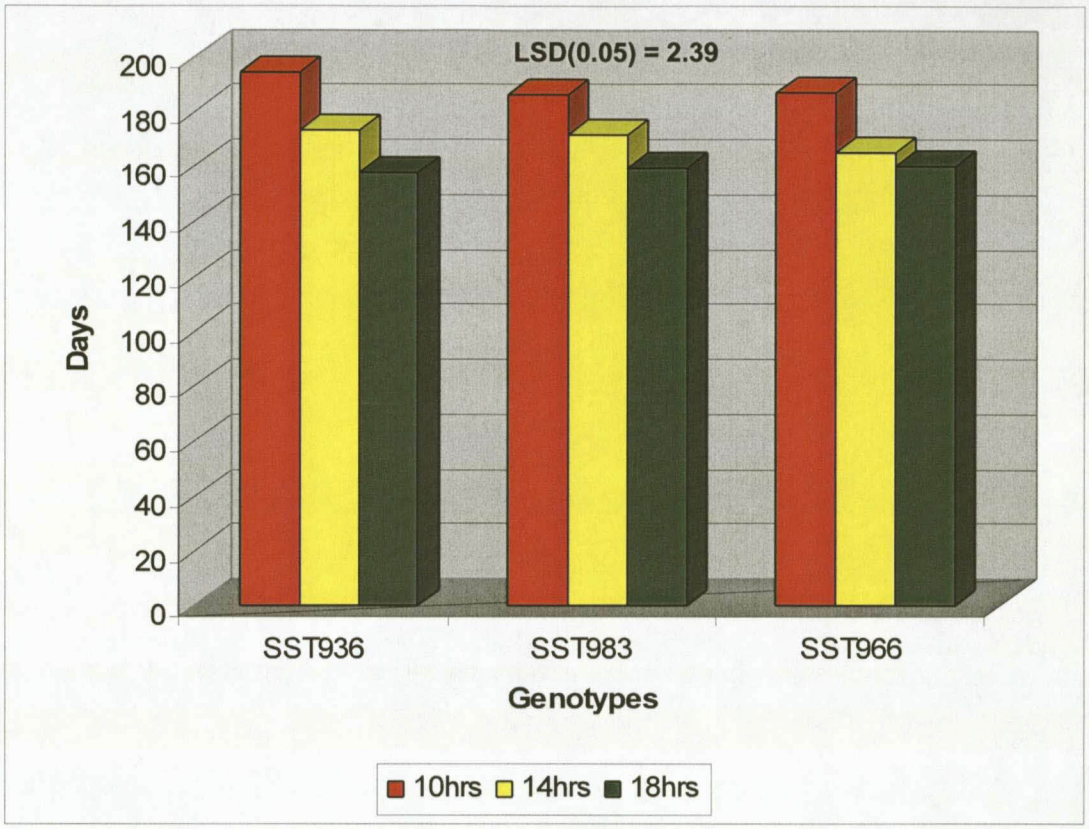

Figure 4.12 Days to physiological maturity of the Group 3 wheat cultivars for three photoperiod treatments

Significant differences were observed for days to physiological maturity between the cultivars in Group 3. SST936 ranked first with the longest period to physiological maturity and was significantly longer than both SST966 and SST983 at the 0.05 significance level, but differed significantly from only SST983 at the 0.01 significance level. SST983 was ranked second, but did not differ significantly from SST966 that was ranked last.

The longest period for days to physiological maturity was recorded for the 10 hour photoperiod (188.7 days) and it was significant longer than the periods recorded for the 14 hour (169.9 days) and the 18 hour (159.2 days)

photoperiods. The 14 hour photoperiod differed significantly from the 18 hour photoperiod.

Significant differences for cultivar x photoperiod were also found. SST936 showed a reduction of 20.7 days in the number of days to physiological maturity when the 10 hour photoperiod treatment was compared to the 14 hour photoperiod treatment and 15.2 days when the 14 hour photoperiod was compared to the 18 hour photoperiod treatment. The response of SST966 (21.6 days) was similar to that of SST936 for the 10 and 14 hour photoperiod treatment comparisons. SST966 had almost no response (4.5 days) to photoperiod when the 14 hour and 18 hour photoperiods were compared. SST983 responded almost identical to photoperiod in terms of number of days to physiological maturity than what it did in terms of number of days to physiological maturity. The observed reduction in days to physiological maturity for SST983 was 14.3 days when the 10 and 14 hour photoperiod treatments were compared and 12.2 days when the 14 and 18 hour photoperiod treatments were compared.

4.3.2.3.3 Days from flowering to physiological maturity (DFTPM)

Since the days from flowering to physiological maturity is a calculation deduced from the number of days to flowering and physiological maturity, it is dependant on the ratio in which these two characters change when subjected to different photoperiod treatments. The response of the Group 3 wheat cultivars in terms of grain fill period is presented in Figure 4.13.

Significant differences were found for cultivars. SST983 (46.63 days) had the longest period between flowering and physiological maturity, and differed significantly only from SST966 (46.57 days). SST966 (44.43 days) had the shortest grain filling period and differed significantly from both SST983 and SST936.

Significant differences were also observed for cultivar x photoperiod interactions. The days from flowering to physiological maturity increased when the cultivars were subjected to longer photoperiod treatments. It is only

with SST936 (0.9 day) that a slight reduction in number of days was found when the 14 hour photoperiod was extended to 18 hours. The response of SST936 when comparing the 10 and 14 hour photoperiods resulted in an increase of 10 days. The number of days from flowering to physiological maturity for SST983 increased with 5.2 days and 2.3 days when the photoperiod was extended from 10 to 14 hours and from 14 to 18 hours respectively. SST966 responded with a lower increase (3.0 days) in the grain filling period from 10 to 14 hour photoperiod treatment and a higher increase (8.2 days) for photoperiods 14 to 18. This is in contrast to what was observed for SST936 and SST983 where the initial (from 10 to 14 hours) increase was larger than the second one.

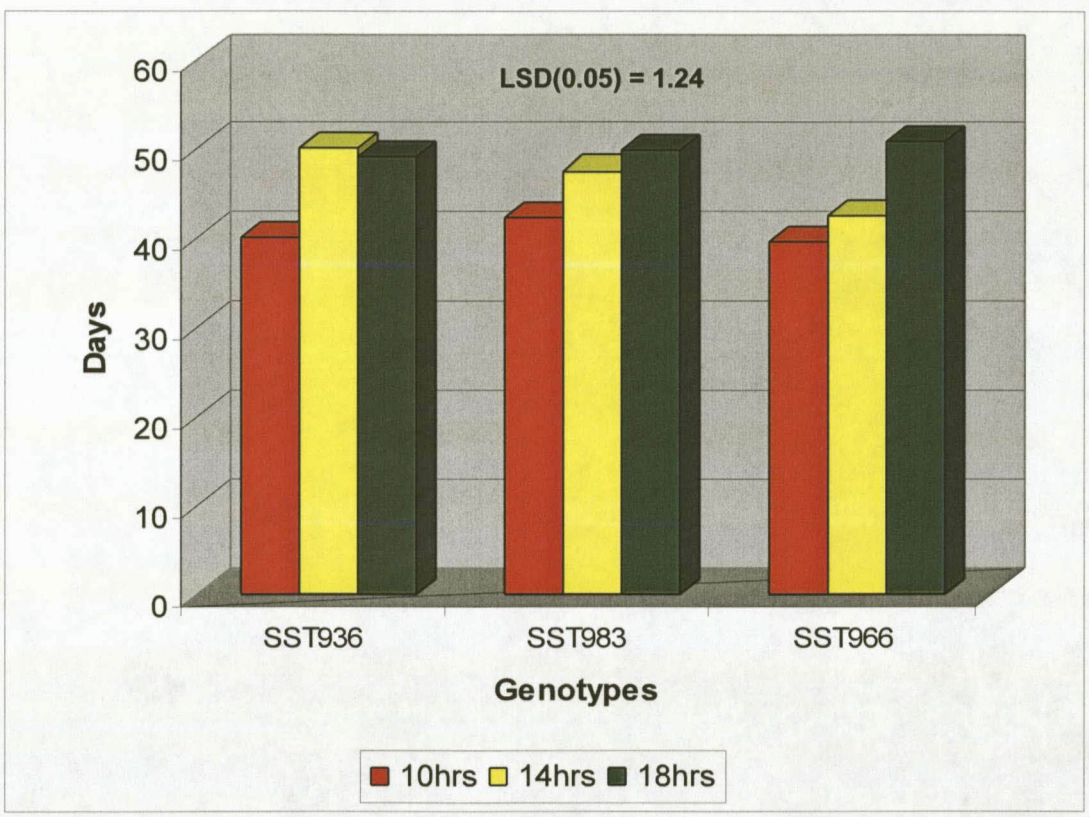

Figure 4.13 Days from flowering to physiological maturity of the Group 3 wheat cultivars for three photoperiod treatments

Discussion

Only the hybrid wheat cultivars from the true winter and winter wheat cultivars classes initiated flowering under a 10 hour photoperiod treatment. All three

hybrid wheats responded to photoperiod treatment and the number of days to flowering and physiological maturity was progressively reduced as the photoperiod increased. SST936 was ranked first for both the longest period to flowering and the longest period to physiological maturity.

The 10 hour photoperiod had the longest period to flowering and physiological maturity, but the shortest period from flowering to physiological maturity. The days needed to reach anthesis and physiological maturity were reduced when the photoperiod treatments were extended to 14 and 18 hours and the grain filling period increased with longer photoperiod treatments.

SST936 and SST966 responded similarly in terms of days to flowering with large incremental reductions from 10 to 14 hour photoperiod treatments and from 14 to 18 hour photoperiod treatments. The difference between the 10 to 14 hour photoperiod treatment and 14 to 18 hour photoperiod treatment for SST936 and SST966 was 16.4 days and 11.9 days respectively. The same calculation resulted in only 4.6 days for SST983. The same phenomenon was observed for days to physiological maturity. For all the cultivars an increase in the length of the photoperiod lead to a net increase of the grain filling period. The 18 hour photoperiod treatment therefore had the longest period from flowering to physiological maturity.

4.3.2.4 Group 4

All the spring wheat cultivars assessed in this study clustered in Group 4 as presented in Figure 4.1. Although, both the hybrid (Group 3) and spring (Group 4) wheats flowered when exposed to only 10 hours day light, these two groups are markedly dissimilar. The hybrid wheats had a much longer growing period than the spring wheats. Four smaller groups could be identified within the Group 4 cluster. SST65 clustered on its own and so did Marico, while SST57, Baviaans, and Palmiet clustered closer to one another to form the third group. The last group comprised of SST822, Inia, SST876, SST88, and Kariega.

The analyses of variance were done for cultivars in the Group 4 cluster and the results are summarised in Table 4.6. Significant differences were observed for replications for all measured characteristics.

Table 4.6 Analysis of variance for reproductive characteristics in the Group 4 photoperiod cluster wheat cultivars

Source	df	DTF	DTPM	DFTPM
Replications	9	512.909**	1040.000**	113.745**
Cultivars	10	2248.006**	4076.655**	968.885**
Treatments	2	38353.873**	42326.035**	2455.170**
Cultivar x treatment	20	1085.194**	2376.036**	1883.097**
Residual	288	787.291	1668.200	1237.455
Total	329	42987.237	51487.455	6658.352
LSD for cultivar at 0.01		1.00	1.45	1.25
LSD for cultivar at 0.05		0.71	1.03	0.88

** significant at level 0.01 and *significant at level 0.05

DTF=Days to flowering, DTPM=Days to physiological maturity, DFTPM=Days flowering to physiological maturity

4.3.2.4.1 Days to flowering (DTF)

Highly significant differences were observed for cultivars in terms of days to flowering. The days to flowering for the Group 4 cultivars are presented in Figure 4. 14. Marico, compared to all the cultivars in Group 4, was significantly the latest cultivar in reaching anthesis. Palmiet ranked the second latest in flowering and was significantly later than all the cultivars in Group 4 except Marico. Palmiet was followed by SST88 that was significantly later to reach anthesis than all other cultivars with the exception of Marico and Palmiet. SST876 differed significantly from the above mentioned three wheat cultivars, and was significantly later in flowering than SST822, Inia, Kariega, and SST65. Four cultivars: SST57, Baviaans, Steenbras, and SST822 did not differ significantly from one another, but all four were significantly later than Kariega and SST65. Inia and Kariega reached anthesis significantly later than SST65, but Inia and Kariega did not differ significantly from one another.

SST65 ranked last and was significantly earlier in flowering than all the other cultivars in Group 4.

Significant differences were found for treatments and the 10 hour photoperiod treatment had the largest number of days to flowering than the other treatments. The number of days to flowering decreased as the photoperiod increased from 10 to 14 to 18 hours. The largest response of 15.2 days was observed form 10 to 14 hours while the increase from a 14 to an 18 hour photoperiod resulted in an 11.1 days reduction in days to flowering.

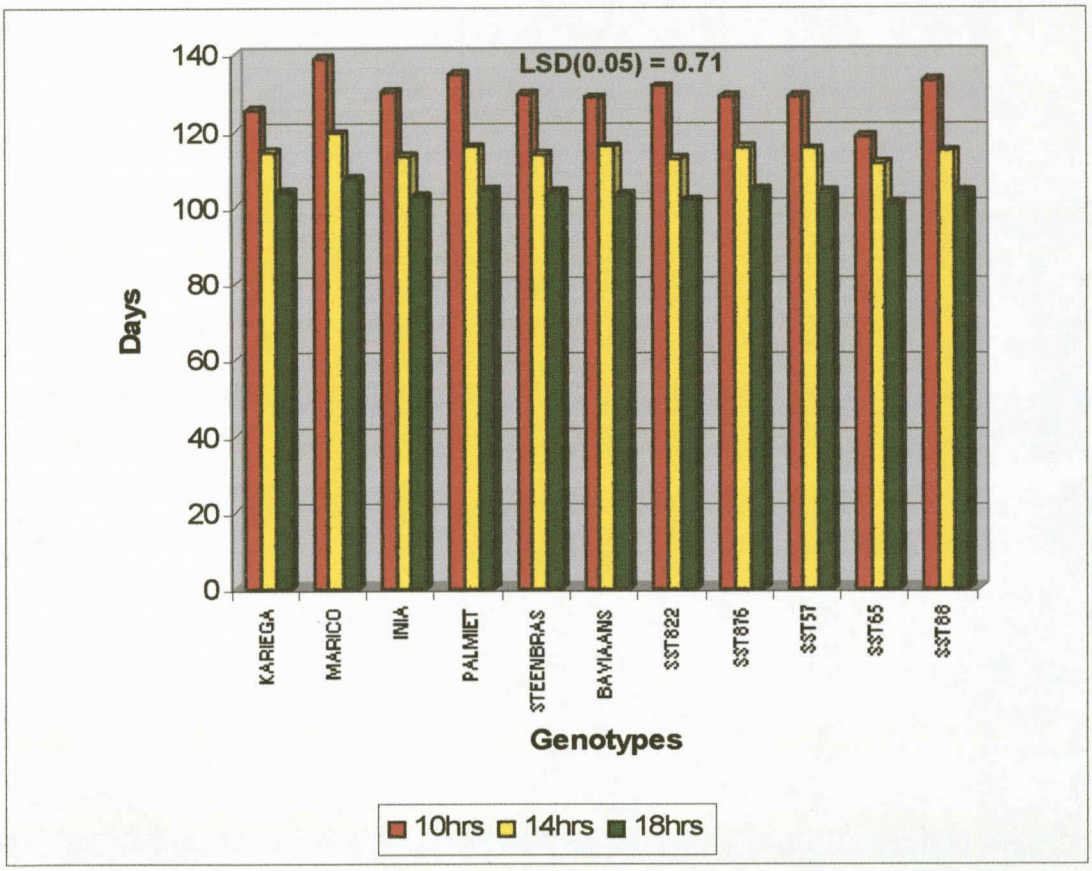

Figure 4.14 Days to flowering of the Group 4 wheat cultivars for three photoperiod treatments

Significant differences for cultivar x photoperiod were observed. Kariega, Baviaans, SST876, and SST57 responded similarly with a more or less equal reduction in number of days to flowering from a 10 to 14 to 18 hour photoperiod. The difference in reduction in days to flowering between the two

SST65 ranked last and was significantly earlier in flowering than all the other cultivars in Group 4.

Significant differences were found for treatments and the 10 hour photoperiod treatment had the largest number of days to flowering than the other treatments. The number of days to flowering decreased as the photoperiod increased from 10 to 14 to 18 hours. The largest response of 15.2 days was observed form 10 to 14 hours while the increase from a 14 to an 18 hour photoperiod resulted in an 11.1 days reduction in days to flowering.

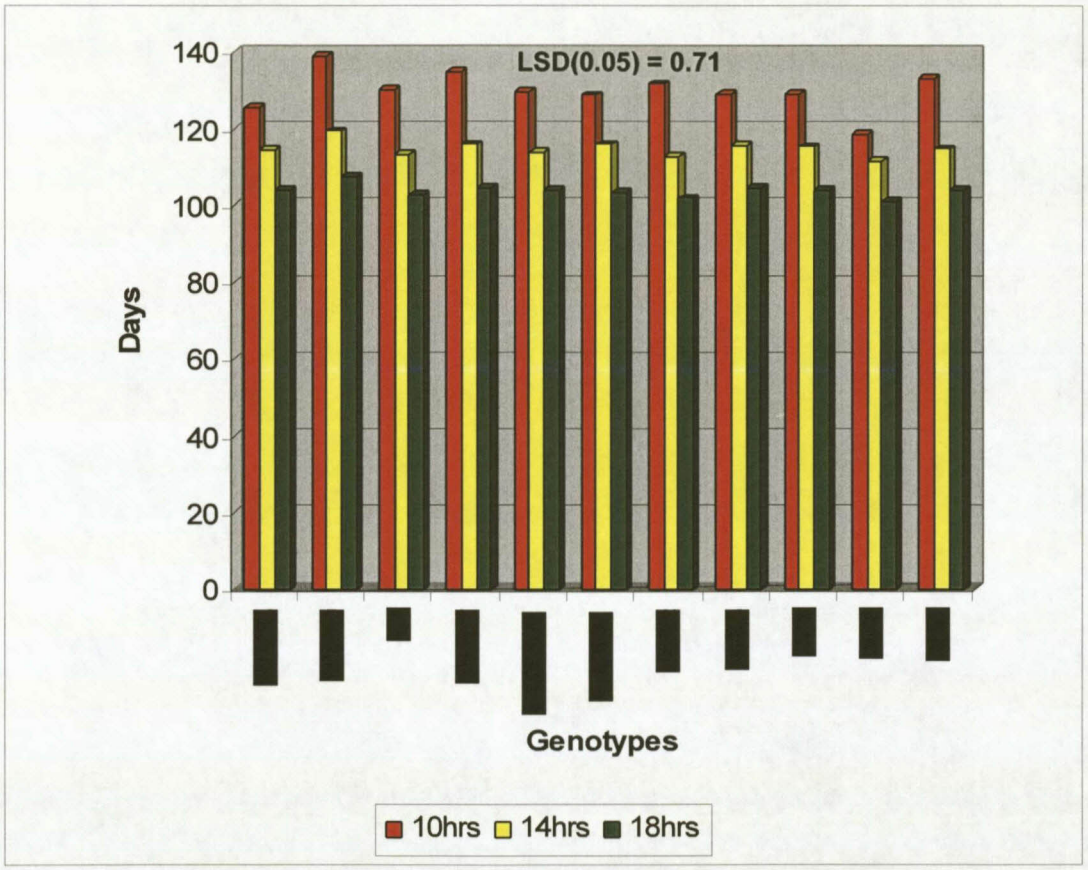

Figure 4.14 Days to flowering of the Group 4 wheat cultivars for three photoperiod treatments

Significant differences for cultivar x photoperiod were observed. Kariega, Baviaans, SST876, and SST57 responded similarly with a more or less equal reduction in number of days to flowering from a 10 to 14 to 18 hour photoperiod. The difference in reduction in days to flowering between the two

longer photoperiods was calculated by subtracting the reduction obtained after an 18 hour photoperiod from the reduction obtained after a 14 hour photoperiod. For both Kariega and Baviaans this difference was only 0.3 days, for SST57 it was 2.1 days, and for SST876 2.6 days. Another group including Marico, Inia, Palmiet, SST822, and SST88 responded differently with a large initial reduction in days to flowering when subjected to a 14 photoperiod. The reduction in days to anthesis was similar to that of Kariega, Baviaans, SST57, and SST876 under an 18 hour photoperiod, but the difference between the 14 hour and 18 hour treatments were larger. The differences were for; Inia 6.7 days, SST88 7.4 days, Marico 7.5 days, Palmiet 7.7 days and SST822 8.6 days. Steenbras (5.2 days) responded somewhere in between these two main groups. The only cultivar that showed an increase in the reduction of days to flowering for the 18 hour photoperiod was SST65 with 3.1 days.

4.3.2.4.2 Days to physiological maturity (DTPM)

Significant differences were observed for days to physiological maturity and the wheat cultivars responded by reducing the number of days to physiological maturity stepwise in relation to an increase in the length of the photoperiod. This is clearly indicated by Figure 4.15.

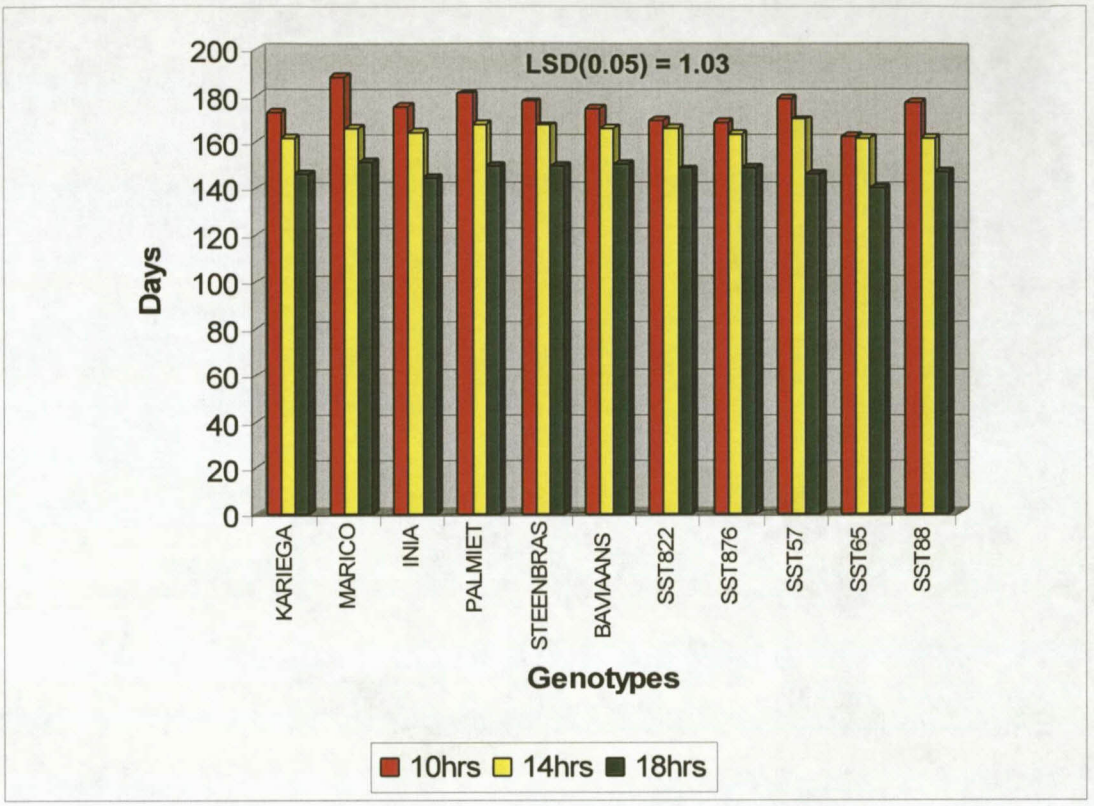

Figure 4.15 Days to physiological maturity of the Group 4 wheat cultivars for three photoperiod treatments

Marico ranked first with the longest period to physiological maturity and it was also significantly longer than that of any of the other wheat cultivars of the Group 4 cluster. Palmiet ranked second and was significantly longer than all the cultivars except Marico. SST57, Steenbras, and Baviaans did not differ significantly from one another. These three cultivars were significantly later in reaching physiological maturity than the remaining six wheat cultivars in the cluster. SST88, Inia, SST822, and Kariega were significantly later than SST876 and SST65, although no significant difference was found between them. SST65 had a significantly shorter period to reach physiological maturity than all other cultivars.

Photoperiod treatments differed significantly. The 10 hour photoperiod treatment had the longest period to physiological maturity (175 days), followed by the 14 hour photoperiod treatment with 165 days. The shortest period (147 days) for days to physiological maturity was observed for the 18 hour photoperiod treatment. The largest average reduction in number of days to

physiological maturity was observed when the photoperiod was extended from 14 to 18 hours.

The wheat cultivars differed significantly in their response to photoperiod, indicating significant differences for cultivar x photoperiod interaction. From Figure 4.14 it is clear that SST65 (20.2 days), SST57 (14.4 days), SST822 (14.0 days), and SST876 (11.2 days) had a larger response under an 18 hour photoperiod than under a 14 hour photoperiod. The difference in response is given in brackets next to the cultivar name. Inia, Steenbras, Baviaans, Palmiet, Kariega, and SST88 also had larger reductions in days to physiological maturity under an 18 photoperiod than under a 14 hour photoperiod, but the difference between these two treatment were lower than that of the first four cultivars. The reductions were: Inia 8.6 days, Steenbras 7.4 days, Baviaans 6.3 days, Palmiet 5.0 days, Kariega 4.6 days, and SST88 4.2 days. Marico was the only cultivar that responded inversely to the others with a larger (7.1 days) response to photoperiod for the 14 hour photoperiod than the 18 hour photoperiod.

4.3.2.4.3 Days from flowering to physiological maturity (DFTPM)

The response of the spring wheat cultivars to photoperiod in terms of grain filling period is summarised in Figure 4.16. All the cultivars, except Marico, responded similarly although not to the same extent.

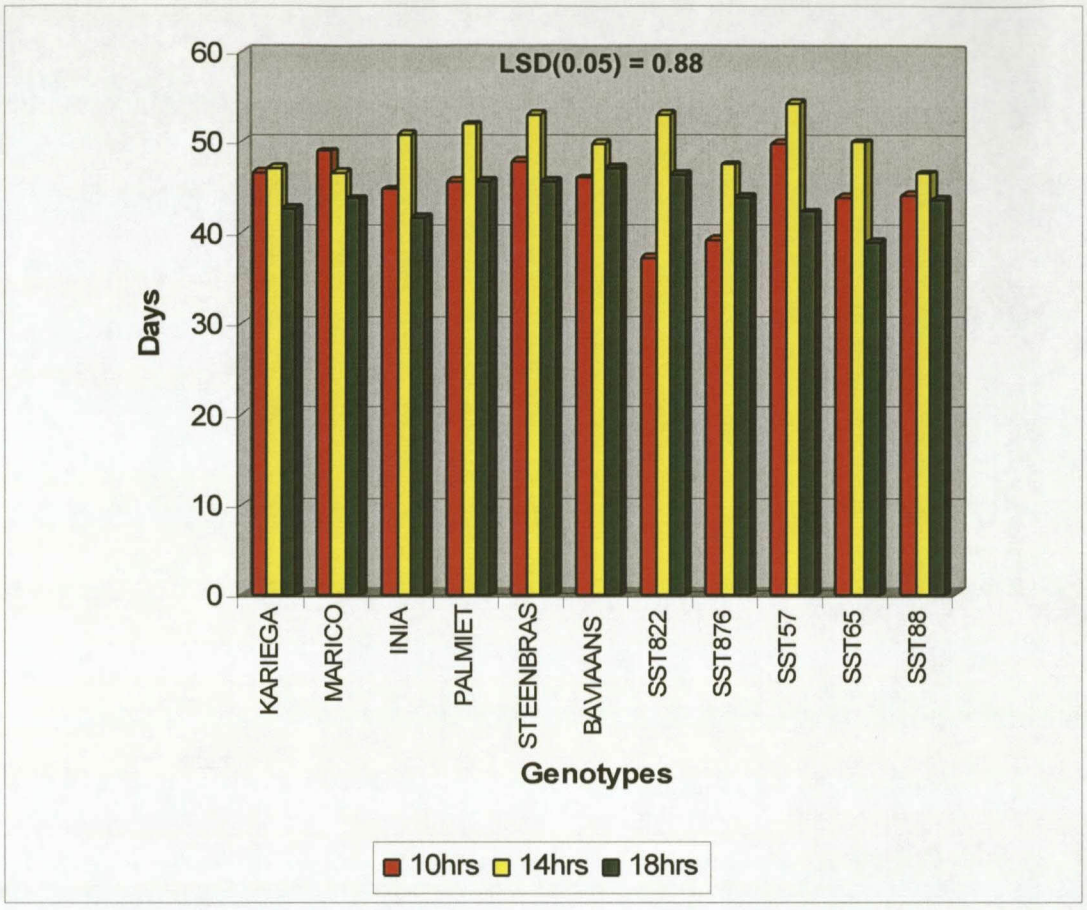

Figure 4.16 Days from flowering to physiological maturity of the Group 4 wheat cultivars for three photoperiod treatments

Significant differences in days from flowering to physiological maturity were observed for cultivars. Steenbras and SST57 had a significantly longer period from flowering to physiological maturity, but they did not differ significantly from one another. Palmiet and Baviaans did not differ significantly, but they had significantly longer grain filling periods than Marico, Inia, SST822, Kariega, SST88, SST65, and SST876. No significant differences were observed for the first four ranking cultivars at a 0.01 significance level. SST876 had a significantly (only at the 0.05 significance level) the shorter grain filling period than the other cultivars.

The three photoperiod treatments differed significantly from one another. The 14 hour photoperiod treatment (49.99 days) had the longest period between flowering and physiological maturity, followed by the 10 hour photoperiod (44.84 days) and the 18 hour photoperiod (43.73 days). It is interesting to note that the grain filling period increased from the 10 to the 14 hour

photoperiod treatment and decreased again when subjected to an 18 hour photoperiod. The net result of the 18 hour photoperiod was a reduction in the period from flowering to physiological maturity.

Significant differences were found for cultivar x photoperiod interactions. The majority of the cultivars had an increase in the period from flowering to physiological maturity under the 14 hour photoperiod treatment, whereas Marico had almost equal reductions in the grain filling period for both the 14 (2.4 days) and the 18 (2.8 days) hour photoperiod. SST822 had a much larger response for the 14 hour photoperiod than for the 18 hour photoperiod and this resulted in a net increase of 9.2 days from a 10 hour to an 18 hour photoperiod treatment. SST822 had the highest increase (15.9 days) in grain filling period for the 14 hour photoperiod treatment. Only two other cultivars had net increases from a 10 hour to an 18 hour photoperiod treatment in the period from flowering to physiological maturity: SST876 with 4.8 days and Baviaans with 1.2 days. The lowest increase in days from flowering to physiological maturity was observed for Kariega (0.4 days) and SST88 (2.3 days)

Discussion

Group 4 included all the spring wheat cultivars that were assessed in this study. Much shorter average days to flowering (10.6 days) separated the Group 4 from the Group 3 cultivars. The number days to flowering was, as expected, reduced with increasing photoperiods. The variability between cultivars was more prominent in the 10 hour photoperiod than in the 18 hour photoperiod and decreased with an increase in the length of the photoperiod. At an 18 hour photoperiod the difference in days to flowering between wheat cultivars was very low (not more than six days). Marico had the highest number of days to flowering at all three photoperiod treatments. SST65, on the other hand, had the shortest time to flowering.

The number of days to physiological maturity followed much the same pattern as the days to flowering by decreasing when the photoperiod increased. It was clear that the cultivars responded differently to the different photoperiod

treatments. In this instance it was noted the response to photoperiod was larger at an 18 hour photoperiod than what was recorded for the 14 hour photoperiod. The 14 hour photoperiod resulted in 10.1 days reduction in days to physiological maturity while a reduction of 17.4 days was realised for the 18 hour photoperiod treatment. When considering the basic development rate of the cultivars, SST65 clearly had the shortest period to physiological maturity and Marico had the longest period to physiological maturity. SST65, SST822, and SST876 had the lowest response of all the spring wheat cultivars to the 14 hour photoperiod treatment. Marico had a larger response to the 14 than to the 18 hour photoperiod treatment and this response was the largest for all cultivars.

The response, in terms of days from flowering to physiological maturity or grain filling period, of all the cultivars except Marico is atypical of what was expected. For all the cultivars (excluding Marico) the number of grain filling days increased when the photoperiod was extended from 10 to 14 hours and then decreased when the photoperiod was further extended to 18 hours. This data suggest that, considering the grain filling period to be an important component of yield determination, a 14 hour period is the optimum day light length for spring wheat cultivars to maximise yield. SST822, SST876, Palmiet, Inia, and SST65 had the highest increase in grain filling days when the photoperiod extended from 10 to 14 hours.

From Figures 4.14 to 4.16 it is clear that the spring wheats differed more from one another in terms of grain filling period than in days to flowering and days to physiological maturity when subjected to an 18 hour photoperiod. All the cultivars were sensitive to photoperiod.

4.4 Conclusions and recommendation

The response of wheat cultivars to photoperiod plays an important role in adaptation of wheat to various environments. The response of the cultivars differed to a greater or lesser extent, resulting in four major clusters to be formed. These clusters were denominated as Group 1, Group 2, Group 3, and Group 4. Groups 1 and 2 were separated from Groups 3 and 4 on the

basis that a 10 hour photoperiod did not result in the initiation of the reproductive phase for all cultivars included in Groups 1 and 2. Group 1 cultivars differed from Group 2 because of their longer growth period, and Groups 3 and 4 were also separated on this basis.

The 30 cultivars were divided into the following groups: Group 1 consisted of SST399 and Group 2 included Limpopo, SST124, Gariep, Elands, Caledon, SST363, SST367, Tugela-DN, Betta-DN, PAN3211, PAN3235, PAN3349, PAN3377, Molen, and Hugenoot. Group 3 encompassed the three hybrid wheats SST936, SST983, and SST966 while Group 4 included all the spring wheat cultivars Kariega, Marico, Inia, Palmiet, Steenbras, Baviaans SST822, SST876, SST57, SST65, and SST88.

SST65, SST876, and SST822 showed relative insensitivity to photoperiod in terms of days to physiological at 14 hours photoperiod, but were sensitive to 18 hours photoperiod. Marico on the other hand responded different from all other cultivars in terms of grain filling period with a reduction in grain filling days for a 14 hour photoperiod, where all other cultivars had an increase in grain filling days.

From this study it is concluded that all the South African wheat cultivars, including the spring wheats, are sensitive to photoperiod. It is also suggested (purely in terms of grain filling period) that the optimum photoperiod for spring wheats (Group 4) was 14 hours, while 18 hours photoperiod was the optimum photoperiod for the true winter, winter, and intermediate wheats (Groups 1 to 3).

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CHAPTER 5

5. RELATIONSHIP BETWEEN VERNALIZATION, PHOTOPERIOD, AND YIELD STABILITY IN SOUTH AFRICAN BREAD WHEATS

5.1 Introduction

The adaptability of hexaploid wheat lends it to be the crop with the largest cultivated area among crop plants. A large part of this adaptability can be attributed to the wheat plant's response to variation in vernalization and photoperiod (Ortiz Ferrara *et al*, 1998). Understanding adaptation in wheat can aid the breeder to better target selected germplasm to specific environments and thereby reduce the risk of crop failure. In completing its life cycle the wheat plant goes through developmental phases from sown seed to ultimately end in seed again. Because seed (grain) is the sole measure of yield in crop plants it is imperative that the crop should be adapted to the environment it is planted in and utilise optimum growing conditions (low stress) when those conditions occur. The degree of interaction of a cultivar with different environments is indicative of the adaptability of the cultivar.

Wheat cultivars that perform well in one environment do not necessarily or by default guarantee good performance in other environments. This is true because of the existence of interactions between cultivars and the environments they are grown in. Cultivar by environment interaction therefore refers to the differential performance of cultivars in different environments.

The aim of this study was to investigate the possibility of the existence of a parallel between response to vernalization and photoperiod, and yield stability.

5.2 Materials and methods

5.2.1 Cultivars

Thirty South African bread wheat cultivars, including spring, intermediate (facultative), and winter wheats were classed according to their vernalization requirement and photoperiodic response and assessed for their yield stability over multiple environments and years. The cultivars were selected to represent cultivars cultivated in the major wheat production areas of South Africa. The cultivars used are summarised in Table 5.1

Table 5.1 Thirty South African bread wheat cultivars assessed for their yield stability

Entry	Cultivar	Company	Growth Habit
1	KARIEGA	Small Grain Institute	Spring
2	MARICO	Small Grain Institute	Spring
3	INIA	Small Grain Institute	Spring
4	PALMIET	Small Grain Institute	Spring
5	STEENBRAS	Small Grain Institute	Spring
6	BAVIAANS	Small Grain Institute	Spring
7	SST822	Monsanto	Spring
8	SST876	Monsanto	Spring
9	SST57	Monsanto	Spring
10	SST65	Monsanto	Spring
11	SST88	Monsanto	Spring
12	LIMPOPO	Small Grain Institute	Intermediate
13	SST124	Monsanto	Intermediate
14	GARIEP	Small Grain Institute	Intermediate
15	ELANDS	Small Grain Institute	Intermediate
16	CALEDON	Small Grain Institute	Intermediate
17	SST363	Monsanto	Intermediate
18	SST367	Monsanto	Winter
19	TUGELA-DN	Small Grain Institute	Intermediate
20	BETTA-DN	Small Grain Institute	Winter
21	PAN3211	Pannar	Intermediate
22	PAN3235	Pannar	Intermediate

Table 5.1 Thirty South African bread wheat cultivars assessed for their yield stability (Continued)

Entry	Cultivar	Company	Growth Habit
23	PAN3349	Pannar	Intermediate
24	PAN3377	Pannar	Winter
25	MOLEN	Small Grain Institute	Winter
26	HUGENOOT	Small Grain Institute	Winter
27	SST936	Monsanto	Winter
28	SST983	Monsanto	Intermediate
29	SST966	Monsanto	Winter
30	SST399	Monsanto	Winter

5.2.2 Growth classes of South African bread wheat cultivars

Data obtained from previous studies carried out on vernalization requirements and photoperiodic responses in wheat were used to classify the wheat cultivars into discreet classes. Vernalization requirements for the cultivars were determined by subjecting the cultivars to eight vernalization treatments, varying from no vernalization to seven weeks vernalization. The cultivars were then transplanted in the field under a natural long day photoperiod. The response of cultivars to photoperiod was determined by exposing the fully vernalised (eight weeks vernalization) cultivars to three photoperiod treatments. These treatments were 10, 14, and 18 hour photoperiod treatments. Data from both studies were combined into one cluster analysis.

5.2.3 Yield stability

The yield stability of the South African bread wheats was calculated from data obtained from the national cultivar evaluation trials planted by the Small Grain Institute (SGI). These trials were conducted over three planting seasons and five environments. The major South African wheat production areas were covered by the trials and included the summer rainfall, rainfed and irrigated regions, and the winter rainfall, rainfed regions.

Trials in the summer rainfall, rainfed regions were planted from the beginning of May to mid July as five row plots, five meters long with an inter-row-spacing

of 45 cm. These trials were planted at a seeding rate of 15 kg/ha in the Western Free State to 35 kg/ha for a late planting in the Eastern Free State. Three major production regions were used: Eastern Free State, Central Free State, and Western Free State. Only the centre three rows of each plot were harvested.

Trials in the summer rainfall, irrigated regions and winter rainfall rainfed regions were planted from the beginning of May as six row plots, six meters long with an inter-row-spacing of 17 cm. These trials were planted at a seeding rate of 120 kg/ha. Two major production regions were used for the irrigation areas: cooler and warmer irrigation regions. The two regions used in the winter rainfall region were the Swartland and Rûens. All six rows for both the irrigated and winter rainfall trials were harvested.

5.3 Statistical analysis

Statistical analyses were done on the data sets using cluster analysis to group the cultivars and analysis of variance to determine variance for each trial. The yield stability for each cultivar was calculated according to the Eberhart and Russel model (1966). Two computer software programmes: NCSS (2000) for cluster analysis and AGROBASE (1999) for ANOVA's were used.

5.3.1 Cluster analysis

Cluster analysis encompasses a number of different classification algorithms. This analysis is used to organise observed data into meaningful structures. Tree or hierarchal clustering method, the method used in this study, uses dissimilarities or distances between observations when forming the clusters. Starting off, each object is in a class by itself after which the threshold is lowered to declare two or more objects to be members of the same cluster. This continuous process results in linking more objects together and aggregate larger and larger clusters of increasing dissimilar elements. In the final step all objects are joined together.

The chosen type distance in the study is a Euclidean distance and is the geometric distance in the multidimensional space. Euclidean distance was calculated as follows:

Distance(x, y) = $\{\sum_i (x_i - y_i)^2\}^{1/2}$

When several objects have been linked together it is important to determine the distances between the new clusters. To accomplish this, a linkage or amalgamation rule is needed to link clusters together that are sufficiently similar. In this study the unweighted pair-group average method was used. In this method, the distance between two clusters are determined by the average distance between all pairs of objects in the two clusters.

5.3.2 Analysis of variance

Analysis of variance is an arithmetic technique by which total variation presented in a set of data is partitioned into different components. Data was analyzed according to a RCBD, using AGROBASE (1999). Significant differences between cultivar means were separated using a least significant difference (LSD) at P≤ 0,05.

Eberhart and Russel's (1966) procedure defines a stable cultivar as one of which the regression coefficient equals one (b = 1.0) and the deviations from the regression is as small as possible ($S^2d_i = 0$). The first stability parameter b is calculated as:

$$b_1 = \sum_j Y_{ij} I_j / \sum_j I^2_j \quad \text{and}$$

the second stability parameter as:

$$S^2 d_i = \left[\sum_j \hat{\delta}^2_{ij} / (n-2) \right] - s_e^2 / r$$

In the words of Eberhart and Russel (1966): "This model provides a means of partitioning the cultivar-environment interaction into two parts: 1) the variation

due to response of the variety to varying environmental indexes; and 2) the unexplainable deviations from the regression on the environmental index."

5.3.3 Linear correlation

The linear correlation was calculated using AGROBASE (1999) computer software. The correlation matrix displays two sets of figures. The first set represents the correlation estimates while the second number set represents the probabilities of the estimates. A probability near to zero indicates significant correlation, and near to one indicates no correlation. The calculation of correlation estimates and probability is not given.

5.4 Results and Discussions

5.4.1 Cluster analysis

Clustering (using actual values) of 30 South African bread wheat cultivars in terms of vernalization requirement and response to photoperiod is illustrated in Figure 5.1. Clusters A and B represent the highest point of dissimilarity and discriminates between two clear groups. Cluster A constitutes of all the true winter cultivars, while cluster B includes the winter, intermediate and spring wheats. The next highest level of dissimilarity was found at clusters B(i) and B(ii), representing cultivars with and without minimum vernalization requirement respectively. Cluster B(ii) is subdivided into B(ii)a and B(ii)b and these two sub clusters discriminate between intermediate and spring wheat cultivars respectively.

Cluster A includes the true winter wheats: SST966, SST936, SST399, and Molen. The winter wheat class (B(i)) includes SST983, SST376, Caledon, Hugenoot, PAN3235, Betta-DN, and Elands. SST363, PAN3377, Gariep, SST124, PAN3211, Tugela-DN, PAN3349, and Limpopo form the intermediate wheat class (B(ii)a), while the spring wheat class (B(ii)b) constitutes of SST57, SST65, Marico, SST822, Baviaans, Steenbras, Palmiet, SST88, SST876, Inia, and Kariega.

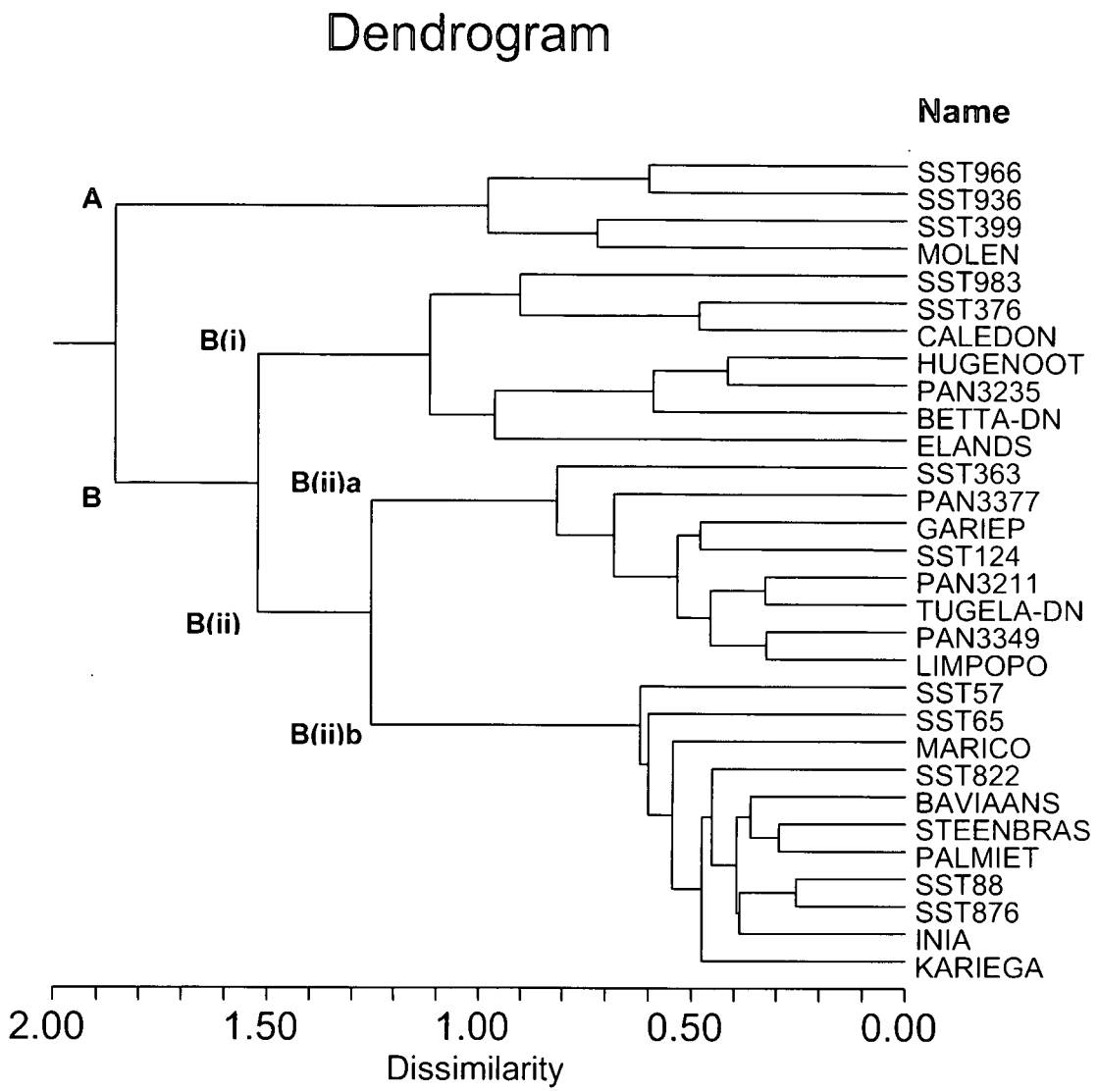

Figure 5.1 Cluster analysis of 30 wheat cultivars in terms of vernalization requirement and response to photoperiod

Cophenetic Correlation = 0.893683
Delta(0.5) = 0.147791
Delta(1.0) = 0.202184

5.4.2 Analysis of variance

Clustering the 30 wheat cultivars into similarity groups enables one to do analyses of variance for wheat cultivars with similar requirements for vernalization and photoperiod. Analyses of variance are important to

determine differences in the response of wheat cultivars within the same cluster due to cultivar, or cultivars x environment interaction.

No matter how cultivars respond to vernalization or photoperiod, maximum yield and yield stability still remain the crucial characters the breeder will select for. With yield comes reliability and therefore stability over varying environments. Poehlman and Sleper (1995) attribute adaptation of wheat cultivars to different environments to the general relatedness of physiological characteristics to vernalization requirement, cold tolerance, and photoperiodic response. Other authors (Mosaad *et al*, 1995, Ortiz-Ferrara *et al*, 1998, and Worland *et al*, 1998) also concluded that photoperiod response and vernalization requirement are major attributors to the adaptability of wheat. Subsequently the question can be raised whether any correlation between the genetic constitution of cultivars, in terms of vernalization and photoperiod, and yield stability exists.

5.4.3 Yield stability analyses

5.4.3.1 Summer rainfall, rainfed regions

The first group of cultivars include all the true winter, winter, and intermediate wheat cultivars. This group represents the cultivars that are traditionally planted in the summer rainfall, rainfed regions of South Africa. The Free State province forms the largest area of the summer rainfall region and is subdivided into three regions: Western Free State, Central Free State, and Eastern Free State.

5.4.3.1.1 Eastern Free State

The Eastern Free State is characterised by higher rainfall, lower temperatures, and lower evaporation requirement. Results for the analyses of variance for the Eastern Free State region are summarised in Table 5.2.

Table 5.2 Analyses of variance for yield of true winter, winter and intermediate wheat cultivars in the Eastern Free State

Source	df	SS	MS	F-value	Pr> F
Total	1019	20881902.760			
Cultivars	16	6382623.185	398913.949	11.53	0.0000
Env + invar x Env.	68	14499279.575	213224.700		
Env in linear	1	10774294.056			
Var x Env.(linear)	16	1960713.488	122544.593	3.54	0.0003
Pooled deviation	51	1764272.031	34593.569		
Residual	935	5400006.553	5775.408		

From Table 5.2 it is clear that cultivar x environmental interaction exists between these cultivars. The stability values for these cultivars planted in the Eastern Free State are summarised in Table 5.3.

Table 5.3 Stability analysis for yield of true winter, winter and intermediate wheat cultivars in the Eastern Free State

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	21063.5417	1.2157	0.303	1.2757	1245.7725	**Limpopo**
2	204277.3001	11.7901	0.000	0.5568	62317.0253	**SST124**
3	84736.1957	4.8906	0.002	1.1647	22469.9905	**Gariep**
4	13421.1343	0.7746	0.508	1.1964	-1301.6967	**Elands**
5	17638.7817	1.0180	0.384	1.1277	104.1858	**Caledon**
6	137719.5257	7.9486	0.000	0.5655	40131.1005	**SST363**
7	5968.4636	0.3445	0.793	0.1166	-3785.9202	**SST367**
8	443271.3536	25.5838	0.000	1.5335	141981.7098	**Tugela-DN**
9	37442.5014	2.1610	0.091	1.1358	6705.4257	**Betta-DN**
11	32434.8137	1.8720	0.133	1.0618	5036.1965	**PAN3235**
12	100171.7893	5.7815	0.001	1.2065	27615.1883	**PAN3349**
13	30046.7503	1.7342	0.158	1.3119	4240.1754	**PAN3377**
15	247670.7274	14.2946	0.000	0.3722	76781.5011	**Hugenoot**
16	38171.2740	2.2031	0.086	0.3609	6948.3499	**SST936**
17	183270.6147	10.5776	0.000	1.5228	55314.7968	**SST983**
18	125435.9055	7.2397	0.000	1.4974	36036.5604	**SST966**
19	41531.3585	2.3970	0.067	0.9939	8068.3781	**SST399**

According to Eberhart and Russel (1966) cultivars with Beta values close to one and low deviations (zero) from the regression line (S^2d) are considered to be stable. Negative deviation values are considered equal to zero. From Table 5.3 Limpopo, Gariep, Elands, Caledon, PAN3235, PAN3349, PAN3377,

and SST399 revealed very stable Beta values, but only Limpopo, Elands, SST367, and Caledon had relative low S^2d values. SST367 was very stable in terms of the S^2d value, but was unstable according to the Beta value. Two wheat cultivars, Molen and PAN3211 were not included in the analysis because too few data points were available. Molen was, however, included in the analyses for the Central Free State region.

5.4.3.1.2 Central Free State

The Central Free State has moderate temperatures, rainfall, and evaporation requirement with relative shallow soils. Results of the analysis of variance for the Central Free State region are summarised in Table 5.4.

Table 5.4 Analyses of variance for yield of true winter, winter and intermediate wheat cultivars in the Central Free State

Source	df	SS	MS	F-value	Pr> F
Total	863	7521430.072			
Cultivars	17	5591278.596	328898.741	11.62	0.0000
Env + in var x Env	54	1930151.476	35743.546		
Env in linear	1	355248.839			
Var x Env (linear)	17	555666.425	32686.260	1.15	0.3466
Pooled deviation	36	1019236.212	28312.117		
Residual	792	2781783.171	3512.352		

No significant interaction for cultivar x environment was observed for the four Central Free State yield test sites, although the cultivars differed significantly in yield. It is, however, interesting to look at the stability values as presented in Table 5.5. Caledon, SST363, and PAN3377 had Beta values very close to one, while SST124, Gariep, Elands, and PAN3349 showed small deviation values. Elands again had a negative deviation value that effectively equals zero and a Beta value of 0.59 indicating stability for both the Eastern and Central regions of the Free State.

Table 5.5 Stability analysis for yield of true winter, winter and intermediate wheat cultivars in the Central Free State

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	18086.6928	2.5747	0.077	2.3966	5530.9939	**Limpopo**
2	10646.3203	1.5156	0.220	-0.0873	1810.8077	**SST124**
3	11020.9966	1.5689	0.209	2.5923	1998.1458	**Gariep**
4	5359.4034	0.7629	0.467	0.5916	-832.6508	**Elands**
5	33447.3700	4.7614	0.009	1.0393	13211.3325	**Caledon**
6	40142.3323	5.7145	0.003	1.0023	16558.8137	**SST363**
7	75907.5284	10.8058	0.000	0.5632	34441.4117	**SST367**
8	67360.0841	9.5890	0.000	0.9976	30167.6896	**Tugela-DN**
9	52485.8536	7.4716	0.001	-0.2712	22730.5743	**Betta-DN**
11	34033.2449	4.8448	0.008	0.7148	13504.2700	**PAN3235**
12	3024.2960	0.4305	0.650	0.3796	-2000.2045	**PAN3349**
13	16943.4504	2.4120	0.090	1.0547	4959.3727	**PAN3377**
14	29115.2866	4.1447	0.016	-0.3844	11045.2908	**Molen**
15	35002.1336	4.9827	0.007	1.8061	13988.7143	**Hugenoot**
16	322179.8068	45.8638	0.000	3.4946	157577.5509	**SST936**
17	32015.3059	4.5575	0.011	1.7320	12495.3004	**SST983**
18	35143.6945	5.0029	0.007	2.3573	14059.4947	**SST966**
19	197322.4120	28.0898	0.000	-1.9791	95148.8535	**SST399**

5.4.3.1.3 Western Free State

Climatically the Western Free State is characterised by low rainfall, high temperatures and a high evaporation requirement. Results for analysis of variance of cultivars planted in the Western Free State are presented in Table 5.6. No significant differences were observed for cultivar x environment interaction.

Table 5.6 Analyses of variance for yield of true winter, winter and intermediate wheat cultivars in the Western Free State

Source	df	SS	MS	F-value	Pr> F
Total	1139	23351062.413			
Cultivars	18	2289637.468	127202.082	3.53	0.0001
Env + in Var x Env	76	21061424.945	277124.012		
Env in linear	1	18389914.535			
Var x Env (linear)	18	615070.054	34170.559	0.95	0.5294
Pooled deviation	57	2056440.355	36077.901		
Residual	1045	6246434.581	5977.449		

Significant differences were observed between wheat cultivars even though the interactions between cultivar and environment were disappointingly low.

The stability values for cultivars planted in the Western Free State are summarised in Table 5.7. Although no significant differences were observed for cultivar x environment interaction, there were cultivars with higher levels of stability as indicated by the Beta and S^2d values. All the cultivars had relative stable Beta values and the differences between cultivars for stability therefore lie in the S^2d values. Gariep, Elands, SST363, SST367, Betta-DN, PAN3211, PAN3235, SST983, and SST966 had relative low deviation values and it can thus be assumed that these cultivars are more stable that the remaining cultivars.

Table 5.7 Stability analysis for yield of true winter, winter and intermediate wheat cultivars in the Western Free State

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	94330.9545	5.2604	0.001	0.8370	25466.2021	**Limpopo**
2	114736.4824	6.3983	0.000	0.6645	32268.0448	**SST124**
3	27071.1925	1.5096	0.210	1.1463	3046.2815	**Gariep**
4	32135.9263	1.7921	0.147	0.9193	4734.5261	**Elands**
5	104123.5267	5.8065	0.001	1.0170	28730.3929	**Caledon**
6	5275.4169	0.2942	0.830	1.0311	-4218.9771	**SST363**
7	18968.9138	1.0578	0.366	0.7493	345.5219	**SST367**
8	197768.3453	11.0286	0.000	1.1165	59945.3324	**Tugela-DN**
9	27781.8700	1.5493	0.200	0.9534	3283.1740	**Betta-DN**
10	34040.6468	1.8983	0.128	0.7659	5369.4329	**PAN3211**
11	22438.4905	1.2513	0.290	0.9914	1502.0475	**PAN3235**
12	86432.4570	4.8199	0.002	0.9008	22833.3696	**PAN3349**
13	58013.3675	3.2351	0.022	0.9247	13360.3398	**PAN3377**
14	743867.1011	41.4819	0.000	0.8605	241978.2510	**Molen**
15	73929.4405	4.1227	0.006	1.0362	18665.6975	**Hugenoot**
16	95323.8014	5.3157	0.001	1.3113	25797.1511	**SST936**
17	27858.1431	1.5535	0.199	1.2635	3308.5983	**SST983**
18	15635.0128	0.8719	0.455	1.2694	-765.7784	**SST966**
19	276709.2660	15.4307	0.000	1.2419	86258.9727	**SST399**

5.4.3.1.4 Yield stability, and vernalization and photoperiodic response in true winter, winter and intermediate wheat cultivars

Thus far the yield stability values for all the true winter, winter, and intermediate wheat cultivars have been presented. It is seems relevant to investigate if vernalization and photoperiod genetic constitution plays a role in yield stability of bread wheat cultivars planted in the summer rainfall region of South Africa.

Since all the wheat cultivars were exposed from zero to seven weeks vernalization the cumulative change in days to flowering, physiological maturity, and flowering to physiological maturity were correlated against the stability values obtained from the Eberhart and Russel (1966) stability analysis. Only the deviation parameter was used from the stability analysis, while change in the measured characteristics was expressed as percentage change from the first to the last observable value. The same methodology was followed for the photoperiod treatments.

The response of cultivars to vernalization and photoperiod for each cultivar is defined as the absolute value obtained by calculating the percentage change in days to flowering, physiological maturity and flowering to physiological maturity. A linear correlation with this value and the deviation from the regression as obtained from the stability analysis was calculated. The correlation matrix is presented in Table 5.8.

The following values were included in the correlation matrix: stability value for the Eastern Free State (EFSD), stability value for the Central Free State (CFSD), days to flowering in vernalization trial (VRNF) and photoperiod trial (PPDF), days to physiological maturity in vernalization trial (VRNM) and photoperiod trial (PPDM), grain filling days in vernalization trial (VRNG) and photoperiod trial (PPDG). The first set of numbers in the correlation matrix represents estimates, while the second set represents the probabilities. A probability value close to zero indicates significant correlation, while a value near to 1.00 indicates no correlation.

Table 5.8 Correlation matrix between wheat cultivars for vernalization, photoperiod and yield stability in the Free State

	EFSD	CFSD	WFSD	VRNF	VRNM	VRNG	PPDF	PPDM
CFSD	-0.0945							
	0.7183							
WFSD	0.4293	0.1065						
	0.0855	0.6841						
VRNF	0.0131	-0.4460	-0.3035					
	0.9602	0.0727	0.2363					
VRNM	0.0920	-0.1916	-0.3630	0.8690				
	0.7254	0.4613	0.1521	0.0000				
VRNG	0.1639	0.1174	-0.3197	0.4638	0.8405			
	0.5297	0.6535	0.2110	0.0607	0.0000			
PPDF	-0.1611	-0.1107	-0.1201	0.3058	0.1367	-0.1022		
	0.5367	0.6723	0.6462	0.2326	0.6008	0.6964		
PPDM	-0.0759	-0.3287	-0.2351	0.1534	-0.0450	-0.2265	-0.0641	
	0.7721	0.1978	0.3638	0.5567	0.8640	0.3821	0.8068	
PPDG	-0.1673	0.4817	0.2230	-0.4453	-0.3310	-0.1309	0.0292	-0.6963
	0.5210	0.0502	0.3895	0.0732	0.1943	0.6165	0.9115	0.0019

Stability values for Eastern Free State (EFSD), Central Free State (CFSD), Western Free State (WFSD), Vernalization flowering (VRNF), Vernalization maturity (VRNM), Vernalization grain fill (VRNG), Photoperiod flowering (PPDF), and Photoperiod maturity (PPDM)

The results presented in Table 5.8 suggest that response to vernalization, in terms of days to flowering, plays some role in the yield stability values in the Central and Western Free State regions. This is manifested in the relatively lower probability values for VRNF and CFSD, and VRNF and WFSD than for VRNF and EFSD. Furthermore it is also suggested that response to vernalization, in terms of days to physiological maturity and grain filling days, is not strongly correlated with yield stability values. Photoperiod seems to be poorly correlated with yield stability values in the Western and Eastern Free State, although a stronger correlation was observed for the Central Free State stability values and response to photoperiod in terms of days to physiological maturity and grain filling days.

Discussion

It is known that wheat cultivars traditionally planted in the Western Free State fall in the true winter wheat class and include SST966, SST399, and Molen. These cultivars have strong vernalization requirements and, as is evident from Chapter 3, a minimum cold treatment period of six weeks is needed to satisfy

their vernalization requirement. Admittedly the correlation data could be skewed towards the true winter wheats because the response of these cultivars to vernalization was only determined between six and seven weeks vernalization treatment, while that of the intermediate wheats was determined between zero and seven weeks vernalization treatment. Although there were some correlations between vernalization response and yield stability, these correlations were not strong enough to conclude with confidence that the genetic constitution in terms of vernalization requirement plays a major part in yield stability in wheat planted in the Free State regions of South Africa.

No clear trend for photoperiod sensitivity was observed and again where correlations were observed, these correlations did not qualify the response, of cultivars to photoperiod, to confidently contribute to yield stability. Care should also be taken in interpreting the correlation data because the cultivars were not necessarily planted during optimal conditions for each class. True winter, winter and intermediate wheats should be planted at different dates in some regions.

5.4.3.2 Summer rainfall, irrigated regions

The irrigated areas are mainly divided into the warmer and cooler irrigation regions. The wheat cultivars planted in these areas are mainly spring wheats with no vernalization requirement.

5.4.3.2.1 The warmer irrigation region

The warmer irrigation region differs from the cooler irrigation region in winter temperatures. The winter temperatures in the warmer irrigation regions are higher than that of the cooler irrigation region and evaporation requirement is thus also higher. It is also accepted that the warmer irrigation region has lower yields than the cooler irrigation region. The analysis of variance for the warmer irrigation region is summarised in Table 5.9.

Significant differences were observed for cultivar x environment interactions. The cultivars also differed significantly from one another. The stability values

for spring wheat cultivars planted in the warmer irrigation region are presented in Table 5.10.

Table 5.9 Analyses of variance for yield of spring wheat cultivars in the summer rainfall, warmer irrigation regions

Source	df	SS	MS	F-value	Pr> F
Total	587	23709927.593			
Cultivars	6	1856788.666	309464.778	14.53	0.0000
Env in Var Env.	42	21853138.927	520312.832		
Env in linear	1	20580520.108			
Var Env (linear)	6	526977.431	87829.572	4.12	0.0031
Pooled deviation	35	745641.387	21304.040		
Residual	539	4813198.830	8929.868		

Table 5.10 Stability analysis for yield of spring wheat cultivars in the warmer irrigation regions

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	16438.2598	0.3682	0.870	1.1752	-5642.2160	**Kariega**
2	137003.9594	3.0684	0.010	1.0519	18470.9239	**Marico**
3	186306.1475	4.1727	0.001	0.9145	28331.3615	**Inia**
5	179211.3334	4.0138	0.001	0.6489	26912.3987	**Steenbras**
6	38297.0119	0.8577	0.509	1.0808	-1270.4656	**Baviaans**
7	29334.9507	0.6570	0.656	1.0499	-3062.8778	**SST822**
8	159049.7245	3.5622	0.004	1.0789	22880.0769	**SST876**

From Table 5.10 it is clear that Kariega, Baviaans, and SST822 are the most stable cultivars as illustrated by the low deviations from the regression. It is also expressed in the Beta values close to one. Inia, Steenbras, SST876, and Marico seem to be less stable in this environment. Steenbras also had a very low Beta value.

5.4.3.2.2 Cooler irrigation region

The cooler irrigation region has higher yields than the warmer irrigation region and is also characterised by lower winter temperatures. The analysis of variance for the cooler irrigation region is summarised in Table 5.11.

From Table 5.11 it is clear that significant differences were observed between the cultivars, but there was no significant difference found for cultivar x

environment interactions. The stability values for these cultivars in the cooler irrigation region are presented in Table 5.12.

Table 5.11 Analyses of variance for yield of spring wheat cultivars in the summer rainfall, cooler irrigation regions

Source	df	SS	MS	F-value	Pr>F
Total	455	104718960.2			
Cultivars	6	7727247.0	1287874.5	3.76	0.0072
Env in Var x Env.	35	96991713.3	2771191.8		
Env in linear	1	87190980.8			
Var x Env (linear)	6	205294.7	34215.8	0.10	0.9958
Pooled deviation	28	9595437.8	342694.2		
Residual	414	9183676.634	22176.366		

Table 5.12 Stability analyses for yield of spring wheat cultivars in the summer rainfall, cooler irrigation regions

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	843053.7888	9.5040	0.000	0.9652	188587.0813	**Kariega**
2	215356.7613	2.4278	0.047	0.9816	31662.8244	**Marico**
3	7131945.5747	80.4003	0.000	1.0139	1760810.0278	**Inia**
5	90784.8566	1.0234	0.395	1.0994	519.8483	**Steenbras**
6	807047.1199	9.0981	0.000	1.0285	179585.4141	**Baviaans**
7	230500.7340	2.5985	0.036	0.9481	35448.8176	**SST822**
8	276748.9693	3.1199	0.015	0.9633	47010.8764	**SST876**

Steenbras is the only spring wheat cultivar that shows stability in the cooler irrigation areas. Inia, Kariega and Baviaans rated very poor on yield stability, while Marico, SST822, and SST876 had intermediate stability values. All eight spring wheat cultivars showed very stable Beta values.

5.4.3.2.3 Yield stability, and vernalization and photoperiodic response in irrigated spring wheat cultivars

All the wheat cultivars in the vernalization and photoperiod trials responded at the same treatment levels and can thus be compared on equal terms. All the cultivars in this group do not require a minimum vernalization period, but do respond to cold treatments. The correlation between vernalization and photoperiodic response, and yield stability was determined using the absolute response of the cultivars to vernalization and photoperiod, and the deviation

parameter from the Eberhart and Russel (1966) stability analysis. The correlation matrix is presented in Table 5.13.

Significant correlations are again found where the probability value is low. From Table 5.13 it is evident that response to vernalization and photoperiod does not play an important part in yield stability of spring wheat cultivars planted in the irrigated regions.

Table 5.13 Correlation matrix between wheat cultivars for vernalization, photoperiod and yield stability in the Irrigation regions

	WISD	CISD	VRNF	VRNM	VRNG	PPDF	PPDM
CISD	0.4042						
	0.4997						
VRNF	0.7622	0.2024					
	0.1341	0.7441					
VRNM	0.4790	-0.0409	0.707				
	0.4143	0.9479	0.1818				
VRNG	-0.1712	-0.3613	-0.0449	0.6508			
	0.7831	0.5501	0.9429	0.2273			
PPDF	0.1136	0.0470	0.2465	-0.3514	-0.6289		
	0.8556	0.9401	0.6894	0.5619	0.2557		
PPDM	0.4111	0.2679	-0.0414	-0.3245	-0.5002	0.2873	
	0.4917	0.6630	0.9473	0.5942	0.3908	0.6393	
PPDG	-0.3176	-0.2421	-0.0958	-0.4916	-0.4682	0.4844	-0.4064
	0.6026	0.6948	0.8782	0.4003	0.4264	0.4083	0.4972

Stability values for Warmer irrigation (WISD), Cooler irrigation (CISD), Vernalization flowering (VRNF), Vernalization maturity (VRNM), Vernalization grain fill (VRNG), Photoperiod flowering (PPDF), and Photoperiod maturity (PPDM)

The correlation matrix is the result of parameters such as stability value of cultivars in the warmer irrigation regions (WISD), yield stability of cultivars in the cooler irrigation regions (CISD), response the cultivars to vernalization and photoperiod in terms of days to flowering (VRNF, PPDF) and physiological maturity (VRNM, PPDM), and grain filling days (VRNG, PPDG). It is noteworthy to mention that a relative strong correlation is found between yield stability and response to vernalization in the warmer irrigation regions, although this correlation is statistically not significant. This can be seen in the low probability value of 0.1341.

Discussion

It is generally accepted that spring wheat does not need vernalization to reach anthesis, although vernalization treatment decreased the number of days to flowering and physiological maturity in almost all the cultivars (Chapter 3). Wheat under irrigation is also less exposed to drought stress and therefore it seems logical to find no correlation for yield stability and the adaptive characters: vernalization and photoperiod. Wheat cultivars with a smaller response to vernalization, however, suggest better yield stability in the warmer irrigation regions.

No correlation could be found between photoperiodic response and yield stability in irrigated spring wheat. This could be attributed to the short photoperiod required to initiate the reproductive phase in spring wheat.

5.4.3.3 Winter rainfall, rainfed spring wheat

The Winter Rainfall Region has a typical Mediterranean climate without what is considered vernalization temperatures (zero to four degrees centigrade). The Winter Rainfall Region is subdivided into two smaller regions, the Rûens and the Swartland, with slightly different growing conditions.

5.4.3.3.1 The Rûens region

The Rûens region is considered to have poorer soils, rainfall, and lower yields than the Swartland. There are seasons, however, that the yield is much higher in some areas and even out-yielding wheat planted in the Swartland. The analysis of variance for spring wheat cultivars grown the Rûens region is summarised in Table 5.14.

Table 5.14 Analyses of variance for yield of spring wheat cultivars in the winter rainfall, Rûens region

Source	df	SS	MS	F-value	Pr>F
Total	359	25851137.178			
Cultivars	6	8646296.264	1441049.377	58.65	0.0000
Env + in Var x Env.	28	17204840.913	614458.604		
Env in linear	1	16195651.521			
Var x Env (linear)	6	493234.883	82205.814	3.35	0.0179
Pooled deviation	21	515954.509	24569.262		
Residual	325	5175078.345	15915.972		

Evidently from Table 5.14 a moderate significance was observed for cultivars x environment interactions. The spring wheat cultivars differed significantly in terms of yield. The stability values for these cultivars are summarised in Table 5.15.

From the seven spring wheat cultivars presented in Table 5.15, four had good stability values. These were: Kariega, Baviaans, SST57, and SST65. Palmiet, Steenbras, and SST88 showed relative high stability values indicating poorer yield stability.

Table 5.15 Stability analyses for yield of spring wheat cultivars in the winter rainfall, Rûens region

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	7961.2043	0.1667	0.919	1.0924	-13262.2374	**Kariega**
2	95637.1883	2.0030	0.113	1.1686	15963.0906	**Palmiet**
3	168423.7338	3.5274	0.015	0.7122	40225.2725	**Steenbras**
4	38661.0855	0.8097	0.489	0.9556	-3028.9436	**Baviaans**
5	47776.1649	1.0006	0.393	0.8813	9.4161	**SST57**
6	17933.4175	0.3756	0.771	0.9227	-9938.1663	**SST65**
7	139561.7150	2.9229	0.034	1.2672	30604.5995	**SST88**

5.4.3.3.2 The Swartland region

The Swartland generally has a better yield potential and soils better suited for wheat production than the regions in the Southern Cape (Rûens). However, occasionally the climatic conditions are harsh and poor yields are recorded. The analysis of variance for cultivars in the Swartland region is presented in Table 5.16.

Table 5.16 Analyses of variance for yield of spring wheat cultivars in the winter rainfall, Swartland region

Source	df	SS	MS	F-value	Pr>F
Total	489	48472735.101			
Cultivars	6	5150520.365	858420.061	8.91	0.0000
Env in Var x Env.	42	43322214.736	1031481.303		
Env in linear	1	36343512.222			
Var x Env (linear)	6	3607388.513	601231.419	6.24	0.0002
Pooled deviation	35	3371314.001	96323.257		
Residual	441	7433159.886	16855.238		

Significant differences for cultivars and cultivar x environment interactions were observed. The yield stability values for the cultivars in the Swartland region are summarised in Table 5.17.

Table 5.17 Stability analyses for yield of spring wheat cultivars in the winter rainfall, Swartland region

Var	SS	F-Ratio	Pr.>F	Beta	Deviation	Name
1	136198.4256	1.6161	0.154	0.7073	10384.4473	**Kariega**
2	1466362.9064	17.3995	0.000	1.7347	276417.3434	**Palmiet**
3	538018.1817	6.3840	0.000	0.9329	90748.3985	**Steenbras**
4	452205.9314	5.3658	0.000	0.7716	73585.9484	**Baviaans**
5	291883.2572	3.4634	0.004	0.9506	41521.4136	**SST57**
6	166187.9838	1.9719	0.082	1.0040	16382.3589	**SST65**
7	320457.3149	3.8025	0.002	0.8988	47236.2252	**SST88**

The deviation values for cultivars planted in the Swartland region are relatively high although Kariega and SST65 showed lower deviation values. These lower values suggest that Kariega and SST65 are more stable than Palmiet, Steenbras, Baviaans, SST57, and SST88. Palmiet was the most unstable cultivar, but this could be due to the difference in data used. Because Palmiet is an older cultivar, data from 1997 to 1999 had to be used to calculate stability values. The Beta values also indicate SST65 is stable. It is important to read the deviation value with the Beta value and it can therefore be assumed that SST57 is also relatively stable.

5.4.3.3.3 Yield stability, and vernalization and photoperiodic response in winter rainfall spring wheat cultivars

Since the winter temperatures in the winter rainfall region seldom reach levels as low as 4 degrees centigrade, it is expected that no vernalization requirement wheat cultivars are planted in this region. All the cultivars targeted for planting in the winter rainfall regions reached anthesis without any vernalization treatment as illustrated in Chapter 3. Some cultivars: Kariega, Steenbras, and Baviaans are also planted in the irrigated, summer rainfall region. Correlations between the stability of cultivars and their response to vernalization and photoperiod treatments are shown in Table 5.18.

Table 5.18 Correlation matrix between wheat cultivars for vernalization, photoperiod and yield stability in the Winter rainfall regions

	WRSD	WSSD	VRNF	VRNM	VRNG	PPDF	PPDM
WSSD	0.3674						
	0.5429						
VRNF	0.4805	0.2255					
	0.4126	0.7153					
VRNM	0.2724	0.2891	0.8923				
	0.6575	0.6371	0.0417				
VRNG	-0.2074	0.2644	0.1985	0.6182			
	0.7378	0.6673	0.7489	0.2664			
PPDF	0.6552	0.6926	0.2775	0.1068	-0.1919		
	0.2301	0.1949	0.6513	0.8643	0.7571		
PPDM	0.4834	0.3426	0.5530	0.2057	-0.5050	0.6742	
	0.4095	0.5724	0.3337	0.7399	0.3855	0.2119	
PPDG	-0.3905	-0.5145	0.2153	0.0533	-0.3246	-0.5893	0.1854
	0.5157	0.3751	0.7280	0.9322	0.5941	0.2957	0.7653

Stability values for Rûens (WRSD), Swartland (WSSD), Vernalization flowering (VRNF), Vernalization maturity (VRNM), Vernalization grain fill (VRNG), Photoperiod flowering (PPDF), and Photoperiod maturity (PPDM)

In Table 5.18 the measured parameters are stability values for the Rûens and Swartland regions (WRSD, WSSD), the absolute response of cultivars to vernalization and photoperiod treatment in terms of days to flowering (VRNF, PPDF), days to physiological maturity (VRNM, PPDM), and days from flowering to physiological maturity (VRNG, PPDG). From Table 5.18 it is evident that vernalization requirement has little to no correlation with yield

stability in the Winter Rainfall Regions of the Rûens and Swartland. The only relative correlation found was between yield stability and the photoperiodic response, in terms of days to flowering, of cultivars planted in the Swartland region, although the correlation is not significant.

Discussion

The expected low correlation of yield stability and response to vernalization is confirmed with the results obtained from the correlation matrix. These cultivars were selected for this target region and logically vernalization should not influence yield stability to a large extend. There seems to be a weak correlation between photoperiodic response and yield stability of cultivars planted in the Swartland, and even the Rûens region. Both Kariega and SST65 had lower responses to photoperiod treatment than the remaining five cultivars and from Tables 5.15 and 5.17 it is suggested that these two cultivars are more stable than the others.

5.5 Conclusions and recommendation

Classifying wheat in growth habit groups is important in targeting germplasm to specific environments. The combined cluster analysis (vernalization and photoperiodic response), for the 30 cultivars evaluated, agrees with the cluster analysis for vernalization by dividing the 30 cultivars into four main classes. These classes are true winter, winter, intermediate, and spring wheat cultivars.

True winter, winter, and intermediate wheat cultivars are planted in the Free State under dry land conditions were vernalization temperatures occur during the early phases of plant development. Vernalization response seems to influence yield stability in the lower rainfall regions (central and western Free State), while photoperiodic response is less influential. Vernalization response in spring wheat only correlates with cultivars planted in the warmer irrigation regions, while no correlations were found for the cooler irrigation, Rûens, and Swartland regions. It is suggested that response to photoperiod attributes more to yield stability in the Rûens and Swartland than in other parts of the wheat growing areas of South Africa.

Elands stands out as a cultivar with good yield stability in all three Free State environments. Another interesting observation is the yield stability of the intermediate wheat cultivar SST363 in the Western Free State. True winter types are predominantly planted in the Western Free State and this is also manifested in the stability of the hybrid wheat SST966 in the Western Free State.

Although this study investigated the correlation or relation of yield stability and response of cultivars to vernalization and photoperiod, it is recommended that further study is necessary to confidently accept or reject the existence of yield stability and genotypic response to vernalization and photoperiod correlations. It is further recommended that trial planning should be conducted in such a way that true winter, winter, and intermediate wheat cultivars are not included in the same trial, but planted in the class type they represent.

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CHAPTER 6

6. SUMMARY

The aim of this study was to determine the response of South African bread wheat cultivars to vernalisation and photoperiod and to group the genotypes accordingly. In addition to this the way in which the response of genotypes to vernalisation and photoperiod attributes to yield stability was also investigated.

Thirty South African wheat cultivars were included in two separate trials to evaluate their response to vernalisation and photoperiod treatments. The wheat cultivars were selected to represent cultivars planted in all the main wheat production regions of South Africa. The range of genotypes included cultivars with no vernalisation requirement to cultivars with very strong vernalisation requirements.

The vernalisation trial consisted of 30 South African wheat cultivars subjected to eight vernalisation treatments, ranging from zero to seven weeks vernalisation. Each treatment had eight replicates on which days to heading, flowering and physiological maturity were observed. Cluster analysis was done to group the cultivars into similarity groups. Four groups were identified: 1) True winter wheats encompassing: Molen, SST936, SST966, SST399, and 2) Winter wheats that included Betta-DN, Caledon, Elands, Hugenoot, PAN3235, SST367, and SST983, 3) Intermediate wheats consisting of Gariep, Limpopo, PAN3211, PAN3349, PAN3377, SST124, SST363, and Tugela-DN, and 4) Spring wheats including Baviaans, Inia, Kariega, Marico, Palmiet, Steenbras, SST57, SST65, SST88, SST822, and SST876.

The photoperiod trial involved 30 South African wheat cultivars subjected to three photoperiod treatments (10, 14, and 18 hours day light). Ten replicates were included for each treatment. Days to heading, flowering

and physiological maturity were recorded for all cultivars. Cluster analysis was performed and four discreet response classes identified. The classes were denominated as Group 1, Group 2, Group 3, and Group 4. Group 1 consisted of only one cultivar SST399. Group 2 included all the following true winter, winter, and intermediate wheat cultivars: Molen, Betta-DN, Caledon, Elands, Hugenoot, PAN3235, SST367, Limpopo, Gariep, PAN3211, PAN3349, PAN3377, SST124, SST363, and Tugela-DN. The only cultivars in Group 3 are the hybrid wheats: SST936, SST966, and SST983. Group 4 included all the spring wheat cultivars: Baviaans, Inia, Kariega, Marico, Palmiet, Steenbras, SST57, SST65, SST88, SST822, and SST876.

Data obtained from the vernalisation and photoperiod trials were used in conjunction with data from cultivar evaluation trials to determine the relationship between the response to vernalisation, photoperiod and yield stability. Yield data from the three main wheat production areas: Free State (14 sites), Irrigation areas (13 sites), and the Western Cape (12 sites) were used to calculate yield stability. Correlations between response to vernalisation, photoperiodic and yield stability were found to be weak, although stronger correlations were observed between vernalisation response and yield stability in the Western Free State, Central Free State, and warmer irrigation areas.

The data from this study suggest that wheat should be classes as true winter, winter, intermediate, and spring wheats, and that trial layouts should be planned according to these classes.

CHAPTER 7

7. OPSOMMING

Die doel van hierdie studie was om die reaksie van Suid-Afrikaanse broodkoring cultivars op vernalisasie en fotoperiode behandelings te bepaal en die cultivars dienooreenkomstig te klassifiseer. Aanvullend tot die klassifikasie van broodkoring cultivars is 'n ondersoek geloods na die waarskynlikheid dat 'n genotipe se reaksie op vernalisasie en fotoperiode bydrae tot opbrengsstabiliteit in broodkoring.

Dertig Suid-Afrikaanse broodkoring cultivars is in twee afsonderlike proewe ingesluit om hierdie cultivars se reaksie op vernalisasie en fotoperiode behandelings te evalueer. Die cultivars is gekies op grond van verteenwoordiging van cultivars in die belangrikste verbouingsstreke van Suid Afrika, wat genotipes met geen, en sterk vernalisasiebehoeftes insluit.

Die vernalisasie proef het bestaan uit 30 Suid Afrikaanse broodkoring cultivars wat onderhewig was aan agt vernalisasie behandelings wat gewissel het van geen vernalisasie tot sewe weke vernalisasie behandelings. Elke behandeling het agt herhalings gehad waarop dae tot aarverskyning, blom en fisiologiese volwassenheid aangeteken is. 'n Trosanalise is uitgevoer om die cultivars in verwantskapsgroepe te klassifiseer. Vier groepe is uit hierdie analise geïdentifiseer naamlik: 1) Egte winter tipes, wat Molen, SST966, SST936, SST399 en insluit, 2) Winter tipes bestaande uit Betta-DN, Caledon, Elands, Hugenoot, PAN3235, SST367 en SST983, 3) Intermediêre tipes insluitend Gariep, Limpopo, PAN3211, PAN3349, PAN3377, SST124, SST363 en Tugela-DN en 4) Lente tipes insluitend Baviaans, Inia, Kariega, Marico, Palmiet, Steenbras, SST57, SST65, SST88, SST822 en SST876.

Die fotoperiode proef het 30 Suid Afrikaanse broodkoring cultivars ingesluit wat aan drie fotoperiodiese behandelings (10, 14, en 18 ure dagliglengte) blootgestel is. Elke behandeling is tien maal herhaal en dae tot aarverskyning, blom en fisiologiese volwassenheid is aangeteken. 'n

Trosanalise is uitgevoer om die cultivars op grond van hulle reaksie op fotoperiode in verwantskapsklasse te deel. Die analise het vier diskrete klasse geïdentifiseer wat Groep 1, Groep 2, Groep 3 en Groep 4 genoem is. Groep 1 bestaan slegs uit een cultivar, SST399, terwyl Groep 2 die volgende egte winter, winter en intermediêre cultivars insluit: Molen, Betta-DN, Caledon, Elands, Hugenoot, PAN3235, SST367, Limpopo, Gariep, PAN3211, PAN3349, PAN3377, SST124, SST363 en Tugela-DN. Groep 3 het al die basterkoring cultivars bevat, naamlik: SST936, SST966 en SST983. Groep 4 is opgemaak uit al die lente tipes: Baviaans, Inia, Kariega, Marico, Palmiet, Steenbras, SST57, SST65, SST88, SST822 en SST876.

Data wat uit die vernalisasie en fotoperiode proewe verkry is, is in samehang met data uit die cultivar evaluasie proewe gebruik, om vas te stel of daar 'n verwantskap tussen vernalisasie, fotoperiode en opbregsstabiliteit is. Opbrengsdata van die belangrikste koringproduksiegebiede: Die Vrystaat (14 lokaliteite), Besproeiingsgebiede (13 lokaliteite) en die Weskaap (12 lokaliteite) is gebruik om opbrengsstabiliteit te bereken. Korrelasies tussen vernalisasie, fotoperiode en opbrengsstabiliteit was oor die algemeen swak, maar sterker korrelasies is wel tussen die reaksie op vernalisasie en opbrengsstabiliteit in die Wes Vrystaat, Sentraal Vrystaat en warmer besproeiingsgebiede gevind.

Die data wat uit hierdie studie verkry is, dui aan dat broodkoring behoort as egte winter, winter, intermediêre en lente tipes geklassifiseer te word en dat proewe binne klasverband opgestel moet word.

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