Effects of Temperature, Photoperiod, and Vernalization on the Growth, Development, and Predictions by the CERES-Wheat Model, for Spring Wheat Cultivars

by

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A Thesis
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Effects of Temperature, Photoperiod, and Vernalization on the Growth, Development, and Predictions by the CERES-Wheat Model, for Spring Wheat Cultivars

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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of Manitoba in partial fulfillment of the requirements of the degree

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To my wife Barbara, my daughter Chemaah, my sisters Beatrice and Gina, and my parents Alex and Margaret .....

Abstract

Organizations such as the Canadian Wheat Board rely on yield forecasts to plan grain handling and marketing strategies. Therefore, a model that accurately predicts yield would be useful. In plant breeding programmes involving advanced line evaluations at different locations, lack of adequate resources may be a limitation. Differences among genotypes at different locations are due to genetic as well as environmental effects. These studies investigated the effects of temperature, photoperiod, and vernalization on the growth and development of spring wheat cultivars, and assessed the ability of the CERES-wheat model to predict yield in yield trials conducted in western Canada. Field experiments were conducted at Winnipeg and Carman, Manitoba, using three seeding dates at each location, to provide data for model calibration and validation. Controlled environment studies elucidated environmental effects which may be difficult to discern under field conditions. Data on phenology, yield-related components, weather, and model-required soil properties were collected for all trials. High temperatures accelerated the growth of vernalization-insensitive cultivars by decreasing time to anthesis and time to maturity, and reduced the number of main stem leaves and yield-related components. High temperatures decelerated the growth of vernalization-sensitive cultivars and prolonged the length of the vegetative growth period. Differential cultivar phyllochron responses to temperature increases were evident. Therefore, the use of modified

thermal time calculations in the CERES-wheat model may not be appropriate for all genotypes. To reduce errors in phyllochron interval calculations, crop modellers may need new equations to address temperature sensitivity of cultivars. Cultivar differences in time to heading, anthesis, and maturity, were attributable to differences in the time to terminal spikelet initiation. The CERES-wheat model was sensitive to changes in seeding date and locations, and was capable of deciphering cultivar differences. Cultivar genetic coefficients determined under an early seeding environment at one location could be used at another location in the same region. The CERES-wheat model however, showed several weaknesses which included a general tendency to underestimate grain yield, phyllochron interval, and dry matter production. Also, its predictive power declined with delays in seeding date. The extensive data requirement of the CERES-wheat model are deterrents to its use. These concerns need to be addressed by the model builders if researchers are to find the CERES-wheat model less demanding and user-friendly.

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Table of contents

Page

List of tables

List of figures

Page

List of appendices

Foreword

This thesis is written in a manuscript style. Three manuscripts are presented. Each manuscript includes an abstract, introduction, materials and methods, results and discussion, and conclusions. A general introduction and literature review precede the manuscripts. A general discussion, references, and appendices terminate the thesis. All manuscripts are formatted to conform with the requirements of the Canadian Journal of Plant Science in which some of them are intended to be published.

1.0 INTRODUCTION

Wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L), and corn (*Zea mays* L.) are the three most widely grown crop species in the world (Reitz, 1967). Broad adaptation, coupled with the ease of storage, transportation, and processing, account for the widespread use of cereals as sources of food and feed. Wheat is a major ingredient of many food products (e.g., breads, biscuits, doughnuts, noodles etc.).

Over the years, plant breeders have made significant improvements in wheat grain yield (Cox et. al., 1988). However, the effects of environmental factors such as diseases, insect pests, temperature, photoperiod, moisture, and competition with weeds for moisture, nutrients, and sunlight, may prevent the full intrinsic yield potential of wheat cultivars from being realized.

Demographers project the world's population to increase from the present 6 billion to more than 10 billion by 2050 (Bongaarts, 1994). Thus, the production of enough food to feed the increasing world population is a concern. Crop yields may be increased in three major ways: 1) increasing the genetic yield potential of cultivars, 2) removing or reducing the constraints that interfere with the expression of the intrinsic yield potential of cultivars, and 3) proper management practices and decisions (e.g., the right choice of cultivar for planting in a specific environment).

Farmers are usually faced with the difficulty of balancing the advantages and disadvantages of early seeding to maximize yield while minimizing risk. Early

seeding could lead to disease avoidance, better realization of yield potential, and provide increased marketing opportunities and profit (Canada-Manitoba Farm Business Management Council, 1996). However, early seeding (in temperate regions), could result in exposure to an increased risk of spring frost, susceptibility to herbicide residue, and seed rot. If farmers could have an *a priori* knowledge of the cultivar that would yield best under varying seeding dates, risks could be minimized and grain yields maximized. Crop modelling could be one way of achieving this.

The fact that year-to-year fluctuations in crop yields are largely due to environmental variations has lead to numerous efforts to model crop-environment relationships and develop yield-prediction systems (Haun, 1982). Crop cultivars may differ in the duration of their phasic development, as well as in their responses to different environmental conditions. Therefore, a crop simulation model which accounts for genotypic differences would be useful to: 1) the plant breeder, for the assessment of cultivar adaptability to different locations, 2) the producer, for making management decisions (e.g., the choice of which cultivar to plant under certain anticipated or forecasted environmental conditions for the growing season), and 3) marketing organizations, for yield forecasts to aid the development of effective marketing strategies.

One model which is receiving increasing world-wide attention because of its ability to differentiate between cultivar characteristics, is the Crop Estimation through

Resource and Environment Synthesis (CERES)-wheat model (Ritchie, 1991). To investigate the feasibility for use in a particular region, a model should be calibrated and validated with a data base appropriate to the particular region (Otter and Ritchie, 1984).

The main objectives of this study were to: 1) characterize the effects of temperature, photoperiod and vernalization, on the plant growth and development of six spring wheat cultivars (AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat), (under controlled environment), 2) investigate the effects of delayed seeding on the growth, development, and performance of the spring wheat cultivars, and 3) determine the cultivar characteristics (genetic coefficients) for the six spring wheat cultivars, and also calibrate and validate the CERES-wheat model under Manitoba conditions by investigating the effects of delayed seeding on model predictions.

2.0. LITERATURE REVIEW

2.1. Stages of development of the wheat plant

2.1.1. The wheat grain

The mature wheat grain is a caryopsis (a small, dry, indehiscent, one-seed fruit with a thin, tight pericarp), and consists of an embryo, and the endosperm (Briggle, 1967). The embryo consists of: 1) the scutellum, a modified leaf that absorbs sugars and other nutrients from the starchy endosperm, during germination, 2) the epiblast, a leaf-like structure that fails to develop into a true leaf, 3) the coleoptile, another leaf-like structure that protects the first true leaf during emergence from the soil, 4) primordia for the first three to four true leaves, 5) the radicle, which is covered by a protective layer of tissue called the coleorhiza, and two to five seminal root primordia (Cook and Veseth, 1991). The outer pericarp is characterized by cells with thickened cell walls, arranged in a closely packed fashion, with the long axes of the cells parallel to the length of the grain. There is a thin cuticle on the outer epidermal cell wall (Briggle, 1967). Sandwiched between the outer epidermis and the endosperm is a single layer of cells, called the aleurone layer. The aleurone cells are thick-walled and closely packed with no intercellular spaces between them. The thin-walled endosperm cells contain many starch granules embedded in a proteinaceous matrix.

2.1.2. Germination and emergence

When a mature non-dormant wheat grain is exposed to moisture and temperature above 3°C (Addae and Pearson, 1992), the seed imbibes moisture and swells, and the embryo begins to grow. The coleorhiza emerges through the pericarp and elongates. The enclosed primary root forces its way through the coleorhiza, and the first pair of lateral roots become visible. The coleoptile is the first shoot structure to appear (Karow et al., 1993). The endosperm provides the energy source for these initial growth activities.

Sowing depth and seed-soil contact affect seedling emergence. The coleoptile can grow to a length of only 7.5-10 cm. If the seed is planted deeper than this, the first true leaf will emerge below the soil surface and may be damaged as it grows (Karow et al., 1993).

2.1.3. Root development

The root system of cereal plants is typically fibrous (Reilly, 1982). The root meristem is protected by the root cap. The first evidence of structural growth is the emergence of the radicle, followed by two seminal roots formed at the scutellar and epiblast nodes (Cook and Veseth, 1991; Karow et al., 1993). When these three roots begin to absorb water, the coleoptile elongates and emerges. As the plant matures, the nodal root system develops from the crown (Karow et al., 1993). Each node of the main stem and the tillers may produce up to four crown roots. First and second

order branching of the seminal roots may occur when the main stem has about three leaves, and five to six leaves respectively. Similarly, first and second order branching of crown roots from a given node may begin when the associated tiller has three leaves. Roots start to elongate when cells immediately behind the root cap enlarge.

2.1.4. Shoot development

2.1.4.1. Leaf development

The production and appearance of leaves are fundamental processes in the growth and development of a cereal plant. The rate of leaf emergence is slower than that of leaf initiation, and leaf emergence rates differ between environments and genotypes (Kirby, 1984). The total number of main stem leaves is related to the duration of the development interval prior to floral initiation, as well as to the rate of leaf primordia initiation (Kiniry et al., 1991). In general, the rate of development is defined as the inverse of thermal time [growing degree days (GDD)] required to reach a certain developmental stage. Del Pozo et al., (1987) suggested that the rate of leaf development increases linearly within a defined range of temperatures. Measurement of leaf appearance on the main stem, although time consuming, is non-destructive, and offers a developmental measurement for determining response function(s) of plant development to environmental factors such as temperature, and photoperiod (Ritchie and NeSmith, 1991). Environmental factors interact with the plant genotype to produce leaves in an orderly and predictable fashion (Frank and Bauer, 1995).

Phyllochron interval is defined as the thermal time (GDD) required for successive leaves to pass through the same developmental stage. Phyllochron interval is related to air temperature (Klepper et al., 1982), and is used for determining the duration of specific developmental phases, which in turn are used in determining the timing of management practices (e.g., fertilizer and/or pesticide application) (Frank and Bauer, 1995). On the other hand, other researchers have reported that soil temperature provides a greater predictive accuracy in cereals (Ong, 1983; Jamieson et al., 1995; Bollero et al., 1996). However, McMaster and Wilhelm (1998) reported that the additional effort and expense of using soil temperature in predicting wheat phenology are not justified.

Several investigators have suggested that the phyllochron interval is fixed for the growing season by the prevailing environmental conditions during seedling emergence (Klepper et al., 1982; Bauer et al., 1984). The number of main stem leaves has thus been reported to be a linear function of accumulated GDD (in either field or controlled environments). However, Darrock and Baker (1990), and Duguid (1990) found that a quadratic polynomial model best described the number of main stem leaves with respect to GDD, and therefore contended that the phyllochron interval is not constant over the leaf development phase.

2.1.4.2 Tillering

A typical characteristic of most cereal plants is the development of secondary

stems, or tillers. Tillering is an important process in determining wheat yields. Tillering patterns of genotypes may be assessed by either determining the maximum tillers and final spike numbers on a plant/crop basis (Hucl and Baker, 1989), or by determining tiller mortality or tiller survival (Shanahan et al., 1985).

There is a well coordinated synchrony between leaf and tiller development of cereals in general, and wheat in particular (Klepper et al., 1983). Tillers (T) are named after the leaf (L) from whose axil they developed. For example, the tiller that emerges from the axil of the first leaf would be labelled T1 (Karow et al., 1993). T1 appears as the fourth leaf elongates, and T2 develops with the appearance of the fifth leaf, etc. Wheat is a determinate plant, and therefore only leaf primordia formed before floral initiation develop into mature leaves (Karow et al., 1993). However, not all axillary buds produce tillers (Klepper et al., 1982). Some reports state that tillering patterns remain unaffected over a wide range of environmental conditions (Fraser et al., 1982; Klepper et al., 1982). On the other hand, some workers have observed both genotypic differences in tillering pattern (Hucl and Baker, 1989), and significant environmental effects (Black and Siddoway, 1977; Shanahan et al., 1985) on tillering. Tillering is closely correlated to yield because the number of tillers plays a role in determining maximum yield potential. Therefore, factors that affect tillering will also influence maximum yield potential.

Plant density may affect the number of tillers produced per plant. Wheat plants

may tiller more to compensate for a low plant population, or tiller less in response to a high plant population (Cook and Veseth, 1991). Generally, stress causes tiller emergence to be delayed or suppressed. Furthermore, under stress conditions (e.g., high temperature) the tillering capacity of the wheat plant to compensate for a low plant population, is reduced (Rahman and Wilson, 1978). Wheat plants growing in an unfavourable seed bed (e.g., dry and crusted) may produce neither a T0 (coleoptile tiller) nor a T1 tiller (Klepper et al., 1982). In a good seed bed, where moisture and nutrients are non-limiting, a high percentage of plants will have T0 and T1 tillers (Karow et al., 1993). Once produced, each tiller develops leaves at a similar rate as the main stem (Klepper et al., 1983).

There is a disagreement as to when tillering ceases. According to Baker and Gallagher (1983) tillering ceases at the double ridge stage. Darwinkel (1983), however, found that tiller production ceased at a progressively later date with decreasing rate of sowing. Rawson (1971) suggested that tillering ceases at about the same time as terminal spikelet differentiation, and is followed by a period of tiller mortality which begins after the main shoot initiates floral development. Masle (1984) established that cessation of tillering and the senescence of tillers are immediate consequences of nutrient, and moisture deficiency. Kirby (1984) suggests that the cessation of tillering and tiller mortality may be both genetic and environment dependent.

2.1.5. Reproductive phase

The change from vegetative to reproductive development results from hormonal signals triggered in the plant, and is dependent upon: 1) the genotype 2) temperature, and/or 3) photoperiod (Cook and Veseth, 1991). During the transition from vegetative to reproductive growth, the growing points first elongate and then produce reproductive nodes (clusters of undifferentiated cells destined to become structures on the spike) at about twice the rate at which the vegetative growing points develop. The reproductive nodes give rise to axillary buds, from which future spikelets are formed. The first series of spikelet primordia, representing the single-ridge stage, are followed by a second series to establish the double-ridge stage. At this point, the maximum number of spikelets is fixed.

The rate and duration of spikelet initiation are determinants of spikelet number. Generally, an inverse relationship exists between the rate and duration of spikelet initiation. However, a deviation from a strict inverse relationship was observed by Rahman and Wilson (1978). Spikelets have the potential to produce as many as seven to nine kernels, however most produce one to five kernels (depending on genetic and environmental factors). The terminal spikelet is formed at late jointing when the growing point is pushed above ground. Onset of the terminal spikelet initiation causes a cessation of spikelet production (Wong and Baker, 1986). Therefore the number of spikelets puts a basic limitation on potential yield. In spring wheat, for

example, this conversion which leads to the fixation of spike size, is completed by the time the main stem has acquired approximately 5.5 leaves (Cook and Veseth, 1991).

2.1.6. Stem elongation

Stem elongation is a critical part of the life cycle of a cereal plant in relation to yield, because it coincides with changes in the partitioning of assimilates, resulting in the accumulation of reserves for use during the ensuing grain filling period (Kirby and Appleyard, 1982). The stem of a cereal plant could have 7 to 15 internodes, but usually only the uppermost five to six internodes elongate (the lower internodes remain short). Elongation of internodes is sequential, starting with the fourth internode from the base. When this internode is about half grown, the next uppermost internode starts to elongate, until the internode beneath the spike (the peduncle - the longest) is fully elongated (Kirby and Appleyard, 1982). The application of certain growth regulators at the stem elongation stage may modify the activity of the internode meristem, to shorten the stems (Kirby et al., 1994). Dwarfing genes may also affect stem elongation in cereals (Austin et al., 1980; Mahalakshmi et al., 1991).

2.1.7 Anthesis

The lemma and palea enclose three stamens, a single pistil, and two lodicules situated at the base of an ovary (Simmons, 1987). At anthesis the anthers become

yellow and the enclosed pollen grains are dehisced before the florets open. Some of the pollen grains shed within the flower fall on the feathery stigma, which leads to self fertilization. The thin-walled parenchyma of the lodicules swell at the base and force the lemma and palea apart. At the same time, the filaments of the stamens lengthen rapidly, and push the anthers out of the floret (Peterson, 1965). This leads to the opening of the flower, and exposure of the anthers (Briggle, 1967). Anthesis on the main stems may occur over a period of three to five days, and usually starts from the middle of the spike and continues upward and downward (Cook and Veseth, 1991). Within a spikelet there is a time lag between occurrence of anthesis in the primary and secondary florets, and anthesis in the tertiary and other florets.

It is important that environmental conditions (e.g., temperature, moisture, nutrients) just before and during anthesis be conducive for maximum fertilization. Under certain environmental conditions, high yields are obtained when flowering occurs before plants suffer high temperature stress (French et al., 1979). Entz and Fowler (1989) attributed reduced yield under high pre-anthesis drought conditions to reduction in dry matter accumulation, kernel number, and harvest index. Low kernel number implies low spikelet initiation and/or poor fertilization. In Australia, reduced yields were observed when flowering occurred too early, and was followed by frost damage (Kohn and Storrier, 1970). Temperatures above 30°C cause stress and pollen injury, which significantly reduces fertilization (Smika and Shawcroft, 1980).

2.1.8. Grain filling

Fertilization of the ovules by the pollen leads to the beginning of grain filling. Kernels may be filling in the florets of the middle spikelets while flowering is still in progress at the ends of the spike, and/or tertiary florets. Generally, dry matter accumulation is slow during early grain filling, and is followed by a nearly linear increase in kernel dry weight, until maximum seed mass is attained (Simmons, 1987; Cook and Veseth, 1991).

Grain yield is dependent on sink capacity (the number of fertile florets to be filled) and photosynthetic capacity during the grain filling period (Evans and Wardlaw, 1976). Generally, net photosynthesis does not limit grain production in wheat (Judel and Mengel, 1982). Therefore, apart from the effects of the prevailing environmental conditions, the rate at which grain filling occurs, and the duration of the grain filling period are the two post anthesis determinants of final grain dry weight. Nass and Reiser (1975) did not observe any relationship between grain yield and the duration of grain filling. Gebeyehou et al. (1982a) observed a positive correlation between the length of the grain filling period and kernel weight, and advocated that lengthening the grain filling period should increase grain yield, provided that the resultant late maturity does not result in increased susceptibility to late summer drought stress or early fall frosts. On the other hand, a high grain filling rate will be especially desirable in a short growing season area (Nass and Reiser,

1975).

Several equations have been used to describe grain filling in wheat; ranging from quadratic (Nass and Reiser, 1975; Bruckner and Frohberg, 1987), and cubic polynomials (Gebeyehou et al. 1982b), to logistic (Darrock and Baker, 1990; Duguid and Brûlé-Babel, 1994) equations. Genotype and environment influence the rate and duration of grain filling (Gebeyehou et al. 1982a & b; Duguid and Brûlé-Babel, 1994). Because the phenotypic correlation between the rate and duration of grain filling was close to zero, Gebeyehou et al., (1982b) proposed that simultaneous selection of both rate and duration of grain filling should be possible, without increasing the duration of the grain filling period.

Most of the dry matter contributing to grain yield is newly assimilated during grain filling, but conditions such as drought can cause a reduction in new assimilate supplies, and the plants must then rely on previously stored assimilates for grain filling (Gallagher et al., 1976). Generally it is accepted that the mobilization and transportation of assimilates in leaves and culms do contribute to grain filling (Austin et al., 1977). In order to realize the yield potential laid down during the vegetative phase, adequate water and nutrient supply, as well as appropriate temperature and irradiance are important during the grain filling period.

2.1.9 Maturity

Unlike anthesis, time to maturity in wheat is a difficult trait to assess.

Technically, maturity in cereal crops may be defined as the time at which maximum kernel dry mass is attained [physiological maturity (PM)]. In wheat, kernel moisture content at PM has been reported to range from 38 to 44 % (Housley et al,, 1982). Hanft and Wych (1982) reported the PM of eight wheat cultivars to be in the moisture content range of 13 to 28 %. Clarke (1983) attributed this wide range of reported moisture content at PM to genetic and/or environmental factors.

Knowledge of PM may be important to the researcher who may use it as a selection criterion, or to the grower who may swath the crop at PM to hasten dry down and/or avoid frost damage (Copeland and Crookston, 1985). Several methods of assessing PM have been suggested. The appearance of a dark pigment strand in the chalazal tissue between the endosperm and the vascular bundle, has been observed to be associated with PM (Zee and O'Brien, 1970; Hanft and Wych, 1982). Other visual markers which have been confirmed as indicators of PM in wheat include complete loss of green colour from the glumes (Hanft and Wych, 1982) or the peduncle (Copeland and Crookston, 1985) of hard red spring wheat, and 75% loss of green colour from the glumes of the primary spike in durum wheat (Gebeyehou et al., 1982a). Pinthus (1963) reported that the glumes of certain durum wheats did not lose their green colour at PM. In genotypes which possess coloured glumes, the use of loss of green colour from the glume could be difficult. Smith and Donnelly (1991) suggested that for any given environment, the precise visual marker(s) to be used for

PM assessment should be determined rather than assumed. In some groups of genotypes, days to heading or anthesis, which is easily and rapidly scored, has been shown to exhibit a positive correlation with time to PM (Cross, 1975). However, Sommerville and Briggs (1979) argued that since heading or anthesis and PM are separated in time, it is possible to mis-classify some genotypes if days to heading or anthesis is the only measure used for PM assessment.

2.2. Effects of environmental factors on wheat growth and development

Crop growth and development is a complex combination of crop responses to weather and soil conditions. Each cultivar appears to have a unique set of controls and requirements in phenological development (Pirasteh and Welsh, 1980). Environmental factors which limit attainable yields of cereal crop plants, vary according to geographical location (Williams, 1971; Touré et al., 1995).

Grain yield of a wheat plant is influenced by the number of plants per metre square, the number of fertile spikes per plant, the number of kernels per spike, and kernel weight. The vegetative growth phase of the wheat plant can be divided into three relatively distinct periods - leaf initiation, spike initiation, and spike growth. Long leaf initiation and spike initiation periods are usually associated with high spikelet number. Prevailing environmental conditions before and/or during floral initiation can affect the size and number of spikelets, which can directly affect yield.

Thus, environmental conditions that shorten the pre-anthesis phase are likely to result in fewer spikelets, and consequently, reduced grain yield.

In general, during almost all the growth stages of a cereal plant, external conditions will affect one or more components of the seed yield. Moisture, temperature, photoperiod, and vernalization responses and their interactions with genotype have been identified as the most important factors in the control of number of kernels per spike (Halse and Weir, 1970). In light of the confounding effects of temperature, vernalization, and photoperiod requirements on plant development and maturity, perhaps the description of a cultivar as "early-maturing" needs to be done with some qualification.

2.2.1 Temperature

Temperature affects the rates of most biological processes involved in crop growth and development. Factors that influence the response(s) of a plant to stressful conditions are the genetic potential of a plant to adapt, the stage of growth, and the duration of exposure (Gusta and Chen, 1987). For example, depending on the winter wheat cultivar, and the age of the leaves, temperatures as low as -18°C can be tolerated, but the reproductive tissues may be injured at temperatures between -3°C and 2°C (Single and Marcellos, 1974). Wheat plants appear to be programmed genetically not to push the growing point above the soil surface until enough heat units have accumulated (Cook and Veseth, 1991).

Wheat is sensitive to high soil temperature when first planted, and during seedling emergence and tillering. Wheat seeds may fail to germinate when soil temperatures are above 30°C. High temperatures during terminal spikelet initiation, stem elongation, heading, and flowering, may also cause stress or injury (Cook and Veseth, 1991). Exposure of wheat plants at most stages of development to temperatures above 30°C, may result in: 1) a shut down of transpiration, 2) reduced rate of photosynthesis, 3) an increase in the respiration rate (Larcher et al., 1973), 4) inactivation of key enzymes - e.g., sucrose synthase and starch synthase (Jenner, 1991), and 5) acceleration in the rate of plant growth and development. As a result, photosynthates may not be adequate to meet the demands of respiration and growth of new leaves and tissues. Such effects of high temperature stress usually result in suppressed growth and reduced yield, but rarely cause lethal injury to the plants (McWilliam, 1980). Under non-irrigated field conditions, the effects of high temperature are frequently confounded by the effects of water stress. This makes it difficult to adequately define heat stress in field-grown plants.

2.2.2 Photoperiod

Photoperiod influences the flowering of plants. A short-day plant flowers more rapidly as photoperiod decreases, and a long-day plant flowers more rapidly as photoperiod increases (Major, 1980). A day-neutral crop is not sensitive to day length. Generally, wheat is considered to be a long-day plant (Vince-Prue, 1975).

When wheat is grown within the optimal photoperiod range (15 to 17 h), there is no delaying effect on floral development (Major, 1980). Photoperiod sensitive cultivars respond to an increase in day length by decreasing the time to heading, which in most cases occurs concomitantly with a decrease in the number of main stem leaves and spikelets. Cao and Moss (1989a) observed a direct proportional relationship between photoperiod and leaf emergence rate. In another study, Cao and Moss (1989b) observed a linear positive relationship (R^2=0.93) between phyllochron interval and the combined action of temperature and photoperiod (thermo/photo ratio).

Day length insensitivity may be considered an advantageous trait for spring wheat breeding programs, for the following reasons: 1) day length insensitive genotypes are more broadly adapted world-wide, and could thus be more readily exchanged among breeding programs, 2) the day length insensitive trait could be incorporated into a wide range of spring wheat genotypes, which could result in yields as high as, or higher than, the day length sensitive counterparts, 3) day length insensitivity allows for rapid cycling through winter nurseries and greenhouses (Marshall et al., 1989), and 4) day length insensitivity allows cultivars to develop rapidly in countries where wheat is grown under relatively short day lengths of the winter season (Wall and Cartwright, 1974). The inheritance of photoperiod response in spring wheat is attributed to three major genes (Ppd1, Ppd2, and Ppd3), and several modifier genes with minor effects, (Marshall et al., 1989). A dominant allele at any

locus promotes photoperiod insensitivity.

2.2.3. Vernalization

Vernalization is the acquisition or acceleration, of the ability of a plant to flower due to exposure to a cold treatment (Chouard, 1960), and could occur during seed storage or after planting. Vernalization can occur at temperatures ranging from 0°C to 10°C, with an optimum around 7°C. Vernalization response serves as delineator of wheat into the two major groups, winter and spring. Winter wheat requires a cold treatment in order to respond to the conditions that produce flowering, whereas, spring wheat is relatively unresponsive (Jedel et al., 1986). However, this distinction is not absolute. Five major genes have been identified to control response to vernalization (vrn1, vrn2, vrn3, vrn4, and vrn5) (Law, 1966; Pugsley, 1971; 1972). For a winter habit to be expressed all five genes should be present in the recessive form. The presence of a dominant allele in any one of the five vernalization genes results in the expression of a spring habit. A continuous gradation of intermediate vernalization requirements exists between extreme winter and extreme spring types. According to Griffiths and Lyndon (1985), vrn1 and vrn3 are functionally similar. The vrn1 and vrn3 genes are said to be allelic variations located at similar sites on chromosomes 5A and 5D, respectively. In another study, vrn1 genotypes (vrn1vrn1, and vrn1vrn2) showed a threshold response in which only vernalization periods of about five weeks were sufficient to completely vernalize the

plants (Berry et al., 1980). The workers further observed that in unvernalized plants, the presence of vrn2 (recessive allele) delayed anthesis by 10 days. Thus the vrn2 allele intensified the threshold response, but did not alter the type of response. On the other hand, Vince-Prue (1975) attributed such threshold response characters to vrn3 and/or vrn4.

A cumulative response which is characterized by a quantitative decrease in the length of the vegetative period with increased duration of cold treatment, was found in vrn1 genotypes, vrn1vrn1 and vrn1vrn2. However, a period of vernalization greater than 7 weeks did not significantly decrease days to anthesis (Berry et al., 1980; Jedel et al., 1986). The vrn1 allele has been characterized to control the cumulative response to vernalization treatment, and vrn3 and vrn4 initiate the response to vernalization treatment, whereas vrn2 and vrn5 alleles are characterized as intensifiers of both responses (Berry et al., 1980; Flood and Halloran, 1984). Thus, the genotype of a cultivar is important, since the specific vernalization genes will influence the response characteristics of a cultivar.

Investigations by Griffiths and Lyndon (1985) support the idea that vernalization alters the ability of the shoot apex to respond to subsequent day length, rather than a direct effect on its growth. The vernalized state is communicated autocatalytically through cell divisions, to all meristematic tissues originating at the apex of the embryo. Therefore, communication reaches tillers too, even though they

may be formed after the vernalization treatment (Chouard, 1960). Changes in hormonal communication or the turning on of certain genes have been implied to explain this effect.

2.2.4. Water

Water affects every aspect of wheat growth from seed germination to seed set and final yield. The amount of water needed to optimize crop growth and development is the water needed for transpiration as well as maintenance of green, succulent tissues at a minimum turgor. Cell division and cell expansion are extremely sensitive to water deficit (Hsiao, 1973). Water stress affects certain stages of growth more than others.

Under water stress, Qaurrie and Jones (1977) observed a significant reduction in leaf area, due to reduced cell division, an increase in the size of stomata, and a reduction in the number of spikelets. Other reports indicated that water stress resulted in: 1) a 55% reduction in tiller number (Keim and Kronstad, 1981), 2) a 22 to 77% reduction in above ground biomass (depending upon the magnitude of the stress), and 3) a 66 to 93% reduction in root growth (Blum et al., 1983). If water shortage occurs during tiller initiation, tillers may fail to develop or abort. Water stress could also result in poor pollen viability, and a subsequent reduction in grain set (Saini and Aspinall, 1981). Water stress severely reduces net photosynthesis (Wardlaw, 1971).

2.3. Phytotron experiments

The phytotron can provide a controlled environment for the study of plant growth and development, and the relationships between plants and their environment. The phytotron allows the control of several physical parameters of the environment, including light quality and intensity, day length, air temperature, humidity, plant nutrition, and concentration of gases (Harper and Roberts, 1988).

Controlled environment conditions are artificial and therefore different from natural conditions in the field. For example, in artificially lit chambers, the quantity of light available (500 to 600 μ E m^{-2} s^{-1}) is significantly lower than full sunlight in the field (2,000 μ E m^{-2} s^{-1}). The spectral composition also differs from that of sunlight (Salisbury, 1992; Whisler et al., 1986). Thus, the application of controlled environment results to field situations should be approached with caution (Bickford and Dunn, 1972). It must be recognized, however, that controlled environment facilities can be used to obtain accurate knowledge of plant reactions to specific environmental factors. Such information, is often difficult to obtain in the field where the factors are variable, mostly interrelated, and almost uncontrollable (Harper and Roberts, 1988). Baker (1988) recognized the importance of controlled environment experiments in helping to identify important cultivar by environment crossover interactions. Controlled environment studies have the potential to greatly improve the understanding of cultivar response(s) to specific environment(s). This could lead to

more directed and efficient research on crop adaptation, improvement, and production.

Since it is impossible to separate crop responses to the various environmental factors in the field, field data alone is unsuitable for the development of crop simulation models (Whisler et al., 1986). Therefore, crop modellers use controlled environment facilities to study the effects of individual factors on crop growth, and the pattern of relationship between the levels of those factors. Field data is then used to adjust the parameter values in the equations developed from controlled environment data.

2.4. Crop growth modelling

Soil, climate, and genotype, affect the crop response to irrigation, fertilizer, and other management practices. Determining the appropriate crop management strategies has major economic and environmental implications (Hoogenboom, 1998). Modelling the soil/crop/atmosphere system can make a valuable contribution to a better understanding of the processes that determine crop responses, and the prediction of crop performance in different production areas.

2.4.1. Empirical versus mechanistic models

A crop simulation model may be defined as a quantitative description which consists of mathematical representations of the various physiological processes that

underlie crop growth and development (Hunt and Pararajasingham, 1995). There are two types of crop models: 1) empirical (descriptive or correlative), and 2) mechanistic (explanatory). Generally, empirical models are based on regression analysis, and contain a single function relating crop yield to environmental variables (Fischer, 1984). This limits the use of empirical models to the environment under which they were developed. Mechanistic models, on the other hand, use mathematical functions, some of which may be empirical, to represent the known or presumed mechanisms that relate the variables and explain their observed behaviour. Mechanistic models describe the physiological processes that control crop growth and development (Whisler, et al., 1986). Unlike empirical models, mechanistic models have a broad range of environments in which they may be used.

The fact that mechanistic models are large, complex, and have demanding input data requirements, makes their validation difficult, and also reduces their acceptability to researchers (Fischer, 1984). Researchers are likely to embrace a model that has minimal requirements for input data, which must be reasonably easy to collect or estimate from standard agricultural experimental practices.

2.4.2. History and description of the CERES-Wheat model

In 1983 (to 1993), the United States Agency for International Development (USAID) initiated a project called International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT), which was based at the University of Hawaii

(Thornton, 1994). The mandate of IBSNAT was to develop and improve methods for technology transfer using models of crops and soils, and analysis tools to compare alternative management practices at sites where weather and soil data were available (Jones, 1994). IBSNAT attracted scientists from different parts of the world, including United States of America, Canada, United Kingdom, Netherlands, and Australia. This project produced the Decision Support System for Agrotechnology Transfer (DSSAT) software (version 2.1, 1989, and an improved version 3.0, 1994). After 1993, the networks continued under the auspices of a new consortium involving the former IBSNAT and Dutch modelling groups, the International Consortium for Agricultural Systems Applications (ICASA).

DSSAT v3.0 consists of a set of computer programs which are accessible under a shell designed for entry, storage, and manipulation of weather, soil, and crop data. Thus, using DSSAT crop simulation modelling could be performed, and the outputs analysed (Thornton, 1994). The DSSAT program has ten crop models: maize, wheat, rice, barley, sorghum, millet, soybean, peanut, phaseolus bean, potato and cassava. Taro, sugar cane, and tomato models are yet to be added. All the models share a common input-output format, and are similar in the level of detail required. The models operate on a daily prediction mode, which is based on an understanding of biophysical processes.

2.4.2.1. The CERES-Wheat model

The CERES-Wheat model is written in standard FORTRAN 77, and can be easily compiled to run on almost any computer (Hodges and Ritchie, 1991). The CERES-Wheat model assesses nine growth stages (Table 2.1). Progress through the growth stages is driven by accumulation of daily thermal time (DTT) units. DTT is calculated from air temperature values, and modifications in the DTT calculations are made depending upon the range of minimum and maximum temperatures under

Table 2.1. Growth stages of the CERES-Wheat model (From Hodges and Ritchie, 1991).

Growth stage	Description
1	Emergence to floral initiation.
2	Floral initiation to beginning of ear growth.
3	Beginning of ear growth to anthesis.
4	Anthesis to beginning of grain filling.
5	Grain filling duration.
6	Maturity.
7	End of the last crop to planting.
8	Planting to germination.
9	Germination to emergence.

consideration (Table 2.2). DTT ranges from a maximum of 26 when air temperatures are between 26 to 34°C, to a minimum of 0 when air temperatures are above 60°C or below 0°C. Base temperature (Tbase), indicates the temperature at which no plant growth is assumed.

2.4.2.2. Basic data file requirements

Input parameters required by the CERES-wheat model cover management practices, cultivar differences, soil type(s), and weather information. Management inputs include planting date, plant density, seeding depth, row spacing, initial soil conditions (moisture and fertilizer), and harvesting details. Cultivar input parameters required by the model are: the number of main stem leaves, duration from planting to terminal spikelet initiation, as well as anthesis, and maturity dates. Location-specific input parameters involve the climatic and soil parameters. Climatic data includes solar radiation, daily maximum and minimum air temperatures, and daily precipitation. Soil data inputs include bulk density, percentage of clay, silt and sand, pH, major nutrient content, field capacity, wilting percentage, and moisture content at different soil depths.

2.4.2.3. Genetic coefficients

The CERES-Wheat model recognizes that cultivars may differ in the duration of the different developmental phases, as well as in how they respond to changes in environmental factors. The CERES-Wheat model does this by assigning genotype

Table 2.2.[a] **Equations used in the CERES-Wheat model for thermal time calculations (From Hodges and Ritchie, 1991).**

Air temperature range (°C)	Equation
TEMPCN > Tbase and TEMPCX < 26°C	$DTT = TEMPCR - Tbase$
TEMPCN < Tbase and TEMPCX < 26°C	$DTT = \frac{(TEMPCX - Tbase)}{2} \times \frac{(TEMPCX - Tbase)}{(TEMPCX - TEMPCN)}$
26°C<TEMPCX<34°C	$DTT = 13 \times \left\{1 + \left[\frac{(TEMPCX - 26)}{(TEMPCX - TEMPCN)}\right]\right\} + \frac{TEMPCN}{2} \times \left[\frac{(TEMPCX - 26)}{(TEMPCX - TEMPCN)}\right]$
TEMPCX and TEMPCN >26°C but <34°C	$DTT = 26$
TEMPCX >34°C and TEMPCN >26°C	$DTT = \left\{\frac{(60 - TEMPCX)(TEMPCX - 34)}{(TEMPCX - TEMPCN)}\right\} + 26 \times \left\{\frac{1 - (TEMPCX - 34)}{(TEMPCX - TEMPCN)}\right\}$
TEMPCX >34°C and TEMPCN <26°C	$DTT = \left\{\frac{(60 - TEMPCX)(TEMPCX - 34)}{(TEMPCX - TEMPCN)}\right\} + 26 \times \left\{\frac{1 - (TEMPCX - 34)}{(TEMPCX - TEMPCN)}\right\} \times \left\{\frac{1 - (26 - TEMPCN)}{(TEMPCX - TEMPCN)}\right\} + \left\{\frac{(TEMPCN + 26)}{2}\right\} \times \left\{\frac{(26 - TEMPCN)}{(TEMPCX - TEMPCN)}\right\}$

[a] Definitions for terms in table 2.2 are as follows:

TEMPCX = maximum critical temperature, TEMPCN = minimum critical temperature, TEMPCR = mean critical temperature, and Tbase=base temperature.

Critical temperatures are equal to their corresponding air temperatures (TEMPCX = TEMPMX, TEMPCN = TEMPMN).

However when air temperatures are below freezing, the following equations are used:

TEMPCN = 2. + TEMPMN * [0.4 + 0.0018 * (SNOW - 15) **2], SNOW=Snow cover.

TEMPCX = 2. + TEMPMX * [0.4 + 0.0018 * (SNOW - 15) **2],

$TEMPCR = \frac{(TEMPCN + TEMPCX)}{2}$. Snow cover is limited to a maximum of 15 cm.

specific characteristics called, genetic or cultivar coefficients (Table 2.3). The genetic coefficients are determined by the genetic calculator (Gencalc) in the model, and are then used as new inputs for the final simulation.

2.4.2.4. Simulation output

The simulation output produced by the CERES-Wheat model is detailed and consists of six sections. The output of greatest interest to researchers is the one that compares measured and predicted values of variables of interest (Table 2.4).

2.4.3. Other empirical models

Some examples of empirical models are: the Simple Heat Units (or degree-day system [attributed to Reaumur, (1735) - cited by Shaykewich, (1995)], the Bio-thermal development model (Robertson, 1968), and the Walker model, (Walker 1989). The Simple Heat Units operates on the suggestion made by Reaumur [(1735) - cited by Shaykewich, (1995)] that, the temperature sum was a better estimator of plant phenology than calendar days. A flaw in the Simple Heat Units model is the assumption of a linear relationship between plant development and temperature, with no maximum (Shaykewich, 1995). Robertson's (1968) Bio-thermal development model operates on the premises that the daily rate of development was dependent on nonlinear functions of both temperature and photoperiod. According to Robertson (1968), a plant responds differently to the environment during different developmental periods. Therefore, in the Bio-thermal development model, Robertson used a

Table 2.3. The seven genetic coefficients for the CERES-Wheat model (From Godwin et al., 1994)

Symbol	Description
P1V	Vernalization coefficient; the relative amount that development is slowed for each day of unfulfilled vernalization, assuming that 50 days of vernalization is sufficient for all cultivars.
P1D	Photoperiod coefficient; the relative amount that development is slowed when plants are grown in a photoperiod 1h shorter than the optimum (which is considered to be 20 h).
P5	Relative grain filling duration based on thermal time (degree days above a Tbase=1°C), where each unit increase above zero adds 20 degree days to an initial value of 430 degree days.
G1	Kernel number per unit weight of stem (less leaf blades and sheath) plus spike at anthesis.
G2	Kernel filling rate under optimum conditions.
G3	Non-stressed dry weight of a single stem (excluding the leaf blades and sheaths) and spike when elongation ceases.
PHINT	Phyllochron interval; the thermal time between successive leaf tip appearance.

Table 2.4 Growth and development variables used by the CERES-Wheat model for comparing simulated values with measured values (Adapted from CERES-wheat model output file, Godwin et al., 1994).

1.	Anthesis date (days after planting)
2.	Physiological maturity (days after planting)
3.	Grain yield (kg/ha)
4.	Unit kernel weight (g)
5.	Grain number (grain/m^2)
6.	Grains per spike
7.	Maximum leaf area index (m^2/m^2)
8.	Biomass (kg/ha) at anthesis
9.	Biomass N (kg N/ha) at anthesis
10.	Biomass (kg/ha) at harvest maturity
11.	Stalk (kg/ha) at maturity
12.	Harvest index (kg/kg)
13.	Final leaf number (on main stem)
14.	Grain nitrogen (kg N/ha)
15.	Biomass nitrogen (kg N/ha)
16.	Stalk nitrogen (kg N/ha)
17.	Seed nitrogen (%)

different equation for each of five different phases of development (planting, jointing, emergence, heading, soft dough and ripening).

The Walker model, is used by the Canadian Wheat Board for yield forecasts. The model is based on the assumption that the paramount yield-limiting factor in western Canada is drought. The model calculates a drought index to quantify the severity of drought during the growing season. This index is calculated from historic and current growing season weather data gathered from all weather stations in the wheat-producing areas within a region. The required weather data are: daily maximum and minimum temperatures, and daily precipitation. Drought stress is modelled as a function of the difference between supply and demand of moisture. A weighted mean drought index is then calculated from the individual weather station drought index values, to give a regional mean drought index (equations 1-3) (Walker, 1989). Regional average wheat yields are also determined. The regional average wheat yields are then regressed onto the regional mean drought index to give a predictive equation. The equation is used for yield prediction with the current season drought index (from forecasted or real-time weather data).

Some examples of mechanistic models are: Erosion/Productivity Impact Calculator (EPIC) (Williams et al., 1983), Agricultural and Food Research Council (England) (AFRC) (Weir et al., 1984), AmirSinclair (Amir, and Sinclair, 1991), and Crop Estimation through Resource and Environment Synthesis (CERES)-wheat model

$$\bar{D} = \sum_{i=1}^{m} D_i * W_i \; / \; \sum W_i \qquad (1)$$

$$D = \sum_{j=1}^{n} G_j \qquad (2)$$

and $$G_j = \min (G_{pj}, G_{wj}) \qquad (3)$$

where: $\bar{D}$ = mean weighted drought index for the year, and m is the number of weather stations,

D = drought index over the growing season at each station i, and n is the number of days,

W = weights applied to each station i, according to the intensity of cultivation and proximity of other weather stations; weights range between 1 to 6,

G_j = daily plant growth,

G_w = plant growth variable as a function of the cumulative difference between moisture supply and demand, and

G_p = plant growth phenology factor (range from 0-1).

For stress to be avoided G_w should be greater than G_p.

(Ritchie and Otter, 1985). These models are sophisticated and versatile, and are based on the physiological processes of the crop.

2.4.4. Why the CERES-wheat model?

CERES-wheat is the only model that possesses a descriptor, which allows for the characterization of individual cultivars through the genetic coefficient sub-routine. Thus, in addition to being able to simulate plant growth, development, and grain yield, the CERES-wheat model could be useful in assessments of cultivar adaptability for different locations (Otter and Ritchie, 1984). The Walker model predicts yield, but not crop growth and development (Walker, 1989). Other models such as the AFRC predict phenology but not yield (Weir et al., 1984). The CERES-wheat model was chosen for this work because, it simulates phenology and grain yield, and is able to distinguish among cultivars. The present thermal time units used by the CERES-wheat model to estimate phenological development, is based on Reaumurs', [(1735) - cited by Shaykewich, (1995)] original simple heat units concept. However, the CERES-wheat model uses specific air temperature equations to address the flaw in the simple heat unit concept. If the CERES-wheat model is adapted for western Canada, an important wheat growing region in Canada, it could aid various management decisions, involving the producers, marketing agencies, and plant breeders.

3.0 EFFECTS OF TEMPERATURE, PHOTOPERIOD, AND VERNALIZATION, ON THE GROWTH, DEVELOPMENT AND PERFORMANCE OF SPRING WHEAT CULTIVARS, GROWN UNDER CONTROLLED ENVIRONMENTS.

3.1 Abstract

An understanding of the effects of temperature, photoperiod, and vernalization is essential to the development of breeding strategies for improvement of cultivar adaptation, time to maturity, and yield. It is also important to crop modelling. The objective of this study was to assess the effects of temperature, photoperiod, and vernalization, on the growth, development, and performance of six spring wheat cultivars (AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat). Three levels each of temperature regime, and photoperiod, in all possible combinations, were used to simulate different environmental conditions. Phenological characteristics, and yield components were measured. High temperatures shortened the time to anthesis and maturity, and reduced the number of main stem leaves, tillers, spikelets, kernels per spike, and total grain mass per spike. Phyllochron intervals were higher under warmer environments, which suggests a reduction in thermal-use-efficiency by the plants, and/or a possible existence of a threshold temperature tolerance level beyond which a cultivar does not respond to further temperature increase. Long photoperiod reduced the time to anthesis and maturity. Increases in photoperiod and/or vernalization treatment caused a reduction in the number of spikelets, fertile spikelets,

kernels per spike, and unit kernel mass in AC Taber and Biggar, which require partial vernalization . These results suggest the possibility of using partial vernalization genes to alter the phasic development of spring wheat.

3.2. Introduction

Temperature, photoperiod, and vernalization, are among the factors that may prevent realization of the intrinsic yield potential of spring wheat cultivars. According to Larcher et al. (1973), exposure of wheat plants to high temperatures above 30°C may reduce transpiration, and the rate of photosynthesis, and increase the rate of respiration. High temperatures may lead to inactivation of key enzymes (e.g. sucrose synthase and starch synthase), and accelerate the rate of plant growth and development (Jenner, 1991). Both vernalization requirement, and photoperiod influence the flowering time of wheat plants. Vernalization treatment conditions the plant to respond favourably to photoperiod to initiate flowering (Griffiths and Lyndon, 1985). Generally, wheat is considered to be a quantitative long-day plant (Vince-Prue, 1975), and therefore photoperiod sensitive cultivars flower under long photoperiod.

Wheat growth and development has been well characterized at lower temperatures but not at higher temperatures (Single and Marcellos, 1974; Cao and Moss, 1989b; Duguid, 1990; Addae and Pearson, 1992). Also in the field, high temperatures are often accompanied by drought stress and it is difficult to separate the effect of temperatures from that of drought (Harper and Roberts, 1988). Under controlled environments it is possible to separate the effects of lack of moisture, from the effects of high temperatures (Baker, 1988).

Crop cultivars may differ in the duration of their phasic development, and in their responses to different environmental conditions. Characterization of the specific effects of high temperatures, photoperiod, and vernalization requirement, should be beneficial to the proper understanding of cultivar responses to these environmental factors. It should help to elucidate observations in the field, where the effects of high temperature are usually confounded by the effects of lack of moisture. The understanding of cultivar response(s) to specific environmental factors, could lead to greater precision in breeding programs to alter phasic development in wheat, for cultivar adaptation, improvement, and/or higher yields, as well as modelling of wheat growth and yield. The objective of this study was to determine and characterize the effects of high temperature, photoperiod, and vernalization on growth, phasic development, yield-related components, and yield of wheat.

3.3. Materials and methods

Two sets of experiments were conducted in growth cabinets. In the first set, the effects of high temperatures and photoperiod were studied on five spring wheat cultivars, AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC). The cultivars were selected to represent a range of spring wheat classes, and different characteristics. AC Taber, Biggar, and Oslo belong to the Canada Prairie Red Spring Wheat Class, Katepwa and Roblin are Canada Western Hard Red Spring Wheat genotypes, while Wildcat belongs to the Canada Western Extra Strong Red Spring Wheat Class (formerly Canada Utility Spring Wheat Class). Wildcat is the only cultivar that is not recommended for growth in Manitoba, because of its poor resistance to stem and leaf rust and bunt. AC Taber and Biggar are known to possess partial vernalization requirements (DePauw, personal communication). The effect of vernalization on AC Taber, Biggar (BG), and Katepwa (a standard vernalization non-responsive cultivar) under controlled environment conditions, was investigated in the second experiment.

Seeds were sown directly in 15-cm diameter clay pots filled with 1.37 kg of soil mixture. The potting soil was a 2:1:1 mixture (by volume) of sterilized soil, sand, and peat moss, respectively. Pots were well watered prior to planting. The pots were examined daily and watered whenever the surface soil in the pots (one inch deep) was dry. A recommended rate of 2.5 g/l of water of 20:20:20 fertilizer (nitrogen,

phosphorus, and potassium, respectively) (Peters Fertilizer Products, W.R. Grace & Co., Fogelsville, Pa. 18051) was used once a week for watering the plants. The fertilizer contained the following trace element: 0.05% magnesium, 0.05% iron, 0.0031% manganese, 0.0068% boron, 0.0025% zinc, 0.0036% copper, and 0.0009% molybdenum.

The light irradiance was 500 ±10 μ E m^{-2} s^{-1}, as measured at the soil surface to a height of 1 m from the light panel, with a Li-Cor LI-185B quantum sensor, Li-Cor Inc., Lincoln, NE. Lighting in the growth cabinets was a mixture of Grolux and Cool white tubes in the proportion of 1:3, respectively. All seeds used for the controlled environment studies were obtained from plants grown under field conditions at Arborg, 1993 (provided by Mr. Darin Gibson, Ph.D. Candidate, Dept. of Plant Science, University of Manitoba, Winnipeg, MB, Canada).

3.3.1 Temperature and photoperiod experiments

Three temperature regimes and three photoperiod levels in all possible combinations, were used to simulate different environmental conditions. The temperature regimes were: 22°C/17°C (light/dark temperatures, respectively) [standard growth cabinet temperature regime and photoperiod settings for wheat growth, Dept. of Plant Science, Univ. of Manitoba], 26°C/20°C, and 30°C/23°C. The high end of the temperature regimes, was added to ensure the inclusion of possible natural conditions in the study. The photoperiod levels were 14 h, 16 h, and 18 h. Relative humidity

was not controlled and fluctuated between 50-70%. According to Hoffman (1979), for temperatures between 20°C to 30°C, relative humidity within 60 to 80% is appropriate for optimum plant growth. Five spring wheat cultivars (AC Taber, Katepwa, Oslo, Roblin, and Wildcat) were used for this study. Plants were grown in plant growth cabinets, Enconaire Model GRW-36 (Enconaire, U.S.A.) with Grolux and Cool white tubes in the proportion of 1:3, respectively. A completely randomized design with 18 replicates (pots) for each cultivar, was used for each temperature/photoperiod experiment. Four seeds were planted in each pot. At about the 2-leaf stage, the plants were thinned to one seedling per pot. This prevented overcrowding, ensured uniformity of seedling development, and made phenological data collection easier. The experiments were repeated once. Care was exercised to ensure similar environmental conditions and management practices for the same repeated experiments.

3.3.2 Vernalization experiment

AC Taber, and Biggar which possess partial vernalization requirements (DePauw, personal communication), and Katepwa (a standard vernalization non-responsive cultivar) were exposed to different vernalization treatments. A split plot experimental design with four replications was used, with cultivar as the main plot, and length of vernalization treatment as the subplot. The vernalization treatments were 4°C ± 1°C (Griffiths and Lyndon, 1985) for zero (control), 10, 20, 30, 40, or 50

days. The experiment was repeated once. The type of growth cabinet and management conditions were similar to the temperature/photoperiod experiment. The following procedure was followed:

1) For each cultivar, 50 seeds per vernalization treatment were used.

2) The cold treatments were timed to ensure that all vernalization treatments were completed on the same day. All seedlings and the control seeds were planted on the same day.

3) Seeds for a particular treatment were first surface-sterilized in 0.525% solution of sodium hypochlorite (10 ml of Javex mixed with 90 ml of sterilized distilled water) for 2-3 minutes. After draining the solution, the seeds were rinsed three times with sterilized distilled water.

4) The sterilized seeds for a particular treatment (except the control) were then put on wet filter paper in a petri dish and placed in a dark cold room (Davidson et al., 1985) which was set at 4°C ± 1°C (Griffiths and Lyndon, 1985).

5) Samples were examined weekly to ensure that the filter papers were moist (sterilized distilled water was used), and also to open the lid of the petri dishes to cause brief aeration of the containers (Hillman, 1969).

6) At the end of the synchronized cold treatments, the control seeds (soaked in water for about five minutes), and the seedlings were planted into 15-cm diameter pots filled with 1.37 kg of soil mixture (2:1:1, by volume of sterilized soil, sand, and peat moss,

respectively).

7) Four seedlings or seeds per pot were planted. One plant per pot was kept for phenological data collection, and the remaining seedlings were used for destructive sampling.

8) To prevent devernalization, the seedlings were first grown for a week in a growth cabinet set at 15°C/12°C (Ritchie, 1991), and 16 h photoperiod. After this, the plants were transferred into a growth cabinet (same as previous description) set at 22°C/17°C (day and night temperatures, respectively) and 16 h photoperiod (standard growth cabinet temperature regime and photoperiod settings for wheat growth, Dept. of Plant Science, Univ. of Manitoba).

3.3.3 Measurements

All measurements were made for both the temperature/photoperiod, and vernalization experiments. Leaf development was measured at five-day intervals (or four-day interval at the latter stages of leaf development), using the Haun scale (Haun, 1973). In the Haun scale, leaf stage is measured as the number of fully expanded leaves plus the ratio of the laminar length of the last visible growing leaf, to that of the preceding leaf.

The number of leaves produced by the main stem was recorded. The time to anthesis (from planting date), and maturity, plant height, and the number of spike-bearing tillers per plant, were measured. The following yield-related variables were

measured on the main stem: the spike length, total mass of grains, the total number of kernels, the total number of spikelets, and the number of sterile and fertile spikelets. To determine phyllochron interval [the growing degree-days(GDD) required to produce a leaf] for the different cultivars under varying environmental conditions, the daily growing-degree-days (DGDD) was calculated as:

$$GDD=\sum DGDD, \text{ and}$$

$$DGDD=[(T_{max} + T_{min})/2]-T_{base},$$

where T_{max} and T_{min} are daily maximum and minimum temperatures, respectively, and T_{base} is the minimum temperature at which growth is assumed to cease. T_{base} was assumed to be 0°C (Cao and Moss, 1989c; Baker et al., 1986). The phyllochron interval was determined by graphing the cumulative number of leaves on the main stem (on the y-axis) against the cumulative growing-degree-days (on the x-axis), and then determining the inverse of the slope of the line (Ritchie, 1991).

The time to terminal spikelet initiation (TSI) was determined for the vernalization experiment. From the 3-leaf stage, plants were sampled on alternate days and destructively dissected and observed under a light microscope to determine the onset of TSI, in relation to the leaf stage. These observations for TSI were done on the main stems. The vernalization coefficient (P1V) (as used in the CERES-Wheat model) was determined by the following procedures and equations (Ritchie, 1991):

a) Relative development rate (RDR) was calculated as:

$$RDR = \frac{\text{Days to TSI for 50 vernalization days}}{\text{Days to TSI for } < 50 \text{ vernalization days}} \quad (1)$$

The lower the RDR value, the longer the cultivar takes to reach TSI. Fifty vernalization days are assumed to be sufficient to completely vernalize all cultivars (Ritchie, 1991).

b) Number of vernalization days (V) was then plotted against RDR to determine the value of a constant K from the equation:

$$RDR = 1 - K(50 - V). \quad (2)$$

c) The value of K was used to determine P1V, using the equation:

$$P1V = K*183 - 0.55. \quad (3)$$

3.3.4 Analyses

The temperature/photoperiod experiments were analysed separately from the vernalization experiments. Data were analysed using the analysis of variance (ANOVA) (Appendices 1 & 2) procedure of the Statistical Analyses System (SAS v.6.12) computer programs (SAS, 1989). In cases where there were missing data, the SAS (SAS v. 6.12) general linear model (GLM) procedure was used. Since the maximum number of treatments in an experiment was five (cultivars), mean comparisons were done by using the least significant difference (LSD) test at 5% probability.

3.4 Results and discussion

3.4.1 Number of leaves produced on the main stem

For the temperature/photoperiod experiment, analysis of variance showed differences due to temperature to be significant for the number of leaves produced on the main stem (Table 3.1). Temperature effect produced significant differences among the cultivars for the number of main stem leaves, but changes in photoperiod did not have any significant effect on the number of main stem leaves produced by the cultivars (Table 3.1). AC Taber and Biggar produced the highest number of leaves (9 to 11 leaves), while the remaining cultivars produced 7 to 9 leaves (Fig 3.1 a). Temperature by photoperiod by cultivar interactions had minor effect on the number of leaves produced on the main stem. These results indicate that the production of leaves on the main stem of spring wheat is temperature dependent, and that different cultivars respond to temperature differently.

Vernalization treatment had a significant effect on the number of main stem leaves produced by the cultivars (Table 3.2). For example, 10 days and 40 days vernalization treatments produced 8-9 leaves and 7 leaves, respectively (Fig 3.1 b). Vernalization treatment by cultivar interaction was significant for PHINT, indicating that, the cultivars responded differently to vernalization treatments (Table 3.2). Generally, as the vernalization treatment duration increased, there was significant reduction in the number of main stem leaves produced by all

Table 3.1. Analyses of variance of number of leaves on the main stem, phyllochron interval (PHINT), number of tillers per plant, and plant height of spring wheat cultivars, grown under controlled temperatures (22°C/17°C, 26°C/20°C, and 30°C/23°C) and photoperiods (14 h, 16 h, and 18 h).

Source of		Mean Squares			
variation	df	Leaves	PHINT	Tillers	Plant height
Temperature(T)	2	106.9*	77801.2*	1242.6*	32832.6*
Photoperiod (P)	2	15.4	47492.4*	381.2*	15756.2*
T * P	4	40.4	1640.3*	334.4*	3160.8*
Expt (T*P)	9	19.4*	188.4*	20.9*	131.3*
Cultivar (C)	4	453.0*	62757.2*	549.9*	7263.1*
T*C	8	9.9*	2589.1*	17.6*	471.4*
P*C	8	10.1*	3188.5*	21.6*	379.6*
T*P*C	16	7.7*	1547.6*	12.4*	250.0*
Error	1566	0.5	46.3	1.9	20.3

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 1.

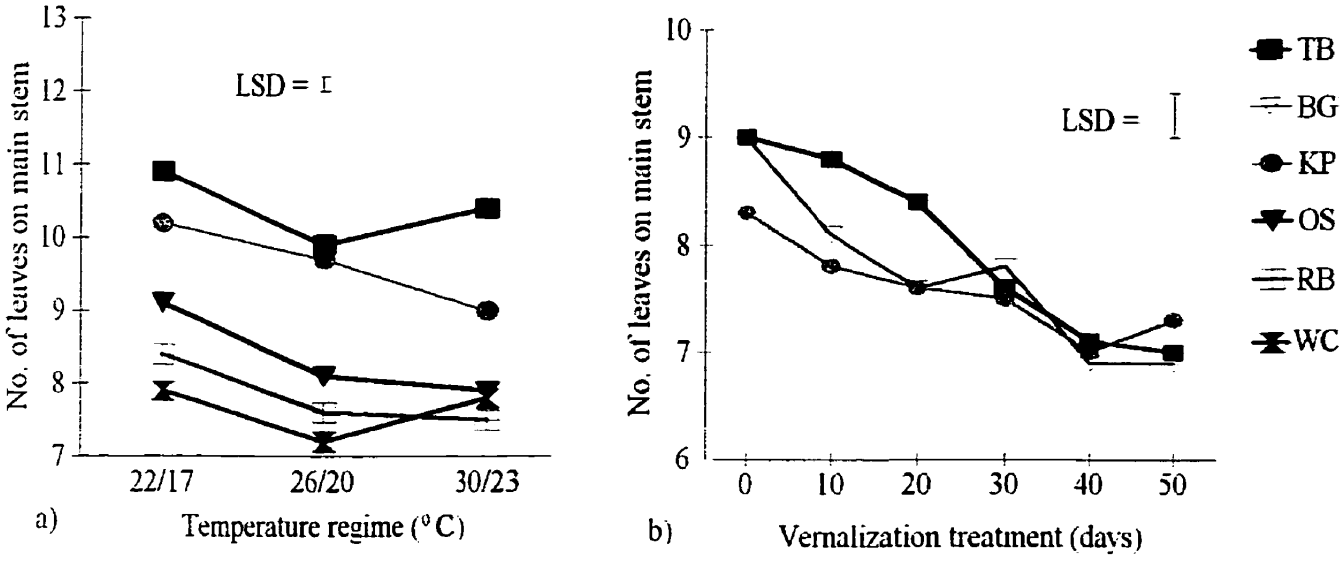


Fig. 3.1. a) Number of main stem leaves produced by AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), and b) number of main stem leaves produced by AC Taber, Biggar, and Katepwa for different vernalization treatments. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

cultivars (Fig. 3.1b). According to Wall and Cartwright (1974), this may be attributed to a reduction in the number of nodes on the main stem, and a subsequent reduction of the number of main stem leaves. Cutforth et al. (1992) observed similar findings. The number of main stem leaves produced by AC Taber was significantly different from that produced by Biggar, and Katepwa, for 10 and 20-day vernalization treatments (Fig. 3.1b). Vernalization treatment above 30 days however, eliminated cultivar differences for main stem leaf number.

Table 3.2. Analyses of variance of number of leaves on the main stem, phyllochron interval (PHINT), number of tillers per plant, plant height, time to anthesis, and time to maturity of spring wheat cultivars, given different vernalization treatments (vntrt), and grown under controlled environment of 22°C/17°C (day and night temperature, respectively) and 16 h photoperiod.

Source of		Mean squares			
variation	df	Leaves	PHINT	Tillers	Height
Experiment(E)	1	0.69*	702.3*	90.3*	1002.8*
Block (E)	6	0.09	989.9*	1.6	49.6
Cultivar (C)	2	2.15	6376.8*	127.7	1004.8
Vntrt (V)	5	11.07*	680.6	7.8*	310.7*
E*C	2	0.26	67.0	8.6*	82.2*
E*V	5	0.39	738.8	0.3	25.1
C*V	10	0.69	2279.4*	1.6	14.1
E*C*V	10	0.23	684.7	1.7	39.8
Error	102	0.18	6721.0	1.2	22.2

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 2.

3.4.2 Phyllochron interval

Based on analysis of variance, differences due to temperature, photoperiod, cultivar, and their interactions were all significant for phyllochron interval (Table 3.1). Under higher temperature regimes, the phyllochron interval for all cultivars was higher than for lower temperature regimes (Fig. 3.2a), and differences among cultivars were

significant. This indicates that, for a particular cultivar, the phyllochron interval is not constant but dependent on the temperature range under which it is grown. This may explain why the phyllochron interval for a cultivar varies with planting dates under field conditions (chapter 4). These results suggest that: 1) as temperature increased, more thermal energy was needed to produce a leaf, 2) thermal-energy-use efficiency is inversely proportional to temperature, and/or 3) there is/are threshold temperature tolerance level(s) (which may be cultivar specific) beyond which an overestimation of phyllochron interval occurs. These results are in agreement with findings made by Cao and Moss (1989c), and Duguid (1990).

As photoperiod increased, however, the phyllochron intervals of cultivars decreased. In other words, the thermal-use-efficiency increased (especially for AC Taber and Katepwa) (Fig. 3.2b). This further supports the idea that the phyllochron interval is not fixed, but varies (non-linearly) with changes in temperature and/or photoperiod. The length of light exposure (photoperiod) was considered in calculating the total photo thermal units, but did not change the conclusions above, since the daily accumulated heat units and the daily photo-thermal heat units values were close (Appendix 3). According to Rawson (1986), increases in temperature trigger acceleration of organ production without any increase in net photosynthesis. It should be noted that under field conditions where temperature and photoperiod do change during the growing season, the effects of temperature and photoperiod are likely to be

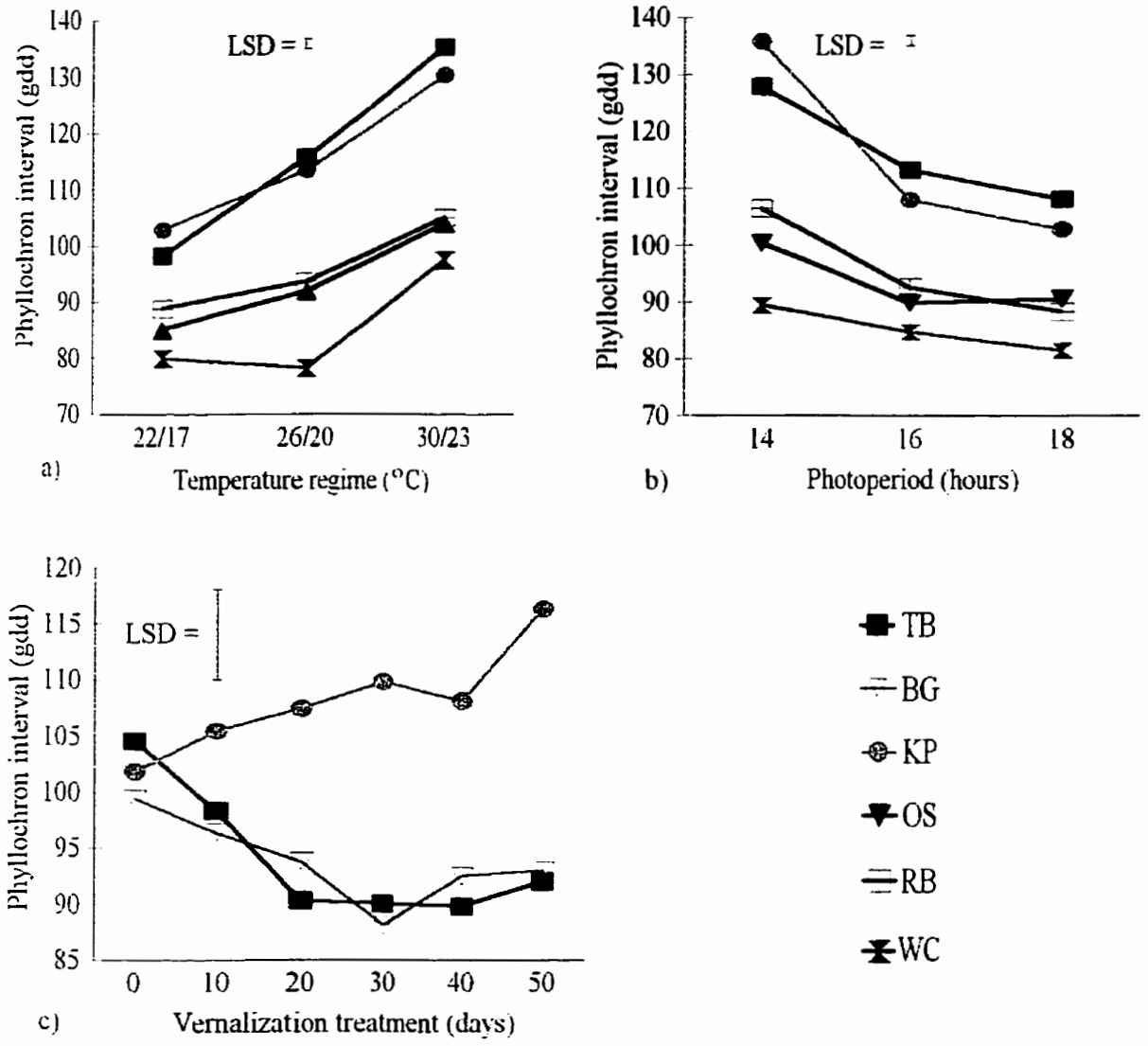


Fig. 3.2. Phyllochron interval of a) AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), b) AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat, grown at different photoperiods (14, 16, 18h) (averaged over all temperature regimes), and c) AC Taber, Biggar, and Katepwa, for different vernalization treatments. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

different at different phases of wheat growth and development, as implied by Shaykewich (1995).

The differential cultivar phyllochron interval responses to temperature increases (Fig. 3.2a), suggests the need to develop cultivar temperature sensitivity equations. Such a temperature coefficient should improve the phenological predictions of wheat crop growth models, such as the CERES-Wheat model, which use phyllochron intervals to calculate the onset of wheat phenological stages.

Based on the analysis of variance, the effect of vernalization on phyllochron interval was not significant (Table 3.2). However, differences due to cultivar, and cultivar by vernalization interaction, were significant. This indicates that phyllochron interval is not affected by vernalization treatment per se, but by intrinsic cultivar characteristics and their interaction with vernalization. Vernalized AC Taber and Biggar had phyllochron intervals between 90-98 (GDD), while Katepwa had 105-115 (GDD) (Fig. 3.2c). This observation suggests that, Katepwa, unlike AC Taber and Biggar, does not possess any partial vernalization requirement (DePauw, personal communication). It appears that the rate of leaf development and growth are increased for AC Taber and Biggar, whereas that of Katepwa is slowed down to some extent. The vernalization coefficient (P1V) values support this reasoning (Table 3.3); the responses of AC Taber and Biggar to vernalization were similar, and different from Katepwa.

3.4.3 Number of seed-bearing tillers per plant

Temperature, photoperiod, and cultivar main effects were all significant for the number of tillers per plant (Table 3.1). Although all interactions were significant for the number of tillers, only temperature by photoperiod interaction was of practical significance. These results indicate that the number of seed-bearing tillers produced by a cultivar is dependent on both temperature and photoperiod. The highest number of tillers was produced under the 22°C/17°C temperature regime. Under warmer environments, all cultivars produced fewer tillers (Fig. 3.3a). For example, Katepwa, the highest tillering cultivar, produced an average of 9, 7, and 5 tillers under 22°C/17°C, 26°C/20°C, and 30°C/23°C temperature regimes, respectively. Thus, the high temperature environment caused a reduction in both the number of tillers per plant (Fig. 3.3a) and the number of leaves produced on the main stem (Fig. 3.1 a). Tiller initiation and tiller abortion are critical pre-anthesis developmental processes for the establishment of adequate sink capacity for grain filling period (Shanahan et al., 1984; Warrington et al., 1977). This may partly explain why yield reductions occur under warm/hot environments, and/or late seeding conditions. Maas et al. (1994) obtained similar results under a salinity stress condition. The genotypic differences and significant environmental effects on tillering, observed in this study, agree with observations made by Hucl and Baker (1989), and Shanahan et al. (1985).

Table 3.3. **Vernalization coefficient (P1V) of spring wheat cultivars, determined under controlled environment conditions (22°C/17°C, light/dark temperature, respectively, and 16 h photoperiod).**

Cultivar	P1V *
AC Taber	1.53
Biggar	1.52
Katepwa	0.65

* P1V was determined from the following equations (Ritchie, 1991):

$$P1V = K \times 183 - 0.55,$$

$$RDR = \frac{\text{Days to TSI for 50 vernalization days}}{\text{Days to TSI for } < 50 \text{ vernalization days}} = 1 - K(50 - V),$$

where K = constant,
V = vernalization days,
RDR = relative development rate, and
TSI = terminal spikelet initiation.

The effect of photoperiod on tiller production was opposite to the effect of temperature. With the exception of AC Taber, all the cultivars produced significantly more seed-bearing tillers under a photoperiod greater than 14 h (Fig.3.3b). Katepwa was the highest tillering cultivar (produced 6-8 tillers), whereas AC Taber produced the least number of tillers (4 tillers).

Vernalization effect was significant for the number of tillers produced by a cultivar (Table 3.2). Katepwa, a relatively high tiller producing cultivar was affected by the vernalization treatment, whereas the effect on the tillering ability of AC Taber and Biggar was negligible (Fig. 3.3c). Katepwa produced 5-8 tillers, as opposed to 3-4.5 tillers produced by AC Taber and Biggar. Griffiths and Lyndon (1985) reported similar effects of vernalization on the growth of wheat; the growth of the non vernalization-responsive cultivar was decreased to a greater extent than the vernalization-responsive cultivars.

3.4.4. Plant height

Temperature, photoperiod, and cultivar main effects, as well as temperature by photoperiod interaction were all significant (Table 3.1) for plant height. The other interaction had minor significant effects on plant height. These results show that plant height is influenced by both temperature and photoperiod and that the cultivars exhibit differential responses to these environmental factors. Wildcat produced the tallest plants under all environments (Fig. 3.4a & b), whereas Katepwa produced short

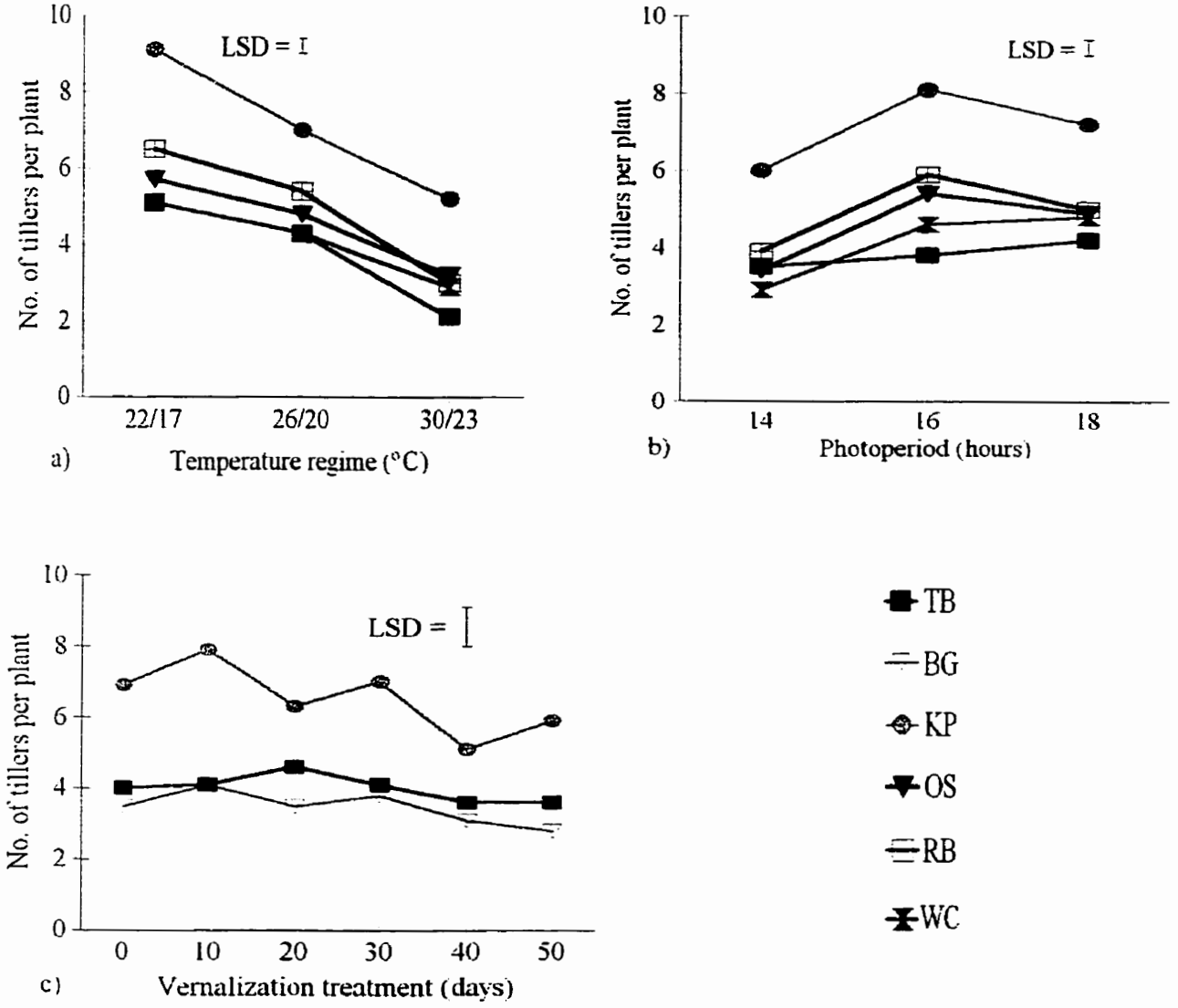


Fig. 3.3. Number of tillers per plant of a) AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), b) AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat, grown at different photoperiods (14, 16, 18h) (averaged over all temperature regimes), and c) AC Taber, Biggar, and Katepwa, for different vernalization treatments. Vertical bars represent LSD at 0.05 level of probability.

plants. In general, higher temperatures, and long photoperiods (18 h), led to the production of shorter plants (Fig. 3.4a & b). It appears that under relatively warmer environments, stem elongation is negatively affected, probably due to the acceleration of plant growth and development, and the reduction of the number of main stem nodes (Wall and Cartwright, 1974). These observations, however, are opposite to plant height results obtained from field studies (chapter 4). Under natural conditions in the field, plant height increased with delays in seeding date (which corresponds to warmer conditions), and Katepwa produced the tallest plants under all field environments. This discrepancy may be partly attributed to the differences in spectral composition between controlled environment (indoors) and natural conditions in the field. Sunlight is richer in blue and green wavelengths than is light from flourescent tubes (Salisbury and Ross, 1992). Plant spacing in the field is closer than in controlled environment experiments, and therefore plants in the field may grow taller due to greater competition among plants, than occurs under controlled environment.

Analysis of variance showed a signifanct vernalization effect on plant height (Table 3.2). Increases in vernalization treatment resulted in significant reductions in plant height (Fig. 3.4c). Katepwa was the tallest among the three cultivars. AC Taber and Biggar were similar in height. AC Taber and Biggar are known semi-dwarf cultivars (DePauw, personal communication). The vernalization treatment resulted in a reduction of the number of nodes on the main stems, which consequently reduced

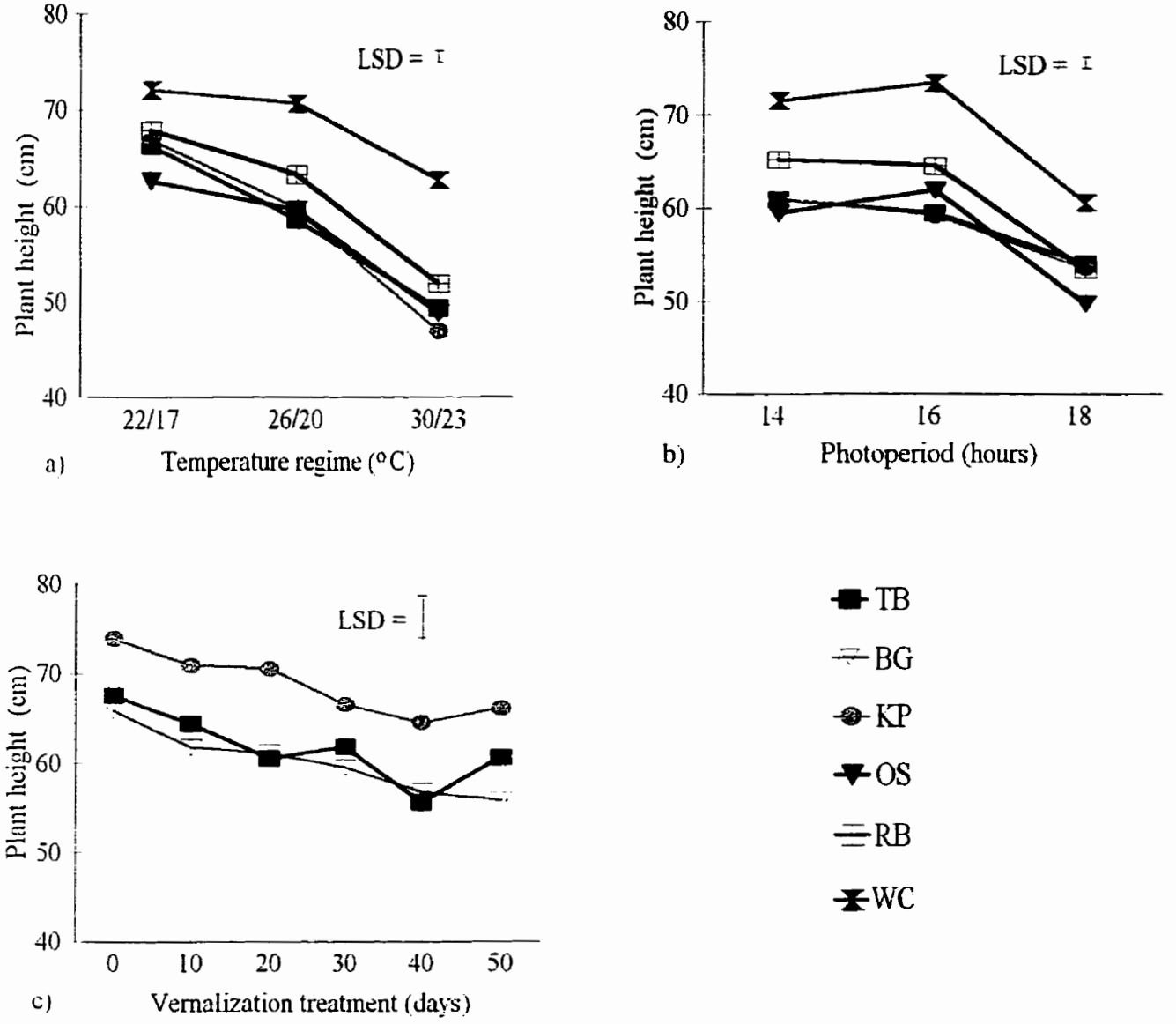


Fig. 3.4. Plant height of a) AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), b) AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat, grown at different photoperiods (14, 16, 18h) (averaged over all temperature regimes), and c) AC Taber, Biggar, and Katepwa, for different vernalization treatments. Vertical bars represent LSD at 0.05 level of probability.

the plant height.

3.4.5. Time to reach anthesis and maturity (from planting date)

Time to reach anthesis and maturity were measured in both days and GDD. Based on analysis of variance, differences due to temperature, photoperiod, cultivar, and their interactions were all significant for both anthesis and maturity, irrespective of the units of expression (days versus GDD) (Table 3.4). However, the effects due to the interactions were relatively small. This indicates that, temperature and photoperiod influence time to anthesis and maturity. Cultivars showed significant differences in the time (days) taken to reach both anthesis and maturity. AC Taber took the longest time to reach anthesis under all temperature regimes, and photoperiods (Fig. 3.5 a & b, respectively). Higher temperatures and longer photoperiod reduced the time (days) to reach anthesis for most cultivars, but increased the GDD to anthesis (Fig. 3.5a, b & Fig. 3.6a, b, respectively). Wildcat, Roblin, and Oslo which produced $\approx$ 2 fewer leaves on the main stem (Fig. 3.1a), than AC Taber and Katepwa, reached anthesis 10 - 15 days earlier. Cultivars with relatively shorter vegetative growth phases, reached anthesis earlier. Longer photoperiods also reduced the time (days) taken for cultivars to reach anthesis (Fig. 3.5b), but the impact was more pronounced on AC Taber and Katepwa than on the other cultivars. These results agree with observations made by Pirasteh and Welsh (1980), and support the concept that different cultivars possess unique controls and requirements in phenological development.

Table 3.4 Analyses of variance of time to anthesis (days), anthesis measured in growing degree days (AGDD), time to maturity (days), and maturity measured in growing degree days (MGDD) of spring wheat cultivars, grown under controlled temperatures (22°C/17°C, 26°C/20°C, and 30°C/23°C) and photoperiods (14 h, 16 h, and 18 h).

Source of		Mean squares			
variation	df	Anthesis	AGDD	Maturity	MGDD
Temperature (T)	2	10104.0*	2681653.9*	36155.1*	2858862.7*
Photoperiod (P)	2	13943.3*	7374119.4*	30034.3*	15539500.0*
T * P	4	902.0*	517951.0*	887.7*	452603.8*
Expt (T*P)	9	401.9*	185746.4*	1856.5*	904506.1*
Cultivar (C)	4	27822.1*	15049073.8*	19663.7*	10571395.6*
T*C	8	267.8*	388061.9*	171.4*	234529.6*
P*C	8	1433.0*	777533.0*	1242.2*	645689.7*
T*P*C	16	52.8*	38722.2*	173.9*	96609.5*
Error	1548	4.9	2590.4	7.3	3835.5

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 1.

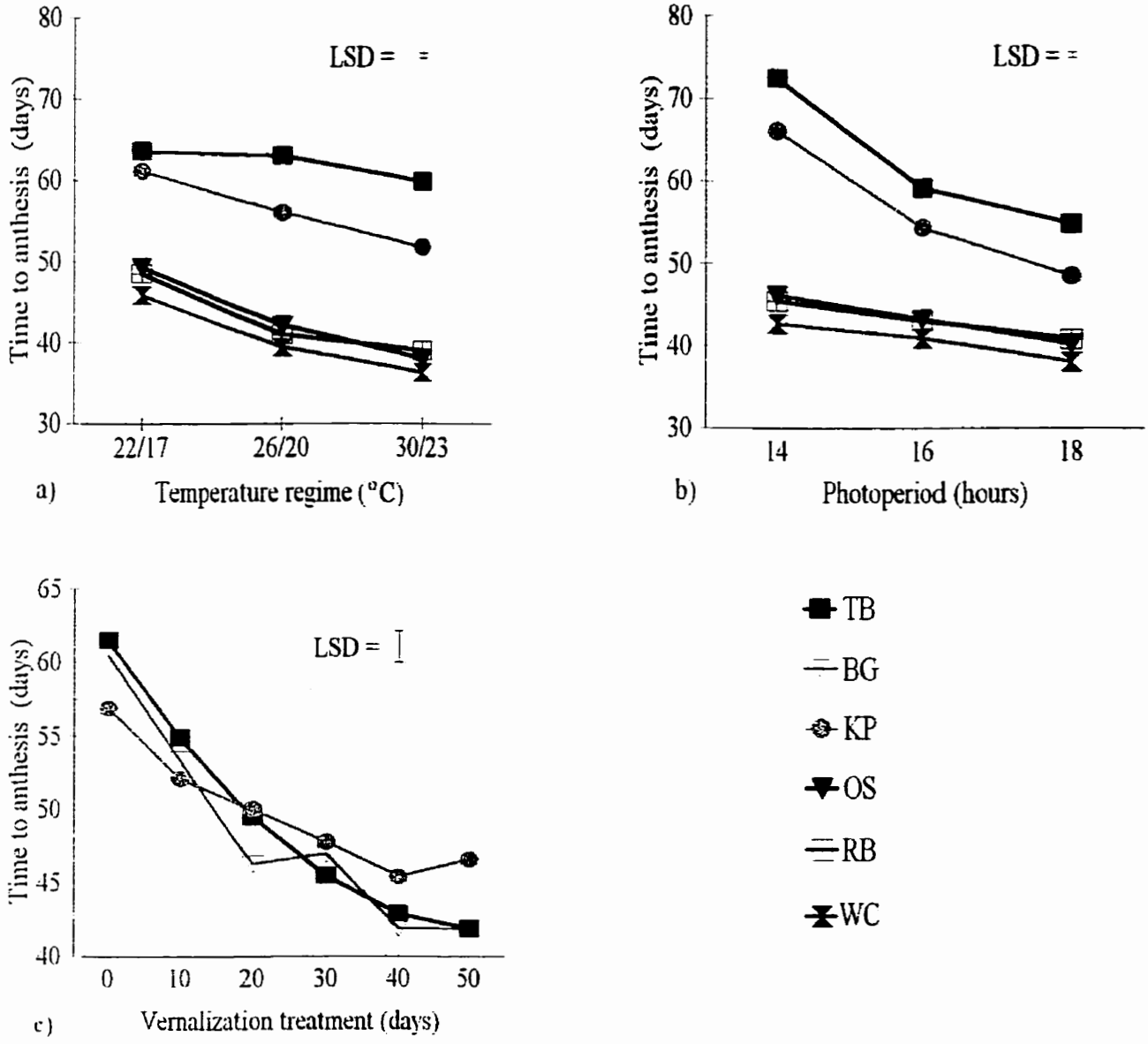


Fig. 3.5. Time to anthesis (days) of a) AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), b) AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat, grown at different photoperiods (14, 16, 18h) (averaged over all temperature regimes), and c) AC Taber, Biggar, and Katepwa, for different vernalization treatments. Vertical bars represent LSD at 0.05 level of probability.

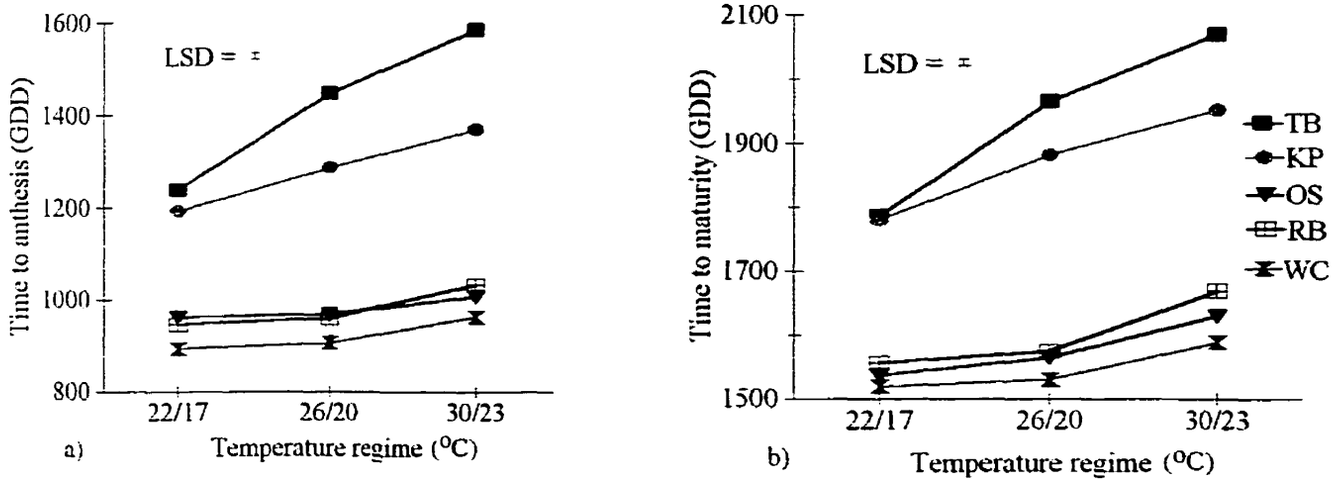


Fig. 3.6. Time (GDD) to a) anthesis and b) maturity, of AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods).

The reduction in efficiency of heat units usage for plant development (section 3.4.2) was reflected for anthesis and maturity periods, only when time was expressed in growing- degree-days. Under lower photoperiod conditions (14 hr), more heat units were required by all cultivars to reach both anthesis and maturity (Fig. 3.7 a & b).

Vernalization treatment, and cultivar by vernalization interaction were significant for both anthesis and maturity, irrespective of how they were expressed (days versus GDD) (Table 3.5). Therefore, the vernalization treatment affected the time to reach anthesis and maturity.

Table 3.5. Analyses of variance of time to anthesis (days), anthesis measured in growing degree days (AGDD), time to maturity (days), and maturity measured in growing degree days (MGDD) of spring wheat cultivars, given different vernalization treatments (vntrt), and grown under controlled environment of 22°C/17°C (day and night temperature, respectively) and 16 h photoperiod.

Source of		Mean squares			
variation	df	Anthesis	AGDD	Maturity	MGDD
Experiment(E)	1	191.4*	72900.0*	1601.7*	611393.7*
Block (E)	6	28.5*	10848.1*	16.2*	6182.0*
Cultivar (C)	2	21.4	8137.4	158.5	60383.7
Vntrt (V)	5	960.5*	365434.8*	770.4*	293368.2*
E*C	2	2.4	909.4	56.8*	21718.9*
E*V	5	13.8*	5302.9*	12.8*	4872.4*
C*V	10	34.2*	13035.3*	52.2*	19922.1*
E*C*V	10	2.1	790.3	6.5	2478.4
Error	102	4.5	1711.6	4.8	1817.7

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 2.

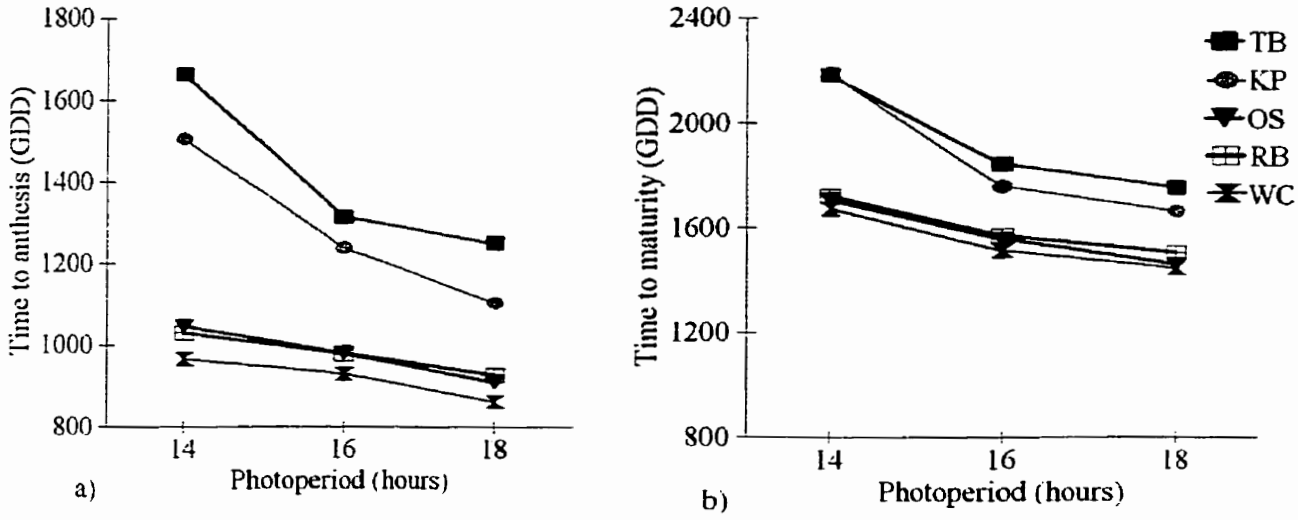


Fig. 3.7. Time (GDD) to a) anthesis and b) maturity, of AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different photoperiods (14 , 16 & 18 h), (averaged over all temperature regimes).

The time to reach anthesis for all cultivars was reduced as vernalization treatment was increased (Fig. 3.5c). The rates of plant development for the late maturing cultivars (AC Taber and Biggar) were accelerated to such a degree that at the 20-day vernalization treatment (or longer), AC Taber and Biggar reached anthesis at either approximately the same time as, or earlier than Katepwa. There were no significant differences between responses at 40-day and 50-day vernalization treatments.

The relative trends observed for time (days) to reach maturity among the cultivars in the temperature/photoperiod experiment (Fig. 3.8a & b) were similar to that of anthesis (Fig. 3.5a &b). AC Taber and Katepwa which took the longest times to reach anthesis, also took the longest times to reach maturity. Increases in temperature or photoperiod had similar effects; both were inversely related to the time (days) taken by the cultivars to reach maturity. For the vernalization experiment, the trend for the time to maturity was also similar to that of anthesis (Fig. 3.5c & Fig. 3.8c). This suggests that the vernalization treatment mostly affected the vegetative growth phase, and that any differences in time to maturity may be attributed to the differences in time to anthesis (Wong and Baker, 1986). Comparison of anthesis, grain filling (maturity minus anthesis), and maturity periods (GDD) revealed that all the cultivars had similar grain filling duration (500-520 GDD) (Fig. 3.9). This may imply that the genes controlling the length of grain filling in these cultivars may be conserved. This observation further suggests that for AC Taber and Biggar, the partial vernalization requirement genes appear to play little or no role in post-anthesis development. These results agree with observations made by Wong and Baker (1986). Similar trends in time to anthesis and time to maturity suggests that maturity differences among cultivars may be attributed to differences in the duration of the vegetative growth phase period (Wong and Baker, 1986).

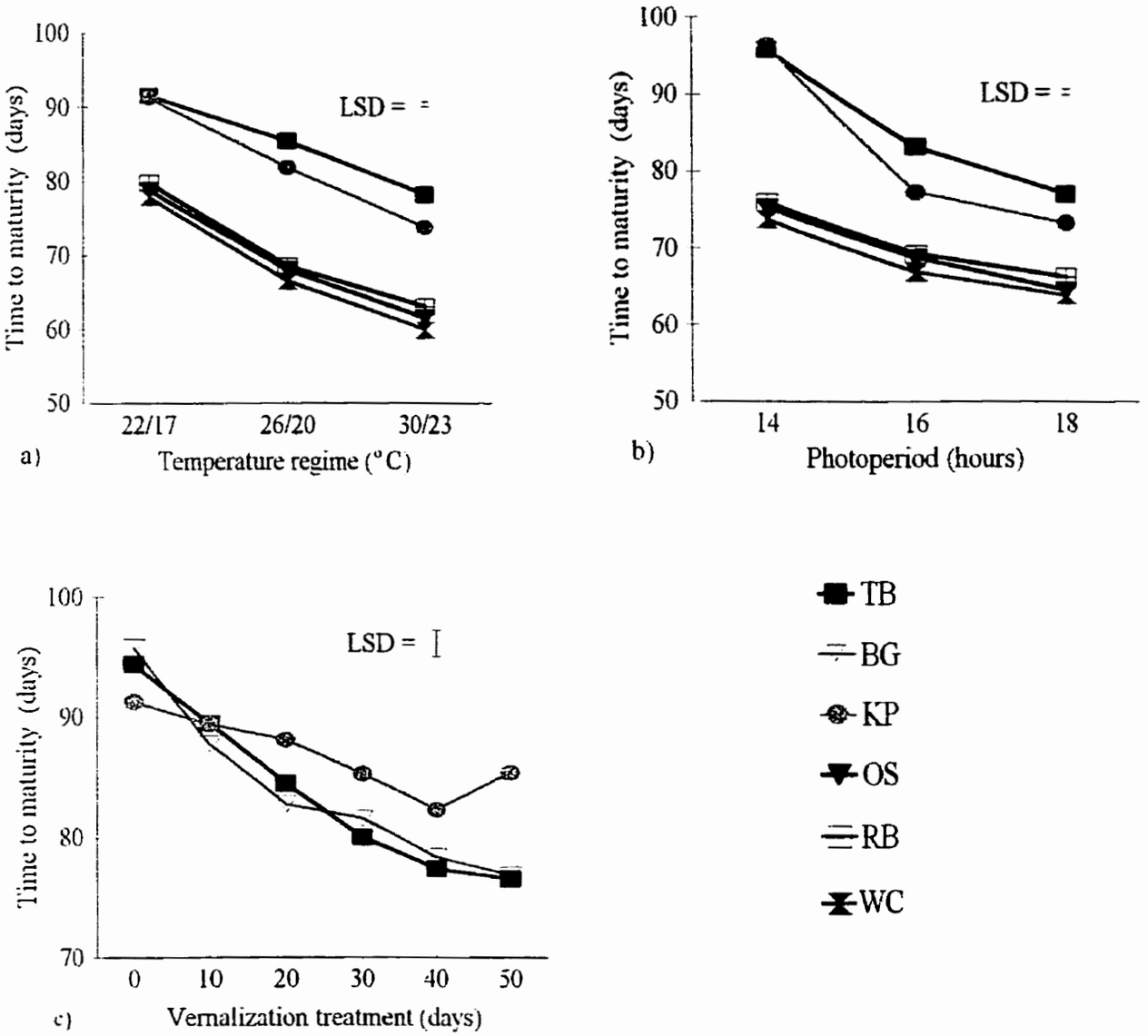


Fig. 3.8. Time to maturity (days) of a) AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), b) AC Taber, Biggar, Katepwa, Oslo, Roblin, and Wildcat, grown at different photoperiods (14, 16, 18h) (averaged over all temperature regimes), and c) AC Taber, Biggar, and Katepwa, for different vernalization treatments. Vertical bars represent LSD at 0.05 level of probability.

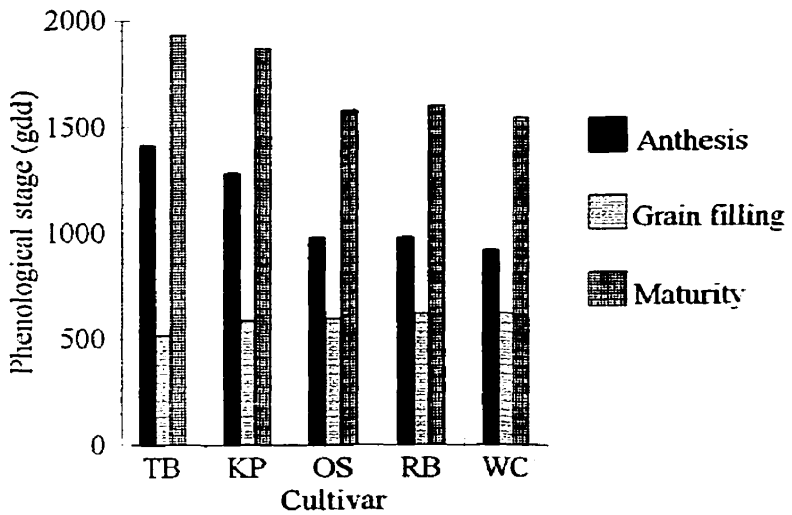


Fig. 3.9 Anthesis, grain filling, and maturity period of AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC) (averaged over all temperature regimes and photoperiods), showing similarity of grain filling duration among cultivars.

3.4.6 Main stem spike length and number of spikelets

Temperature, photoperiod and cultivar main effects influenced the spike length, number of spikelets, and the number of fertile spikelets (Table 3.6). All interaction effects except temperature by photoperiod, have minor effects. Katepwa and Roblin produced the shortest main stem spikes and were not significantly different from each other (Fig. 3.10a) . The spike length of AC Taber and Wildcat were not significantly

Table 3.6 Analyses of variance of main stem spike length (SPKL), number of spikelets on the main stem (SPKTS), and fertile spikelets on the main stem (FERTSPT) of spring wheat cultivars, grown under controlled temperatures (22°C/17°C, 26°C/20°C, and 30°C/23°C) and photoperiods (14 h, 16 h, and 18 h).

Source of		Mean	squares	
variation	df	SPKL	SPKTS	FERTSPT
Temperature (T)	2	112.8*	1980.8*	3350.4*
Photoperiod (P)	2	453.3*	40.0*	116.1*
T * P	4	354.2*	33.2*	100.9*
Expt (T*P)	9	8.2*	34.3*	27.2*
Cultivar (C)	4	192.7*	907.2*	309.4*
T*C	8	7.6*	43.6*	56.2*
P*C	8	12.9*	33.7*	98.6*
T*P*C	16	6.9*	5.0*	44.1*
Error	1566	0.4	2.0	3.7

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 1.

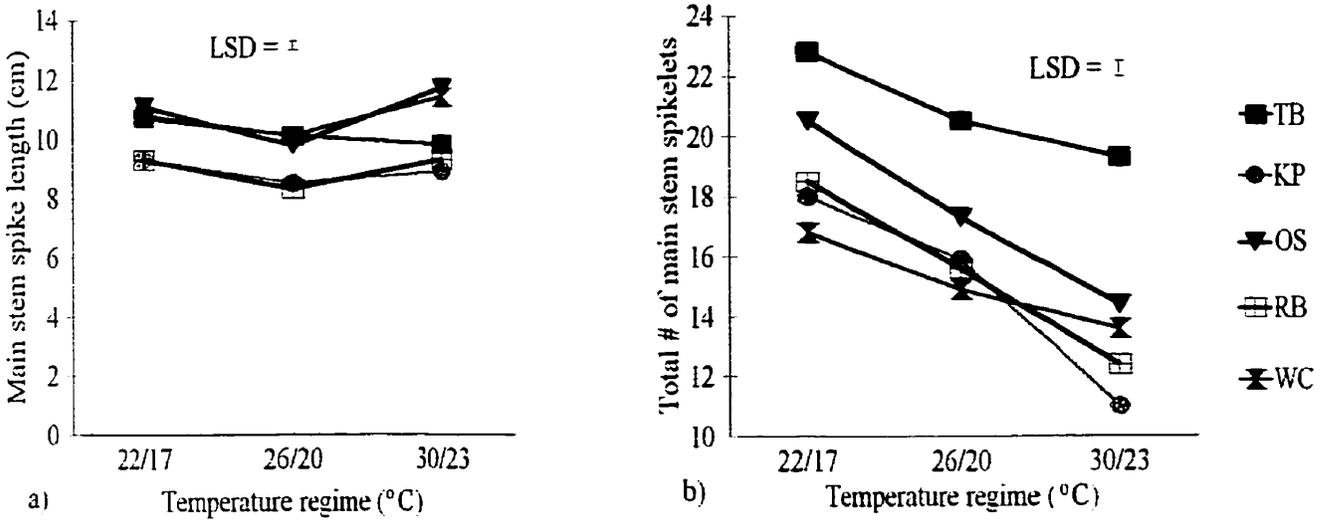


Fig. 3.10. a) Spike length (cm), and b) number of spikelets on the main stem of spring wheat cultivars [AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], grown at different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

different from each other, except under 30°C/23°C temperature regime. Any increase in spike length however, did not prove to be biologically important, since it did not translate into increases in the total number of spikelets on the main stem spike of Oslo and Wildcat (Fig. 3.10b). For all cultivars, the number of spikelets, a yield potential index, declined as temperature increased. AC Taber produced the highest number of

main stem spikelets under all environments. The decrease in the number of main stem spikelets with increases in temperature, agrees with observations made by several workers (Warrington et al., 1977; Campbell and Davidson, 1979; Ford et al., 1981; and Shpiler and Blum, 1986). The decrease in the number of main stem spikelets with increases in temperature may be a result of the acceleration of the vegetative growth phase, which corresponds with the general reduction of number of main stem leaves (section 3.4.3, Fig. 3.1a) (Bagga and Rawson, 1977). These results, however, contradict observations by Halse and Weir (1970) who reported a lack of high temperature effect on the number of spikelets per spike. This discrepancy may be explained by the different ranges of temperature regimes used. The highest temperature regime used by Halse and Weir (1970) was 18/13°C (light/dark temperatures, respectively), as opposed to 30/23°C in the present study. Also, this may explain why certain differences in cultivar response were observed under the high temperature regime in this study.

Increases in photoperiod did not have any significant effect on the spike length of AC Taber, but for the other cultivars the longest spikes were produced at (16 h) (Fig. 3.11). These results support suggestions made by Rawson (1971) that, further increases in spikelet number per spike should be possible through the manipulation of genes that control responses to photoperiod and vernalization within the plant.

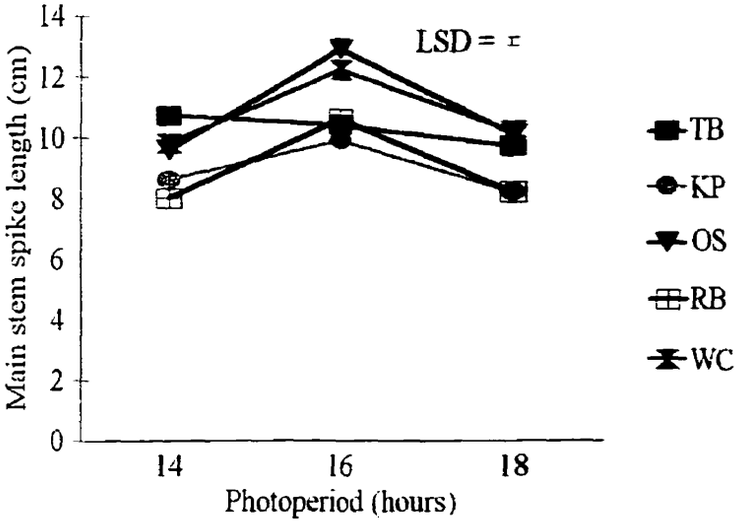


Fig. 3.11. Spike length (cm) on the main stem of spring wheat cultivars [AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], grown under different photoperiods (averaged over all temperature regime (22°C/17°C, 26°C/20°C, 30°C/23°C). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

Temperature, photoperiod, and cultivar effects, and their interactions significantly affected the number of main stem fertile spikelets (Table 3.6). Temperature and photoperiod effects were important in determining the number of seed-producing spikelets, and were cultivar dependent. Under warmer environments, the number of spikelets that produced at least one seed, declined (Fig. 3.12a). This observation was

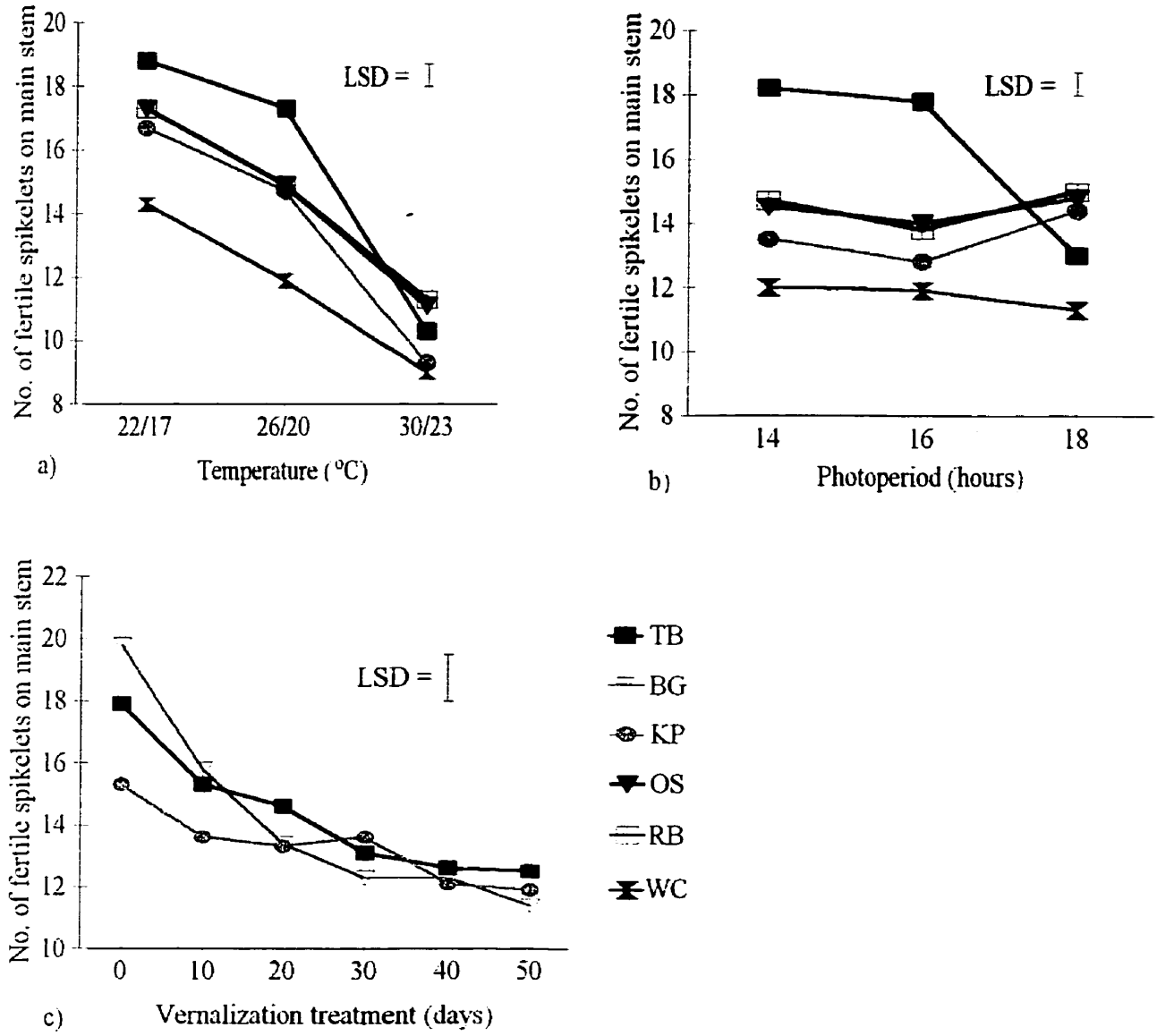


Fig. 3.12. Fertile spikelets on the main stem of spring wheat cultivars [AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], grown at: a) different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), b) different photoperiods (14, 16, 18h) (averaged over all temperature regimes), and c) for different vernalization treatments. Vertical bars represent LSD at 0.05 level of probability.

true for all cultivars, but under the warmest environment (30°C/23°C), the reduction was greatest for AC Taber, and Katepwa. Amores-Vergara and Cartwright (1984) also observed a reduction of spikelet number, and spikelet survival, under high temperature conditions. Frank et al. (1987) established that the temperature from the 6^{th} - 8^{th} day prior to terminal spikelet initiation is crucial for determining the number of spikelets per spike. Similarly, Russell and Stuber (1985) observed that the period of tassel initiation (in maize) is very sensitive to temperature. Similar results have been reported for spring wheat grown under water stress conditions (Frank et al., 1987), salt stress conditions (Grieve et al., 1993), and vernalization treatment (Wall and Cartwright, 1974). Generally, these stress factors decreased the duration of the vegetative/reproductive phase of development, reduced the number of leaves produced by the main stem, and the number of spikelets.

Lengthening the photoperiod duration, however, significantly affected only AC Taber (vernalization-responsive cultivar) which produced 18 fertile spikelets under 22°C/17°C and 26°C/20°C, and 13 fertile spikelets under 30°C/23°C (Fig. 3.12b). Oosterhuis and Cartwright (1983), also observed reduced numbers of fertile spikelets with increases in photoperiod. Expressing the number of fertile spikelets as a percentage of the total number of spikelets on the main stem supported the above conclusions. The percentage of fertile spikelets was greatly reduced by both high temperature, and long photoperiod (Fig. 3.13a & b). These results may partially explain why reduced wheat

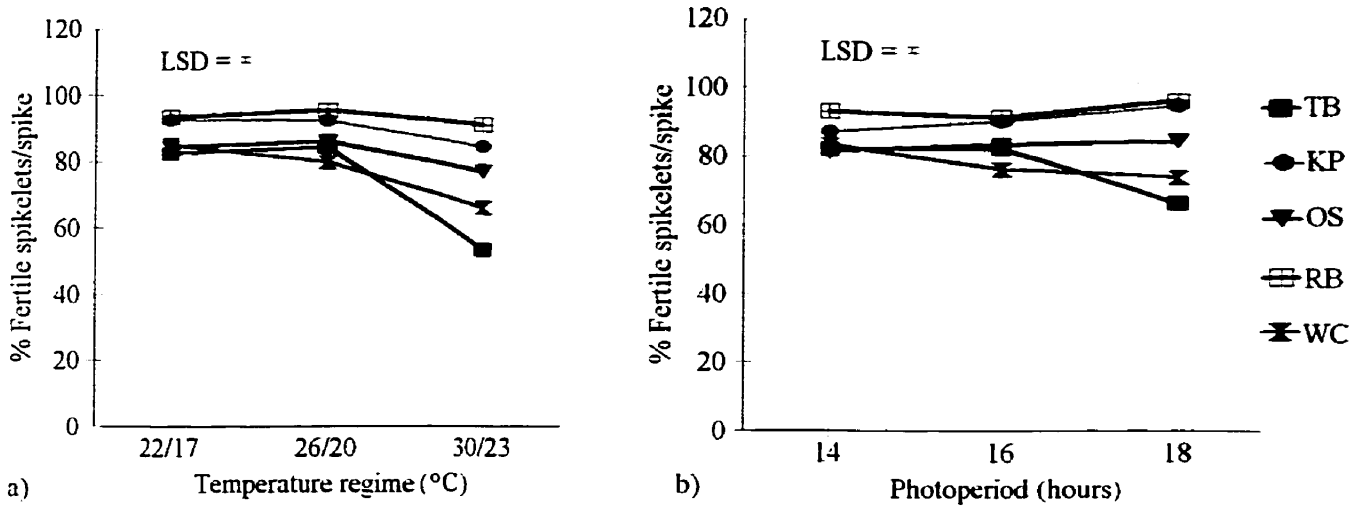


Fig. 3.13. Percentage fertile spikelets per main stem of spring wheat cultivars [AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], grown at: a) different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), and b) different photoperiods (14, 16, 18h) (averaged over all temperature regimes).

grain yields accompany late planting (warmer temperatures) in farmers' fields. AC Taber was affected the most, whereas Roblin and Katepwa were the least affected. At the lowest and medium temperature regimes and photoperiod levels, all cultivars had at least 80 % fertile spikelets per spike, with Katepwa and Roblin having at least 90 % fertile spikelets per spike (Fig. 3.13a & b). These results appear to suggest that Katepwa and Roblin have broader environmental adaptation than the other cultivars.

Vernalization treatment and cultivar effects significantly affected spike length and the number of spikelets produced on the main stem spike (Table 3.7). For the number of spikelets, the vernalization treatment by cultivar interaction was also significant. These results suggest that the difference in cultivar response to vernalization is more pronounced on the establishment of the potential number of spikelets, than the length of the spike. As the duration of the vernalization treatment was increased, only minor reductions in spike length were observed (Fig. 3.14a). Increases in the duration of vernalization treatment caused a reduction in the number of spikelets produced on the main stem, and this effect was more pronounced on AC Taber and Biggar than on Katepwa (Fig. 3.14b). Differences between AC Taber and Biggar were not significant. As previously shown, the vernalization treatment shortened the spikelet development phase (section 3.4.1, Fig. 3.1b, section 3.4.5, and Fig. 3.5c), which subsequently reduced the number of spikelets per spike (Wall and Cartwright, 1974). It could be inferred that a longer time for spikelet initiation is required for a higher spikelet number (Rawson, 1971). These results support the conclusions of Rawson (1970), and Wall and Cartwright (1974), that a shortening of the pre-heading phase in spring wheats is likely to result in fewer spikelets per spike, and potentially reduce grain yield. Vernalization seems to affect vernalization-responsive cultivars by reducing the duration of the vegetative growth phase, and thus causing a sequence of reductions in the number of main stem leaves, phyllochron interval, and the potential number of spikelets (Woodruff,

Table 3.7 Analyses of variance of main stem spike length (SPKL), number of spikelets on the main stem (SPKTS), and fertile spikelets on the main stem (FERTSPT) of spring wheat cultivars, given different vernalization treatments (vntrt), and grown under controlled environment of 22°C/17°C (day and night temperature, respectively) and 16 h photoperiod.

Source of		Mean	squares	
variation	df	SPKL	SPKTS	FERTSPT
Experiment (E)	1	1.5	12.3*	1.8
Block (Expt)	6	0.2	1.8	1.2
Cultivar (C)	2	27.5*	189.4*	14.6*
Vntrt (V)	5	14.7*	92.7*	105.8*
E*C	2	0.2	5.8*	1.2
E*V	5	0.5	4.0*	3.5
C*V	10	0.6	6.3*	9.6*
E*C*V	10	0.5	1.2	2.3
Error	102	0.4	1.7	2.2

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 2.

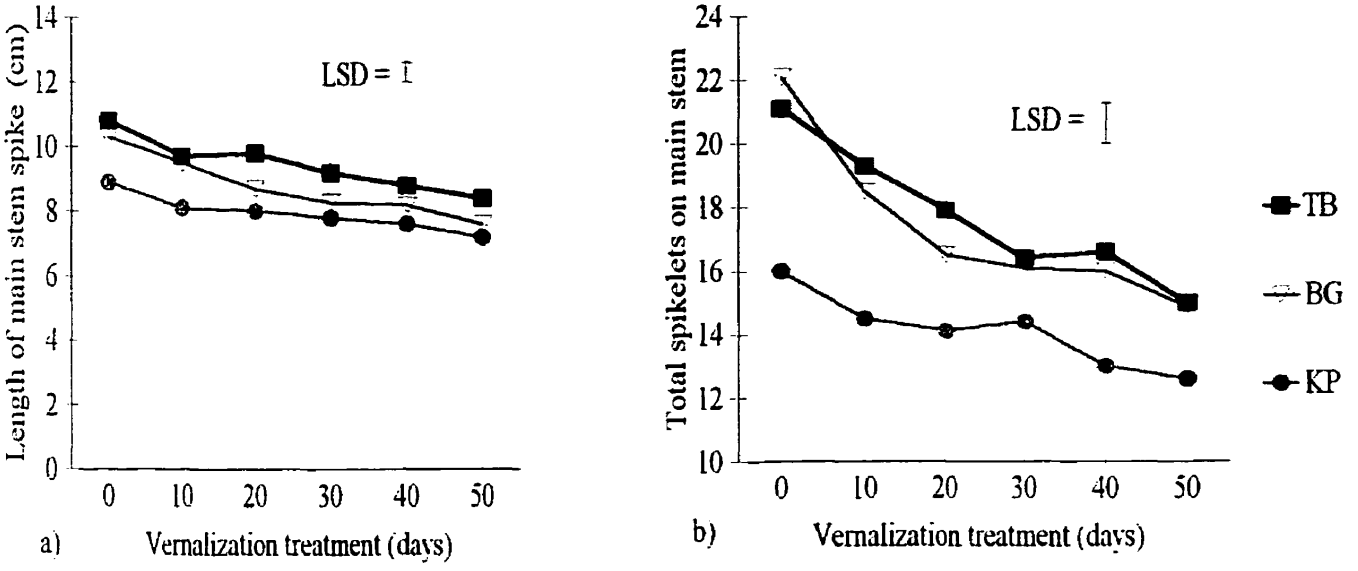


Fig. 3.14. a) Spike length, and b) number of spikelets on the main stem of three spring wheat cultivars [AC Taber (TB), Biggar (BG), and Katepwa (KP)], at different vernalization treatments. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

1983).

Effects of vernalization treatment, of cultivar, and of cultivar by vernalization interaction on fertile spikelets were also significant (Table 3.7). Therefore, vernalization treatment plays an important role in determining the number of fertile spikelets. The number of fertile spikelets declined as the duration of vernalization treatment was increased (Fig. 3.12 c). It is interesting to note that increased vernalization treatment duration beyond 20 days, eliminated any cultivar differences.

3.4.7. Number of kernels, total mass of kernels, and unit kernel mass

Temperature, but not photoperiod, significantly affected the number of kernels per main stem spike, total mass of kernels, and unit kernel mass (Table 3.8). Temperature by cultivar, photoperiod by cultivar, and temperature by photoperiod by cultivar interactions were significant. The effects of temperature and photoperiod were cultivar dependent. Shanahan et al. (1985) reported that grain yield is more consistently correlated with the number of kernels per spike, than unit kernel mass. In this work, as the temperature increased, the number of kernels per spike decreased (Fig. 3.15a), with significant crossover interactions. For example, Roblin which produced the least number of kernels under 22°C/17°C, ranked first under the hottest environment. Shanahan et al. (1984) made similar observations under water stress (usually associated with high temperatures, under field conditions). Lengthening the photoperiod had no effect on the number of kernels per spike produced by Wildcat (Fig. 3.15b). The other cultivars produced more kernels per spike with increasing photoperiod, except AC Taber, which produced about 30% fewer kernels at 18 h photoperiod than at < 18 h.

The mass of the total number of kernels on the main stem spike of all cultivars were negatively affected by increases in temperature (Fig. 3.15c). For example, AC Taber, Wildcat, and Oslo produced 1.6-1.7 g of kernels per main stem spike, under 22°C/17°C, but produced only 0.5-0.7g under 30°C/23°C. Crossover interactions were also observed among the cultivars under the different photoperiods (Fig. 3.15d).

Table 3.8 Analyses of variance of number of kernels per main stem spike (Kernels/spike), total mass of kernels per spike (TMK/spike), and unit kernel mass, of spring wheat cultivars, grown under controlled temperatures (22°C/17°C, 26°C/20°C, and 30°C/23°C) and photoperiods (14 h, 16 h, and 18 h).

Source of variation	df	Mean squares		
		Kernels/spike (#)	TMK/spike (g)	Unit kernel mass (mg)
Temperature (T)	2	25963.3*	55.8*	8954.3*
Photoperiod (P)	2	505.8	0.1	197.0
T * P	4	717.4	0.1	374.9
Expt (T*P)	9	506.6*	0.5*	109.0*
Cultivar (C)	4	1255.0*	3.6*	4532.9*
T*C	8	768.9*	1.2*	201.9*
P*C	8	1015.3*	2.2*	708.0*
T*P*C	15	289.3*	0.2*	120.5*
Error	827	35.6	0.04	21.1

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 1.

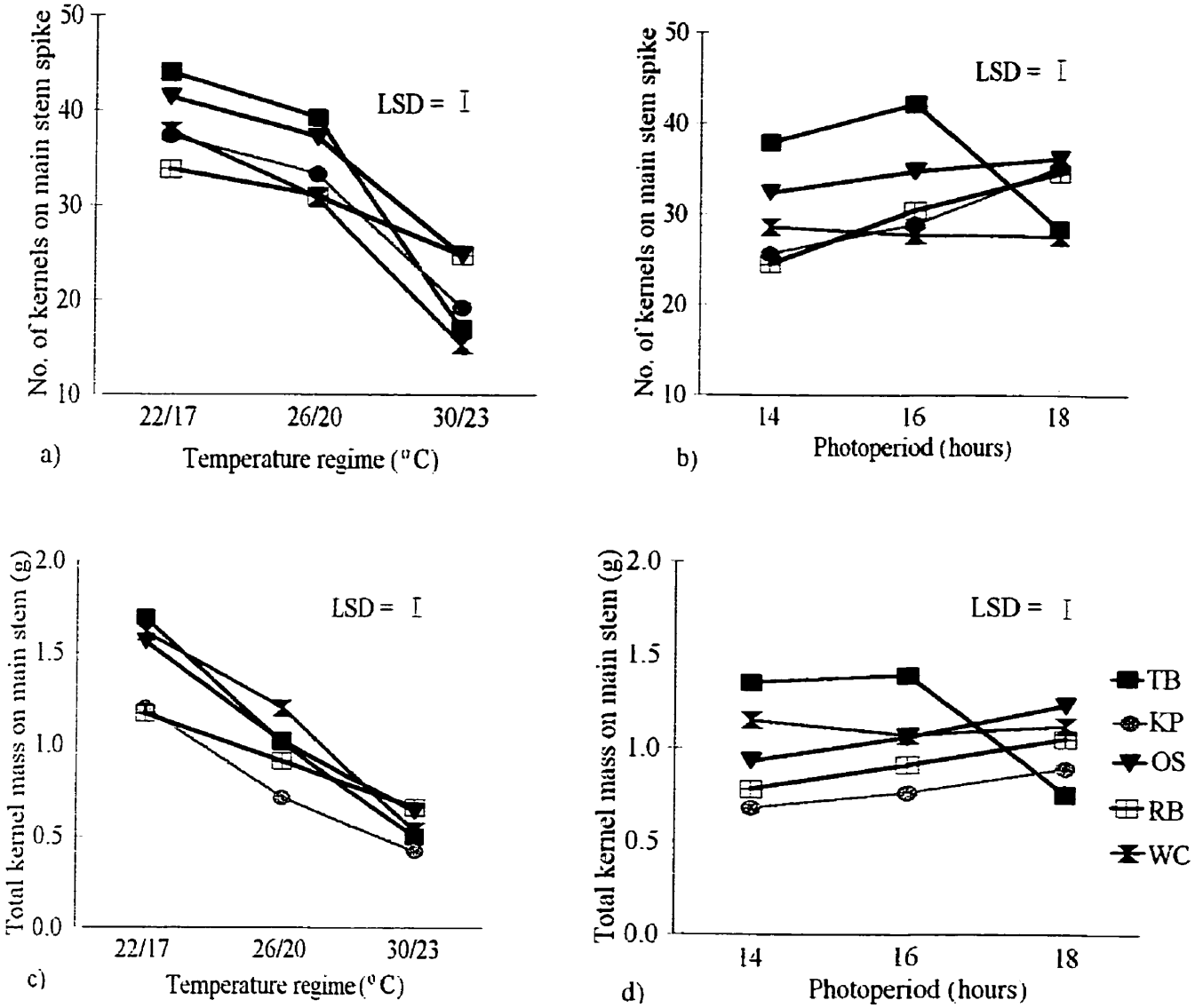


Fig. 3.15. a) Number of kernels on the main stem (averaged over all photoperiods - 14, 16, 18h), b) number of kernels on main stem (averaged over all temperature regimes - 22°C/17°C, 26°C/20°C, 30°C/23°C), c) total kernel mass on main stem (averaged over all photoperiods - 14, 16, 18h), and d) total kernel mass on main stem (averaged over all temperature regimes - 22°C/17°C, 26°C/20°C, 30°C/23°C), of five spring wheat cultivars [AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)]. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

AC Taber, which had the highest total kernel mass per main stem (1.4 g) under 14 h and 16 h, produced the lowest (0.75 g) under 18 h photoperiod. This may be due to the fact that AC Taber is vernalization-responsive while the other cultivars are not. Therefore, the 18 h photoperiod satisfied the vernalization requirement for AC Taber and shortened its vegetative growth period. Subsequently, the mass of grains per spike was reduced for AC Taber, but not the other cultivars. Katepwa, Oslo, and Roblin on the other hand, responded positively to lengthening photoperiod by increases in grains per main stem spike.

Increases in temperature also had a negative effect on the unit kernel mass of all cultivars (Fig. 3.16a). For example, for AC Taber, the reduction in unit kernel mass was as high as 43% (38 mg at 22°C/17°C compared to 21.8 mg at 30°C/23°C). Increases in photoperiod however, affected the unit kernel mass of only Oslo and AC Taber. The unit kernel mass of Oslo increased, while that of AC Taber decreased with increases in photoperiod (Fig. 3.16b). Comparing the unit kernel mass of AC Taber at 14 h (35 mg), and 18 h (23 mg) photoperiod, the reduction was 34%.

Vernalization and cultivar effects were significant for number of kernels per spike, and total mass of kernels on the main stem (Table 3.9). These results support the reasoning that, the effects of vernalization is operative in the vegetative phase of the wheat plant (Wall and Cartwright, 1974). Therefore vernalization affects the number of kernels which are established during spikelet formation in the vegetative growth phase, but not the unit

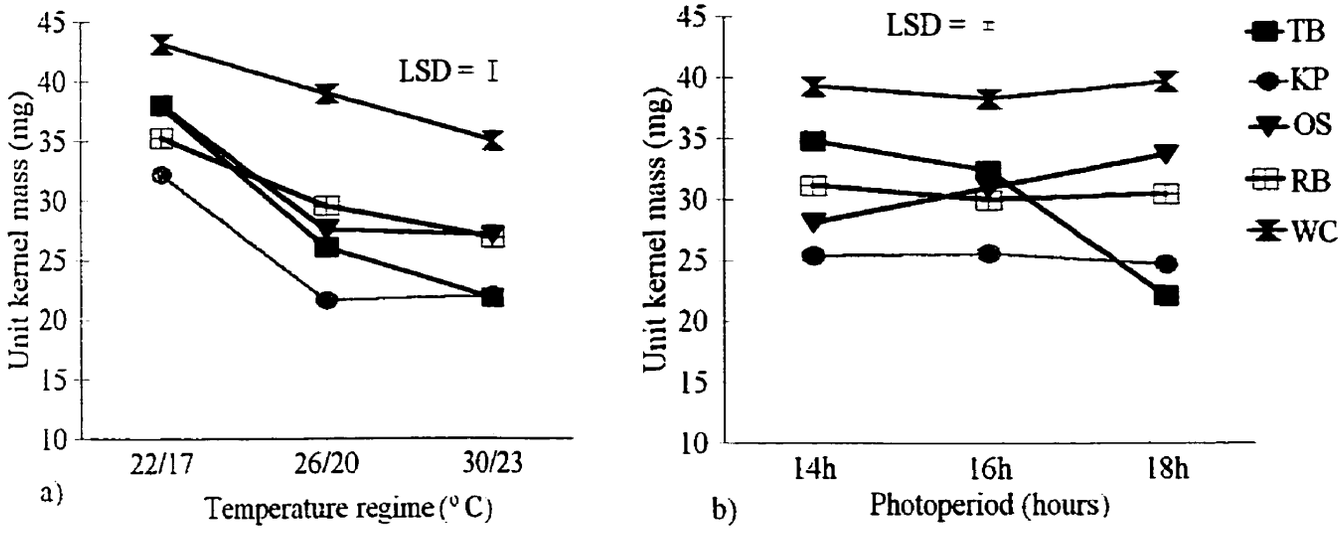


Fig. 3.16. Main stem unit kernel mass (mg) of five spring wheat cultivars [AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], grown at: a) different temperature regimes (22°C/17°C, 26°C/20°C, 30°C/23°C), (averaged over all photoperiods), and b) different photoperiods (14, 16, 18h) (averaged over all temperature regimes). Vertical bars represent LSD (least significant difference at 0.05 level of probability.

kernel mass, which is determined during grain filling (Frank et al., 1987). The total mass of kernels on the other hand is determined by both the number of kernels and the unit kernel mass. Increasing the length of vernalization treatment reduced the number of kernels per spike, and therefore, the total mass of kernels per spike on the main stem (Fig. 3.17 a & b). At shorter vernalization treatments, the number of kernels (for 10 days vernalization treatment), and total mass of kernels (for 10 to 20 days vernalization treatment) for Katepwa were significantly different from those of AC Taber and Biggar,

Table 3.9 Analyses of variance of number of kernels per main stem spike (Kernels/spike), total mass of kernels per spike (TMK/spike), and unit kernel mass, of spring wheat cultivars, given different vernalization treatments (vntrt), and grown under controlled environment of 22°C/17°C (day and night temperature, respectively) and 16 h photoperiod.

Source of variation	df	Mean squares		
		Kernels/spike (#)	TMK/spike (g)	Unit kernel mass (mg)
Experiment (E)	1	82.5	0.59*	319.1*
Block (Expt)	6	22.1	0.06	20.2
Cultivar (C)	2	953.8*	2.82*	480.1*
Vntrt (V)	5	1201.6*	1.76*	8.3
E*C	2	71.8	0.02	98.3
E*V	5	105.6	0.19	36.2
C*V	10	106.6*	0.13	28.9
E*C*V	10	32.9	0.05	49.9
Error	102	58.1	0.08	25.5

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 2.

but differences between AC Taber and Biggar were non significant (Fig. 3.17 a, & b). These observations are consistent with the knowledge that AC Taber and Biggar have a partial vernalization requirement (DePauw, personal communication), but Katepwa does not. However, the differences disappeared with vernalization treatments greater than ten days (Fig. 3.17 a & b). These observations suggest that vernalization treatments of 10 to 20 days would be sufficient to satisfy the vernalization requirement of vernalization-responsive spring wheat cultivars.

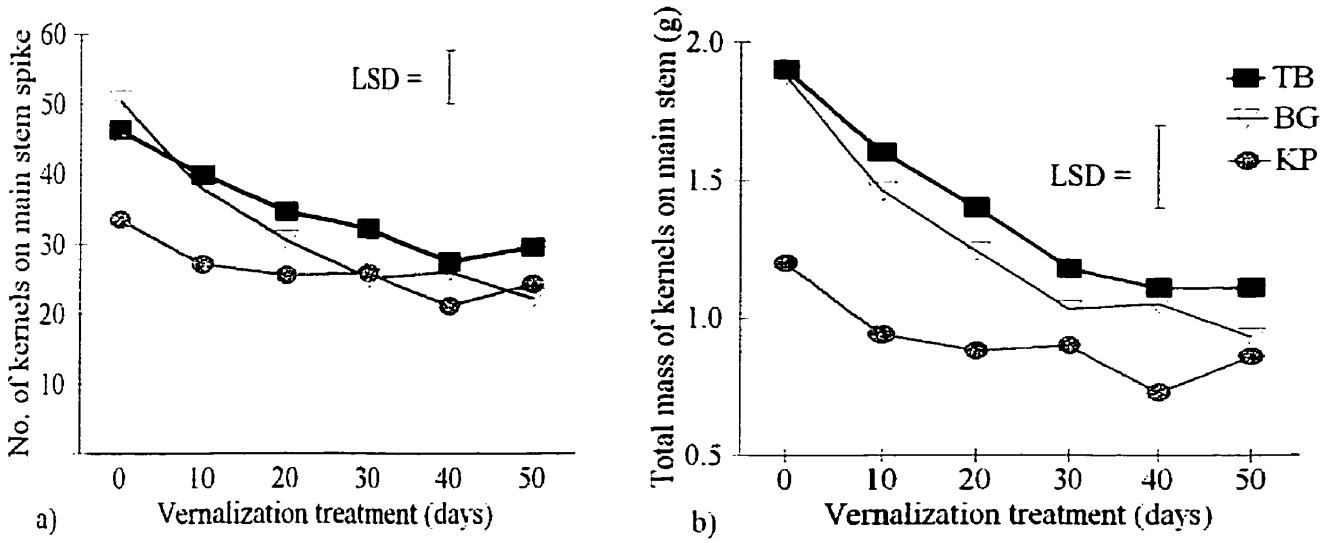


Fig. 3.17. a) Total number of kernels, and b) total kernel mass, on the main stem of spring wheat cultivars at different vernalization treatments. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

3.4.8. Conclusions

Plants grown under high temperature conditions produced fewer main stem leaves, and fewer tillers per plant. The length of the vegetative growth period (time to anthesis), as well as the time to maturity, when expressed in days, were shortened under higher temperatures. A thermal-use-inefficiency, for time to anthesis and to maturity was observed when time was expressed in GDD. The grain filling period is non-responsive to environment and no cultivar differences were observed. Therefore, the similarity in trends observed between anthesis and maturity suggests that maturity differences among cultivars may be attributed to differences in the duration of the vegetative growth phase period. Thus, time to anthesis could serve as a screening procedure for maturity differences.

High temperatures reduced yield-related components like the number of spikelets, fertile spikelets, kernels per spike, and total kernel mass per spike. This may explain why yield reductions occur with delayed planting in the field, and why lower wheat yields are obtained when spring wheat is grown under sub-tropical or tropical conditions.

Increasing temperatures resulted in higher phyllochron intervals. This suggests the following: 1) a reduction in thermal-use-efficiency occurs under warmer conditions, 2) possibly, there is/are threshold temperature tolerance level(s) beyond which cultivars do not respond to any further increases in temperature, and this could lead to overestimation of phyllochron intervals. When grown under less than 16 h photoperiod, tiller

production of the spring wheat cultivars tested was low. As photoperiod was increased, the times to anthesis and to maturity (days) were reduced. For the unsatisfied vernalization-responsive cultivar (AC Taber), further reductions occurred in the number of spikelets, number of kernels per spike, total kernel mass per spike, and unit kernel mass. The satisfaction of partial vernalization requirement in cultivars that possess it, also led to the reductions of the number of main stem leaves, phyllochron interval, time to anthesis and to maturity (days), number of spikelets, number of fertile spikelets, number of kernels, and total kernel mass per spike. It appears that the high-yielding potential of cultivars with a partial vernalization requirement, may be compromised to some extent by the vernalization treatment.

These observed differences in cultivar responses to the different environmental conditions point to the need for accounting for these cultivar differences in crop modelling. These observations further suggest that the predictability of wheat maturity and yield, based on temperature and photoperiod, may be more difficult than originally expected.

4.0 EFFECTS OF SEEDING DATE ON THE GROWTH, DEVELOPMENT, PHENOLOGY, AND PERFORMANCE OF FIELD-GROWN SPRING WHEAT CULTIVARS.

4.1 Abstract

Variable times of seeding present different sets of environmental conditions to which a crop is subjected, which in turn affect the phenology, performance and yield of the crop. Six spring wheat cultivars were grown under rain-fed conditions, at two locations (Winnipeg, and Carman, Manitoba, Canada) and three seeding dates per location. The objectives were to determine the effect of different environments on the growth, development, and yield of spring wheat cultivars, and to provide current field data for the calibration and validation of the CERES-wheat model. Each of the six field trials was sown in a four replicate randomized complete block design. Daily maximum and minimum temperatures, rainfall, and solar radiation data were collected. Field data collected included leaf measurements (using the Haun leaf scale), total number of main stem leaves, onset of terminal spikelet initiation, number of seed-bearing spikes (at maturity), date of heading, anthesis, and maturity, and total plot grain yield. Yield component measurements made on the main stem included: total number of spikelets, number of fertile spikelets, number of kernels, total kernel mass per spike, and unit kernel mass. Differences in heading, anthesis, and maturity dates of cultivars, were similar to cultivar differences observed for terminal spikelet

initiation (TSI). Therefore, cultivar differences observed at heading, anthesis, and/or maturity, may be attributed to the differences in the time to TSI. Phyllochron intervals (degree-days required to produce a leaf) differed among cultivars and seeding date. Therefore, the use of a common phyllochron interval for all cultivars in crop modelling may be inappropriate. Late seeding caused a reduction in the number of seed-bearing spikes, especially in the vernalization-responsive cultivars. The grain filling patterns of the cultivars appeared to be similar during the lag and linear phases, but significantly different during the late phase of grain filling. The grain filling pattern was best described by a quadratic model. Significant genotype by environment interactions were observed and require further investigation. The cultivars examined differed in their phenological development, yield, and yield components under different environments. These differences and interactions must be recognized and accounted for when trying to predict crop maturity and yield over a wide range of environments.

4.2. Introduction

Environmental conditions that a crop is subjected to may vary significantly with differences in seeding dates. Among other factors, variations in environmental conditions are largely responsible for year-to-year fluctuations in crop yields. It is often difficult to balance the advantages and disadvantages of early seeding to maximize yields and minimize risk. Early seeding is often recommended to avoid disease, realize maximum yield potential, and provide increased marketing opportunities and profit (Canada-Manitoba Farm Business Management Council, 1996). However, early seeding may increase the risk of spring frost damage, susceptibility to herbicide residue, and seed rot. The time of sowing has a major influence on the rate of development of wheat, and in some environments, highest yields have been reported to occur when flowering occurs before plants suffer high temperature stress (French et al., 1979).

Each cultivar appears to have a unique set of controls and requirements in phenological development (Pirasteh and Welsh, 1980). Therefore, crop cultivars may differ from one another in the duration of their phasic development. High temperatures during the switch from vegetative to reproductive development, stem elongation, heading, and flowering, may cause stress or injury (Cook and Veseth, 1991). Under non-irrigated field conditions, the effects of high temperature are usually confounded by the effects of water stress.

The magnitude of cultivar by location interactions has been shown to be highly correlated to cultivar adaptability (Baker, 1988). Thus, plant breeders conduct performance tests at different locations in different years, to determine the magnitude of the genotype by environment (GxE) interaction. In order for a cultivar to be commercially successful in western Canada, it must perform well across the range of environments in which the cultivar may be grown. Delays in seeding may present the need to choose a different cultivar, in order to maximize yield and profit. The Crop Estimation through Resource and Environment Synthesis (CERES)-wheat model, a crop simulation model which possesses a genetic coefficient descriptor, may have the potential to aid such management decisions a priori.

Work done so far in Canada and other places, on the calibration and evaluation of the CERES-wheat model, has relied on historic data for much of the required data for the model (Otter and Ritchie, 1984; Otter et al., 1986; Moulin and Beckie, 1993; Chipanshi et al., 1997; Pecetti and Hollington, 1997). Such historic data usually lacks some of the information needed to effectively calibrate and evaluate the model in an unbiased manner, since the historic experiments may not have been planned with crop modelling in mind. This forces model evaluators to estimate the missing information, which usually affects the conclusions made from such studies. To effectively evaluate and assess the claims of a crop model, it is imperative to conduct and collect data from current field research for crop modelling requirements.

The objectives of this study were: 1) to determine the growth, development, phenology patterns, and yield of six spring wheat cultivars, grown in the field under different seeding dates in Winnipeg and Carman, Manitoba, Canada, 2) to determine any genotype by environment interactions under the different environments, and 3) to provide current field data for the calibration and validation of the CERES-Wheat model, (chapter 5).

4.3. Materials and methods

Six spring wheat cultivars, AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), were grown in the field under rain-fed conditions at two locations and three seeding dates per location in 1996. The cultivars were selected to represent a range of spring wheat classes and different characteristics. AC Taber, Biggar, and Oslo belong to the Canada Prairie Red Spring Wheat Class, Katepwa and Roblin are Canada Western Hard Red Spring Wheat genotypes, while Wildcat belongs to the Canada Western Extra Strong Red Spring Wheat Class (formerly Canada Utility Spring Wheat Class). Wildcat is the only cultivar that is not recommended for growth in Manitoba because of its poor resistance to stem rust, leaf rust, and bunt. AC Taber and Biggar are known to possess partial vernalization requirements (DePauw, personal communication).

The experiments were conducted in the summer of 1996 at Winnipeg (latitude 49.8°, longitude 97.2°), and Carman (latitude 49.5°, longitude 98.0°) (70 km from Winnipeg), Manitoba, Canada. The soil type for the Carman experimental plots was the Winkler series, which is a moderately well drained Orthic Black soil (Mills and Haluschak, 1993), while the soil type for the Winnipeg experimental plots was a silty clay Riverdale Floodplain (McPherson, 1987). The Winnipeg plots were sown to barley the previous year, whereas those in Carman had been fallowed the previous year. Trials were planted on three different dates to provide a wide range of

environments. The seeding dates were: Winnipeg - May 8 (WSD1), May 27 (WSD2), June 10 (WSD3); Carman - May 13 (CSD1), May 24 (CSD2), and June 4 (CSD3). Each of the six field trials was sown in a four replicate randomized complete block design. Plots were planted in duplicate; one set was used for destructive sampling. Each plot consisted of six 3-m rows spaced 17.5 cm apart. Plots were maintained weed-free by hand weeding. The seeding rate was adjusted for each cultivar on the basis of grain dry weight and germination percentage to have about 950 viable seeds sown per plot (200 seeds/m^2). Pre-seeding soil nitrogen (N) testing was conducted, and the level of available nitrogen (N) in the soil was raised to 150 kg N ha^{-1} (standard protocol) with ammonium nitrate (34-0-0), by hand broadcasting 76 kg N ha^{-1} at Winnipeg, and 48 kg N ha^{-1} at Carman. The fertilizer was applied when the plants were at the 2-3 leaf stage. Daily maximum and minimum temperatures, rainfall, and solar radiation data were collected at Winnipeg from the Department of Plant Science weather station, and at Carman from the Environment Canada weather station. The weather stations were located within 30 m of the respective sites.

At the two leaf stage, five plants were chosen at random in each non-destructive plot and were labelled for leaf development monitoring on the main stem. Leaf stage was measured at four to five-day intervals, using the Haun scale (Haun, 1973). The total number of leaves per main stem, was determined. The phyllochron

interval (growing-degree-days required to produce a leaf) was calculated by the reciprocal of the regression coefficient of Haun leaf stage on accumulated growing-degree-days (GDD). Accumulated GDD were calculated by the summation of daily GDD (DGDD). DGDD was calculated as:

$$DGDD = \{(T_{max} + T_{min})/2\} - T_{base}$$

where T_{max} and T_{min} = daily maximum and minimum temperatures, respectively, and T_{base} is the minimum temperature at which growth is assumed to cease. In these experiments, T_{base} was assumed to be 0°C (Baker et al., 1986; Cao and Moss, 1989c).

To determine the terminal spikelet initiation stage, five plants (per sampling date) for each cultivar were collected at random from the duplicate plots used for destructive sampling; the leaf stages were recorded before cutting the leaves. The samples were kept in water in petri dishes and were later dissected in the laboratory, under a light microscope, to determine the onset of terminal spikelet initiation (TSI). The time between sampling and dissection was not more than 5 h. Sampling for TSI began when plants were at the 1.5-2.0 leaf stage and continued at four to five-day intervals until the TSI was identified.

The following measurements were made on the centre one metre section of the two middle rows of each plot, and the mean from the two rows was used for each plot analysis: number of plants, number of stems at anthesis, anthesis dry matter (cut from the destructive sampling plots), maturity dry matter (cut from the non-destructive

sampling plots), and number of seed-bearing spikes (at maturity). The samples collected for dry matter determinations were oven-dried at 80°F for 72 h before dry matter was determined. Tiller abortion was determined from the difference between number of stems at anthesis and the number of seed-bearing spikes. Other measurements made were: date of heading, anthesis, and maturity, plant height, and total plot yield. Heading and anthesis dates were determined when 50% of the spikes in a plot had reached heading and anthesis, respectively. Maturity date was determined when 50% of the spikes in a plot had lost all green colouration (Hanft and Wych, 1982; Smith and Donnelly, 1991). The following yield-related variables were measured on ten random samples of main stem spikes at maturity (taken from the destructive sampling plots): spike length, total number of spikelets, number of fertile spikelets, number of kernels, total kernel mass per spike, and unit kernel mass.

To study the nature and differences in grain filling among the cultivars, random samples of ten spikes per cultivar were harvested from the destructive sampling plots at three to five-day intervals, starting from 12 days post anthesis to 43 days post anthesis. The samples were oven-dried at 80°F for 72 h, and then five kernels from the middle section of each spike were removed and bulked. The dry mass of each bulked sample of seeds was determined and used to calculate the unit kernel mass for each sampling date.

Data were analysed using the analysis of variance (ANOVA) (Appendix 4)

procedure of Statistical Analyses System (SAS v.6.12) computer programs (SAS, 1989). Since the maximum number of treatments in an experiment was not more than six (cultivars), mean comparisons were done by the least significant difference (LSD) test at 5% probability. Regression analysis and basic regression diagnostics were used to assess the nature of the relationship between kernel mass and thermal time, and to determine the curve that best describes the grain filling pattern.

4.4 Results and discussion

4.4.1 Summary of environmental conditions at Winnipeg and Carman, 1996

Total precipitation for the months of May, June, August, and September of the 1996 growing season, were higher at Winnipeg than Carman, but the total precipitation for July was higher at Carman than Winnipeg (Fig. 4.1 a). The average maximum temperature patterns through May-September, were similar at both locations. Average maximum temperatures at Winnipeg were slightly higher than at

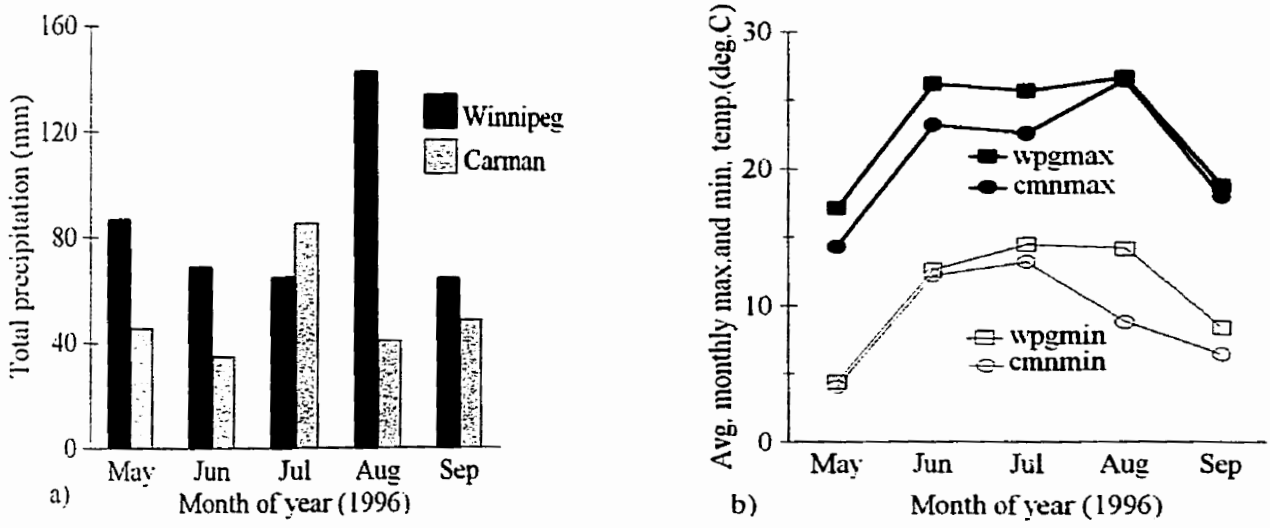


Fig. 4.1 a) Total monthly rainfall, and b) monthly average maximum and minimum temperatures, at Carman and Winnipeg for May through September of 1996 [wpgmax, wpgmin = Winnipeg maximum and minimum temperatures, respectively, cmnmax, cmnmin = Carman maximum and minimum temperatures, respectively].

Carman, from May through July, whereas the average minimum temperatures at Winnipeg were slightly higher than at Carman for July through September (Fig. 4.1 b). Therefore, the average monthly temperatures at Winnipeg were higher than those at Carman throughout the entire growing season.

4.4.2 Leaf number at terminal spikelet initiation, total number of leaves, and phyllochron interval.

Location and cultivar, as well as location by seeding date, location by cultivar, and location by seeding date by cultivar interactions significantly affected the leaf number at terminal spikelet initiation and the total number of leaves on the main stem (Table 4.1). However, the interaction effects were minor and therefore not of practical significance. Both AC Taber and Biggar initiated terminal spikelet at a later leaf stage than the other cultivars (Fig. 4.2 a & b), and also produced the highest number of main stem leaves (Fig. 4.2 c & d). For all cultivars terminal spikelet initiation occurred at between 2.5-3 leaves prior to the appearance of the main stem flag leaf (compare Fig 4.2 a with 4.2 b; compare Fig. 4.2 c with 4.2 d). With most of the cultivars producing 7-9 main stem leaves, these results are in agreement with observations by Frank et al. (1987), that terminal spikelet initiation is complete at about 5.5 leaf growth stage. These results suggest that, cultivar differences in the duration of vegetative growth phase may be dictated primarily by the number of main

Table 4.1. Analyses of variance of number of main stem leaves at terminal spikelet initiation (TSILN), total number of main stem leaves (leaves), and phyllochron interval (PHINT), of field-grown spring wheat cultivars, at two locations and three seeding dates.

Source of		Mean	Squares	
variation	df	TSILN	Leaves	PHINT
Location (L)	1	11.73*	6.25*	275.01*
Block / Location	6	0.04	0.01	5.60
Seeding date (SD)	2	6.50	5.90	11.10
L * SD	2	0.42*	1.56*	123.03*
Cultivar (C)	5	16.92*	17.52*	1060.00*
L * C	5	0.20*	0.45*	20.00*
SD * C	10	0.63	0.49	131.70*
L * SD * C	10	0.34*	0.49*	26.06*
Error	102	0.02	0.05	10.91

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 4.

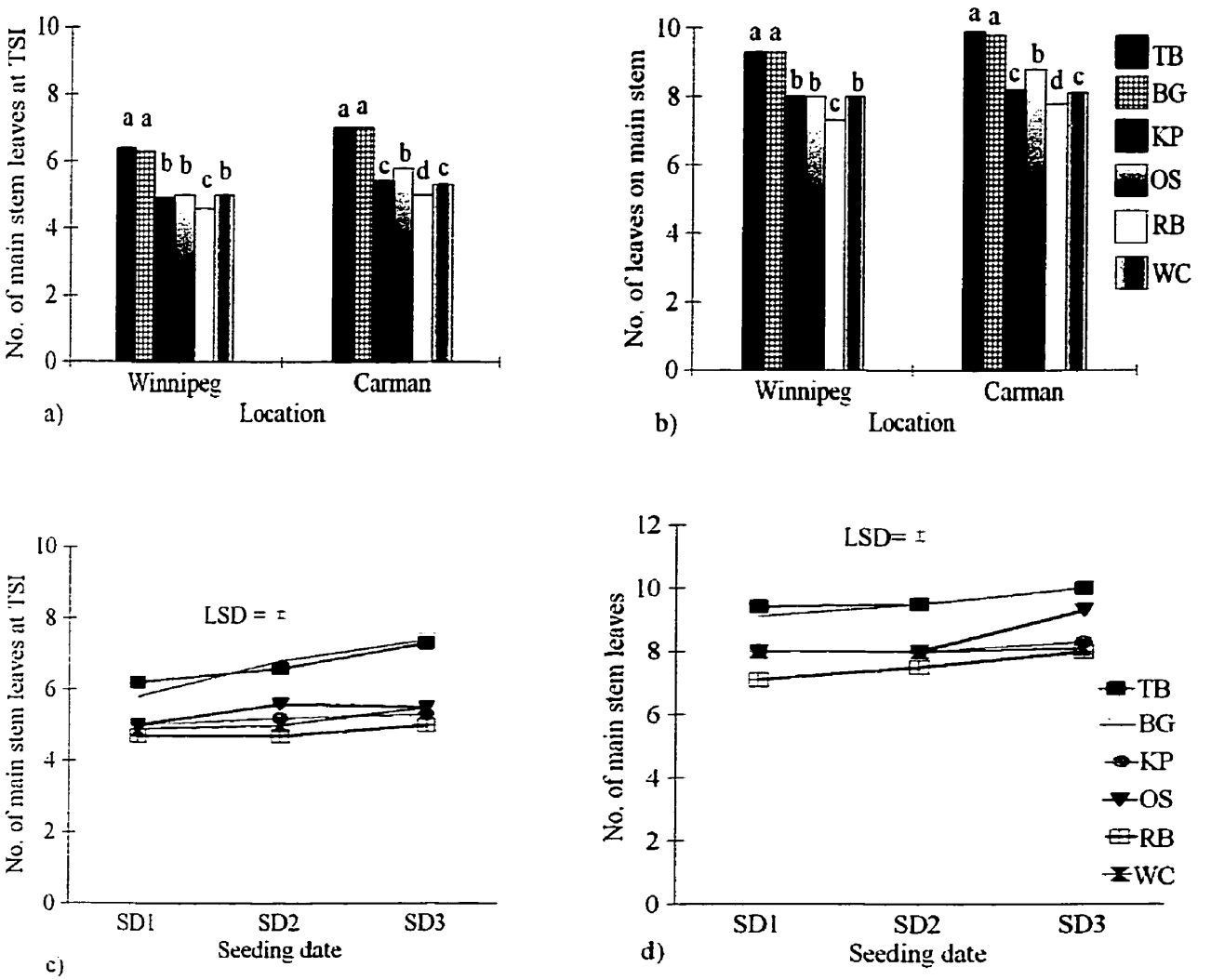


Fig. 4.2 Number of main stem leaves produced by spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], a) at terminal spikelet initiation for different locations, (averaged over all seeding dates), b) at different locations, (averaged over all seeding dates), c) at terminal spikelet initiation for different seeding dates (averaged over both locations), and d) at different seeding dates (averaged over both locations). Vertical bars represent LSD (least significant difference) at 0.05 level of probability, and bars having the same letter at a particular location are not significantly different according to the LSD test.

stem leaves produced under any given environment.

The analysis of variance showed significant differences in phyllochron interval due to location and cultivar, as well as location by seeding date, location by cultivar, cultivar by seeding date, and location by seeding date by cultivar interactions (Table 4.1). The significant seeding date by cultivar interaction supports the observations by Cao and Moss (1989a) that under field conditions the phyllochron of wheat varies with seeding date. However, these results contradict the assertion by Hodges (1991) that a cultivar should have a characteristic phyllochron regardless of the time of planting or location. When the phyllochron intervals for the different cultivars at the two locations were compared, the ranking remained the same, with phyllochron intervals only 2-5 GDD/leaf higher at Winnipeg than at Carman (Fig. 4.3 a). The average phyllochron interval determined across locations within the same growing region, may be appropriate for crop phenology modelling and yield predictions.

Katepwa had the highest average phyllochron interval of 93 GDD/leaf, followed by AC Taber and Biggar with 85 GDD/leaf (Fig. 4.3 b). Wildcat had the lowest average phyllochron interval of 75 GDD/leaf. The presence of differential cultivar responses to environmental conditions, implies that the use of a common phyllochron interval of 75 GDD/leaf for spring wheat cultivars, as suggested by Ritchie (1991), is not appropriate, and may lead to erroneous phasic and morphological development predictions by crop models (e.g., the CERES-wheat

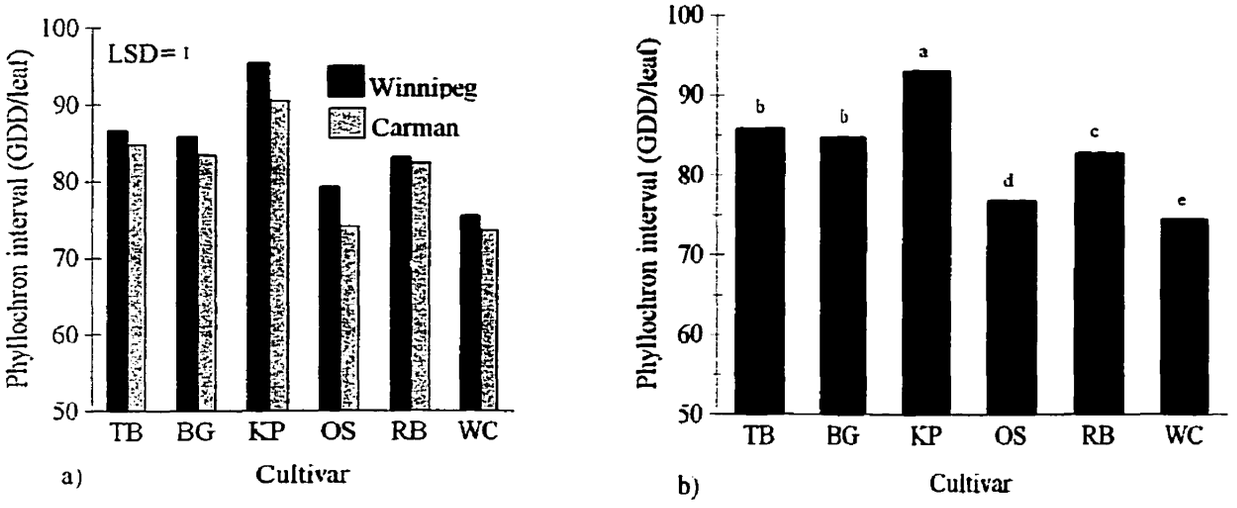


Fig. 4.3 a) Comparison of phyllochron intervals at Winnipeg and Carman, and b) average phyllochron interval (averaged over both locations), for spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)]. Bars having the same letter are not significantly different according to the LSD (least significant difference) test at 0.05 level of probability test. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

model). Thus, determining the actual phyllochron interval for specific spring wheat cultivars is imperative, and should improve model predictions.

4.4.3 Number of stems (including main stem) at anthesis, number of seed-bearing spikes at maturity, and tiller abortion.

The number of stems at anthesis, the number of seed-bearing spikes at maturity, and the number of tillers aborted were significantly affected by location, seeding date and cultivar (Table 4.2). Where significant, interaction effects (except

location by seeding date effect on the number of stems at anthesis) were of minor practical significance (Table 4.2). The number of stems at anthesis is an indicator of tillering capacity, which has an effect on yield. At both locations, Katepwa had the highest number of stems at anthesis, which was significantly different from the other cultivars (Fig. 4.4 a). The number of stems at anthesis, and the number of seed-bearing spikes were both higher at Carman than at Winnipeg for all cultivars (Fig. 4.4 a & b). Katepwa produced the highest number of stems and seed-bearing spikes at all seeding dates (Fig. 4.4 c & d). When planting was delayed, the number of seed-bearing spikes for AC Taber and Biggar declined significantly (Fig. 4.4 d). AC Taber and Biggar were the most sensitive cultivars to delayed seeding, probably due to their response to vernalization (DePauw, personal communication). These results agree with observations reported in chapter three, that temperature increases reduced yield-related components (section 3.4.3). These results show that spring wheat cultivars may respond differently to different environmental conditions, and therefore, the use of a common vernalization coefficient (0.5) for all spring wheat cultivars in crop modelling (Pecetti and Hollington, 1997; Chipanshi et al., 1997) needs further investigation.

The difference between the number of seed-bearing spikes, and the number of stems at anthesis was used as a measure of tiller abortion. The negative values in Fig. 4.5 a represent the appearance of tillers after anthesis. Post-anthesis

Table 4.2. Analyses of variance of the number of stems at anthesis (ANSTEM), number of seed-bearing spikes at maturity (MATSBS), and tiller abortion (TLABOT), of field-grown spring wheat cultivars, at two locations and three seeding dates per location. [Values for ANSTEM and MATSBS were obtained from the average of the two centre 1-m rows, and TLABOT=ANSTEM - MATSBS].

Source of		Mean	Squares	
variation	df	ANSTEM	MATSBS	TLABOT
Location (L)	1	90801.78*	13244.17*	35375.34*
Block / Location	6	188.88	120.49	341.56
Seeding date (SD)	2	1231.97*	2097.22*	5296.78*
L * SD	2	1529.26*	968.42*	119.19
Cultivar (C)	5	3971.44*	2512.61*	1343.32*
L * C	5	141.09*	320.27*	539.39
SD * C	10	144.47	326.11*	547.33
L * SD * C	10	226.07*	105.50	432.74
Error	102	39.06	80.41	82.65

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 4.

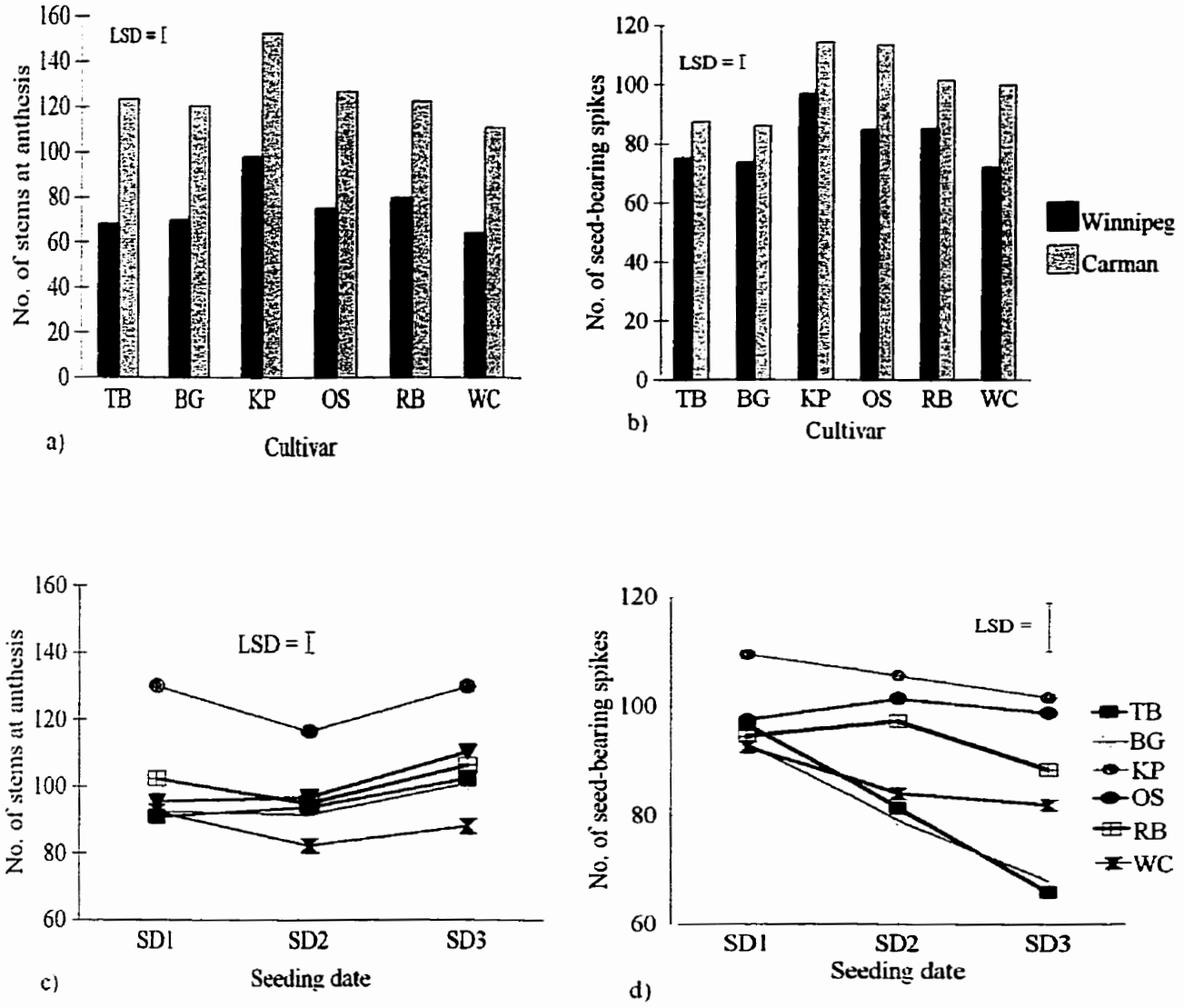


Fig. 4.4 a) Number of stems at anthesis (averaged over all seeding dates) for Winnipeg and Carman, b) number of seed-bearing spikes at maturity (averaged over all seeding dates) for Winnipeg and Carman, c) number of stems at anthesis (averaged over both locations) for different seeding dates, and d) number of seed-bearing spikes at maturity (averaged over both locations) for different seeding dates, of spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)]. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

rainfall and warm temperatures at Winnipeg (Fig. 4.1 a & b) are responsible for this post-anthesis gain in tiller number (Fig. 4.5 a & b). Katepwa, showed a high rate of tiller abortion over all seeding dates, while tiller abortion for AC Taber and Biggar was more pronounced with delayed seeding than the other cultivars (Fig. 4.5 b).

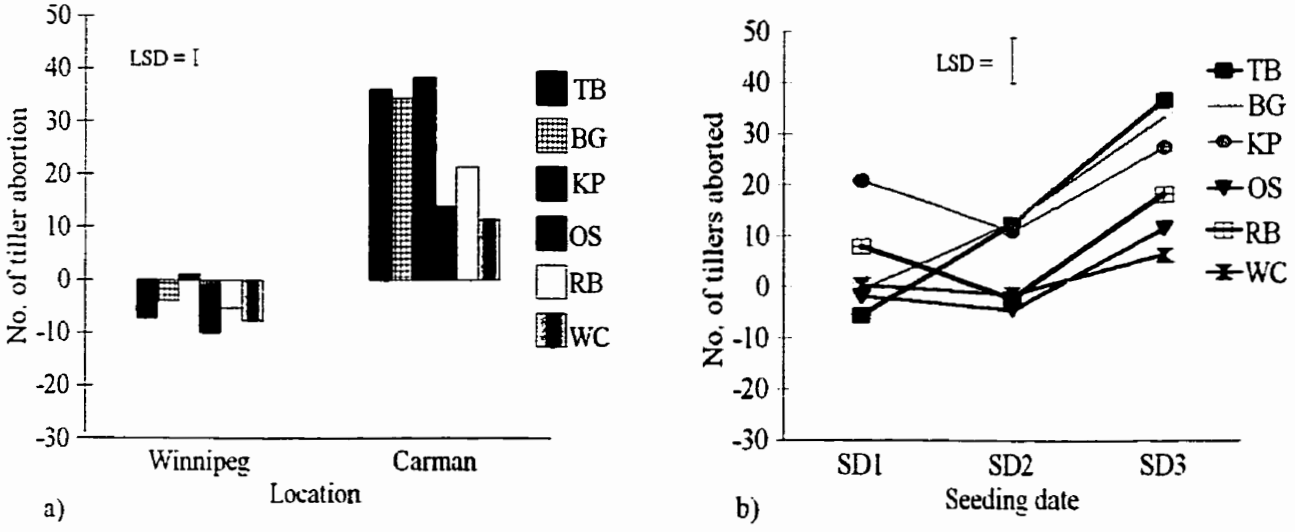


Fig. 4.5. Tiller abortion of spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)] grown at; a) different locations (averaged over all seeding dates) and b) different seeding dates (averaged over both locations). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

4.4.4 Height, dry matter at anthesis, and dry matter at maturity

Plant height, dry matter at anthesis, and dry matter at maturity were significantly affected by location, seeding date and cultivar (Table 4.3). The location by cultivar interaction significantly affected the dry matter at maturity. Plant height of all cultivars were higher at Carman than Winnipeg (Fig. 4.6 a). Katepwa produced the tallest plants at both locations (Fig. 4.6 a). This observation is different from that made under growth cabinet conditions (chapter 3). Also, plant height under growth cabinet conditions ranged between 45 - 75 cm, while the range was 70 - 110 cm in the field. This may be attributed to the differences in spectral composition and light intensity between the controlled environments (indoors) and natural conditions in the field. The far red spectrum, (found in wavelengths of 700-730 nm), is more abundant under natural sunlight conditions, and are known to promote stem elongation (McCree, 1973). Plant competition under field conditions (where plants are closely spaced) is more vigorous, than under controlled environment (where plants are widely spaced in pots). These could also be contributing factors to the observed differences in plant height.

Table 4.3. Analyses of variance of height, dry matter at anthesis (DMANT), and dry matter at maturity (DMMAT), of field-grown spring wheat cultivars, at two locations and three seeding dates per location.

Source of		Mean Squares		
variation	df	Height	DMANT	DMMAT
Location	1	8533.14*	73938.67*	33154.34*
Block / Location	6	41.65	352.33	284.36
Seeding date (SD)	2	2990.76*	7536.73*	6230.04*
L * SD	2	354.42*	1542.25*	2621.30*
Cultivar (C)	5	971.86*	5023.94*	2667.27*
L * C	5	17.06	172.66	1381.34*
SD * C	10	53.05	387.40	201.17
L * SD * C	10	38.22	266.08	312.34
Error	102	8.43	60.73	263.94

* Significant mean square at the 0.05 probability level.

Model for F tests was based on appendix 4.

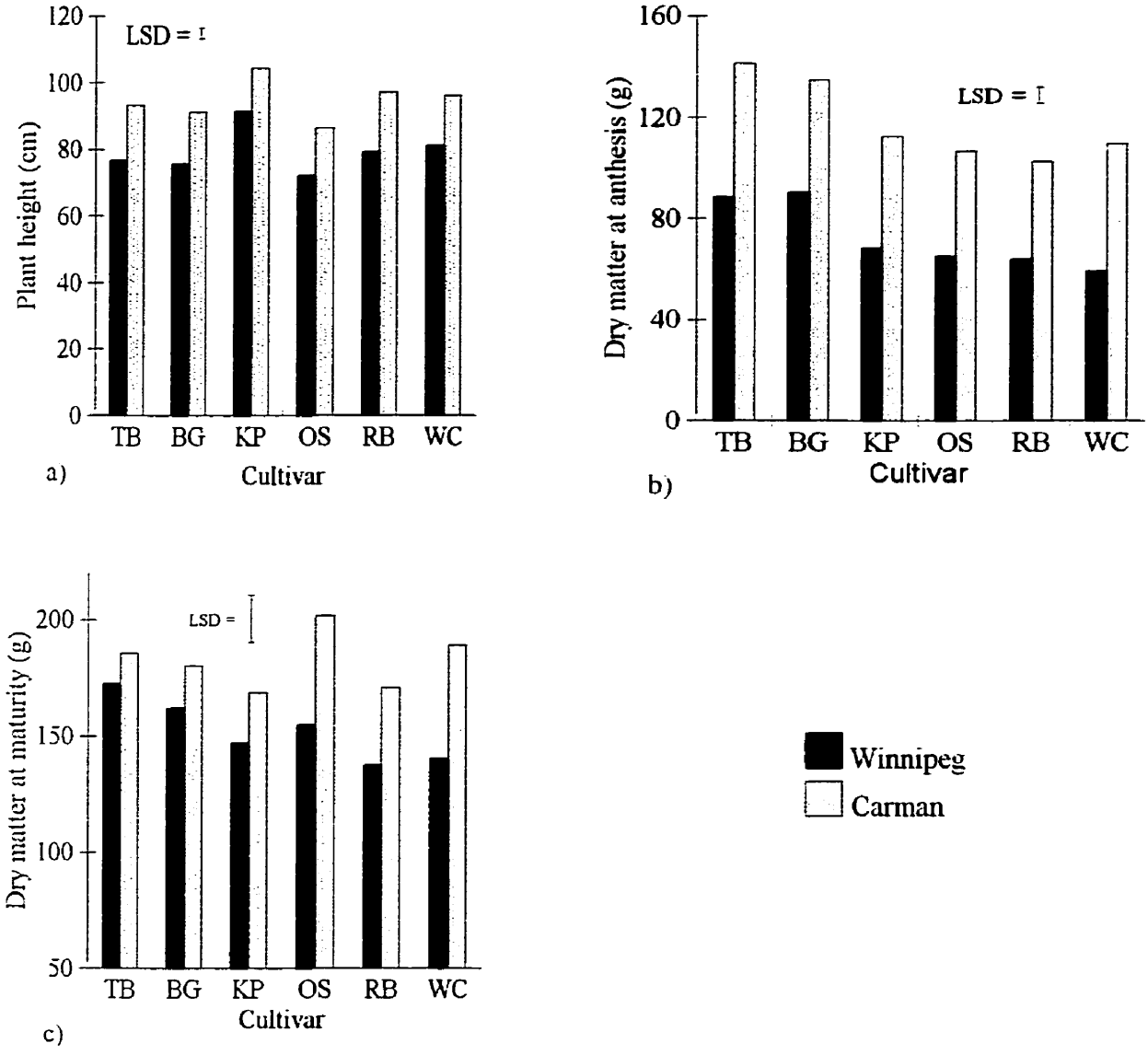


Fig. 4.6. a) Plant height, b) dry matter at anthesis, and c) dry matter at maturity, for spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], grown at Winnipeg and Carman, (averaged over all seeding dates). Vertical bar represent LSD (least significant difference) at 0.05 level of probability.

At both locations AC Taber and Biggar produced the highest anthesis dry matter (Fig. 4.6 b). AC Taber and Biggar produced the highest maturity dry matter at Winnipeg, while Oslo and Wildcat produce the highest maturity dry matter at Carman (Fig. 4.6 c). This may be a reflection of the fact that under warmer conditions, the partial vernalization requirements of AC Taber and Biggar were not satisfied, which led to a prolonged vegetative growth phase, higher number of main stem leaves, and subsequently more anthesis and maturity dry matter production, than most of the other cultivars.

4.4.5 Time to terminal spikelet initiation (TSI), heading, anthesis, and maturity

Time to reach terminal spikelet initiation, heading, anthesis, and maturity were significantly affected by location, and cultivar, as well as location by seeding date, location by cultivar, and location by seeding date by cultivar interactions (Table 4.4). Where significant, the interaction effects were relatively small compared to cultivar main effects, and therefore not of practical significance. The duration of these phenological stages were not constant over environments. AC Taber and Biggar required 600 GDD to reach TSI, as compared to 400 GDD for Oslo, Roblin, and Wildcat (Fig. 4.7a). AC Taber and Biggar required similar GDDs to attain heading, anthesis, and maturity, as did Katepwa, Oslo, Roblin and Wildcat (Fig. 4.7 a).

Table 4.4. Analyses of variance of time to terminal spikelet initiation (TSI) (GDD), heading (GDD), anthesis (GDD), and maturity (GDD), of field-grown spring wheat cultivars, at two locations and three seeding dates per location.

Source of		Mean Squares			
variation	df	TSI	Heading	Anthesis	Maturity
Location	1	309136*	331776*	240753*	374238*
Block / Location	6	0.0	0.0	0.0	22.6
Seeding date (SD)	2	3044	45373	10174	21007
L * SD	2	234541*	245952*	277864*	174859*
Cultivar (C)	5	238512*	261861*	270328*	190336*
L * C	5	2177*	4682*	477*	1219*
SD * C	10	13260	14349*	10793*	11336
L * SD * C	10	5493*	3039*	1734*	6561*
Error	102	0.0	0.0	0.0	22.6

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 4.

Further, all six cultivars accumulated 350-400 GDD from TSI to heading, 50-70 GDD from heading to anthesis, and 750-770 GDD from anthesis to maturity (Fig. 4.7 b). The thermal time requirement from anthesis to maturity agrees with values (750-800 GDD) reported by Cook and Veseth (1991). These results indicate that cultivar differences observed at heading, anthesis, and maturity are primarily attributed to the differences in the time to TSI. This may explain why after TSI was

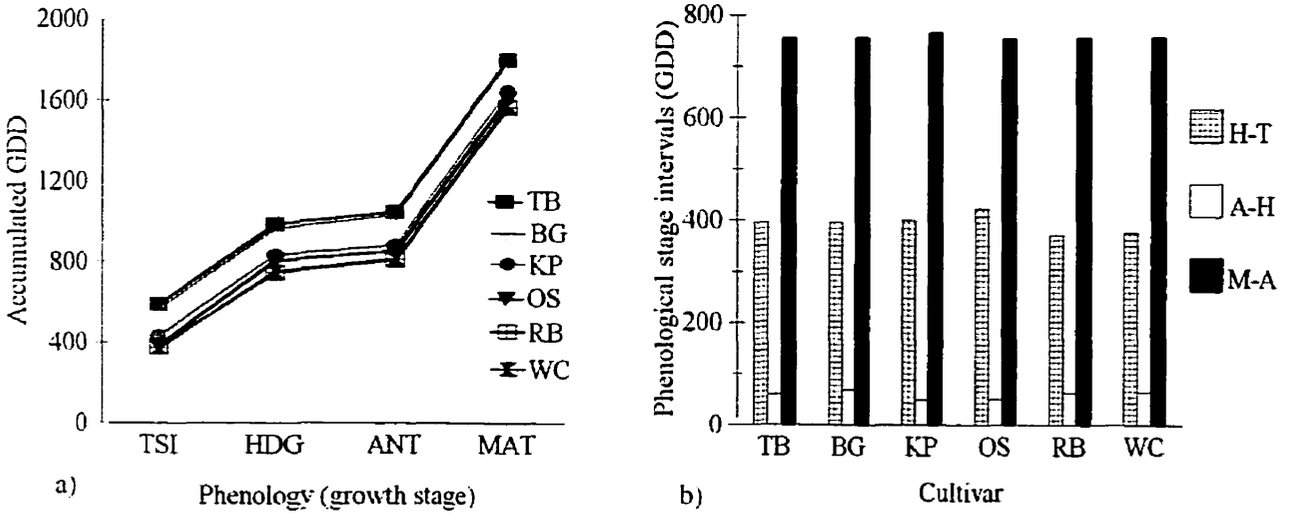


Fig. 4.7. Thermal time requirement for a) terminal spikelet initiation (TSI), heading (HDG), anthesis (ANT), and maturity (MAT), and b) intervals between phenological stages (H-T= interval between terminal spikelet initiation and heading; A-H= interval between heading and anthesis; M-A= interval between anthesis and maturity) of spring wheat cultivars AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC).

reached, all cultivars produced a similar number of leaves (2.5-3.0 leaves) prior to the main stem flag leaf appearance, even though the total number of leaves produced on the main stem were different among cultivars. Wong and Baker (1986) observed similar relationships among heading, anthesis and maturity for the cultivars of their study.

4.4.6 Yield and yield-related components

4.4.6.1 Yield

Yields were significantly affected by the main effects of location, seeding date, and cultivar, as well as by their interactions (Table 4.5). At Winnipeg, AC Taber produced the highest yield, whereas at Carman, Wildcat ranked first (Fig. 4.8 a). Roblin produced the lowest yields at both locations. The changes in yield rank between the two locations suggests that cultivars respond differently to varying environmental conditions. At Winnipeg, most cultivars produced the highest yields at the third seeding date (Fig. 4.8 b). At Carman, however, yields declined with late seeding (Fig. 4.8 c). Yield rankings were similar to dry matter at maturity rankings at each location (compare Fig. 4.8 a with Fig. 4.6 c). The rainfall distribution pattern and the warmer temperatures at Winnipeg (Fig. 4.1 a & b) than Carman, may be responsible for the relative increases in yield with delayed planting at Winnipeg.

Table 4.5. Analyses of variance of grain yield, kernels per main stem spike, and unit kernel weight, of field-grown spring wheat cultivars, at two locations and three seeding dates per location.

Source of		Mean	Squares	
variation	df	Yield	Kernels/spike	Unit kernel wt.
Location (L)	1	265654.34*	672.97*	635.88*
Block / Location	6	98530.21*	5.97	5.11
Seeding date (SD)	2	110772.53*	359.50	114.87*
L * SD	2	1416730.78*	85.08*	0.89
Cultivar (C)	5	490343.04*	1354.90*	144.26*
L * C	5	236780.17*	20.92*	15.45*
SD * C	10	85334.39*	75.38*	38.78*
L * SD * C	10	25576.44*	17.45*	7.05
Error	102	10394.01	4.59	4.26

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 4.

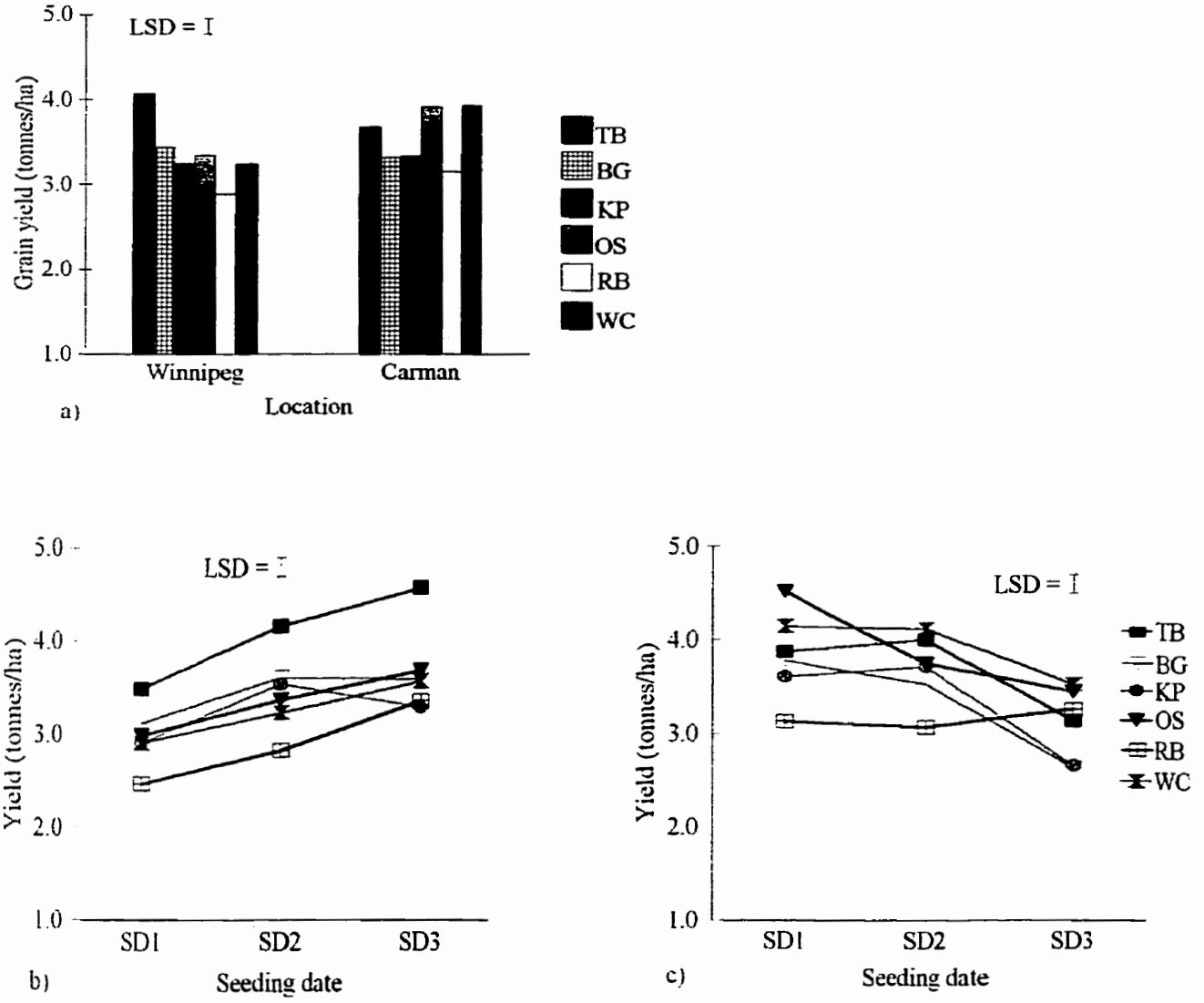


Fig. 4.8 Grain yield of spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)] a) grown at Winnipeg and Carman (averaged over all seeding dates), b) grown at different seeding dates at Winnipeg, and c) grown at different seeding dates at Carman. Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

Tiller abortion was higher at Carman than at Winnipeg (Fig. 4.5 a), and also some pre-anthesis lodging occurred at Carman but not at Winnipeg. Any combination of these factors may be responsible for the observed decline in yields at Carman with late seeding. However, the yields at Carman (except under CSD3) compared favourably with those at Winnipeg. For example, under CSD2, the yields ranged from 3.2 - 4.2 tonnes/ha, as compared to 2.8 - 4.2 tonnes/ha under WSD2. Differences in rainfall distribution pattern, soil fertility, and soil water retention properties may be partly responsible for the observed differences. The presence of a genotype by environment interaction suggests the importance of choosing an appropriate cultivar for seeding in a particular location. For example, at Carman, although Roblin had the lowest yield at SD1 and SD2, it may be a better choice over Katepwa under very late seeding conditions (Fig. 4.8 c). Further work is needed to assess the repeatability and predictability of the observed genotype by environment interactions.

4.4.6.2. Kernels per main stem spike, and unit kernel mass on main stem spike

Kernels per spike were significantly affected by location, and cultivar main effects (Table 4.5). For unit kernel mass, differences due to location, seeding date, and cultivar main effects were significant (Table 4.5). Where significant, the interaction effects on kernels per main stem spike and unit kernel mass were relatively small compared to the main effects, and therefore of minor importance. Location and seeding date are important factors in determining both the number of kernels per spike

and unit kernel mass produced by a cultivar. The cultivars produced more kernels per main stem spike, and bigger kernels at Winnipeg than at Carman (Fig. 4.9 a & b, respectively). Delays in seeding date led to increases in the number of kernels produced on the main stem spike of AC Taber, Biggar, and Wildcat, but had no significant effect on kernel numbers produced by Oslo, Katepwa, and Roblin (Fig. 4.9 c). According to Shpiler and Blum (1986), varieties that produce increased kernel numbers per main stem spike under delayed seeding, usually maintain high yields. This may partly explain why AC Taber ranked first in yield at Winnipeg, while Oslo and Wildcat produced the highest yields at Carman. However, delays in seeding date significantly reduced the kernel mass of AC Taber and Biggar (Fig. 4.9 d). These results demonstrate the compensatory ability of yield components, and agree with findings made by Nass (1973), that the number of kernels produced by the main stem and kernel weight were negatively correlated.

Gebeyehou et al. (1982a), attributed the reduction in kernel weight to the shortening of the grain filling period. Results from the present study do not support the suggestion by Gebeyehou et al. (1982 a), since all cultivars had similar grain filling periods (Fig. 4.7), when measured in growing-degree-days.

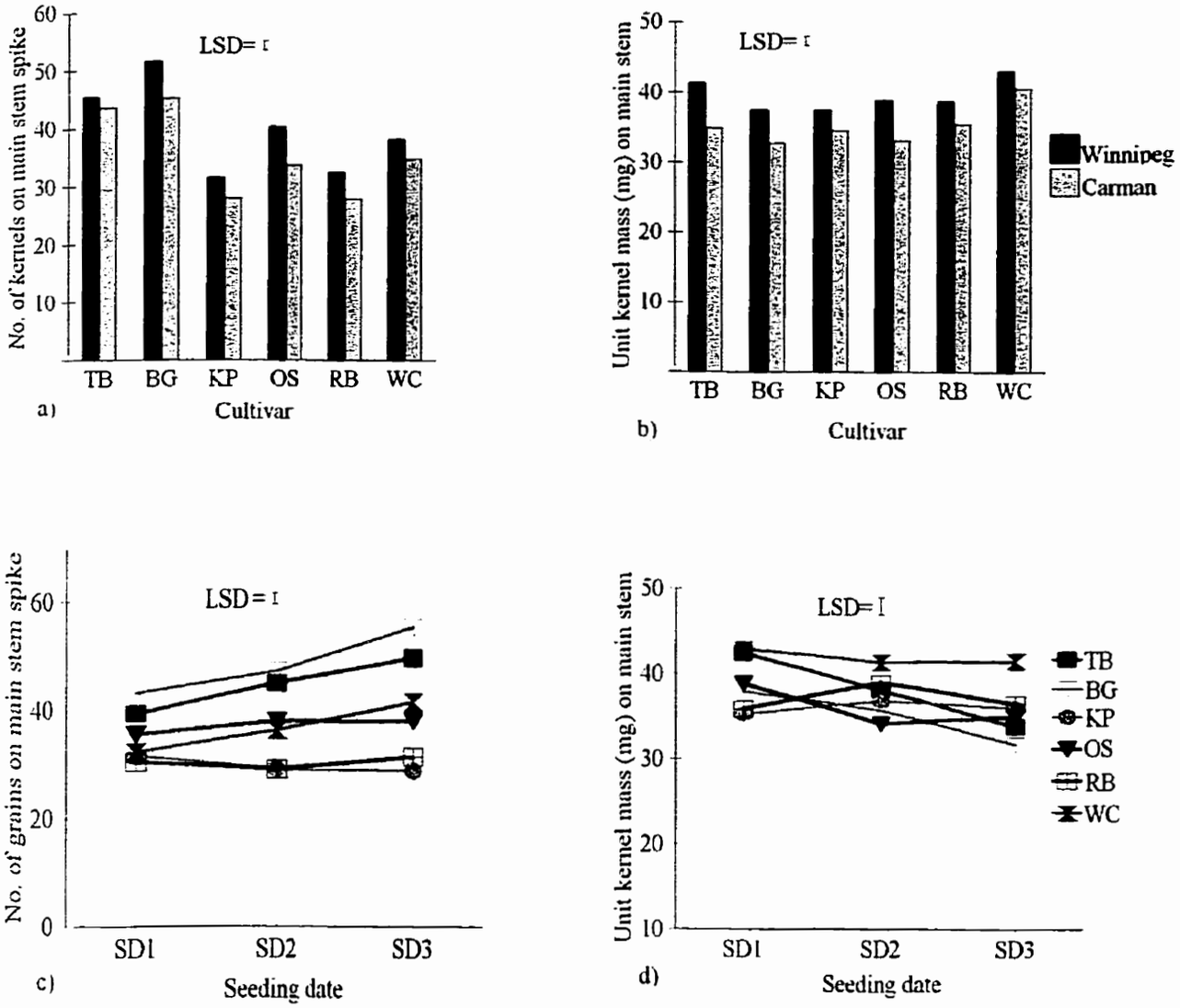


Fig. 4.9 a) Number of kernels on main stem spike at Winnipeg and Carman (averaged over all seeding dates), b) unit kernel mass on main stem spike at Winnipeg and Carman (averaged over all seeding dates), c) number of kernels on main stem spike for different seeding dates (averaged over both locations), and d) unit kernel mass on main stem spike for different seeding dates (averaged over both locations), of spring wheat cultivars AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

4.4.6.3. Spike length, number of spikelets, and number of fertile spikelets.

Spike length and the number of spikelets were significantly affected by location, and cultivar main effects, as well as location by seeding date, location by cultivar, and seeding date by cultivar interactions (Table 4.6). The location by seeding date by cultivar interaction significantly affected the number of spikelets but not the spike length. The number of fertile spikelets were significantly affected by cultivar, as well as location by seeding date, location by cultivar, seeding date by cultivar, and location by seeding date by cultivar interactions. Cultivar main effects are by far the most important of all the significant effects. The effect of environment (location and seeding date) on these yield-related traits is cultivar dependent.

AC Taber and Biggar produced the longest spikes, and the highest numbers of spikelets and fertile spikelets at both locations, and their values were higher at Carman than Winnipeg, whereas the other cultivars had similar values at the two locations (Fig. 4.10 a, b, &c). Delays in seeding date led to increases in spike length for AC Taber, Biggar, Oslo, and Wildcat, but not for Katepwa and Roblin. Katepwa and Roblin had similar spike lengths (7.0-7.5 cm), which were significantly different from the other cultivars (8.5-10.0 cm) (Fig. 4.11 a). As seeding was delayed, the total number of spikelets and the number of fertile spikelets for AC Taber and Biggar increased (Fig. 4.11 b & c), but not for Katepwa, Oslo, Roblin, and Wildcat. The behaviour of AC Taber and Biggar agrees with findings by Wall and Cartwright

Table 4.6. Analyses of variance of spike length (cm), number of spikelets, and number of fertile spikelets, of field-grown spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)], at two locations (Winnipeg and Carman) and three seeding dates per location.

Source of		Mean	Squares	
variation	df	Spike length	Spikelets	Fertile spikelets
Location	1	4.17*	22.25*	0.55
Block / Location	6	0.09	0.36	0.34
Seeding date (SD)	2	10.88	58.39	58.62
L * SD	2	0.79*	9.46*	9.34*
Cultivar (C)	5	28.97*	132.47*	72.88*
L * C	5	0.79*	4.42*	3.39*
SD * C	10	0.30*	8.21*	5.80*
L * SD * C	10	0.08	0.69*	0.79*
Error	102	0.06	0.22	0.25

* Significant mean square at the 0.05 probability level.
Model for F tests was based on appendix 4.

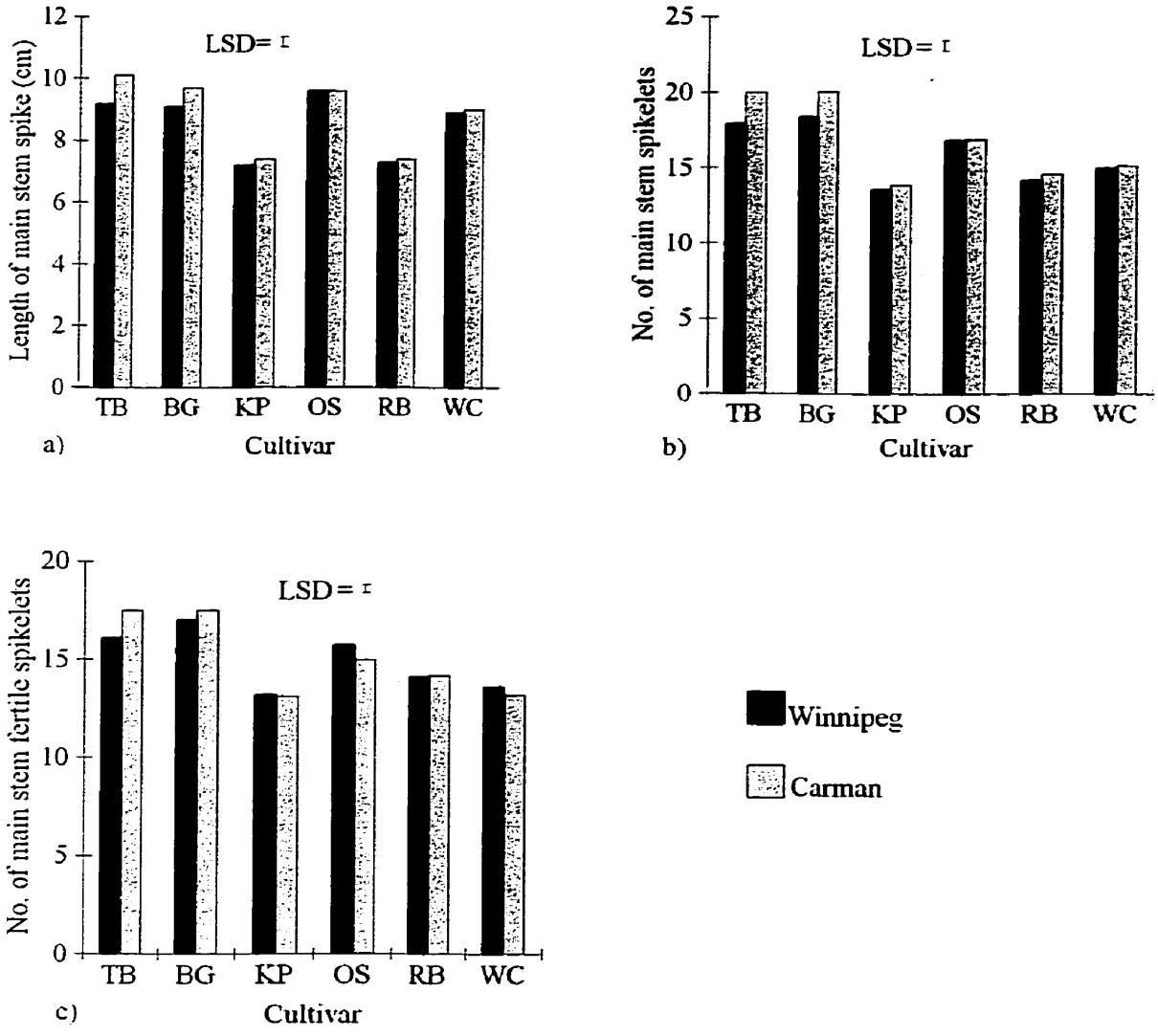


Fig. 4.10 a) Main stem spike length, b) number of main stem spikelets, and c) number of fertile spikelets on main stem, of spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)] (averaged over both locations). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

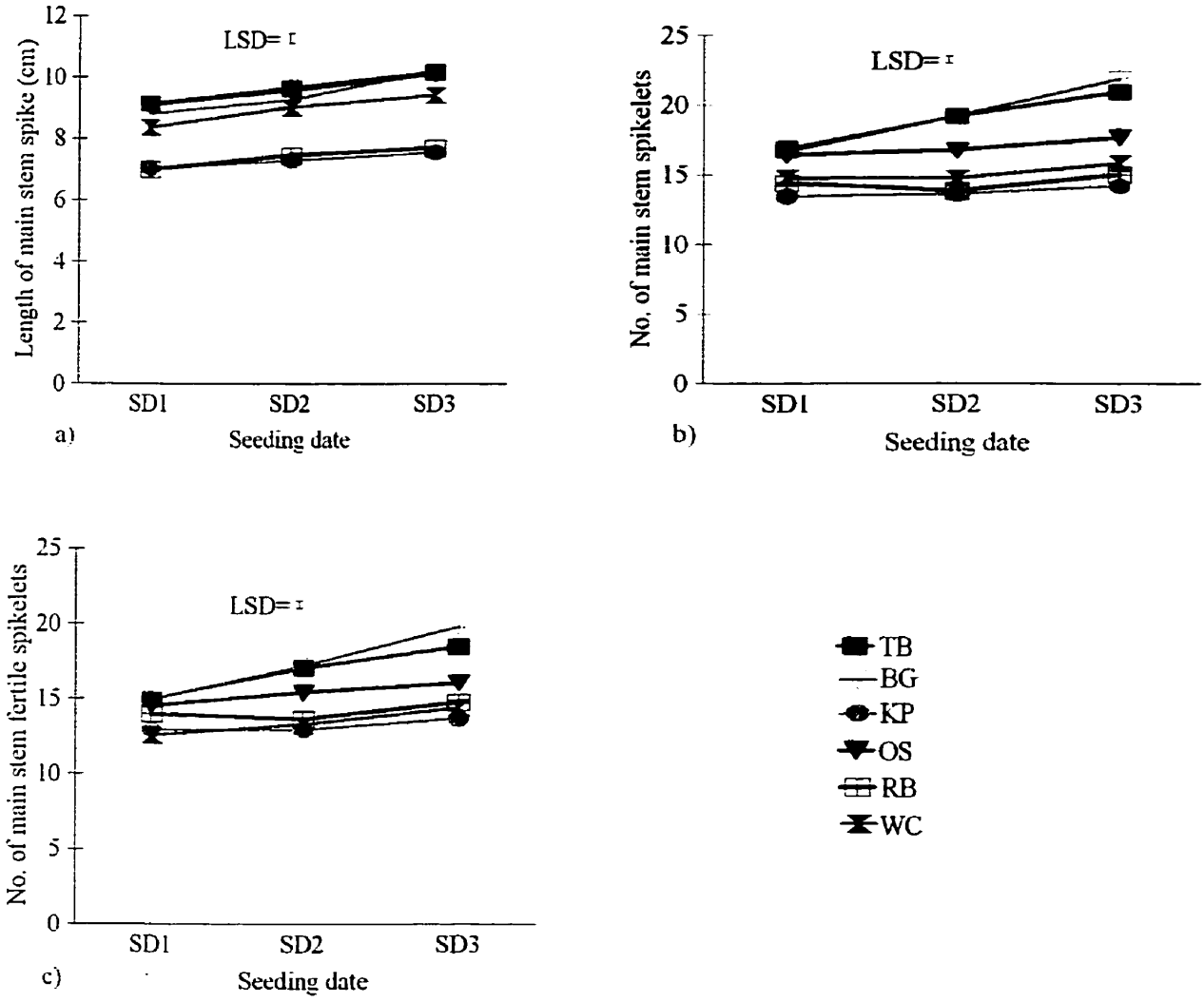


Fig. 4.11 a) Main stem spike length, b) number of main stem spikelets, and c) number of fertile spikelets on main stem, of spring wheat cultivars [AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC)] at different seeding dates (averaged over both locations). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

(1974) who found non-vernalized late maturing cultivars produced more spikelets. The response by AC Taber and Biggar may be explained by the fact that, delayed seeding presented warmer environmental conditions, which reduced or eliminated the vernalization effect of any accumulated temperatures below 10°C, or that the vernalization requirement may not have been satisfied at all. This led to a prolonged vegetative growth phase, and a subsequent prolonged spikelet initiation period for AC Taber and Biggar (Fig. 4.7 a). A prolonged spikelet initiation period led to a higher number of spikelets produced on the main stem spike (Fig. 4.11 b).

4.4.7. Grain filling

Grain filling patterns were assessed by using the three different regression models commonly reported in the literature; i.e., linear, quadratic, and cubic models (Schlotzhauer and Littell, 1987). The relationship between unit kernel mass and time (measured from anthesis) was evaluated as follows:

Linear model: $M = a + bt$

Quadratic model: $M = c + dt + et^2$

Cubic model: $M = f + gt + ht^2 + it^3$

where M was unit kernel mass (mg), t was time (days post anthesis), and *a, b, c, d, e, f, g, h,* and *i* were regression coefficients. Coefficients of determination (R^2) produced by the linear model were high (Table 4.7). However, regression diagnostics (residual plots) showed a bell-shaped pattern instead of a random distribution

(Appendix 5). Based on R^2 values alone, the cubic polynomial model would have been chosen as the best fit of the grain filling curve, since all R^2 values exceeded 0.99 (Table 4.7). Since no decrease was observed after the attainment of maximum kernel dry mass (Fig. 4.12 a, b & c), the cubic polynomial model was not considered appropriate to describe the pattern of grain filling.

Table 4.7. Coefficient of determination for linear (LM), quadratic (QM), and cubic polynomial models (CM), for grain filling of spring wheat cultivars, grown at Winnipeg, and Carman, 1996.

Cultivar	Winnipeg			Carman		
	LM	QM	CM	LM	QM	CM
AC Taber	0.868	0.994	0.997	0.961	0.997	0.998
Biggar	0.807	0.984	0.993	0.943	0.994	0.995
Katepwa	0.895	0.995	0.997	0.922	0.996	0.996
Oslo	0.908	0.992	0.998	0.895	0.984	0.986
Roblin	0.879	0.985	0.998	0.911	0.996	0.998
Wildcat	0.882	0.993	0.998	0.936	0.969	0.981

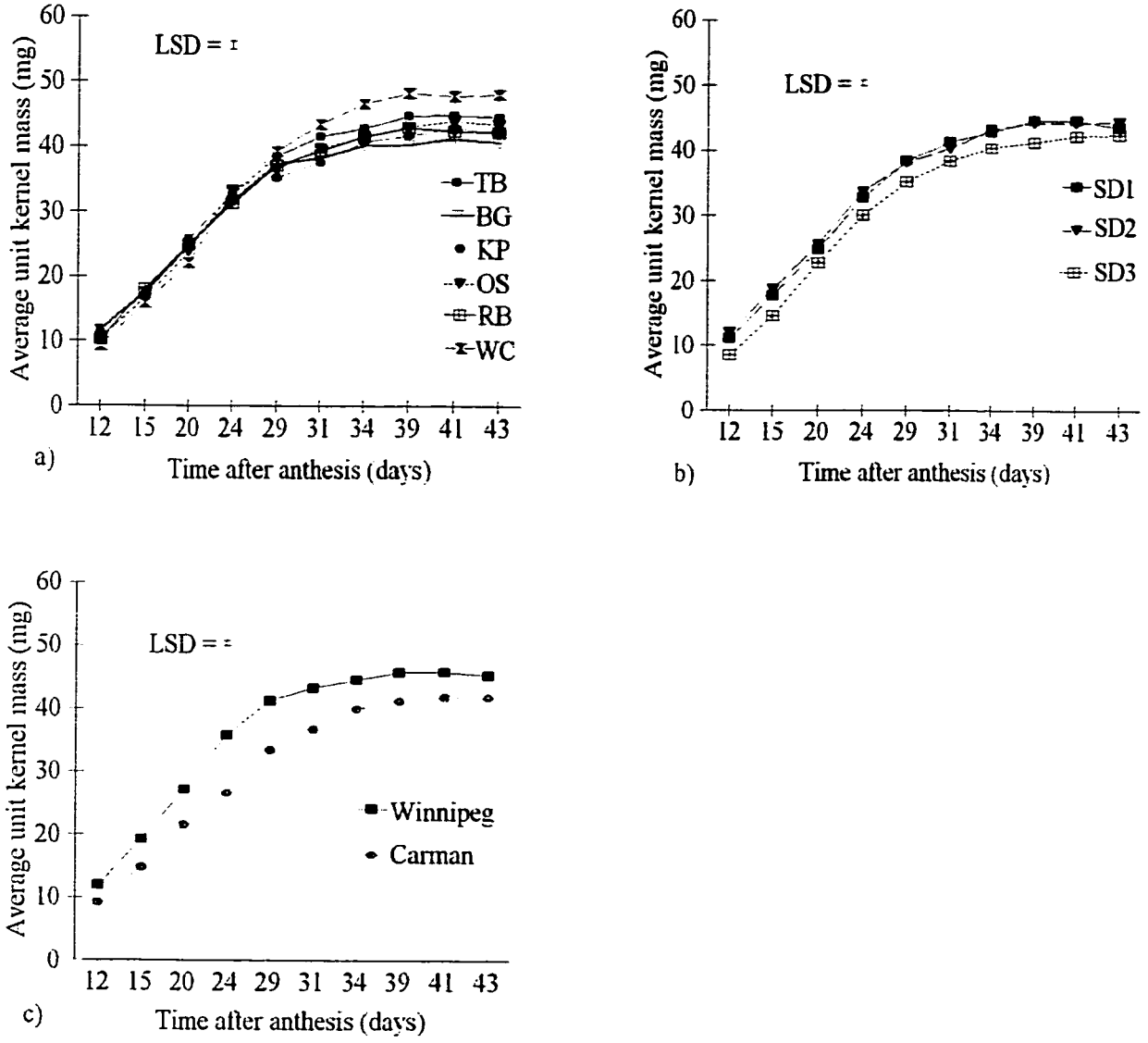


Fig. 4.12 a) Grain filling pattern (averaged over all seeding dates, and locations), b) seeding date effect on the grain filling pattern (averaged over cultivars, and locations), and c) location effect on the grain filling pattern (averaged over cultivars, and seeding dates) of spring wheat cultivars AC Taber (TB), Biggar (BG), Katepwa (KP), Oslo (OS, Roblin (RB), and Wildcat (WC). Vertical bars represent LSD (least significant difference) at 0.05 level of probability.

The R^2 values for the quadratic model ranged between 0.981-0.998, and the residual plots showed a random distribution in all cases (Appendix 6). Therefore, the quadratic model provided the best fit to the grain filling data for all cultivars at both locations. These results agree with the findings of Nass and Reiser (1975), and Bruckner and Frohberg (1987), but disagree with those of Gebeyehou et al. (1982b), and Bauer et al. (1984). Gebeyehou et al. (1982b) chose the cubic model to describe the grain filling process because, according to them, "the coefficients of determination exceeded 0.99 in all cases". The present study emphasizes the point that basing inferences and deductions on R^2 values alone without additional basic regression diagnostic procedures may lead to erroneous conclusions.

Kernel dry matter accumulation at different stages of grain filling was assessed by plotting days after anthesis (when samples were taken) against the average kernel mass. Typical sigmoid-shaped curves, consisting of a lag phase (1-1½ weeks - slow grain filling rate), a linear phase (2-2½ weeks - fast and linear grain filling rate), and the late phase (1-1½ weeks - grain filling rate is slower than the linear phase). After kernel mass had reached its maximum value, there was no decline in kernel mass (Fig. 4.12 a). It was not possible to capture the lag phase because it corresponded to the watery stage (Zadoks 70-72), and therefore when the spikes were oven-dried at 80°F, there was little or no kernel dry matter to weigh. Significant differences among cultivars occurred mainly after the linear grain filling

phase. Wildcat attained the highest kernel mass, followed by AC Taber (Fig. 4.12 a).

During the late phase of grain filling, temperatures were relatively high (Fig. 4.1 b). If the cultivar differences in grain filling were largely due to temperature effects then, based on previous observations, AC Taber and Biggar would tend to have similar grain filling patterns. The difference in grain filling patterns between AC Taber and Biggar suggests that the observed differences in grain filling may be genetic. Judel and Mengel (1982) suggested that the late phase of grain filling appears to correspond to the time during which storage carbohydrates are mobilized and translocated from vegetative plant parts (stems and leaves) to the filling grains. The observed cultivar differences in the late phase of grain filling may therefore be attributed to cultivar differences in the mobilization and translocation of storage carbohydrates from vegetative plant parts to the grains. Austin et al. (1977) estimated the proportion of assimilates which were mobilized and translocated from the vegetative organs to the wheat grain to be approximately 7% of the final grain mass. These observations may suggest, as in Gebeyehou et al. (1982b), that breeding for a higher rate of grain filling should be possible, and should not be affected by the entire duration of grain filling.

The total kernel dry matter accumulation for seeding dates one and two were not significantly different from each other, but seeding date three was significantly lower than seeding dates one and two (Fig. 4.12 b). When planting occurred in June

4-10, the accumulation of dry matter in the kernels was significantly reduced. Comparing the kernel dry matter accumulation at both locations, plants grown at Carman had significantly lower values than plants grown at Winnipeg (Fig. 4.12 c). According to Spiertz (1974), the rate of dark respiration in the stems and flag leaves of wheat plants increases (about two-fold) with increase in temperature (from 15 to 25°C), and this results in a reduction of the content of nonstructural carbohydrates in the vegetative plant parts. Such a reduction affects the quantity of stored carbohydrates that is mobilized and transported for grain filling (Judel and Mengel, 1982). Thus, when grain filling occurs under warmer environmental conditions, dry matter accumulation in the kernels may be reduced, which subsequently reduces final yield (Gebeyehou et al., 1982a). Warmer conditions are usually associated with low moisture availability. However, the higher July rainfall distribution at Winnipeg than Carman (Fig. 4.1 a), may be responsible for the observed differences of higher kernel dry matter accumulation at Winnipeg than Carman.

4.5. Conclusions

At the time of terminal spikelet initiation, all cultivars had similar number of leaves (2.5-3.0 leaves), remaining to emerge. Also, the trends depicted for heading, anthesis, and maturity were similar to those observed for terminal spikelet initiation. Therefore, cultivar differences observed at heading, anthesis, and/or maturity may be attributed to the differences in the time to terminal spikelet initiation.

Phyllochron intervals varied with cultivar and seeding date. These results suggest that the use of a common phyllochron interval of 75 GDD/leaf for spring wheat model predictions (e.g., CERES-wheat model) is inappropriate. The actual average phyllochron interval for specific spring wheat cultivars (e.g., AC Taber and Biggar = 83.5-86.7, Katepwa = 90.6-95.5, Oslo and Wildcat = 73.6-79.3, Roblin = 82.4-83.1) needs to be determined for any given environmental region/area. This should improve model predictions of crop growth stages, maturity, and yield.

Delayed seeding appeared to reduce the number of seed-bearing spikes and kernel mass, especially in the cultivars that possessed a partial vernalization requirement (AC Taber and Biggar). In vernalization-responsive cultivars, delayed seeding led to a prolonged vegetative period (longer terminal spikelet initiation period) and the production of more leaves on the main stem. Thus, the choice of a spring wheat cultivar with a partial vernalization requirement should be related carefully to the length of the growing degree-day period for any particular

environment. The presence of genotype by environment interactions further underscores the importance of choosing an appropriate cultivar for any given location and seeding date.

The quadratic model provided the best fit to the grain filling data for all cultivars at both locations. This study emphasizes the point that basing inferences and deductions on R^2 values alone without additional basic regression diagnostic procedures may lead to erroneous conclusions.

The significant cultivar differences under the different seeding dates and locations provided the needed wide range of database for the crop modelling component (chapter five) of this study.

5.0 PERFORMANCE OF THE CERES-WHEAT MODEL UNDER WESTERN CANADA (MANITOBA) ENVIRONMENT.

5.1 Abstract

Grain marketing agencies depend on wheat yield forecasts for planning grain handling and effective marketing strategies to maximize sales opportunities and profits. The Walker model, used by the Canadian Wheat Board for yield forecasting is based on a drought index and therefore its predictive power diminishes in years of above average precipitation. The Crop Estimation through Resource and Environment Synthesis (CERES)-wheat model claims to have the capability to differentiate among cultivars, as well as world-wide adaptable use. The objectives of this study were to calibrate and validate the CERES-wheat model (version 3.0) under Manitoba conditions, and to compare the yield predictions by the CERES-wheat and the Walker models. Field experiments were conducted in 1996 at Winnipeg and Carman, with three seeding dates per location, to provide current field data for model testing. The predictive power of the CERES-wheat model declined with delays in seeding. Results showed that cultivar genetic coefficients determined under early seeding date conditions in one location could be used for the same cultivar(s) at another location within the same region. Moisture availability appears to be important to the successful simulation of the CERES-wheat model. Under the given conditions of this experiment, the CERES-wheat model provided better yield predictions than the Walker model presently used by the Canadian Wheat Board.

5.2. Introduction

Wheat is an important crop to the Canadian Prairie provinces, with 25-30 million acres in production per year (Canadian Wheat Board, 1996). The Canadian Wheat Board, the main wheat marketing agency in western Canada, depends on pre-harvest yield forecasts to establish the likely quantity of grain available for sale during the year ahead. Such information is essential in planning grain handling and developing effective marketing strategies to maximize sales opportunities and profits.

Presently, the Canadian Wheat Board uses the Walker model (Walker, 1989) for yield predictions. The Walker model is an empirical (descriptive or correlative) model which is based on a drought index. Since the Walker model operates on the assumption that drought is the major factor that limits wheat yield in western Canada, its predictive power diminishes in years of above average precipitation (Dr. Paul Bullock, personal communication). Therefore, a crop model that is capable of accurate predictions under both wet and dry conditions should be beneficial to the Canadian Wheat Board. One such promising model is the Crop Estimation through Resource and Environment Synthesis (CERES)-wheat model (Hodges and Ritchie, 1991).

The CERES-wheat model is a mechanistic (explanatory) model which models the soil/crop/climate system. A unique property of the CERES-wheat model is the presence of a descriptor which is sensitive to differences in cultivar response to soil

and climatic factors. Such a model which accounts for genotypic differences, may also be useful to the plant breeder for assessing cultivar adaptability to different environments.

To investigate the feasibility for use in a particular region, a model should be calibrated and validated with a data base appropriate to the particular region (Otter and Ritchie, 1984). Moulin and Beckie (1993) and Chipanshi et al. (1997) evaluated the CERES-wheat model (version 2.0) under Saskatchewan conditions. Chipanshi et al. (1997) reported acceptable CERES-wheat model predictions for grain yields (using historic data) under Saskatchewan conditions. Moulin and Beckie (1993), however, reported unacceptable CERES-wheat model predictions of annual grain yield. Otter et al. (1986) evaluated the CERES-wheat model with data from different parts of the world and reported good prediction performance of the model. In all evaluations mentioned above, data from previous work were used. Since such previous experiments were not planned to provide the needed measurements for model evaluation, some of the basic input data requirements of the CERES-wheat model had to be estimated (e.g. seeding dates, soil moisture available). Such estimation of data inputs increased the chances of errors in the model predictions.

Skepticism for the application of crop simulation models like the CERES-wheat model, may be attributed to: 1) over-enthusiasm and apparent unrealistic claims by model builders, 2) extensive and sometimes impractical input data

requirements, and 3) lack of 'real world-based' experiments to provide input data for calibration and validation of the model. Therefore, there is a need for more model calibration and validation-directed experiments. According to builders of the CERES-wheat model, cultivar genetic coefficients determined in one region should be similar to those determined in other, possibly contrasting, regions. This assertion requires further examination. However, if the coefficients are functions of the environment in which the measurements are made, then redefinition of the coefficients and /or re-coding of the model may be necessary. To effectively evaluate claims made by the CERES-wheat model, the use of current field-based experiment measurements (not estimates from previous work) is warranted.

The objectives of this study were to use measurements made under current field experiments: 1) to determine whether the cultivar genetic coefficients are affected by the environments in which the measurements are made, 2) to calibrate and validate the CERES-wheat model (version 3.0) under Manitoba conditions, and assess model prediction accuracy of spring wheat phenology and grain yield, and 3) using the same field data to compare predictions by the CERES-wheat model and the Walker model, used by the Canadian Wheat Board for wheat yield prediction.

5.3. Materials and methods

The CERES-wheat model (version 3.0) (Tsuji et al., 1994), and the Walker model (Walker, 1989) were used in this study.

5.3.1 Model input data requirements

5.3.1.1. CERES-wheat model

The CERES-wheat model requires a number of input parameters which cover management practices, cultivar differences, soil type(s), and weather information. Management inputs include planting date, plant population per metre square, seeding depth, row spacing, initial soil conditions (moisture and fertility) at seeding, and yield and yield component data. Cultivar input parameters in the model include the total number of main stem leaves, and time to terminal spikelet initiation, to anthesis, and to maturity.

Location-specific input parameters account for the climate and soil type at a particular location. Climatic data include solar radiation, daily maximum and minimum air temperatures, and precipitation. Soil data inputs include bulk density, percentage of clay, silt and sand, pH, major nutrient content, and moisture content at different soil layers (15cm/30cm increment) up to the 120 cm depth.

5.3.1.2. Walker model

The Walker model requires only weather data (i.e., daily maximum and minimum temperatures, and daily precipitation). The model operates on the

assumption that moisture stress is the major factor that reduces crop yield. There are no management, soil, or cultivar input requirements.

5.3.2 Data sets

Six spring wheat cultivars were grown in the field under rain-fed conditions, at two locations and three seeding dates per location (chapter 4), for model calibration and validation. The cultivars used represent a range of spring wheat classes and different characteristics. AC Taber, Biggar, and Oslo belong to the Canada Prairie Red Spring Wheat Class; Katepwa and Roblin are Canada Western Hard Red Spring Wheat cultivars; while Wildcat belongs to the Canada Western Extra Strong Red Spring Wheat Class (formerly Canada Utility Spring Wheat Class). AC Taber and Biggar are known to be vernalization responsive (DePauw, personal communication).

The experiments were conducted in the summer of 1996 at Winnipeg (latitude 49.8°, longitude 97.2°) and Carman (latitude 49.5°, longitude 98.0°) (70 km from Winnipeg), Manitoba. The fields in Winnipeg had been sown to barley the previous year, whereas those in Carman were fallow the previous year. Planting dates were as follows: Winnipeg: May 8 - seeding date one (WSD1), May 27 - seeding date two (WSD2), June 10 - seeding date three (WSD3); Carman: May 13 - seeding date one (CSD1), May 24 - seeding date two (CSD2), and June 4 - seeding date three (CSD3). This provided a range of environments. Each of the six field trials was sown in a four replicate randomized complete block design. Plots were laid in duplicates, and one

set was used for destructive sampling (e.g., terminal spikelet initiation) . Each plot consisted of six 3-m rows spaced 17.5 cm apart. The centre metre of the two middle rows were marked for data collection. Plots were hand weeded. Seeding rate was adjusted for each cultivar on the basis of grain dry weight and germination percentage, to have about 950 viable seeds sown per plot (200 seeds/m^2). Based on pre-seeding soil tests, available nitrogen (N) was raised to 150 kg N ha^{-1} (based on soil nitrogen testing) with ammonium nitrate (34-0-0). The amount used was 76 kg N ha^{-1} at Winnipeg and 48 kg N ha^{-1} at Carman. The fertilizer was broadcasted by hand at the 2-3 plant leaf stage. Weather data [daily maximum and minimum temperatures (° C), and precipitation (mm)] were collected at both locations from weather stations located within 30 m of each site. The weather stations at Winnipeg ('The Point') and Carman (Agricultural Research Station, University of Manitoba) were maintained by the University of Manitoba and Environment Canada, respectively.

The Haun scale (Haun, 1973) was used to measure leaf development. Five plants per plot from the non-destructive plots were tagged at the two leaf stage and main stem leaf measurements were taken at four- to five-day intervals. The total number of leaves per main stem was determined. Phyllochron interval (growing-degree-days required to produce a leaf) was calculated by the reciprocal of the regression coefficient of the Haun leaf stage versus accumulated growing degree days

(GDD) (Hodges and Ritchie, 1991). Accumulated GDD were calculated by the summation of daily GDD (DGDD). DGDD were calculated as:

$$DGDD = \{(T_{max} + T_{min})/2\} - T_{base}$$

where T_{max} and T_{min} = daily maximum and minimum temperatures, respectively, and T_{base} is the minimum temperature at which growth is assumed to cease. In these experiments, T_{base} was assumed to be 0°C (Cao and Moss, 1989c; Baker et al., 1986).

Terminal spikelet initiation (TSI) was determined by sampling plants at four- to five-day intervals from Haun stage 2.0 to TSI. The leaf stage was recorded before cutting the leaves. Samples were kept in water in petri dishes and later dissected in the laboratory under a light microscope. The time between sampling and dissection was not more than 5 h.

The following measurements were made on the two centre 1-m rows in the destructive plots and the mean for each plot was used to analyse the number of plants emerged (at Haun stage 1.0 - 2.0), the number of spike-bearing shoots at anthesis, anthesis dry matter (cut at ground level), and the number of seed-bearing spikes (at maturity). Dry matter samples were oven-dried at 27 °C for 72 h before dry weights were determined. Tiller abortion was determined from the difference between the number of spike-bearing shoots at anthesis and the number of seed-bearing spikes at maturity. Heading, anthesis, and maturity dates (measured in days, to conform with CERES-wheat units), dry matter at maturity, and total plot grain yield were also

measured. Heading and anthesis dates were determined when 50% of the plants in a plot had reached heading and anthesis, respectively. Maturity date was determined when 50% of the plants in a plot had lost all green colouration on the main stem spikes (Hanft and Wych, 1982; Smith and Donnelly, 1991). Yield-related variables: the number of kernels, kernel mass per spike, and unit kernel mass were also measured for the main stem (at maturity).

Nine additional data sets were supplied by Mr. Darin Gibson (Ph.D. candidate, Dept. of Plant Science, Univ. of Manitoba). Mr. Gibson's experiments were conducted at Winnipeg (1993-1995) ('The Point'), and therefore, the required soil input file was available, and also some of the cultivars used were identical to those used in this study.

5.3.2.1 Soil data

Soil physical properties measured by Mills and Haluschak (1993) for Carman and by McPherson (1987) for Winnipeg were used. The soil type for the Carman experimental plots was the Winkler series, which is a moderately well drained Orthic Black soil, developed on moderately calcareous, deep, stratified, clayey lacustrine deposits (Mills and Haluschak, 1993). The soil type at Winnipeg was described as a silty clay Riverdale Floodplain (McPherson, 1987). At both locations, soil moisture, bulk density, field capacity, and wilting percentage were measured.

5.3.2.1.1 Soil sampling

A three replicate soil sample (0-30 cm depth) was used to determine initial soil nitrate, ammonium, and pH content. The soil analysis was performed by Norwest Labs, Winnipeg, Manitoba. On each seeding date, another three replicate soil sample was taken with a 11.5 cm diameter augur at depths of 0-15 cm, 15-30 cm, 30-45 cm, 45-60 cm, 60-90 cm, and 90-120 cm. The gravimetric water content for each soil layer was measured by weighing a sample of soil, oven drying the soil for 48 h at 110°C, and then re-weighing the soil sample. The difference between the wet soil and the dry soil weights provided a measure of the weight of water in the soil sample. Dividing the weight of water by the weight of the dry soil gave the gravimetric water content, which was multiplied by the bulk density to yield volumetric water content. The available water for plant growth was determined by subtracting the permanent wilting percentage from the field capacity (sections 5.3.2.1.4. and 5.3.2.1.3., respectively).

5.3.2.1.2 Bulk density

A four-replicate soil sample was collected with an 11.5 cm diameter auger to a depth of 15 cm. The soil volume was determined as: $V=(22/7)\ r^2\ h$, (where r is the radius of the auger, and h is the depth of soil collected by the auger). The weight of the oven dried soil divided by the volume of soil, provided the bulk density.

5.3.2.1.3 Field capacity

Field capacity may be defined as the amount of water remaining in a soil two or three days after saturation, when free drainage due to gravity has ceased (Hartmann et al., 1988). A 1.5 m^2 area was marked in an open space at the end of the field by mounding soil (at the perimeter) to 10 cm height. The hollow centre was filled with water to thoroughly saturate the marked area of land, and the water was securely covered with plastic sheets to prevent evaporation. Water was allowed to filter through the soil profile for 72 h. The soil profile was then sampled at incremental depths (as in section 5.3.2.1.1) and the gravimetric soil water content determined. The gravimetric soil water content was multiplied by the bulk density of the corresponding soil layer to obtain the proportion of volumetric soil water content.

5.3.2.1.4 Permanent wilting percentage

The permanent wilting percentage is defined as the soil moisture content at which a plant wilts and cannot recover when placed in an environment of 100% relative humidity. The soil moisture tension at permanent wilting percentage was assumed to be about 15 bars (Hartmann et al., 1988). The pressure membrane at 15 bar method was used to determine the permanent wilting percentage in the laboratory. Soil samples were taken from three different sites of the field to serve as replicates.

5.3.3 Simulation procedure

The Decision Support System for Agrotechnology Transfer (DSSAT v.3), of which the CERES-wheat model is a sub-programme, contains a genetic coefficient calculator (GenCalc) (Hunt et al., 1993), which was used to generate the genetic coefficients. The GenCalc divides the genetic coefficients into 'development' (P1V=vernalization coefficient, P1D=photoperiod coefficient, P5=relative grain filling duration, and PHINT=phyllochron interval, the thermal time between successive leaf tip appearance), and 'growth' (G1=kernel number per unit weight of stem; G2=kernel filling rate;, and G3=non-stressed dry weight of a single stem and spike when elongation ceases) coefficients.

GenCalc was used to determine the genetic coefficients by iterative incremental adjustments of specific coefficients. The model runs a set of coefficients and compares the simulated results with the observed results for a particular reference trait until an acceptable deviation is reached (Appendix 7). An acceptable result is reached when the output coefficient file has no letter associated with the simulated coefficients (Appendix 8).

The first seeding dates at Carman and Winnipeg were assumed to be close to the optimum seeding dates for the local farmers, and data collected for the first seeding dates were used for the determination of the genetic coefficients of the cultivars. The average of cultivar genetic coefficients determined at Carman and

Winnipeg were used to simulate growth of the crop at the other two seeding dates at the two locations.

For further validation of the CERES-wheat model, the independent data sets supplied by Mr. Darin Gibson were used. In collaboration with Mr. Bruce Burnett (Director, Weather and Crop Surveillance, Canadian Wheat Board), the Walker model was applied to the Carman and Winnipeg weather data for yield predictions.

5.3.4 Statistical analysis

According to Willmott (1982), the correlation coefficient and the coefficient of determination are of little practical value in evaluating the predictive capabilities of models because their magnitudes are not consistently related to the accuracy of prediction. More appropriate criteria include: mean bias error (MBE), root mean square error (RMSE), and mean absolute error (MAE) (Fox, 1981; Willmott, 1982). The equations are:

$$MBE = n^{-1} \sum_{i=1}^{n} (P_i - O_i)$$

$$RMSE = [\, n^{-1} \sum_{i=1}^{n} (P_i - O_i)^2 \,]^{0.5}$$

$$MAE = n^{-1} \sum_{i=1}^{n} | P_i - O_i | \qquad \text{(Fox, 1981),}$$

where n is the number of data sets, P = predicted values, and O = observed values.

Willmott (1982) contends that RMSE and MAE are similar measures, and that reporting either one is appropriate. The RMSE and MAE measures indicate the variability around the mean. If there is a close agreement between predicted and observed dates, then the RMSE will be small. Willmott (1982) further suggests the computation of an index of agreement (*d*), which provides a measure of the degree to which a model's predictions are error free. This quality measure is useful for either evaluating a single model, or to compare different models. Willmott's index of agreement varies between 0.0 and 1.0, and for a good model prediction *d* should approach 1. The index is expressed as:

$$d = 1 - \left[\frac{\sum_{i=1}^{n} (P_i - O_i)^2}{\sum_{i=1}^{n} (|P_i^*| + |O_i^*|)^2} \right]$$

where P = predicted values, O = observed values, $P_i^* = P_i - \bar{O}$, $O_i^* = O_i - \bar{O}$, $\bar{O}$ = mean of observed variates, and $0 \leq d \leq 1$.

The three statistics used to evaluate model predictions were: i) MBE, ii) RMSE, and iii) Willmott's index of agreement (*d*). Scatter plots of measured values versus predicted values were also assessed to lend credibility to quantitative comparisons, reveal any possible erroneous computations (Willmott, 1981), and identify the strengths and weaknesses of model predictions with respect to specific

variables. Percentage deviations [(predicted - observed)/(observed) x 100] of yield were calculated to allow for the consideration of model performance on individual cultivars. Where scatter diagrams and regression analysis were used, they served only as a convenient means for evaluating the closeness between predicted and measured values.

5.4 Results and discussion

5.4.1 Genetic coefficients/calibration

In most cases the cultivar genetic coefficients determined for Carman and Winnipeg were either identical or close to each other, except for G1 (Table 5.1). Any significant effect(s) of the few observed differences will be assessed and discussed in section 5.4.5. The P1V (vernalization coefficient) values of AC Taber and Biggar were 0.5, and 0.8, respectively, whereas the values for the other four cultivars were very close to 0.01 (Table 5.1). Thus, the CERES-wheat model (through the GenCalc component) was able to differentiate one group of cultivars that have a partial vernalization requirement from the other group that does not. It should be noted that with the exception of Biggar, all cultivars showed a clear departure from the recommended, and often used, P1V value of 0.5 (Pecetti and Hollington, 1997; Chipanshi et al., 1997) for spring wheat cultivars. This points to the importance of determining and using the appropriate P1V value to avoid erroneous predictions.

The P1D (photoperiod coefficient) values depicted a sensitivity to photoperiod by AC Taber and Biggar, but not the other cultivars (Table 5.1). These observations were consistent with those made under the controlled environment experiments (chapter 3). Simulated PHINT (phyllochron interval) values for a particular cultivar were identical for Winnipeg and Carman (Table 5.1). These results support to the

Table 5.1 Genetic coefficients (determined by GenCalc) for spring wheat cultivars grown at Carman (seeding date one) and Winnipeg (seeding date one).

Cultivar	P1V [z]	P1D	P5	G1	G2	G3	PHINT	
							Sim.	Meas.
AC Taber	**0.8**	**1.0**	**5.4**	**4.7**	**4.5**	**2.6**	**80**	**85**
	0.8	1.0	5.4	5.7	4.8	3.1	80	87
Biggar	**0.5**	**1.0**	**5.4**	**5.1**	**2.4**	**2.2**	**80**	**83**
	0.5	1.0	5.4	6.2	1.2	3.1	80	86
Katepwa	**0.01**	**0.01**	**6.9**	**5.2**	**1.0**	**1.2**	**77**	**91**
	0.01	0.01	6.9	5.6	1.0	1.7	77	96
Oslo	**0.01**	**0.01**	**5.5**	**7.1**	**3.1**	**1.3**	**77**	**74**
	0.01	0.01	5.5	7.1	3.1	1.3	77	79
Roblin	**0.01**	**0.01**	**4.4**	**5.5**	**1.0**	**1.2**	**70**	**82**
	0.01	0.01	5.2	5.5	1.0	1.2	70	83
Wildcat	**0.01**	**0.01**	**6.9**	**5.2**	**1.0**	**1.2**	**77**	**74**
	0.01	0.01	4.8	7.1	3.0	1.1	77	76

[z] Coefficients: P1V=vernalization coefficient; P1D=photoperiod coefficient; PHINT=phyllochron interval, the thermal time between successive leaf tip appearance; P5=relative grain filling duration; G1=kernel number per unit weight of stem; G2=kernel filling rate; and G3=non-stressed dry weight of a single stem and spike when elongation ceases. All coefficients, except PHINT, have scalar values between 0 and 9.

Values in boldface and regular font are for Carman and Winnipeg, respectively.

fact that the GenCalc in the CERES-wheat model is capable of differentiating among cultivar characteristics. However, comparing the simulated PHINT with the measured values (measured in chapter 4), there is a general tendency for the model to under-predict PHINT (Table 5.1). This may lead to underestimation of certain phenological stages which are based on PHINT values. Equations that control the calculations of PHINT in the CERES-wheat model may therefore require reassessment.

Chipanshi et al. (1997) reported a PHINT (phyllochron interval) range of 65 to 70 for spring wheat cultivars grown under Saskatchewan conditions. Ritchie (1991) advocates that for spring wheat grown in latitudes greater than 30°N and 30°S, a PHINT value of 75 should be appropriate. From the present work, only Oslo and Wildcat had PHINT values which were comparable to the cited works (74 to 77) (Table 5.1). The rest of the cultivars had PHINT values between 82 to 91. These results show that phyllochron values are genotype specific, and therefore in validating the CERES-wheat model for any growing region, the actual phyllochron value(s) should be determined. Further work is needed to investigate whether PHINT values determined over broader and distant locations would show PHINT to be environment dependent.

5.4.2 General performance of the CERES-wheat model

Negative MBE values are obtained when predicted values are smaller than measured values. All MBE values for grain yield were negative and ranged from

-0.259 to -1.1 t/ha (Table 5.2). The CERES-wheat model appeared to have a general tendency to underestimate grain yield (Fig. 5.1) (graph plots were mostly below the 1:1 line). Both MBE and RMSE values showed a gradual decline in the predictive power of the model as seeding date was delayed (Table 5.2). Willmott's index of agreement (*d*) reinforces this observation. At both Carman and Winnipeg, the model predictions produced high *d* values for the first seeding dates ($\simeq$0.75), as opposed to low values for delayed seeding dates (0.45-0.54) (Table 5.2). The time of planting does affect the predictive power of the model; the earlier the seeding date the better the prediction. Otter et al. (1986) reported a constant Wilmott's index of agreement (*d*) value of 0.88 for CERES-wheat yield predictions. Results from the present work show that under diverse field conditions the *d* values may be different. The high *d* value reported by Otter et al. (1986) may be partly attributed to the use of estimated values instead of actual measured values, and the repeated use of many data sets in both the calibration and validation processes. The present work contrasts the use of historic data for genetic coefficient estimates, and the repeated use of data sets for both calibration and validation which could lead to erroneous conclusions. The use of current field data for model calibration and validation should therefore be encouraged.

Moulin and Beckie (1993) and Touré et al. (1994) reported that the CERES-wheat model underestimated yield in high-yielding environments and overestimated

Table 5.2 Mean bias error (MBE), root mean square error (RMSE), and Willmott's index of agreement (*d*) for grain yield (t/ha) of spring wheat cultivars (combined over cultivars) grown at Winnipeg and Carman, 1996.

Data set	MBE	RMSE	*d*
	t/ha		
CSD1 [z]	-0.259	0.400	0.74
CSD2	-0.396	0.524	0.54
CSD3	-0.443	0.881	0.45
WSD1	-0.428	0.513	0.72
WSD2	-1.060	1.081	0.48
WSD3	-0.913	1.019	0.45

[z] CSD1, CSD2, & CSD3 = Carman seeding date one, two, & three, respectively; WSD1, WSD2, & WSD3 = Winnipeg seeding date one, two, & three, respectively.

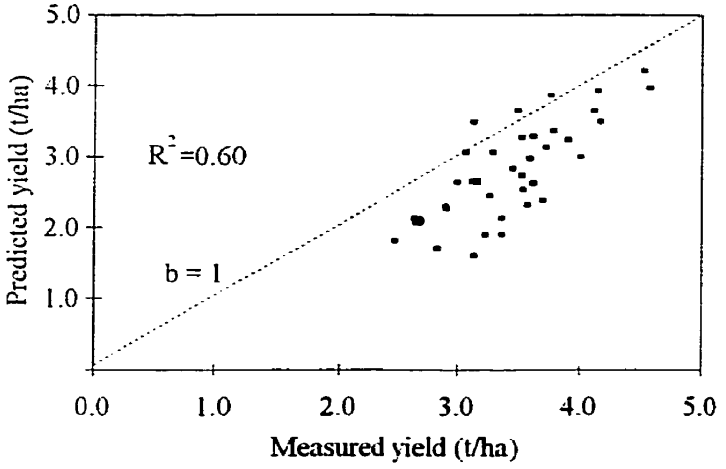


Fig. 5.1. Scatter plot of measured versus predicted grain yield of spring wheat cultivars (combined over cultivars for all seeding dates) grown at Winnipeg and Carman, 1996.

yield in low-yielding environments (genetic coefficients were estimated from calibration with historic data). Only a general tendency for underestimation of grain yield in all environments was observed in the present work.

5.4.3 Model performance on individual cultivars

For CSD1 and CSD2, predicted grain yield values were mostly within 16 % deviation from the measured values (Table 5.3), which is within the limits of model reliability used by other workers (Pecetti and Hollington, 1997; Moulin and Beckie, 1993; Stapper and Harris, 1989; Otter and Ritchie, 1984). Overall, predictions for Winnipeg were poorer than predictions for Carman, which is difficult to explain. At Winnipeg only AC Taber WSD1 & WSD3, Biggar WSD1, Katepwa WSD3, and Oslo WSD1 were within the acceptable 15% grain prediction limit. Nevertheless, the general tendency of the CERES-wheat model to underestimate grain yield was obvious for all seeding dates at both locations (Table 5.3).

5.4.4 Strengths and weaknesses of the CERES-wheat model predictions

The number of leaves produced on the main stem and kernels per metre square were simulated with closer agreement between predicted and measured values (R^2=0.60, in each case) than unit kernel mass, kernels per spike, time to anthesis, and time to maturity (R^2: 0.11 to 0.36) (Figs. 5.2 a, b, c, d, e, & f). The model however, had a general tendency to under-estimate anthesis and maturity dry matter (Fig.5.3 a & b). The poor dry matter prediction tendency, which was more pronounced under

Table 5.3 Predicted (Pred), observed (Obsvd), and percentage deviation (%Dev.) [(predicted - observed)/(observed) x 100] grain yields (kg/ha) of spring wheat cultivars grown at Carman and Winnipeg.

Cultivar	CSD1 [z]			CSD2			CSD3		
	Pred	Obsvd	%Dev.	Pred	Obsvd	%Dev.	Pred	Obsvd	%Dev.
AC Taber	3238	3872	-16.4	2996	4001	-20.1	1606	3137	-48.8
Biggar	3364	3779	-11.0	3260	3525	- 7.5	2126	2643	-19.6
Katepwa	3280	3613	- 9.2	3137	3717	-15.6	2062	2656	-22.4
Oslo	4212	4522	- 6.9	3863	3753	2.9	2826	3452	-18.1
Roblin	3485	3131	11.3	3059	3067	- 0.3	2452	3262	-24.8
Wildcat	3928	4145	- 5.2	3647	4115	-11.4	2734	3525	-22.4
Mean			*- 6.2*			*- 9.5*			*-26.0*
	WSD1			WSD2			WSD3		
AC Taber	3649	3490	4.6	3495	4163	-16.0	3970	4569	-13.1
Biggar	2643	3119	-15.3	2621	3613	-27.5	2968	3590	-17.3
Katepwa	2300	2906	-20.9	2527	3538	-28.6	3060	3290	- 7.0
Oslo	2636	2994	-12.0	2132	3365	-36.6	2376	3690	-35.6
Roblin	1819	2467	-26.3	1705	2833	-39.8	1900	3363	-43.5
Wildcat	2271	2913	-22.0	1897	3227	-41.2	2320	3571	-35.0
Mean			*-15.3*			*-31.6*			*-25.3*

[z] CSD1 = Carman seeding date 1 etc., WSD1 = Winnipeg seeding date 1 etc. Yield predictions for Winnipeg were simulated with genetic coefficients determined from Carman data.

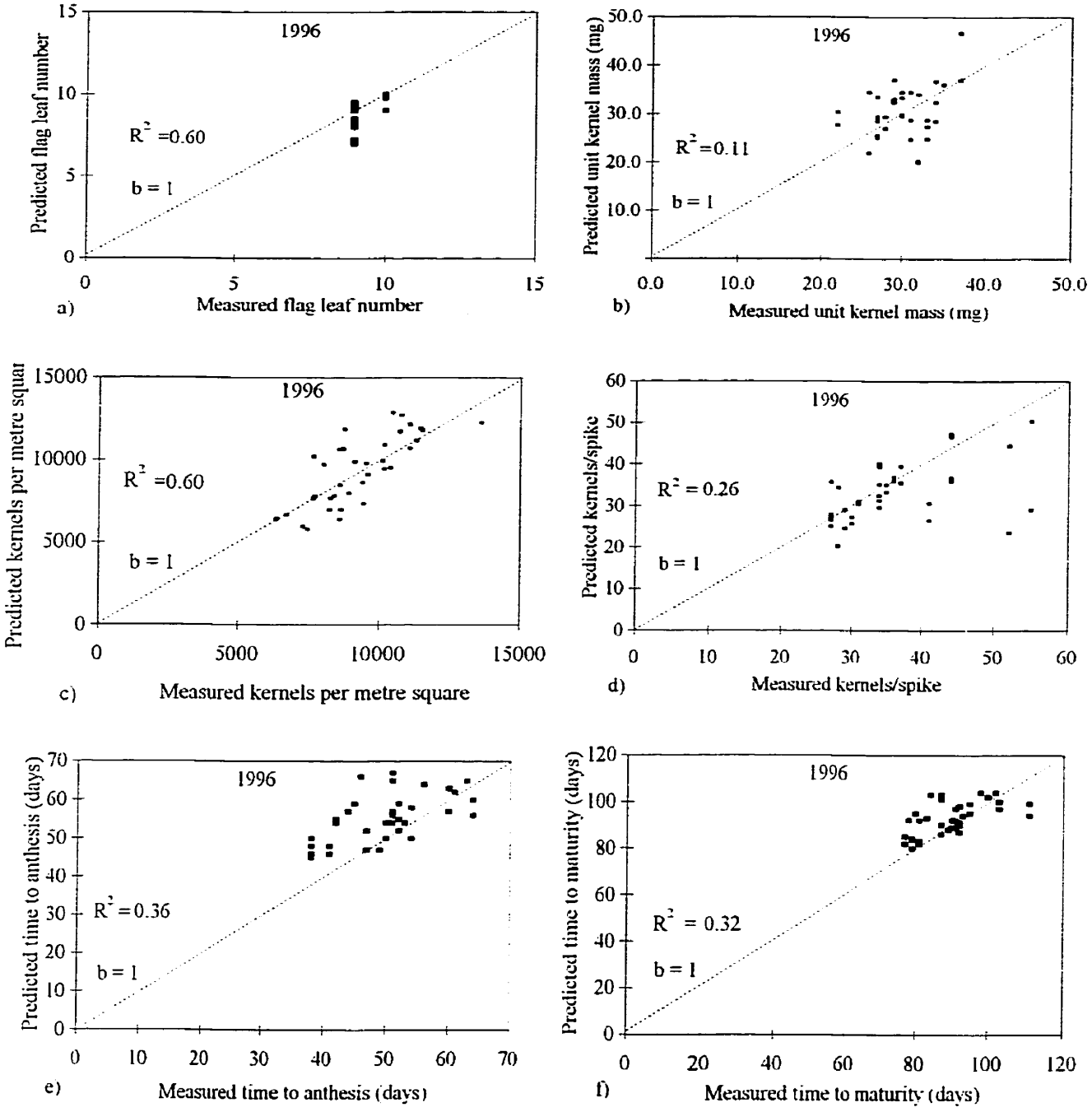


Fig. 5.2. Scatter plot of measured versus predicted values of spring wheat cultivars (combined over cultivars for all seeding dates) grown at Winnipeg and Carman, 1996, for a) number of leaves, b) unit kernel mass, c) kernels/m^2, d) kernels/spike, e) time to anthesis (days), and f) time to maturity (days).

warmer conditions (Table 5.4), may be responsible for the overall poor model performance, especially under late seeding.

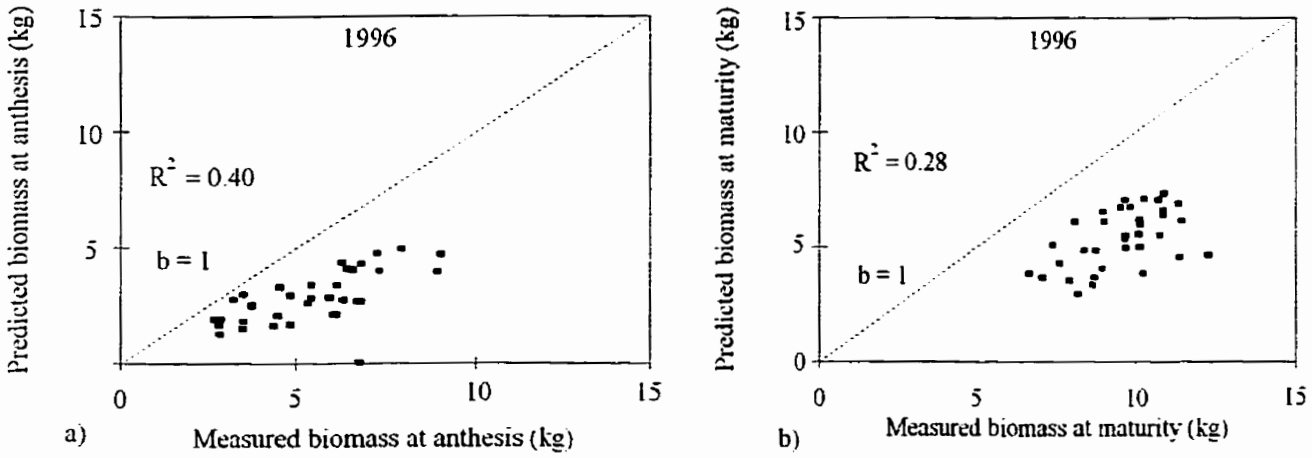


Fig. 5.3. Scatter plot of measured versus predicted values of spring wheat cultivars (combined over cultivars for all seeding dates) grown at Winnipeg and Carman, 1996, for a) dry matter at anthesis, and b) dry matter at maturity.

Table 5.4 Mean bias error (MBE) and root mean square error (RMSE) for flag leaf number, anthesis, maturity, anthesis biomass, maturity biomass, kernel mass, kernels per spike, and kernels per metre square of spring wheat cultivars (combined over cultivars) grown at Winnipeg, and Carman, 1996.

Trait	MBE			RMSE		
	SD1 [z]	SD2	SD3	SD1	SD2	SD3
	Carman					
Flag leaf number	0.79	0.50	0.29	1.02	0.71	0.59
Anthesis (days)	3.67	0.33	-0.50	4.62	3.11	4.92
Maturity (days)	2.83	-1.30	-4.30	3.67	3.42	9.17
Anthesis biomass	-2534	-3166	-3805	2575	3242	3890
Maturity biomass	-3421	-3821	-5582	3505	3906	5714
Kernel mass (mg)	1.12	1.73	5.35	2.26	5.14	7.86
Kernels/spike	0.03	-2.22	-13.8	2.94	5.33	17.2
Kernels/metre sq.	1033	863.7	475.7	1766	1240	1375
	Winnipeg					
Flag leaf number	1.17	1.33	0.50	1.22	1.41	0.71
Anthesis (days)	12.17	8.00	6.17	14.34	8.76	7.38
Maturity (days)	15.50	4.83	2.17	15.59	6.04	4.64
Anthesis biomass	-895	-1875	-3324	943	1931	3722
Maturity biomass	-2886	-4602	-4657	2944	1465	4769
Kernel mass (mg)	2.25	1.85	2.15	5.19	3.33	5.85
Kernels/spike	0.67	1.37	-3.18	1.17	4.38	6.28
Kernels/metre sq.	-223	-1238	-564	373	1383	1469

[z] SD1, SD2, & SD3 = seeding date one, two, & three, respectively.

Dry matter at anthesis is dependent on the duration of the pre-anthesis growth stages (Ritchie, 1991). If the duration of the pre-anthesis growth stages was directly responsible for the lower biomass predicted values, then the model prediction of time to anthesis should also have been underestimated. The CERES-wheat model algorithms for biomass prediction may need modification(s). These results also bring into question the basic assumption in the CERES-wheat model (like most crop models) that plants are at the same temperature as the atmospheric air, and that all processes are driven by air temperature. When plants are small, their development are influenced by soil temperature (Bollero et al., 1996; Addae and Pearson, 1992). Several researchers have reported that soil temperature provides a greater predictive accuracy in cereals (Bollero et al., 1996; Jamieson et al., 1995; Ong, 1983). However, McMaster and Wilhelm (1998) reported otherwise and concluded that the additional effort and expense of using soil temperature in predicting wheat phenology are not justified. Most model validation work use historic data which produce results and conclusions different from those based on field data, as shown by the present study. Although model calibration and validation based on current field data is labour and time-demanding, it is essential for effective evaluation of model accuracy and claims. Similarly, the additional effort and expense of gathering soil temperature data should not deter its use for effective model validation. Further studies are needed in this area.

5.4.5 Location-specific CERES-wheat coefficients, and model predictions

To test whether differences observed between cultivar genetic coefficients determined at Carman and Winnipeg were of significant prediction importance, the two sets of genetic coefficients were used for separate grain yield predictions on the Winnipeg data sets (Fig. 5.4 a & b). Both predictions were similar and the predicted yields were underestimated. The similarity in yield predictions by the two sets of coefficients was confirmed by a high coefficient of determination ($R^2 = 0.98$) (Fig. 5.4 c). This suggests that CERES-wheat model cultivar genetic coefficients determined under early seeding conditions at Winnipeg could be used for the same cultivar(s) under early seeding conditions at Carman. This appears to support the claim for the CERES-wheat model that cultivar genetic coefficients determined in one region should be similar to those determined in other regions (Hodges and Ritchie, 1991).

5.4.6 CERES-wheat model validation with 1993 to 95 Winnipeg data

Unlike the 1996 data (Table 5.2), MBE, RMSE and Willmott's index of agreement (Willmott, 1982) values for the 1993 to 95 data did not show a sequential decline in the predictive power of the model for grain yield, kernels per spike, time to anthesis and time to maturity with delays in seeding (Table 5.5). A comprehensive study involving field data over a number of years and locations may be necessary to explain these differences better. All MBE values for grain yield were negative, which

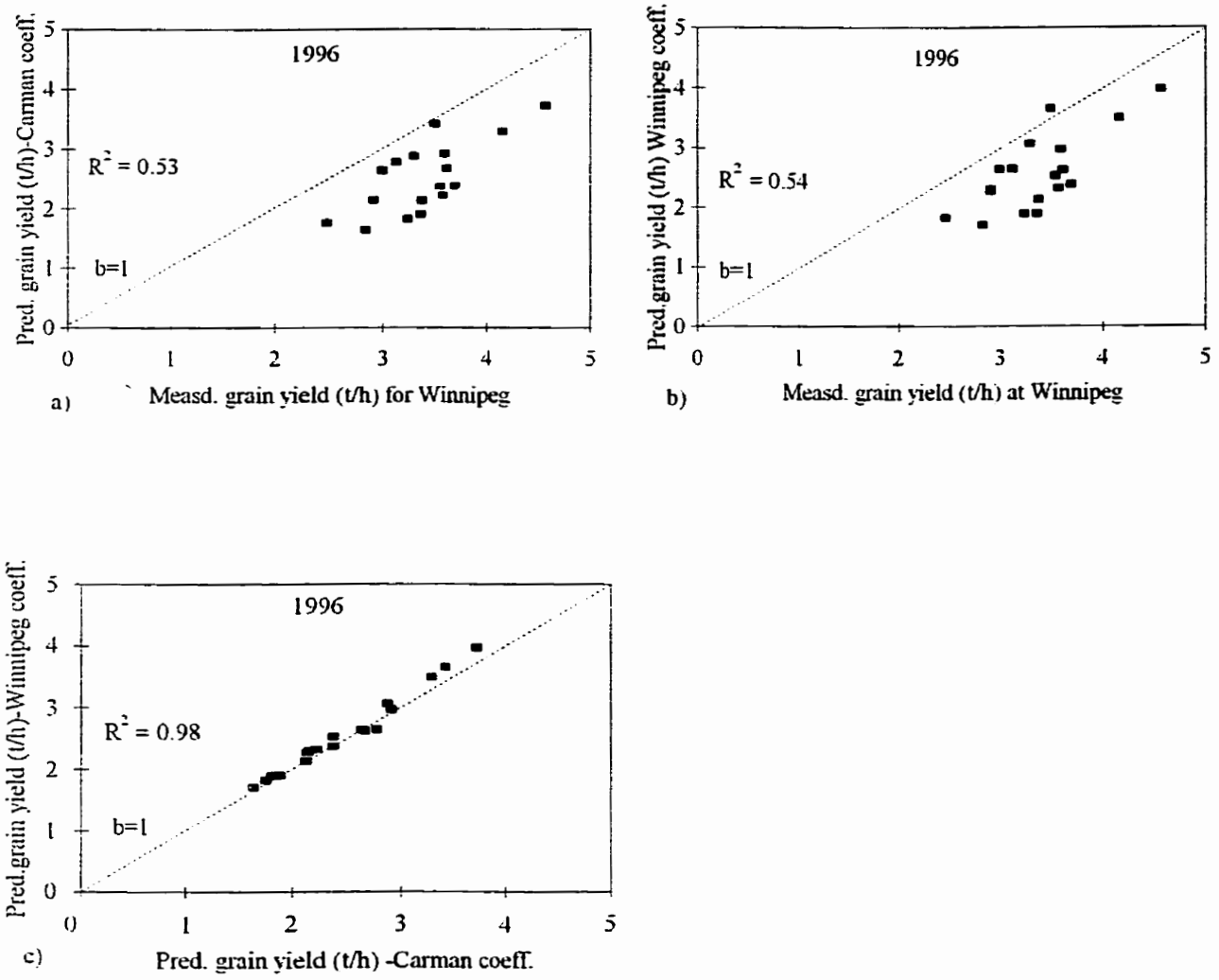


Fig. 5.4. Scatter plot of measured versus predicted values of spring wheat cultivars (combined over cultivars for all seeding dates) grown at Winnipeg and Carman, 1996, for a) Carman coefficient yield predictions, b) Winnipeg coefficient yield predictions, and c) Carman coefficient versus Winnipeg coefficient yield predictions.

Table 5.5 Mean bias error (MBE), root mean square error (RMSE), and Willmott's index of agreement (*d*) for grain yield (kg/ha), anthesis (days), maturity (days), and grains per main stem spike, of spring wheat cultivars (combined over cultivars) grown at Winnipeg, 1993-1995.

Seeding date	1993			1994			1995		
	MBE	RMSE	*d*	MBE	RMSE	*d*	MBE	RMSE	*d*
					Grain yield				
SD1 [z]	-0.02	0.62	0.33	-0.81	0.92	0.64	-3.3	3.2	0.18
SD2	-0.53	0.75	0.48	0.43	0.48	0.89	-3.1	3.2	0.20
SD3	-0.31	0.64	0.52	-1.46	1.56	0.55	-3.7	3.7	0.21
					Anthesis				
SD1	6.2	7.7	0.12	9.6	10.1	0.34	4.4	5.7	0.43
SD2	2.2	3.7	0.72	1.8	4.4	0.65	1.2	3.5	0.67
SD3	0.0	6.4	0.0	11.2	11.6	0.40	14.4	14.7	0.15
					Maturity				
SD1	4.8	6.7	0.17	11.0	11.7	0.41	2.4	4.0	0.68
SD2	0.2	4.8	0.15	8.4	9.3	0.50	0.0	3.6	0.73
SD3	-3.2	8.4	0.0	19.4	19.9	0.27	12.2	13.2	0.29
					Grains/spike				
SD1	-1.26	5.8	0.34	-9.34	9.9	0.50	-18.5	18.8	0.25
SD2	-0.02	6.8	0.40	-4.78	5.5	0.78	-20.6	21.2	0.25
SD3	2.1	6.3	0.85	5.08	11.1	0.63	-26.5	26.9	0.21

[z] SD1, SD2, & SD3 = seeding date one, two, & three, respectively.

agrees with the previously observed general tendency of the CERES-wheat model to underestimate grain yield (section 5.4.2).

Coefficient of determination for predicted versus measured grain yields at Winnipeg for 1993, 1994, and 1995 were, 0.53, 0.29, and 0.02, respectively (Fig. 5.5 a, b and c). Model predictions for 1993 and 1994 grain yield were better than that of 1995 (Table 5.5). The extremely poor model performance for 1995 grain yield [low *d* values (Table 5.5)] is difficult to explain. Although low monthly total precipitation and high temperature conditions characterized the 1995 growing season (Fig. 5.6 a & b), measured grain yields for 1995 were higher than 1993, and comparable to 1994.

Phenological predictions such as time to anthesis and maturity tended to be slightly overestimated (Fig. 5.7 a-f). This weakness in CERES-wheat model predictions could have serious negative effects on the choice of cultivars for the frost-free growing season of specific areas. Since the calculation of phenological stages are chiefly driven by the phyllochron interval, this weakness may be a reflection of the error in the assumption that leaf development is linear used by the CERES-wheat model to calculate phyllochron interval values. According to Shaykewich (1995), under field conditions where temperature and photoperiod change during the growing season, the effects of temperature and photoperiod are likely to be different at different phases of wheat growth and development, but not linear at all stages. This is an important factor that needs to be taken into account by crop modellers.

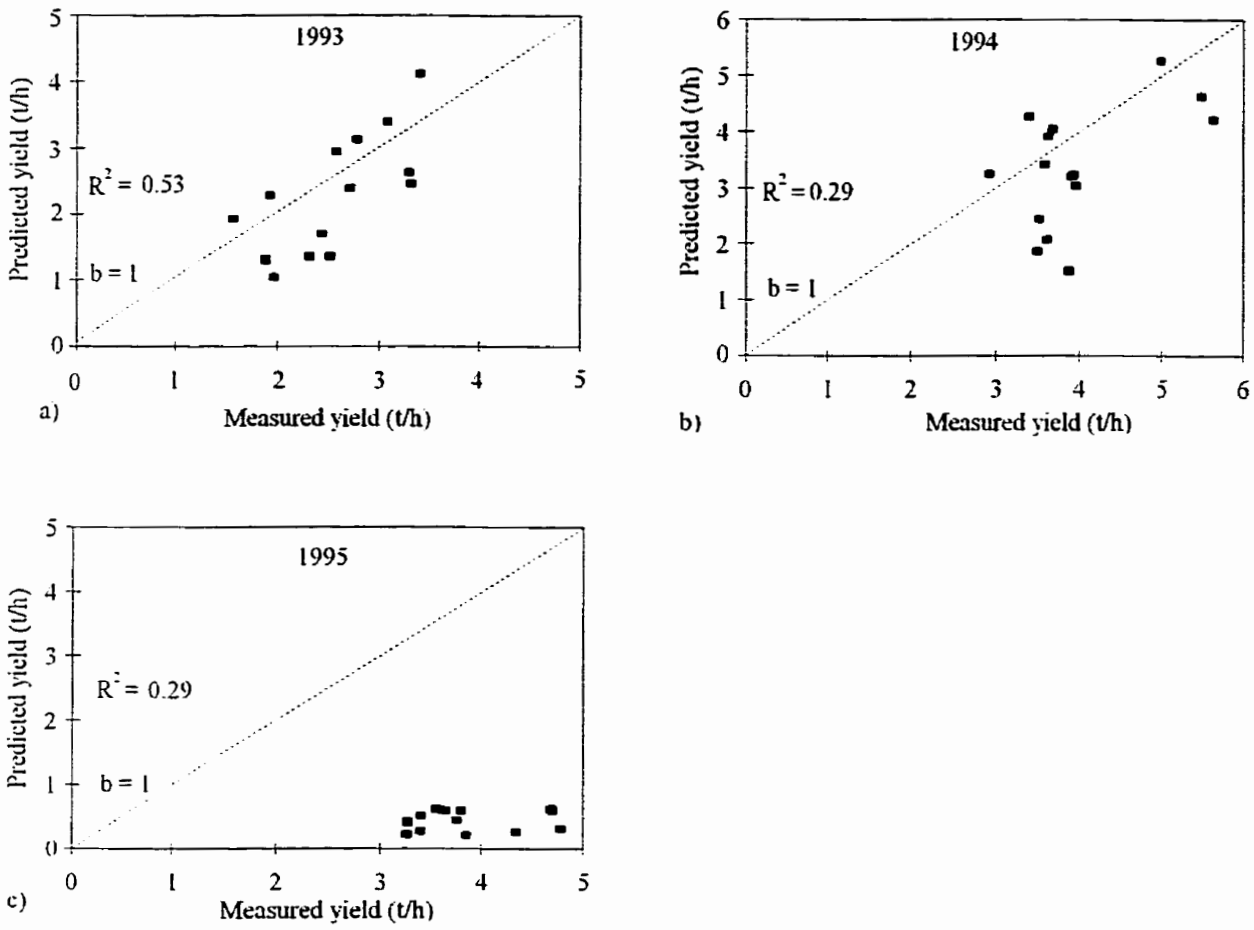


Fig. 5.5 Scatter plot of measured versus predicted grain yield of spring wheat cultivars (combined over cultivars for all seeding dates) grown at Winnipeg in a) 1993, b) 1994, and c) 1995.

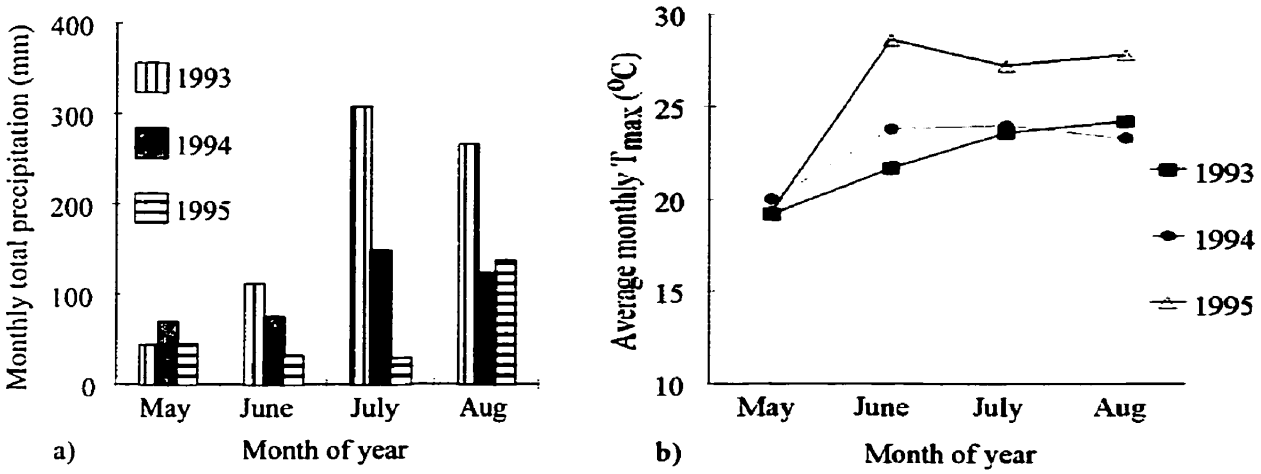


Fig. 5.6 a) Monthly total precipitation and b) average monthly maximum temperature at Winnipeg for May through August of 1993, 1994, and 1995.

5.4.7 Walker model predictions

The same weather data for Winnipeg (1996) and Carman (1996) used to test the performance of the CERES-wheat model, were also used to test the Walker model. The Walker model predictions were simulated and provided by Mr. Bruce Burnette (Director, Weather and Crop Surveillance Department, Canadian Wheat Board). Historic Prairie data from 1982 to 1997 was used to provide a regression of drought stress index versus yield. Drought stress indices for Winnipeg and Carman were determined for 1996 and yield predictions were obtained.

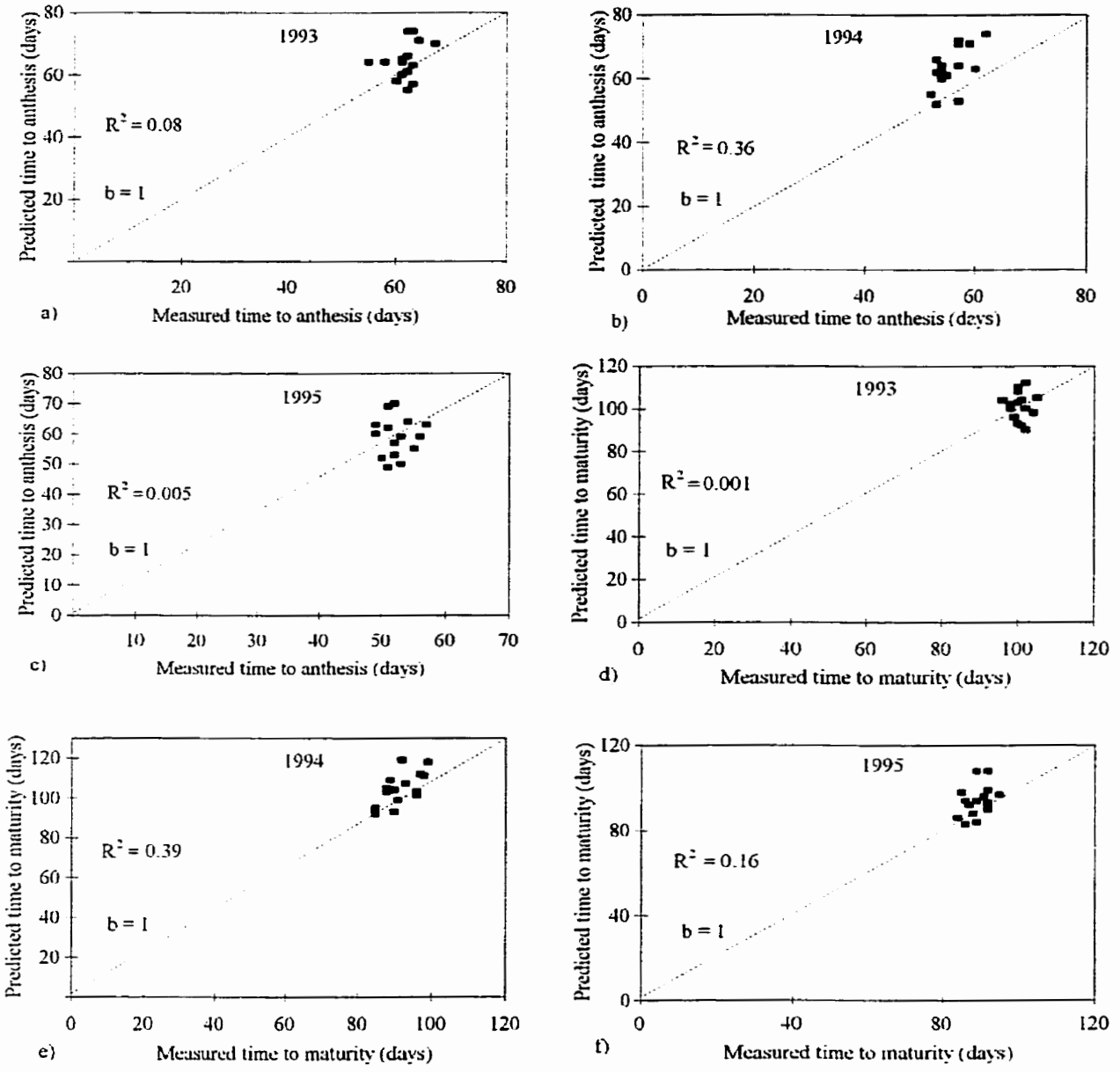


Fig. 5.7 Scatter plot of measured versus predicted values of a) time to anthesis in 1993, b) time to anthesis in 1994, c) time to anthesis in 1995, d) time to maturity in 1993, e) time to maturity in 1994, and f) time to maturity in 1995 for spring wheat cultivars (combined over cultivars for all seeding dates) grown at Winnipeg.

Results indicated that, unlike the CERES-wheat model, the Walker model does not account for yield differences with difference in seeding date or location. Yield predictions by the Walker model were the same for all seeding dates and locations (Table 5.6). Overall, yield predictions by the CERES-wheat model declined as seeding was delayed (Table 5.6).

In general, both models underestimated yield. However, unlike the CERES-wheat model, none of the yield percentage deviations for the Walker model were acceptable (for acceptability deviations should not be greater than 15%) (Table 5.6). The better prediction results of the CERES-wheat than the Walker model may be attributed to the fact that the former model accounts for seeding date and location differences, whereas the latter model does not.

The Walker model was built for large scale predictions, and therefore gives poor results for a small scale localized prediction (Bruce Burnette, personal communication). From these results, it could be stated that the CERES-wheat model has the potential to provide better yield forecasts than the Walker model under the given experimental conditions.

Table 5.6 **Predicted (Pred), observed (Obsvd), and percentage deviation (%Dev.) [(predicted - observed)/(observed) x 100] grain yields (t/h) of spring wheat cultivars** grown at different seeding dates (SD1=seeding date one, etc.), at Winnipeg and Carman, 1996.

Seeding date	Pred. **CERES**	Pred. **Walker**	Obsvd	% Dev. **CERES**	% Dev. **Walker**
			Winnipeg		
SD1	2.55	2.27	2.98	-14.4	-23.8
SD2	2.40	2.27	3.46	-30.6	-34.4
SD3	2.77	2.27	3.68	-24.7	-38.3
Mean	*2.57*	*2.27*	*3.37*	*-23.2*	*-32.2*
			Carman		
SD1	3.58	2.27	3.84	- 6.8	-40.9
SD2	3.33	2.27	3.70	-10.0	-38.6
SD3	2.30	2.27	3.11	-26.0	-27.0
Mean	*3.07*	*2.27*	*3.55*	*-14.3*	*-35.5*

5.5 Conclusions

The CERES-wheat model is capable of characterizing spring wheat cultivars through the determination of genetic coefficients. However, indoor-measured phyllochron intervals for the different cultivars were different from the field-measured values, and the CERES-wheat model showed a tendency to under-estimate phyllochron interval. Phyllochron interval is genotype specific. Therefore, the suggested value of 75 GDD/leaf for spring wheat simulation is erroneous, and the actual value for any particular cultivar needs to be field-determined. Similarly, the common use of 0.5 as the vernalization coefficient for all spring wheat cultivars was not supported by this work and should be discouraged.

In general, the claim that the CERES-wheat model can accurately predict growth and yield under a broad range of environments was not supported by the results from this study. The CERES-wheat model tended to underestimate grain yield. The time of planting affected the predictive power of the model, and predictions were better for the early seeding.

The general performance of the CERES-wheat model under non-moisture stress and non-high temperature environments was acceptable (based on not greater than 15 % deviation of predicted from measured grain yield). However, the model exhibited a specific weakness in biomass predictions. Algorithms controlling biomass calculations may need modifications.

Cultivar genetic coefficients determined under non-moisture stress and non-high temperature environments in one location, could be used for the same cultivar(s) grown at another location within the same region. The general similarity of genetic coefficient values determined at Winnipeg and Carman appear to support to some extent, the CERES-wheat model claim that cultivar genetic coefficients determined at one location could be used for the same cultivar at another location. Based on the Carman results, where delays in seeding were characterized by reduced moisture availability and warmer temperatures, it may be inferred that the predictive power of the CERES-wheat model tended to decrease under the stress generated by low moisture and high temperature conditions. Therefore, in drought years, predictions by the CERES-wheat model will be unreliable.

The CERES-wheat model adequately simulated yield-related components (e.g., kernel mass, kernels per metre square) with close agreement with measured values, but generally under-estimated anthesis and maturity dry matter, and over-estimated anthesis and maturity dates.

Under non-drought conditions (assumed to correspond to early seeding), the CERES-wheat model provided better yield predictions than the Walker model. The CERES-wheat model has the potential to provide more accurate yield forecasts under non-drought conditions than the Walker model. Under low moisture conditions, however, the CERES-wheat model is likely to perform poorly (as in 1995) compared

to the Walker model.

Further investigations on a larger scale (e.g., provincial) using regional variety testing (e.g. Manitoba Variety Testing, or Prairie Registration Recommending Committee for Grains (PRRCG) co-operative trials data and location information would be appropriate and helpful.

6.0 GENERAL DISCUSSION

Crop growth and development is a complex combination of crop responses to weather and soil conditions. Environmental factors which influence attainable yields of cereal crops vary from one geographical location to another (Touré et al., 1995; Williams, 1971). Therefore to efficiently model development and yield of a cereal crop, field measurements of the required input data are imperative. The studies reported in this thesis have been undertaken to elucidate specific environmental effects on plant growth and development, that will give a better understanding of observations made under field conditions, and to provide a field-generated database for the calibration and validation of the CERES-wheat model.

The controlled environment studies revealed that increases in temperature greatly affected the rate of plant growth and development. High temperatures accelerated the growth and development of vernalization-non-responsive spring wheat cultivars, by causing reductions in the total number of leaves produced on the main stem, in the time to anthesis, and in the time to maturity. Similar observations were made for vernalization-responsive cultivars, but only when the vernalization requirement was satisfied. For non satisfied vernalization-responsive cultivars, high temperatures prolonged the length of the vegetative growth period and led to the production of more leaves. High temperatures also reduced yield-related components such as the number of tillers per plant, the number of spikelets per main stem spike,

and the number of kernels per main stem spike. These results are in agreement with reports made by other researchers (Wall and Cartwright, 1974; Pirasteh and Welsh, 1980; Shpiler and Blum 1986; Ford et al., 1981; Campbell and Davidson, 1979; Warrington et al., 1977). In the present study, increases in temperature resulted in the reduction of the number of spikelets on the main stem. This finding contradicts Halse and Weir (1970) who found no effect of high temperature on the number of spikelets per spike in spring wheat. This discrepancy may be explained by the different ranges of temperature regimes used. The highest temperature regime used by Halse and Weir (1970) was 18/13°C (day/night temperatures, respectively), as opposed to 30/23°C in the present study.

Higher phyllochron intervals were obtained under higher temperatures, indicating a thermal-energy-use inefficiency with high temperatures. This may explain why the phyllochron interval for a cultivar varies with seeding dates under field conditions. This observation supports previous findings by Cao and Moss (1989c), and Duguid (1990). The lowering of thermal-energy-use efficiency at high temperatures suggests that there may be an upper limit to temperature tolerance level(s) (which may be cultivar specific) beyond which any further temperature impact may be non effective, or detrimental. Therefore, temperatures above the upper limit may erroneously augment phyllochron intervals, which in turn could lead to erroneous model predictions. The general use of a common modified thermal time

calculations in the CERES-wheat model (Table 2.2), may not be appropriate for all cultivars. Perhaps crop modellers need to develop equations that will specifically address temperature sensitivity of individual cultivars, in order to reduce errors in phyllochron interval determination in particular, and in crop phenology and yield predictions in general. Further investigations to find cultivar threshold temperature tolerance levels is needed.

Ritchie (1991) advocated the use of a common phyllochron interval of 75 for spring wheat cultivars. Pecetti and Hollington (1997), and Chippanshi et al. (1997), used a standard vernalization coefficient value of 0.5 (for spring wheat) in their studies. In this study, the presence of differential cultivar responses to temperature increases, with respect to phyllochron interval and vernalization coefficient, clearly suggest that the use of common phyllochron and vernalization values for all spring wheat cultivars is inappropriate.

All cultivars required 350 to 400 growing-degree-days between terminal spikelet initiation and heading, 50 to 70 growing degree days between heading and anthesis, and 750 to 770 growing degree days between anthesis and maturity. These trends are in agreement with observations made by Wong and Baker (1986) among heading, anthesis, and maturity. The extension of the trends among heading, anthesis, and maturity, to terminal spikelet initiation further suggests that cultivar differences observed in times to heading, anthesis and maturity, may be primarily attributed to the

differences in the time to terminal spikelet initiation. Terminal spikelet initiation could therefore be used as a simple indoor early screening tool to differentiate among spring wheat lines for early maturity, especially where weather constraints and time restrictions exist.

Using R^2 values and basic regression diagnostic procedures, the quadratic model was found to best fit the wheat grain filling pattern. These results agree with findings by Nass and Reiser (1975) and Bruckner and Frohberg (1987), but disagree with those of Gebeyehou et al. (1982b) and Bauer et al. (1984). The present study emphasizes the importance of basing inferences and deductions of grain filling patterns on both R^2 values and basic regression diagnostic procedures, and not on the former alone.

Results of measurements made under controlled environment conditions were generally different from those under field conditions. For example, when grown in controlled environments cultivars required more heat units to attain anthesis (Fig. 3.9), than when grown in the field (Fig. 4.7). However, the trends of differences observed among cultivars were similar under both environments. Therefore, when investigating the general effect(s) of certain environmental factors on plant growth and development, or differences in cultivar response to specific factors, the artificial environment is appropriate, as suggested by Baker (1988), but not for providing practical data for crop modelling.

It is important to note that the CERES-wheat model was sensitive to differential cultivar responses. For example, the CERES-wheat model, through the determination of cultivar genetic coefficients by the GenCalc, was able to differentiate between the vernalization-responsive (AC Taber, and Biggar) and the vernalization-non-responsive cultivars (Katepwa, Oslo, Roblin, and Wildcat). The CERES-wheat model, therefore, appears to have the potential to aid plant breeding research, especially in cultivar adaptability *a priori.* In most of the reported CERES-wheat modelling work to date, cultivar genetic coefficients are usually obtained through calibration with historic data (Otter and Ritchie, 1984; Otter et al., 1986; Moulin and Beckie, 1993; Chipanshi et al., 1997; and Pecetti and Hollington, 1997). Under such situations genetic coefficients such as P1V and PHINT values for spring wheat cultivars are assumed as 0.5 and 75 GDD, respectively. In the present study, different spring wheat cultivars produced different values for P1V and PHINT, which suggest the need to discourage the use of common P1V and PHINT values for CERES-wheat modelling. The genetic coefficients for a particular cultivar need to be determined under field conditions. The present study supports the CERES-wheat model claim, that cultivar genetic coefficients determined at one location, could be used for the same cultivar(s) grown under a similar environment at another location within the same region. Further studies to determine and establish the genetic coefficients for registered cultivars for a particular growing region would therefore be appropriate and

beneficial to CERES-wheat modelling.

Using Willmott's index of agreement, the predictive power of the CERES-wheat model for seed yield under early seeding conditions (at Carman) was acceptable, but declined with delays in seeding date. Further validation with the 1993 to 1995 data also revealed that the predictive power of the CERES-wheat model for seed yield diminished with delays in seeding date. However, this decline was more pronounced in some cultivars than in others. Grain weight, grains per metre square, and the number of grains per main stem spike were simulated with close agreement to measured values, and this is in agreement with observations made by Otter et al. (1986). The CERES-wheat model, however, had a general tendency for underestimation of dry matter at anthesis and maturity. The CERES-wheat model algorithms for biomass prediction may need modification(s). This warrants further research.

Comparison between results produced by the CERES-wheat and the Walker models depicted several performance differences (Table 6.1). Since the Walker model was built for large scale predictions (Mr. Bruce Burnette, personal communication) there is the need for future work to investigate the performances of both models over a larger scale in western Canada.

This work has shown that the CERES-wheat model is capable of deciphering genetic differences among different cultivars, and also genetic coefficients determined

Table 6.1 Comparison of general performance characteristics between the CERES-wheat and the Walker models.

CERES-wheat	Walker
1. Sensitive to changes in seeding date.	Insensitive to changes in seeding date.
2. Sensitive to differences in location.	Insensitive to differences in location.
3. Better grain yield predictions under 1996 conditions at Winnipeg and Carman.	Poorer grain yield predictions under 1996 conditions at Winnipeg and Carman.

by the model at one location may be used for the same cultivar grown at another location within the same region. The CERES-wheat model however, has several weaknesses, which include a general tendency to underestimate grain yield, phyllochron interval, and dry matter. The extensive data requirements by the CERES-wheat model is a deterrent to its use. These concerns need to be addressed by the model builders, if the CERES-wheat model is to find acceptance and adoption in the practical agricultural world. Further investigations with a larger scale testing using, for example, the Prairie Registration Recommending Committee for Grains (PRRCG

co-operative trials) data and location information would be very appropriate and helpful. Whereas researchers may be interested in predictions involving specific genotypes (advanced lines), organizations like the Canadian Wheat Board are rather interested in a large scale wheat yield forecast (not individual cultivars). Further work is therefore needed to assess the effect of a standard set of genetic coefficients for large scale forecasts. For example, will an average phyllochron interval of 83 (average of phyllochron intervals for all six cultivar in the present study) be appropriate for large scale yield forecasts? Sensitivity analysis of the CERES-wheat model data requirements is also needed, and should help to identify and eliminate unnecessary data requirements. Such a study may help to make the data requirements of the CERES-wheat model more practical, and make the model more attractive for use.

7.0 REFERENCES

Addae, P.C., and Pearson, C.J. 1992. Thermal requirement for germination and seedling growth of wheat. Aust. J. Agric. Res. **43**:585-594.

Amir, J., and Sinclair, T.R. 1991. A model of water limitation on spring wheat growth and yield. Field Crops Res. **28**:59-69.

Amores-Vergara, E., and Cartwright, P.M. 1984. Effects of short periods of exposure to high temperature on the phenology and shoot apex development of wheat c. Sonora 64. Aust. J. Agric. Res. **35**:139-148

Austin, R.B., Bingham, J., Blackwell, R.D., Evans, L.T., Ford, M.A., Morgan, C.L., and Taylor, M. 1980. Genetic improvements in winter wheat yield since 1900 and associated physiological changes. J. Agric. Sci. Camb. **94**:675-689.

Austin, R.B., Edric, J.A., Ford, M.A., and Blackwell, R.D. 1977. The fate of the dry matter, carbohydrates and C lost from the leaves and stems of wheat during grain filling. Ann. Bot. **41**:1309-1321.

Bagga, A.K., and Rawson, H.M. 1977. Contrasting responses of morphologically similar wheat cultivars to temperatures appropriate to warm temperate climates with hot summers: a study in controlled environment. Aust. J. Plant Physiol., **4**:877-887.

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

Baker, J.T., Pinter, P.J., Reginato, R.J., and Kanemasu, E.T. 1986. Effects of temperature on leaf appearance in spring and winter wheat cultivars. Agron. J. **78**:605-613.

Baker, R.J. 1988. Analysis of genotype-environmental interactions in crops. Atlas of Sci. (**0894-3761**): Anim. Plant Sci.1-4.

Bauer, A., Frank, A.B., and Black, A.L. 1984. Estimation of spring wheat leaf

growth rates and anthesis from air temperature. Agron. J. **76**:829-835.

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

Bickford, E.D., and Dunn, S. 1972. Lighting for plant growth. pp 221. The Kent State University Press. USA.

Black, A.L., and Siddoway, F.H. 1977. Hard red and durum spring wheat responses to seedling data and NP-fertilization on fallow. Agron. J. **69**:885-887.

Blum, A., Mayer, J., and Gozland, G. 1983. Association between plant production and some physiological components of drought resistance in wheat. Plant Cell Environ. **6**:219-225.

Bollero, G.A., Bullock, D.G., and Hollinger, S.E. 1996. Soil temperature and planting date effects on corn yield, leaf area, and plant development. Agron. J. **88**:385-390.

Bongaarts, J. 1994. Can the growing human population feed itself? Scientific Amer., March 1994. pp 36-42.

Briggle, L.W. 1967. Morphology of the Wheat Plant. *In* K.S. Quisenberry, and L.P. Reitz (eds.), Wheat and Wheat Improvement. Amer. Soc. Agron., Madison, Wisconsin, USA. pp. 89-116.

Bruckner, P.L., and Frohberg, R.C. 1987. Rate and duration of grain fill in spring wheat. Crop Sci. **27**:451-455.

Campbell, C.A., and Davidson, H.R. 1979. Effects of temperature, nitrogen fertilization and moisture stress on yield components, protein content and moisture use efficiency of Manitou spring wheat. Can. J. Plant Sci. **59**:963-974.

Canada-Manitoba Farm Business Management Council. 1996. Information on crop yield response to seeding date. Manitoba Crop Insurance Corporation, Manitoba

Agriculture, Portage la Prairie, MB, Canada. Supplement to the Manitoba Cooperator, April 1996.

Canadian Wheat Board. 1996. The Canadian Wheat Board 1995-96 annual report. Marketing for the future.

Cao, W., and Moss, D.N. 1989a. Day length effect on leaf emergence and phyllochron in wheat and barley. Crop Sci. **29**:1021-1025.

Cao, W., and Moss, D.N. 1989b. Temperature and day length interaction on phyllochron in wheat and barley. Crop Sci. **29**:1046-1048.

Cao, W., and Moss, D.N. 1989c. Temperature effect on leaf emergence and phyllochron in wheat and barley. Crop Sci. **29**:1018-1021.

Chouard, P. 1960. Vernalization and its relations to dormancy. Annu. Rev. Plant Physiol. **11**:191-238.

Chipanshi, A.C., Ripley, E.A., and Lawford, R.G. 1997. Early prediction of spring wheat yields in Saskatchewan from current and historical weather data using the CERES-wheat model. Agric. Forest Meteorol. **84**:223-232.

Clarke, J.M. 1983. Time of physiological maturity and post-physiological maturity drying rates in wheat. Crop Sci. **23**:1203-1205.

Cook, R.J. and Veseth, R.J. 1991. Wheat health management. The American Phytopathological Society. St. Paul, Minnesota, USA. pp 144.

Copeland, P.J. and Crookston, R.K. 1985. Visible indicators of physiological maturity in barley. Crop Sci. **25**:843-847.

Cox, T.S., Shroyer, J.P., Ben-Hui, L., Sears, R.G., and Martin, T.J. 1988. Genetic improvement in agronomic traits of Hard Red Winter Wheat cultivars from 1919 to 1987. Crop Sci. **28**:756-760.

Cross, H.Z. 1975 Diallele analysis of duration and rate of grain filling of seven

inbred lines of corn. Crop Sci. **15**:532-535.

Cutforth, H.W., Jame, Y.W., and Jefferson, P.G. 1992. Effect of temperature, vernalization and water stress on phyllochron and final main-stem leaf number of HY320 and Neepawa spring wheats. Can. J. Plant Sci. **72**:1141-1151.

Darrock, B.A., and Baker, F.J. 1990. Grain filling in three spring wheat genotypes: statistical analysis. Crop Sci. **30**:525-529.

Darwinkel, A. 1983. Ear formation and grain yield of winter wheat as affected by time of nitrogen supple. Neth. J. Agric. Sci. **31**:211-225.

Davidson, J.L., Christian, K.R., Jones, D.B., and Bremner, P.M. 1985. Responses of wheat to vernalization and photoperiod. Aust. J. Agric. Res. **36**:347-359.

Del Pozo, A.H., Garcia-Huidobro, J., Novoa, R., and Villasea, S. 1987. Relationship of base temperature to development of spring wheat. Expl. Agric. **23**:21-30.

Duguid, S.D. 1990. The effect of genotype and temperature on the phenological development and yield of spring wheat. M.Sc. Thesis, University of Manitoba. pp 141.

Duguid, S.D., and Brûlé-Babel, A.L. 1994. Rate and duration of grain fill in five spring wheat (*Triticum aestivum* L.) genotype. Can. J. Plant Sci. **74**:681-686.

Entz, M.H., and Fowler, D.B. 1989. Influence of crop water environment and dry matter accumulation on grain yield of no-till winter wheat. Can. J. Plant Sci. **69**:367-375.

Evans, L.T., and Wardlaw, I.F. 1976. Aspects of the comparative physiology of grain yield in cereals. Adv. Agron. **28**:301-359.

Fischer, R.A. 1984. The role of crop simulation models in wheat agronomy. p. 237-255. *In* W. Day, and R.K. Atkin (eds.), Wheat growth and modelling. NATO ASI Series, Series A: Life Sciences Vol. 86, Plenum Press, New York, NY, USA.

Flood, R.G., and Halloran, G.M. 1984. The nature and duration of gene action for vernalization response in wheat. Ann. Botany **53**:363-368.

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

Fox, D.G., 1981. Judging air quality model performance: a summary of the AMS workshop on dispersion model performance. Bull. Am. Meteorol. Soc. **62**:599-609.

Frank, A.B., and Bauer, A. 1995. Phyllochron differences in wheat, barley, and forage grasses. Crop Sci. **35**:19-23.

Frank, A.B., Bauer, A., and Black, A.L. 1987. Effects of air temperature and water stress on apex development in spring wheat. Crop Sci. **27**:113-116.

Fraser, J., Dougherty, C.T., and Langer, R.H.M. 1982. Dynamics of tiller populations of standard height and semi-dwarf wheats. N.Z. J. Agric. Res. **25**:321-328.

French, R.J., Schultz, J.E., and Rudd, C.L. 1979. Effect of time of sowing on wheat phenology in South Australia. Aust. J. Exp. Agric. Anim. Husb. **19**:89-96.
Gallagher, J.N., Biscoe, P.V., and Hunter, B. 1976. Effects of drought on grain growth. Nature **264**:541-542.

Gebeyehou, G. Knott, D.R. and Baker, R.J. 1982a. Relationships among durations of vegetative and grain filling phases, yield components, and grain yield in durum wheat cultivars. Crop Sci. **22**:287-290.

Gebeyehou, G. Knott, D.R. and Baker, R.J. 1982b. Rate and duration of grain filling in durum wheat cultivars. Crop Sci. **22**:337-340.

Godwin, D.C., Ritchie, J.T., and Singh, U. 1994. Crop models: CERES-wheat. In: G.Y. Tsuji, G. Uehara, S. Balas (eds.), DSSAT version 3, volume 2, IBSNAT, University of Hawaii, Honolulu, Hawaii, USA.

Grieve, C.M., Lesch, S.M., Maas, and Francois, L.E. 1993. Leaf and spikelet primordia initiation in salt stressed wheat. Crop Sci. **33**:1286-1294.

Griffiths, F.E.W., and Lyndon, R.F. 1985. The effects of vernalization on the growth of the wheat shoot apex. Annals of Botany **56**:501-511.

Gusta, L.V., and Chen, T.H.H. 1987. The physiology of water and temperature stress. p. 115-150. *In* E.G. Heyne (ed.), Wheat and wheat improvement. Amer. Soc. of Agron., Madison, WI, USA.

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

Hanft, J.M., and Wych, R.D. 1982. Visual indicators of physiological maturity of hard red spring wheat. Crop Sci. **22**:584-588.

Harper, A.M., and Roberts, D.W.A. 1988. Phytotron manual. Technical Bulletin 1988-4E, Lethbridge Research Station Contribution No. 13., Research Branch, Agriculture Canada.

Hartmann, H.T., Kofranek, A.M., Rubatzky, V.E., and Flocker, W.J. 1988. Plant Science (second edition), Growth, development, and utilization of cultivated plants. Prentice-Hall Inc., New Jersey, USA. p. 168-192.

Haun, J.R. 1973. Visual quantification of wheat development. Agron. J. **65**:116-119.

Haun, J.R. 1982. Early prediction of corn yields from daily weather data and single predetermined seasonal constants. Agric. Meteorol. **27**:191-207.

Hillman, W.S. 1969. Photoperiodism and vernalization. p. 559-601. *In* M.B. Wilkins (ed.), The physiology of plant growth and development. McGraw Hill, London.

Hodges, T. 1991. Temperature and water stress effects on phenology. p. 7-13. *In* T. Hodges (ed.), Predicting Crop Phenology. CRC Press, Boca Raton, Florida, USA.

Hodges, T., and Ritchie, J.T. 1991. The CERES-Wheat phenology model. p. 133-141. *In* T. Hodges (ed.), Predicting Crop Phenology. CRC Press, Boca Raton, Florida, USA.

Hoffman, G.J. 1979. Humudity. p. 141-172. *In* T. W. Tibbitts, and T.T. Kozlowski (eds.), Controlled environment guidelines for plant research. Proc. Controlled environment Conference, March 12-14. Madison, Wisconsin, USA.

Hoogenboom, G. 1998. Rationale: Training program on computer simulation of crop growth and management responses. June 1-12. University of Georgia, and ICASA.

Housley, T.L., Kirleis, A.W., Ohm, H.W., and Patterson, F.L. 1982. Dry matter accumulation in soft red winter wheat seeds. Crop Sci. **22**:290-294.

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. **24**:519-570.

Hucl, P., and Baker, R.J. 1989. Tiller phenology and yield of spring wheat in a semiarid environment. Crop Sci. **29**:631-635.

Hunt, L.A., Pararajasingham, S., Jones, J.W., Hoogenboom, G., Imamura, D.T., and Ogoshi, R.M. 1993. GENCALC: Software to facilitate the use of crop models for analyzing field experiments. Agron. J. **85**:1090-1094.

Hunt, L.A., and Pararajasingham, S. 1995. Cropsim -Wheat: a model describing the growth and development of wheat. Can. J. Plant Sci. **75**:619-632.

Jamieson, P. D., Brooking, I.R., Porter, J.R., and Wilson, D.R. 1995. Prediction of leaf appearance in wheat: a question of temperature. Field Crop Res. **41**:35-44.

Jedel, P.E., Evans, L.E., and Scarth, R. 1986. Vernalization responses of a selected group of spring wheat (*Triticum aestivum* L.) cultivars. Can. J. Plant Sci. **66**:1-9.

Jenner, C.F. 1991. Effects of exposure of wheat ears to high temperature on dry

matter accumulation and carbohydrate metabolism in the grain of two cultivars. I. Immediate responses. Aust. J. Plant Physiol. **18**:165-177.

Jones, J.W. 1994. The international consortium for agricultural systems application (ICASA). p. 1-2. *In* P.K. Thornton, W.T. Bowen, P.W. Wilkens, J.W. Jones, K.J. Boote, and G. Hoogenboom (eds.), Applying Crop Models and Decision Support Systems. Training program on computer simulation of crop growth and management responses, Univ. of Florida, Gainsville, Florida, USA. August 8-19, 1994.

Judel, G.K., and Mengel, K. 1982. Effect of shading on nonstructural carbohydrates and their turnover in culms and leaves during the grain filling period of spring wheat. Crop Sci. **22**:958-962.

Karow, R.S., Klepper, E.L., Rickman, R.W., and Toll, T.R. 1993. Early growth and development of cereals. Oregon State University Extension Service. p. 4.

Keim, D.L., and Kronstad, W.E. 1981. Drought response of winter wheat cultivars grown under field stress conditions. Crop Sci. **21**:11-15.

Kiniry, J.R., Rosenthal, W.D., Jackson, B.S., and Hoogenboom, G. 1991. Predicting leaf development of crop plants. p. 29-42. *In* T. Hodges (ed), Predicting crop phenology, CRC Press Boston, USA.

Kirby, E.J.M. 1984. Significant stages of ear development in winter wheat. p. 7-24. *In* W. Day and R.K. Atkin (eds.), Wheat growth and modelling, NATO ASI Series A, Life Sciences; v. 86, Plenum Press, New York, USA.

Kirby, E.J.M., and Appleyard, M. 1982. Cereal plant development and its relation to crop management. p. 161-173. *In* E.J. Gallagher (ed.), Cereal Production. Proc. 2nd Int. Summer Sch. in Agriculture, Royal Dublin Soc., Butterworths, London.

Kirby, E.J.M., M. Appleyard, and N.A. Simpson. 1994. Co-ordination of stem elongation and Zadoks growth stages with leaf emergence in wheat and barley. J. Agric. Sci., Camb. **122**:21-29.

Klepper, B., Rickman, R.W., and Belford, R.K. 1983. Leaf and tiller identification of wheat plants. Crop Sci. **23**:1002-1004.

Klepper, B., Rickman, R.W., and Peterson, C.M. 1982. Quantitative characterization of vegetative development in small cereal grains. J. Agron. **74**:789-792.

Kohn, G.D., and Storrier, R.R. 1970. Time of sowing and wheat production in New South Wales. Aust. J. Exp. Agric. Anim. Husb. **10**:604.

Larcher, W., Heber, U., and Santarius, K.A. 1973. Limiting temperature for life functions. p. 195-231. *In* H. Precht, J. Christopherson, and H. Hensel (eds.), Temperature and Life, Springer-Verlag, New York, NY. USA.

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

Maas, E.V., Lesch, S.M., Francois, L.E., and Crieve, C.M. 1994. Tiller development in salt-stressed. Crop Sci. **34**:1594-1603.

Mahalakshmi, V., Bidinger, F.R., and Raju, D.S. 1991. Effect of drought stress during grain filling in near-isogenic tall and dwarf hybrids of pearl millet (*Pennisetum glaucum*). J. Agric. Sci. Camb. **116**:67-72.

Major, D.J. 1980. Photoperiod response characteristics controlling flowering of nine crop species. Can. J. Plant Sci. **60**:777-784.

Marshall, L., Busch, R., Cholick, F., Edwards, I., and Frohberg, R. 1989. Agronomic performance of spring wheat isolines differing for day length response. Crop Sci. **29**:752-757.

Masle, J. 1984. Competition among tillers in winter wheat, consequences for growth and development of the crop. p. 33-54. *In* W. Day and R.K. Atkin (eds.), Wheat growth and modelling, NATO ASI Series A, Life Sciences; v. 86, Plenum Press, New York, USA.

McCree, K.J. 1973. A rational approach to light measurements in plant ecology. Curr. Adv. Plant Sci. **5**:39-43.

McMaster, G.S., and Wilhelm, W.W. 1998. Is soil temperature better than air temperature for predicting winter wheat phenology? Agron. J. **90**:602-607.

McPherson, H. 1987. The effects of moisture stress on rapeseed (Brassica napus L.), M.Sc. Thesis, University of Manitoba, Winnipeg, MB, Canada. pp. 118.

McWilliam, J.R. 1980. Adaptation to high temperature stress. C p. 444-447. *In* N.C.Turner and P.J. Kramer (eds.), Adaptation of plants to water and high temperature stress. John Wiley and Sons, New York, N.Y., USA.

Mills, G.F., and Haluschak, P. 1993. Soils of the Carman Research Station. Canada-Manitoba Soil Survey, Special Report Series 93-1, pp. 39.

Moulin, A.P., and Beckie, H.J. 1993. Evaluation of the CERES and EPIC models for predicting spring wheat grain yield over time. Can. J. Plant Sci. **73**:713-719.

Nass, H.G. 1973. Determination of characters for yield selection in spring wheat. Can. J. Plant Sci. **53**:755-762.

Nass, H.G., and Reiser, B. 1975. Grain filling period and grain yield relationships in spring wheat. Can. J. Plant Sci. **55**:673-678.

Ong, C.K. 1983. Response to temperature in a stand of pearl milllet (*Pennisetum typhoides* S. & H.). J. Exp. Bot. **34**:322-336.

Oosterhuis, D.M., and Cartwright, P.M. 1983. Spike differentiation and floret survival in semidwarf spring wheat as affected by water stress and photoperiod. Crop Sci. **23**:711-717.

Otter, S., and Ritchie, J.T. 1984. Validation of the CERES-wheat model in diverse environments. p. 307-310. In W. Day, and R.K. Atkin (eds.), Wheat growth and modelling, NATO ASI Series, Series A: Life Sciences Vol. 86. Plenum Press, New York.

Otter, S., Godwin, D.C., and Ritchie, J.T. 1986. Testing and validating the CERES-wheat model in diverse environments. AGRISTARS, USDA-ARS Technical Report YM 15-00407 JSC-20244, Johnson Space Center, Houston, TX. pp. 155.

Pecetti, L., and Hollington, P.A. 1997. Application of the CERES-wheat simulation model to durum wheat in two diverse Mediterranean environments. Europ. J Agron. **6**:125-139.

Peterson, R.F. 1965. Wheat: botany, cultivation, and utilization. pp 422. Interscience Publishers Inc. N.Y., USA.

Pinthus, M.J. 1963. Comparison of dry matter accumulation and moisture content in the developing kernels of bread wheat, durum wheat, and barley. Israel J. Agric. Res. **13**:117-124.

Pirasteh, B., and Welsh, J.R. 1980. Effect of temperature on the heading date of wheat cultivars under a lengthening photoperiod. Crop Sci. **20**:453-456.

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

Pugsley, A.T. 1972. Additional genes inhibiting winter habit in wheat. Euphytica **21**:547-552.

Quarrie, S.A., and Jones, H.G. 1977. Effects of abscisic acid and water stress on development and morphology of wheat. J. Exp. Bot. **28**:192-203.

Rahman, M.S., and Wilson, J.H. 1978. Determination of spikelet number in wheat. III Effect of varying temperature on ear development. Aust. J. Agric. Res. **29**:459-467.

Rawson, H.M. 1970. Spikelet number, its control and relation to yield per ear in wheat. Aust. J. Biol. Sci., **23**:1-15.

Rawson, H.M. 1971. An upper limit for spikelet number per ear in wheat as controlled by photoperiod. Aust. J. Agric. Res. **22**:537-546.

Rawson, H.M. 1986. High-temperature-tolerant wheat: a discription of variation and a search for some limitations to productivity. Field Crops Res. **14**:197-212.

Reaumur, R.A.F. 1735 (cited by Shaykewich, 1995). Thermetric observations

made at Paris during the year 1735., compared to those made below the equator on the Isle of Mauritius, at Algiers and on a few American islands. Acad. Sci. Memoirs Acad. Sci. Paris. 545.

Reilly, M.L. 1982. Functional aspects of cereal structure. *In* Agriculture, Royal Dublin Soc., Butterworths, London. pp 137-160.

Reitz, L.P. 1967. World distribution and importance of wheat. p. 89-116. *In* K.S. Quisenberry, and L.P. Reitz (eds.), Wheat and Wheat Improvement. Amer. Soc. Agron., Madison, Wisconsin, USA.

Ritchie, J.T. 1991. Wheat phasic development. p. 31-54. *In* J. Hanks and J.T. Ritchie (eds.), Modelling plant and soil systems. Agron. Series 31, Amer. Soc. Agron., Madison, WI, USA.

Ritchie, J.T., and NeSmith, D.S. 1991. Temperature and crop development. p. 5-28. *In* J. Hanks and J.T. Ritchie (eds.), Modelling plant and soil systems. Agron. Series 31, Amer. Soc. Agron., Madison, WI, USA.

Ritchie, J.T., and Otter, S. 1985. Description and performance of CERES-wheat: a user-oriented wheat yield model. USDA-ARS. ARS **38**:159-175.

Robertson, G.W. 1968. A biometeorological time scale for a cereal crop involving day and night temperatures and photoperiod. Int. J. Biometeor. **12(3)**:191-223.

Russell, W.K., and Stuber, C.W. 1985. Genotype x photoperiod and genotype x temperature interactions for maturity in maize. Crop Sci. **25**:152-158.

Saini, H.S., and Aspinall, D. 1981. Effect of water deficit on sporogenesis in wheat. Ann. Bot. **48**:623-644.

Salisbury, F.B. 1992. Limiting factors and maximum yields: a controlled ecological life-support system. p. 560-561. *In* F.B. Salisbury and C.W. Ross (eds.), Plant Physiology, 4th edition. Wadsworth Biology Series, Wadsworth Publishing Company, Belmont, California, USA.

Salisbury, F.B.,and Ross, C.W. 1992. Plant Physiology, 4th edition. Wadsworth

Biology Series, Wadsworth Publishing Company, Belmont, California, USA. pp 682.

SAS Institute. 1989. Software release 6.12. SAS Institute Inc., Cary, NC, USA.

Schlotzhauer, S.D., and Littell, R.C. 1987. SAS system for elementary statistical analysis. SAS Institute Inc. A useful introduction to SAS programming for statistical analysis.

Shanahan, J.F., Smith, D.H., and Welsh, J.R. 1984. An analysis of post-anthesis sink-limited winter wheat grain yields under various environments. Agron. J. **76**:611-615.

Shanahan, J.F., Donnelly, K.J., Smith, D.H., and Smik, D.E. 1985. Shoot developmental properties associated with grain yield in winter wheat. Crop Sci. **25**:770-775.

Shaykewich, C.F. 1995. An appraisal of cereal crop phenology modelling. Can. J. Plant Sci. **75**:329-341.

Shpiler, L., and Blum, A. 1986. Differential reaction of wheat cultivars to hot environment. Euphytica **35**:483-492.

Simmons, S.R. 1987. Growth, development and physiology. p. 77-113. *In* E.G. Heyne (ed.), Wheat and wheat improvement. Amer. Soc. Agron., Madison, WI, USA.

Single, W.V., and Marcellos, H. 1974. Studies on frost injury to wheat. iv. Freezing of ears after emergence from the leaf sheath. Aust. J. Agric. Res. **25**:679.
Smika, D.E., and Shawcroft, R.W. 1980. Preliminary study using a wind tunnel to determine the effect of hot wind on a wheat crop. Field Crops Res. **3**:129-135.

Smith, D.H., and Donnelly, K.J. 1991. Visual markers of maximum grain dry weight accumulation in winter wheat. Crop Sci. **31**:419-422.

Sommerville, S.C., and Briggs, K.G. 1979. Evaluation of maturity assessments in wheat and barley. Can. J. Plant Sci. **59**:505-510.

Spiertz, J.H. 1974. Grain growth and distribution of dry matter in the wheat grain as influenced by temperature, light, and ear size. Neth. J. Agric. **22**:207-220.

Stapper, M., and Harris, H.C. 1989. Assessing the productivity of wheat genotypes in a Mediterranean climate, using a crop simulation model. Field Crops Res. **20**:129-152.

Thornton, P.K. 1994. The decision support system for agrotechnology transfer (DSSAT) version 3.0. p. 3-4. *In* P.K. Thornton, W.T. Bowen, P.W. Wilkens, J.W. Jones, K.J. Boote, and G. Hoogenboom (eds.), Applying Crop Models and Decision Support Systems. Training program on computer simulation of crop growth and management responses, Univ. of Florida, Gainsville, Florida, USA. August 8-19, 1994.

Touré, A., Major, D.J., and Lindwall, C.W. 1994. Comparison of five wheat simulation models in southern Alberta. Can. J. Plant Sci. **75**:61-68.

Touré, A., Major, D.J., and Lindwall, C.W. 1995. Sensitivity of four wheat simulation models to climate change. Can. J. Plant Sci. **75**:69-74.

Tsuji, G.Y., Uehara, G., and Balas, S. 1994. A Decision Support System for Agrotechnology Transfer, DSSAT v.3 Vol.1-3. International Benchmark Sites Network for Agrotechnology Transfer, University of Hawaii, Honolulu, Hawaii.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw Hill, London. p. 262-291.

Walker, G.K. 1989. Model for operational forecasting of western Canada wheat yield. Agric. For. Meteorol. **44**:339-351.

Wall, P.C., and Cartwright, P.M. 1974. Effects of photoperiod, temperature and vernalization on the phenology and spikelet numbers of spring wheats. Ann. Appl. Biol. **76**:299-309.

Wardlaw, I.F. 1971. The early stages of grain development in wheat: response to water stress in a single variety. Aust. J. Biol. Sci. **24**:1047-1055.

Warrington, I.J., Dunstone, R.L., and Green, L.M. 1977. Temperature effects at three development stages on the yield of the wheat ear. Aust. J. Agric. Res. **28**:11-25.

Weir, A.H., Day, W., and Sastry, T.G. 1984. Using a whole crop model. p. 339-355. In: W. Day, and R.K. Atkin (eds.). Wheat growth and modelling. NATO ASI Series, Series A: Life Sciences Vol. 86.

Whisler, F.D., Acock, B., Baker, D.N., Fye, R.E., Hodges, H.F., Lambert, J.R., Lemmon, H.E., McKinion, J.M., and Reddy, V.R. 1986. Crop simulation models in agronomic systems. Adv. Agron. **40**:141-208.

Williams, G.D.B. 1971. Wheat phenology in relation to latitude, longitude and elevation on the Canadian Great Plains. Can. J. Plant Sci. **51**:1-12.

Williams, J.R., Dyke, P.T., and Jones, C.A. 1983. EPIC - a model for assessing the effects of erosion on soil productivity. p. 553-5472. In: W.K. Lauenroth, C.V. Skogerboe, and M. Flug (eds.). Analysis of ecological modelling. Proc. Third International Conference, Fort Collins, CO. Elsevier Scientific Publ. Co., New York, N.Y.

Willmott, C.J. 1981. On the validation of models. Phys. Geogr. **2**:184-194.

Willmott, C.J. 1982. Some comments on the evaluation of model performance. Bull. Amer. Meteorol. Soc. **63**:1309-1313.

Wong, L.S.L., and Baker, R.J. 1986. Developmental patterns in five spring wheat genotypes varying in time to maturity. Crop Sci. **26**:1167-1170.

Woodruff, D.R. 1983. The effect of a common date of either anthesis or planting on the rate of development and grain yield of wheat. Aust. J. Agric. Res., **34**:13-22.

Zee, S.Y., and O'Brien, T.P. 1970. Studies on the ontogeny of the pigment strand in the caryopsis of wheat. Aust. J. Biol. Sci. **23**:1153-1171.

8.0 APPENDICES

Appendix 1. Analysis of variance for controlled environment temperature and photoperiod experiment, showing expected mean squares and F test.

Model:
Experiment (ϵ) = random; Temperature (T), Photoperiod (P), and Cultivar (C) = fixed.

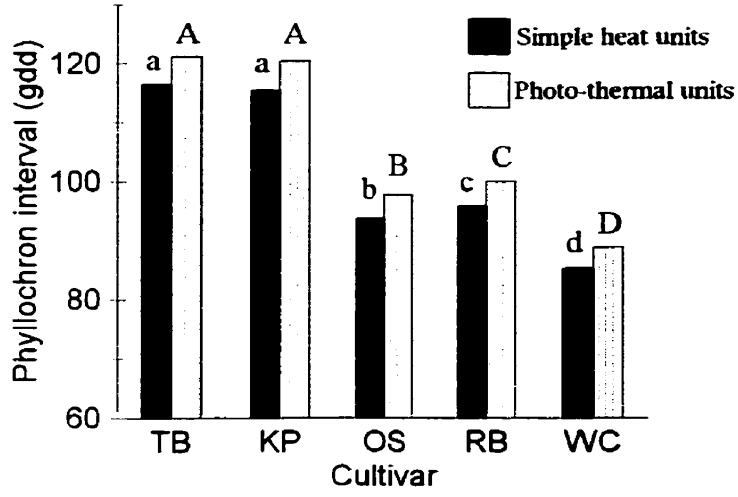
Source of variation	df	Mean squares (MS)	F test
T	(t-1)	$\delta^2_e + PEC\,[\Sigma T^2/(t-1)] + C\delta^2_{E(TP)}$	$MS_T / MS_{E(TP)}$
P	(p-1)	$\delta^2_e + TEC[\Sigma P^2/(p-1)] + C\delta^2_{E(TP)}$	$MS_P / MS_{E(TP)}$
T*P	(t-1)(p-1)	$\delta^2_e + EC[T/T-1]\delta^2_{TP} + C\delta^2_{E(TP)}$	$MS_{TP} / MS_{E(TP)}$
Expt (T*P)	(ϵ-1)(tp)	$\delta^2_e + C\delta^2_{E(TP)}$	$MS_{E(TP)} / MS_e$
C	(c-1)	$\delta^2_e + TEP[\Sigma C^2/(c-1)]$	MS_C / MS_e
T*C	(t-1)(c-1)	$\delta^2_e + PE\,[C/C-1][T/T-1]\,\delta^2_{CT}$	MS_{CT} / MS_e
P*C	(p-1)(c-1)	$\delta^2_e + TE\,[C/C-1][P/P-1]\,\delta^2_{CP}$	MS_{CP} / MS_e
T*P*C	(t-1)(p-1)(c-1)	$\delta^2_e + E[C/C-1][P/P-1][T/T-1]\,\delta^2_{CTP}$	MS_{CPT} / MS_e
Error (e)		δ^2_e	

Appendix 2. Analysis of variance for controlled environment vernalization experiment, showing expected mean squares and F test.

Model:
Experiment (ϵ) = random; Cultivar (C), Vernalization (V) = fixed.

Source of variation	df	Mean squares (MS)	F test
E	(ϵ-1)	$\delta^2_e + BCV\delta^2_E + ECVC\delta^2_{B(E)}$	$MS_E / MS_{B(E)}$
Block(E)	(b-1)(ϵ)	$\delta^2_e + ECVC\delta^2_{B(E)}$	$MS_{B(E)} / MS_e$
C	(c-1)	$\delta^2_e + EBV\,[\Sigma C^2/(c-1)] + BV[C/C-1]\,\delta^2_{EC}$	MS_C / MS_{EC}
V	(v-1)	$\delta^2_e + EBC\,[\Sigma V^2/(v-1)] + BC[V/V-1]\,\delta^2_{EV}$	MS_V / MS_{EV}
E*C	(ϵ-1)(c-1)	$\delta^2_e + BV[C/C-1]\,\delta^2_{EC}$	MS_{EC} / MS_e
E*V	(ϵ-1)(v-1)	$\delta^2_e + BC[V/V-1]\,\delta^2_{EV}$	MS_{EV} / MS_e
C*V	(c-1)(v-1)	$\delta^2_e + EB[C/C-1][V/V-1]\delta^2_{CV} + B[C/C-1][V/V-1]\delta^2_{ECV}$	MS_{CV} / MS_{ECV}
E*C*V	(ϵ-1)(c-1)(v-1)	$\delta^2_e + B[C/C-1][V/V-1]\delta^2_{ECV}$	MS_{ECV} / MS_e
Error (e)		δ^2_e	

Appendix 3. Comparison of simple heat units[z], and photo-thermal units determination of phyllochron intervals for AC Taber (TB), Katepwa (KP), Oslo (OS), Roblin (RB), and Wildcat (WC), grown under controlled environment [22°C/17°C, 26°C/20°C, 30°C/23°C, day/night temperatures, respectively, and 14, 16, and 18h photoperiod]



[z] Simple heat units: $DGDD = [(T_{max} + T_{min})/2] - T_{base}$,

Photo-thermal units: $$DGDD = \frac{[(P/24)T_{max}] + [((24-P)/24)\,T_{min}] - T_{base}}{2}$$

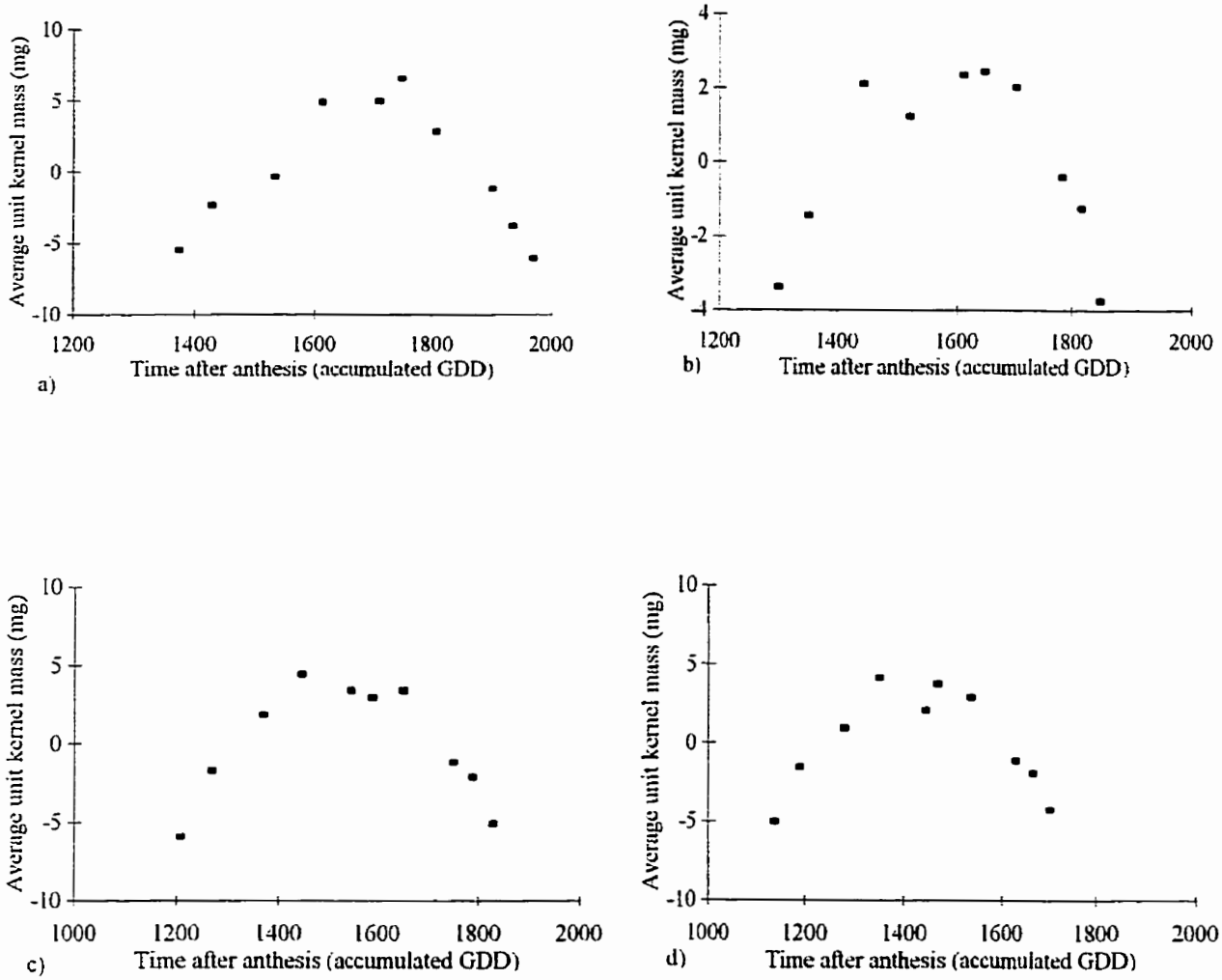
where DGDD is daily accumulated growing-degree-days, P is hours of photoperiod, T_{max} and T_{min} are light and dark temperatures, respectively, and T_{base} is the minimum temperature at which growth is assumed to cease. T_{base} was assumed to be 0°C (Cao and Moss, 1989c; Baker et al., 1986).

Appendix 4. Analysis of variance for spring wheat cultivars grown at Carman and Winnipeg, 1996, for three seeding dates per location, showing expected mean squares and F test.

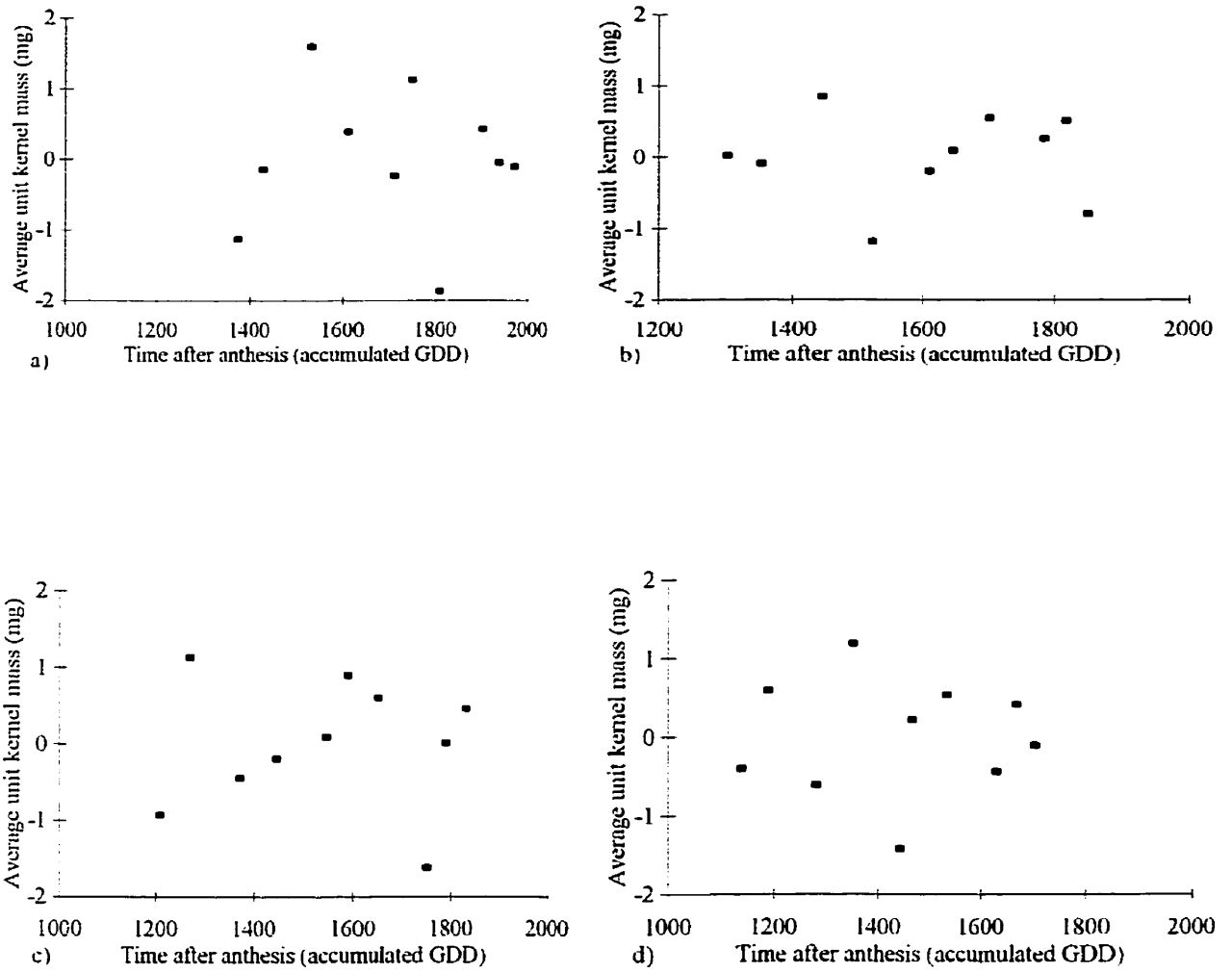
Model:
Location (L) = random; Seeding date (S), and Cultivar (C) = fixed.

Source of variation	df	Mean squares (MS)	F test
L	(l-1)	$\delta^2_e + BSC\delta^2_L + SCL\delta^2_{B(L)}$	$MS_L / MS_{B(L)}$
Block/L	(b-1)(l)	$\delta^2_e + SCL\delta^2_{B(L)}$	$MS_{B(L)} / MS_e$
SD	(s-1)	$\delta^2_e + BCL[\Sigma S^2/(s-1)] + BC[S/S-1]\delta^2_{LS}$	MS_S / MS_{LS}
L*SD	(l-1)(s-1)	$\delta^2_e + BC[S/S-1]\delta^2_{LS}$	MS_{SL} / MS_e
C	(c-1)	$\delta^2_e + BSL[\Sigma C^2/(c-1)] + BS[C/C-1]\delta^2_{CL}$	MS_C / MS_{CL}
L*C	(l-1)(c-1)	$\delta^2_e + BS[C/C-1]\delta^2_{CL}$	MS_{CL} / MS_e
SD*C	(s-1)(c-1)	$\delta^2_e + BL[S/S-1][C/C-1]\delta^2_{SC} + B[S/S-1][C/C-1]\delta^2_{LSC}$	MS_{CS} / MS_{LSC}
L*SD*C	(l-1)(s-1)(c-1)	$\delta^2_e + B[S/S-1][C/C-1]\delta^2_{LSC}$	MS_{LSC} / MS_e
Error (e)		δ^2_e	

Appendix 5. Examples of graphs showing non-random distribution of residuals from a linear model of grain filling values for a) AC Taber grown at Winnipeg, b) AC Taber grown at Carman, c) Katepwa grown at Winnipeg, and d) Katepwa grown at Carman.



Appendix 6. Examples of graphs showing random distribution of residuals from a quadratic model of grain filling values for a) AC Taber grown at Winnipeg, b) AC Taber grown at Carman, c) Katepwa grown at Winnipeg, and d) Katepwa grown at Carman.



Appendix 7. Examples of genetic coefficient reference trait comparison output performed by the CERES-wheat model for field-grown spring wheat cultivars at Carman seeding date one (CSD1).

Seed date	Cultivar	Coefficient[z]	Simulated	Measured	Reference Trait
CSD1	Biggar	P1V	60	60	Anthesis date (days)
CSD1	Biggar	P1D	60	60	Anthesis date (days)
CSD1	Biggar	PHINT	60	60	Anthesis date (days)
CSD1	Biggar	P5	60	60	Maturity date (days)
CSD1	Oslo	G1	13561	13620	Grains m^{-2}
CSD1	Oslo	G2	31	30	Kernel weight (mg)
CSD1	Oslo	G3	33.6	34	Kernels per spike

[z] Coefficients: P1V=vernalization coefficient; P1D=photoperiod coefficient; PHINT=phyllochron interval, the thermal time between successive leaf tip appearance; P5=relative grain filling duration; G1=kernel number per unit weight of stem; G2=kernel filling rate; and G3=non-stressed dry weight of a single stem and spike when elongation ceases.

Appendix 8. Example of computer-produced iterative output by the CERES-wheat model, of genetic coefficient for AC Taber grown at Carman seeding date one (CSD1).

Simul.	Seed date	P1V[z]	P1D	P5	G1	G2	G3	PHINT
1	CSD1	0.75	0.98N	5.4	7.2U	7.0U	0.6U	80
2	CSD1	0.75	0.10	5.4	7.2U	9.7U	0.6U	80
3	CSD1	0.75U	0.10U	5.4U	4.7	7.4	2.6	80
4	CSD1	0.75U	1.00U	5.4U	4.7	5.0	2.6	80U
5	CSD1	0.75U	1.00U	5.4U	4.7	4.0	2.6	80U
6	CSD1	0.80U	1.00U	5.4U	4.7	4.9	2.6	80U
7	CSD1	0.80	1.00	5.4	4.7U	4.5U	2.6U	80U

[z] Coefficients: P1V=vernalization coefficient; P1D=photoperiod coefficient; PHINT=phyllochron interval, the thermal time between successive leaf tip appearance; P5=relative grain filling duration; G1=kernel number per unit weight of stem; G2=kernel filling rate; and G3=non-stressed dry weight of a single stem and spike when elongation ceases. All coefficients except PHINT, have scalar values, between 0 and 9.

Letters after the values are coded as: N=no response to changes in coefficient, and U=coefficient not specified by user for changes.