A STUDY OF THE VERNALIZATION RESPONSES IN A NUMBER OF SPRING WHEAT (*TRITICUM AESTIVUM*) CULTIVARS

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Patricia Ellen Jedel

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TABLE OF CONTENTS

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

ABSTRACT

Jedel, Patricia Ellen. M. Sc. The University of Manitoba, October, 1982. A Study of the Vernalization Responses in a Number of Spring Wheat (Triticum aestivum) Cultivars. Major Professor; L. E. Evans.

Ten wheat, Triticum aestivum, cultivars of importance to spring wheat breeding programs were assessed for their responses to vernalization treatments.

Benito, Glenlea, Marquis, Neepawa, Prelude, Sinton and Yecora had little or no response to 0, 2 and 6 weeks of cold ($4^{o}C$) treatment; while Cajeme, Fielder and Pitic had positive responses to vernalization.

Patterns of response to 0-9 weeks of cold treatment were assessed. Prelude and Sinton were non-responsive to any duration of vernalization. Benito, Glenlea, Marquis, Neepawa and Yecora were relatively insensitive to the one- to seven-weeks cold treatments, while 8 and/or 9 weeks did initiate small threshold responses. Cajeme, Fielder and Pitic had graded, cyclic responses with their vernalization requirements fulfilled by 4 or 5 weeks of cold treatment.

Field plantings of vernalized grain of Cajeme, Fielder and Pitic did not alter the graded vernalization pattern of these cultivars. Fertile tiller numbers were unaffected but total tiller number were significantly reduced with 2-, 4- and 6-weeks cold treatments.

The development of responses in Cajeme and Pitic consisted of a lag period, a period of rapid initiation, and a plateau with satisfaction of the vernalization requirement.

Devernalization by high temperature ($25^{o}C$) was reduced with longer cold durations and/or a period at $15^{o}C$. Intermediate temperature durations of 1, 3 and 6 days effectively stabilized vernalization responses of Cajeme, Fielder and Pitic, with the three-day treatment being optimum.

Response to vernalization decreased with plant age. The 0- and 7-days old plants were more receptive than the 14- and 21-days old plants; while the 28-days old plants were non-responsive to vernalization treatments.

The temperatures of $1^{o}C$, $5^{o}C$ and $11^{o}C$ were found to be equally effective in vernalizing Cajeme and Pitic.

Light conditions of short days or darkness during cold treatment did not affect vernalization response.

Measurement of final leaf number, days to flag leaf emergence and days to anthesis were concluded to be the most consistent and accurate assessments of vernalization.

Segregation analyses of the F2 generations were made for Cajeme-Yecora, Glenlea x Pitic and Neepawa-Pitic crosses. Genic constitutions were proposed.

INTRODUCTION

Chouard (1960) defined vernalization as "an acquisition or acceleration of the ability to flower by a chilling treatment." Gotoh (1975) described all of the wheats tested in his study that were accelerated by cold treatments as "winter" wheats. Martinic (1973) demarcated wheats with vernalization responses as winter wheats only if they failed to head properly with spring planting and as intermediate wheats if they headed with spring planting. These two examples illustrate the non-standardization of the classification of spring and winter wheats on the basis of vernalization response. Spring and winter wheats may or may not have vernalization responses as was found by Gotoh (1975) in his assessment of winter cultivars and by Halloran (1977) in his assessment of spring cultivars.

Characteristics such as vernalization and photoperiodic response play an important role in the control of crop maturity and thereby are important factors governing yield (Wall and Cartwright 1974). The adaptation of a cultivar to a defined set of climatic and environmental conditions is controlled through the physiological processes that include the vernalization response (Martinic 1973). It is therefore incumbent when striving for well-adapted cultivars with dependability of maturity and yield to understand the vernalization response and to assess the response best suited for the conditions wherein the cultivar will grow.

The purpose of this study was to present findings on the vernalization responses of a number of spring wheat cultivars of importance in Western Canadian breeding programs. The areas of investigation included in this thesis were the following.

1. By cold duration studies assessments of ten spring wheat cultivars for their response to vernalization were made to:
   a) classify cultivars as responsive or non-responsive; and
   b) describe patterns of response.
2. For selected cultivars, the effect of various factors on the vernalization response were assessed:
   a) high temperature after cold treatments;
   b) intermediate temperatures after cold treatments;
   c) plant age (with green plant cold treatments);
   d) temperature of the cold treatments; and
   e) light during cold treatments.
3. Genetic analyses of vernalization from a number of responsive x non-responsive crosses were made.

LITERATURE REVIEW

Characterization of Vernalization

Effects on Plant Development

Vernalization is a physiological process that enables plants to respond to the appropriate light and temperature conditions that produce flowering (Purvis 1961). When the vernalization requirement has been partially or completely fulfilled, the point whereat the vegetative apex becomes competent to respond to the photoperiodic stimulus is advanced (Cooper 1956, Riddell and Gries 1958b, Marcellos and Single 1971). Wiegand et al. (1981) reported that as vernalization hastened the termination of the vegetative stage and initiation of the reproductive stage, all phases of post-vegetative development were chronologically advanced. In cereals, the morphology of the apex changes from single ridges to double ridges at the initiation of the reproductive structures (Purvis 1934, Bonnett 1936, Fisher 1973).

Reviews by Whyte (1948) and Chouard (1960) covered the history of works on vernalization. Purvis (1961) reviewed the physiological works on vernalization. Chailakhyan (1968), Evans (1971) and Zeevart (1976) presented coverage of the concepts of flower induction and vernalin.

Phenological development. Vernalization responses are difficult to quantify because standard measures of the response such as days to

heading and days to anthesis are assessments that include responses to environmental conditions after the inductive cold treatment (Marcellos and Single 1971, Wiegand et al. 1981). Cooper (1956) considered that measurements of the vernalization response that were based upon calendar time scales were limited in their usefulness because of differences in temperatures between years and locations.

Measurements of days to initiation of floral primordia was proposed by Purvis (1934) to be an important measurement in elucidating the correlation between vernalization and flowering. Investigators such as Riddell and Gries (1958b), Pugsley (1963), Halse and Weir (1970), Rawson (1970), Marcellos and Single (1971), Devay et al. (1976), and Federov (1976) have used days to initiation as an indication of the effects of vernalization on phenological development. The major disadvantages of the use of this measurement were its destruction of plant material and the necessity for handling sufficient numbers of plants to meet this demand (Cooper 1956).

Measurement of days to heading or ear emergence is one of the most widely used methods for determining the effects of vernalization, having been employed by Lojkin (1936), Kostjucenko and Zarubailo (1937), Wort (1939), Krekule (1961), Pugsley (1963), Syme (1968, 1973), Levy and Peterson (1972), Martinic (1973), Klaimi and Qualset (1974), Wall and Cartwright (1974), Halloran (1976), Law et al. (1976), Ford (1977, 1978), Cahalan and Law (1979), and Ford et al. (1981). Levy and Peterson (1972) found that days to heading was a more sensitive measurement of vernalization than final leaf number for distinguishing cultivar differences to vernalization among spring wheats. Cooper

(1956) stressed two disadvantages of this measurement as the influence of post-cold treatment temperatures and the indirect measurement of not only the time to initiation but also rate of ear elongation.

Friend and Gregory (1953), Riddell and Gries (1958b), Pauli et al. (1962), Halse and Weir (1970), Syme (1973), Salisbury et al. (1979), and Berry et al. (1980) used the measurement of days to anthesis as indicators of vernalization effects.

A less commonly used measurement has been days to flag leaf emergence or unfolding (Chujo 1966a & b, 1967, 1969, and Gotoh 1975, 1977, 1979, 1980). Gotoh (1975) stated that days until flag leaf emergence were more reliable than days to anthesis or heading as some cultivars failed to head or headed incompletely.

Leaf development. A reduction of leaf number with vernalization has been well documented. Purvis (1934) suggested using final leaf number as a measurement of vernalization response in rye. McKinney and Sando (1935) reported that final leaf number was reduced by initial cold treatments in Harvest Queen winter wheat.

Cooper (1956) found the rate of leaf appearances to be linear and unaffected by the initiation of floral primordia on the shoot apex. Final leaf number was a quantitative measurement of inflorescence development little affected by post-cold treatment temperature. Cooper concluded that using final leaf number of the main culm as a measure of reproductive development was a good technique for discriminant analysis of genotypic response to vernalization.

Halloran (1967) and Halloran and Boydell (1967) used final leaf number as a measurement of vernalization response in aneuploid series

studies to determine controlling chromosomes and dosage effects of these chromosomes.

Levy and Peterson (1972), Halloran (1975, 1977), and Berry et al. (1980) found that reduced leaf numbers on the main culm was a characteristic of post-cold treatment development of vernalization responsive spring wheats. However, Salisbury et al. (1979) cautioned that final leaf number was not a valid measure of vernalization response under conditions of alternating daily temperatures, when proportions of time at each temperature were not equal.

Devay et al. (1976) found low temperature treatments of Bankuti 1201 winter wheat produced a S-shaped curve for reduction in leaf number with increasing durations of cold treatments. This indicated a maximum and minimum leaf number as was proposed by Purvis and Gregory (1937) for rye.

Spike development. Rahman et al. (1978) determined that the final spikelet number was dependent upon the rate of initiation of primordia and the duration of production of floral primordia. The phase from terminal spikelet production to ear emergence had no effect on final spikelet number (Rawson 1970).

Pinthus (1967) found that the period from seedling emergence to initiation of reproductive development was similar for all of the winter wheats he tested, but earliness of some cultivars occurred due to a shorter initiation to heading period. Rawson (1970) found a similar phenomenon among spring wheat cultivars. Reduction in spikelet number was possibly due to reduced numbers of primordia present on the primary apex at the time of floral initiation and reduced

primordia production after initiation due to a shorter differentation period (Halse and Weir 1970, Rawson 1970).

Pugsley (1966, 1968, 1971), Derera and Ellison (1974), Wall and Cartwright (1974), and Ford (1977) reported that spikelet number decreased with increased cold treatment durations in vernalization responsive wheats. Salisbury et al. (1979) and Berry et al. (1980) were unable to establish relationships between final spikelet number and degree of vernalization response.

Tillering. Vernalization responses have been associated with decreased tiller number. Purvis (1934) found that when flowering of winter rye was delayed by lack of cold treatments, the tiller numbers were on the average higher. However, the tillering activity had not delayed flowering since flowering had occurred with as high a mean tiller number as 28.4 and failed when mean tiller number was only 1.9. Cooper (1956) demonstrated that removal of side tillers did not influence the vernalization response of Lolium rigidum.

McKinney and Sando (1935) noted that conditions favouring earliness also favoured reduced tiller numbers in Harvest Queen winter wheat. Levy and Peterson (1972) found that for spring wheat cultivars with vernalization responses, reduced tiller numbers accompanied increased durations of cold treatments. Pugsley (1968) proposed that vernalization influenced tiller number by the decreased time until floral initiation and ear emergence causing premature termination of tiller development.

Bell (1936) found that the rate of tillering in vernalization responsive cultivars of oats, barley and wheat was higher in vernalized

plots than in control plots during early development; but the shortening of the vegetative phase prevented normal tiller development and the controls ended up with more tillers than the vernalized plants. Purvis (1948) found in a field study of effects of planting date on the attainment of flowering in vernalized Petkus winter rye that a reduction in tiller number accompanied both increasing durations of vernalization treatments and later planting dates. However, the number of ears per earing plant increased as flowering was accelerated.

Duration of Cold Treatment

The degree of response shown by a cultivar is often relative to the duration of the cold treatment (Derera and Ellison 1974, Klaimi and Qualset 1974, Halloran 1977). Lojkin (1936) referred to the minimum cold duration that maximized response as the minimum effective duration of chilling. Martinic (1973) and Gotoh (1975) defined this minimum effective duration as the vernalization requirement of a cultivar. The expression of the vernalization response can be characterized by its pattern of development with extended vernalization periods.

Classification of requirements. Martinic (1973) described three classifications of wheat based upon vernalization requirements:

1. Spring--non-responsive to 1-10^{o}C cold treatments, nil requirement;
2. Intermediate--flowered with spring plantings but were accelerated by five to thirty or more days when vernalized for less than twenty days;

3. Winter--failed to head or headed very late and irregularly when spring planted or grown at temperatures above 12°C, but when vernalized for 20, 30, to 60 or more days uniform early heading was obtained.

Gotoh (1976) cited in Gotoh (1977, 1979, 1980) described criterion and classes for classification of vernalization requirements in wheat. For the test, cold treatments at 8°C under continuous illumination were given to one-leaf seedlings for durations increasing by increments of five days. The duration necessary for completion of the vernalization requirement was determined from the length of the minimum cold treatment that resulted in plants reaching flag leaf emergence of the main culm within 34 days of the end of the cold treatment. Post-cold treatment conditions were at 20°C and under continuous lighting. Class I had no vernalization requirement attaining flag leaf emergence within 34 days without any response to cold treatment. Class II had no vernalization requirement but did display a slight vernalization response to cold treatment. Class III required five days of cold treatment to attain flag leaf emergence within 34 days. Class IV required between ten and thirty days of cold treatment. Class V required either 35 or 40 days of cold treatment. And Class VI required 45 or more days.

Patterns of development. Classification of cultivars by requirement does not account for the developmental pattern of the vernalization response. Patterning of responses takes into account the minimum duration that will produce a response and the cumulative, irregular or threshold nature of the response (Levy and Peterson 1972, Derera

and Ellison 1974, Halloran 1977, Berry et al. 1980).

The most common pattern of response is the cumulative or graded response. This was the type of response Lojkin (1936) described for Turkey Red and Leap's Prolific; with cold treatments varying from thirty to sixty days, the length of the vegetative period decreased quantitatively with increased cold durations. For Petkus winter rye, seven days of cold effectively initiated some response and as the cold treatment increased a graded response was found up until 14 weeks of treatment (Purvis and Gregory 1937). The winter annuals—Triticum aestivum (Squareshead's Master), T. aestivum (Yeoman), T. aegilopoides (2A1), Lolium rigidum (Wimmera), L. italicum (Irish)—showed a regular relationship between length of the cold treatment and acceleration of flowering (Cooper 1956). Klaimi and Qualset (1974) and Devay et al. (1976) found that a quantitative vernalization response occurred with from two to seven weeks of cold treatment for the winter wheats they tested. In spring wheats tested as having vernalization responses, cumulative responses have been found by Riddell and Gries (1958b), Levy and Peterson (1972), Derera and Ellison (1974), Klaimi and Qualset (1974), and Halloran (1977).

Irregular responses include cumulative responses where plateaus and/or retardation occurs with extended cold durations that may or may not, with still further extension of cold durations, show a renewed graded response. Grant (1964) and Derera and Ellison (1974) found retardation with extended cold treatments of winter wheats. Halloran (1977) reported that the developmental patterns of vernalization response in the cultivars Gabo and Mexico 120 had plateaus from

two to five weeks with further acceleration when cold treatments were longer than five weeks.

The patterns of vernalization response with duration were related to the expression of vernalization genes in near-isogenic Triple Dirk wheat lines by Berry et al. (1980). Two classes of response were found: 1) a threshold or all-or-nothing response; and 2) a cumulative or graded response. The threshold response was attributed to the gene action of vrn3 and/or vrn4; and the cumulative response, to the gene action of vrn1. The action of vrn2 was found to intensify the two classes of response.

The relationship between duration of the vernalization treatment and expression of the treatment with varying spring field planting dates was determined by Purvis (1948). With delayed sowings, progress towards flowering was delayed in unvernalized Petkus winter rye and accelerated in spring rye. The response of the winter rye to short durations of cold treatment was greater after early sowings than late; while the response to long periods of cold treatment was greater after late sowings. Purvis attributed the differences due to sowing date to the influence of natural vernalization under field conditions. Zuzens (1981) found the same trends with spring wheats. Non-responsive wheats, Neepawa, Glenlea and Yecora 70 were accelerated by delayed sowings but responsive wheats, Pitic 62, NB339, Fielder and Cajeme 71 were retarded by delayed spring sowings on a percentage basis of the non-responsive wheats.

Reversibility

The reversal of the effects of cold treatments by an antagonist

such as warm temperatures was termed devernalization by Gregory and Purvis (1936b). Reversibility of the vernalization response of partially vernalized plants by devernalization and revernalization has been described as a fundamental property of the vernalization process (Purvis 1961). Purvis and Gregory (1952) also found that assessment of the stability of the vernalization response could be made by exposures to devernalizing conditions.

Devernalization. Lojkin (1936) reported that drying of vernalized seeds and exposing then to warm temperatures (15°C) decreased or nullified the vernalization already produced.

Gregory and Purvis (1936b, 1938b, 1948) and Purvis and Gregory (1952) through restricting growth by an anaerobic environment or limited moisture found that high temperatures (20°C or 35°C) brought about a quantitative reversal of the low temperature (1-2°C) effect in Petkus winter rye. Progress towards flowering obtained from six weeks at 2°C was progressively reduced by increasing the number of intercalated 24-hour periods at 20°C. When the relative periods at low and high temperatures were maintained at a 2:1 ratio and a total of six weeks of cold, but the absolute lengths of the two periods were decreased, the progress towards flowering was retarded. Exposures to 35°C for 8 and 16 hours and 1, 2, 3, 4 and 5 days were found to have little effect on time to flowering of spring rye, but did cause a marked and progressive delay in flowering of winter rye (previously vernalized for six weeks at 1°C). Devernalizing temperatures tested ranged from 15-17°C to 40°C. Following devernalization chilling treatments resulted in revernalization.

Friend and Gregory (1953) reported that the devernalizing effects of high temperatures (25°C) were annulled by six weeks at this high temperature. Friend and Purvis (1963) determined that prolonged exposures of three to six weeks to devernalizing temperatures accelerated flowering only when given after partial vernalization of four or six weeks. The trade-off between devernalization and promotion by high temperature (20°C) occurred at 12 days for partially vernalized whole grains of Petkus winter rye. Heat treatments before vernalization delayed the progress towards flowering of the subsequent cold treatment; but they did not impair the capacity for vernalization providing the duration of the cold treatment was sufficiently long.

Chujo (1966b, 1967) examined the effects of various thermoperiods on the vernalization and devernalization of wheat. The longer the period of intercalated exposure to high temperature the less effective was the low temperature in accelerating days to flag leaf emergence. Chujo found that short (8 hour) exposures to warm temperatures enhanced the cold treatment of 16 hours. However, devernalization was observed when the period of the warm treatment was for more than several days (ibid. 1967).

Devay et al. (1976) reported devernalization of winter wheat by 36 hours at 32°C. The extent of devernalization was greater at the lower durations of cold treatments. Following devernalization, selected plants were revernalized by cold treatments.

Stabilization. The stability of vernalization responses has been increased by increasing the duration of the cold treatment (Gregory

and Purvis 1948, Chujo 1967, Devay et al. 1976). Gregory and Purvis (1948) determined for Petkus winter rye that as the period of low temperature was extended the vernalized condition induced was progressively less easily reversible and finally was completely stable to a three-day exposure to 35°C.

Purvis and Gregory (1952) reported that the stability of the vernalization response was enhanced by an intercalated period at a neutral temperature (15°C) between the low and high temperature treatments. Friend and Purvis (1963) determined that the stabilizing effect of a neutral period was unaffected by the moisture supply during this period. Stabilization was also effected by: 1) restricted water supply during dark, high temperature (20°C or 25°C) treatments; 2) low intensity illumination during the high temperature treatment; and 3) illumination during a neutral period when the heat treatment was in darkness.

Chujo (1967) concluded that 15°C was a neutral temperature for wheat because in thermoperiod studies no devernalization occurred when 15°C was the high temperature treatment. When the cold treatment was at 10°C, greater stability of the vernalization occurred as devernalizing conditions were less effective than when the cold treatment was at lower temperatures.

Cooper (1956), Derera and Ellison (1974), Halloran (1977) and Ford et al. (1981) followed their cold treatments with a period (two days to two weeks) of neutral temperature (10°C to 15°C) to stabilize the induced vernalization.

Stage of Plant Development

Wellensiek (1962) theorized that the prerequisite of vernalization

was active cell division. In theory therefore in any non-dormant stage from pollination to anthesis the perception and induction of the vernalized condition should be possible. Devay et al. (1976) reported that vernalization of imbibed grain took place at temperatures of $0^{o}C$ to $-1^{o}C$ whereat cell division was almost completely inhibited. Therefore, in cereals the prerequisite may be for a non-dormant stage of development where cell division is possible rather than an absolute requirement for mitosis.

Cold treatments are usually given to imbibed or germinated whole grains (Krekule 1961, Derera and Ellison 1974, Weinberger 1975, Halloran 1977, Wiegand et al. 1981). However, vernalization treatments may be achieved by treating excised embryos (Purvis 1944, 1948, and Friend and Purvis 1963) or green plants (Krekule 1961, Derera and Ellison 1974, Gotoh 1975, 1977, 1980, and Ford et al. 1981).

Pre-harvest development. Kostjucenko and Zarubailo (1937) found natural vernalization of seeds during ripening could account for apparent discrepancies between the vernalization requirement of wheats from southern and northern locations in the Soviet Union. In seeds ripened at lower temperatures the vernalization requirement was much reduced as compared with seed ripened at high temperatures. From the early phases of seed formation until the beginning of wax ripeness, the embryo was in a vitally active state; it was very sensitive to external influences and was able to be vernalized. With seed maturation the embryo entered a state of dormancy and was less sensitive to external influence; the embryo lost its ability to be vernalized

until dormancy was broken and the embryo reactivated. Wort (1940) and Riddell and Gries (1958b) discovered variability of development and vernalization response in seeds of wheat cultivars grown in different years and/or locations. This variability was attributed to natural vernalization of the seed during development. Riddell and Gries found differences were eliminated by extended vernalization.

Investigations using mechanical refrigeration have confirmed that vernalization of the seed prior to dormancy is possible. Equivalent degrees of vernalization were obtained by McKinney and Sando (1935) when seed of Harvest Queen winter wheat from the soft-dough stage, the hard-dough stage, and one-year old grain was chilled for 72 days. Gregory and Purvis (1936a) successfully vernalized Petkus winter rye during grain ripening by exposing the ripening ears to twenty days of cold treatment. Gregory and Purvis (1938a) ascertained by applications of low temperature treatments after anthesis and during the period of embryo development that the earliest stage of the embryo tested (five days) was competent to respond to the chilling treatment and as the time of the application approached the onset of dormancy the degree of vernalization attained was decreased. Weibel (1958) found that immature embryos of Comanche winter wheat could be vernalized by harvesting spikes with attached culms 8 to 12 days after anthesis, standing the culms in water and storing them at 0-4.4^{o}C for 40-50 days.

Post-harvest development. The degree of germination during the cold treatment, regardless of this degree prior to the cold treatment, was assessed by Lojkin (1936) to have a major influence on the degree of

vernalization attained, with active growth during vernalization increasing the response. Hansel (1953) verified that the degree of growth of germinated seeds prior to the cold treatment had no effect on the vernalization response reached.

Purvis (1944, 1948) reported that isolated embryos of Petkus winter rye responded to vernalization treatments after an initial lag period of two weeks. The progress towards complete vernalization proceeded at the same rate as in whole grains after this delayed start.

Chujo (1966a) exposed plants of Norin No. 27 at 0, 5, 10, 15, 20, 30, 60 and 90 days after sowing to thirty days at 0°C, 5°C or 10°C. The vernalization response for all temperature treatments decreased with plant age, although overall the plants treated at 0°C exhibited less response than those plants treated at 5°C or 10°C. No hastening of flag leaf emergence was obtained in plants aged 90 days; slight hastening of flag leaf emergence was noted in plants aged 20, 30 and 60 days; and marked hastening of flag leaf emergence was observed in plants aged 0, 5, 10 and 15 days.

Salisbury et al. (1979) determined the genotypic influence of near-isogenic Triple Dirk lines on the expression of vernalization response when the portion of the cold treatment given to green, leafy plants was increased. For example, one week of cold treatment was given to imbibed seeds; these seeds were planted and allowed to grow under warm conditions; and when the plants were of sufficient size, these green plants were returned to the cold room for three more weeks of cold treatment. Two of the near-isogenic Triple Dirk lines exhibited a threshold response. The Vrn1vrn2 genotype responded

when all of the cold treatment was given to the growing plant and the Vrn1Vrn2 genotype responded to the same extent when one-quarter or more of the cold treatment was given to the growing plant. The vrn1-vrn2 genotype displayed a graded response with the response increasing as the portion of exposure to the growing plants increased. The response of the vrn1Vrn2 genotype was unaffected by the manner of the cold treatment.

McWilliam (1968) and Gotoh (1980) noted that response to green-plant vernalization was more effective than conventional seed vernalization. Gott (1957) found that the winter wheat Minter Minfloris was capable of being vernalized at any stage from just germinated seed until six-weeks old plants with 6-7 leaves on the main shoot.

Temperature of the Cold Treatment

As a biological phenomenon, vernalization is unusual because while most biochemical processes are slowed down by low temperatures the vernalization process is induced (Purvis 1961). The temperature of the cold treatments used to vernalize wheat commonly range from $0^{o}C$ to $10^{o}C$ (Grant 1964, Chujo 1966a). The most frequent temperatures encountered in the literature have been $1^{o}C$ to $5^{o}C$, and although cold treatments are often given at a constant temperature, ranges of cold temperatures have also been used as vernalization treatments.

Optimum temperatures. Various investigators have established optimum temperatures for induction of maximal vernalization response; and optimum temperatures appear to be genotypically dependent. McKinney and Sando (1933) determined that the range of $2.8-5.0^{o}C$ was the

optimum vernalization temperature range for Harvest Queen, Currell, and Sol winter wheats. Purvis (1948) obtained equally effective vernalization of Petkus winter rye with cold treatments ranging from 1°C to 7°C. The most effective temperatures for vernalization of the wheat cultivar Akakawaaka were 4°C and 8°C; and of Akabozu, Norin No. 27 and Norin No. 4 were 8°C and 11°C (Chujo 1966a). Chujo (1966b) established the optimum range of vernalization temperatures for Norin No. 27 as 6°C to 10°C and for Norin No. 4 as 6°C to 14°C.

By using a temperature gradient, Trione and Metzger (1970) determined that the optimum temperature of vernalization for the wheat cultivar Burt was 7°C.

Under continuous illumination the 10°C treatment maximized the response of the wheat cultivar Nishimura; however, in darkness cold treatments at either 5°C or 10°C were equally effective (Inouye et al. 1964).

Effective temperatures. Short of testing for optimum temperatures investigators have tested the effectiveness of a wide range of temperatures for inducing vernalization responses. Ahrens and Loomis (1963) vernalized Minter winter wheat as imbibed grain at temperatures of 1°C and 3°C and as seedling plants at 7°C; all treatments were equally effective when given for 6-8 weeks. Pinthus (1967) found 0.5-2.0°C and 1.5-3.0°C temperature treatments to be equally effective when given for 69 days to Cleo, Champlein, Proffeseur Marchal, Capelle Desprez and Hybrid 46 winter wheats.

Lojkin (1936) determined that vernalization of Leap's Prolific and Turkey Red occurred at 1°C but not at -12°C although the latter

was not injurious to the seed. Cold treatments for 67 days at -4.4°C did not accelerate the heading of Harvest Queen, Currell and Sol but effective vernalization did occur at the -1.1°C to 1.7°C treatment (McKinney and Sando 1933). The lower temperature limit for vernalization of Petkus winter rye was established at -4.5°C with a rapid fall in the efficacy of the treatment between 0°C and -4.5°C (Hansel 1953). Trione and Metzger (1970) identified 3°C as the lower limit for effective vernalization of Burt.

Kostjucenko and Zarubailo (1937) detected accelerated development of wheat grown from seeds ripened at temperatures as high as 14°C. Riddell and Gries (1958a) concluded that 15.5°C was effective in partially vernalizing Chinese Spring. The upper limit for Burt was 9°C (Trione and Metzger 1970).

Other Environmental Considerations

There are many environmental factors both during and after the cold treatment that may influence the vernalization response. Gregory and Purvis (1938b) reported that the vernalization of winter rye and wheat was prevented by the anaerobic conditions of a nitrogen atmosphere and oxygen tensions below the norm reduced the vernalization response. Derera and Ellison (1974) used sodium hydroxide pellets to prevent carbon dioxide build-up during cold treatments. And a common procedure during the cold treatment of seeds in closed containers was to aerate the seed at frequent intervals to disperse carbon dioxide (Cooper 1956, Gott 1961, Weinberger 1975).

Halse and Weir (1970) found that short day (10 hours light) and/or cold treatments (12/7°C) during post-vernalization development

reduced the vernalization response of vernalization-sensitive wheat cultivars. Chinoy (1956) determined that the photosensitivity of cultivars with vernalization responses was increased with increasing fulfillment of the vernalization requirement. Initiation in completely vernalized treatments of Petkus winter rye was proportional to the period of post-cold treatment illumination, being fastest under continuous light and slowest in short days (Gott et al. 1955).

Light conditions during vernalization. Fedorov (1976) proposed that the vernalization process was an extension of the photoperiodic response that required short days during the initial period of the development span. And while Purvis and Gregory (1937) found with Petkus winter rye that short day treatments during early development could be substituted for cold treatments in accelerating development, Chujo (1966a, 1966b, 1967) and Gotoh (1975, 1978, 1980) effectively vernalized plants with cold temperature treatments under continuous illumination.

The effects of illumination during vernalization are dependent upon whether the treatment is of seeds or green plants and upon the intensity and duration of the lighting. McKinney and Sando (1935) reported that the vernalization response of Turkey was not significantly influenced by darkness or short days during cold treatment of the seed. Krekule (1961) found that vernalization of green plants was enhanced under field conditions by short days and inhibited by continuous darkness. Pauli et al. (1962) determined that short days enhanced the vernalization response in seed treatments; however, it should be noted that the short day treatments were at 7°C and the

dark treatments were at 1°C.

In a series of studies, Chujo (1969) educed the effects of light during the vernalization of Norin No. 27. Darkness as opposed to continuous illumination during vernalization was found to inhibit the vernalization responses in plants aged 10, 15 and 20 days, whereas 0- and 5-days old plants were not affected. Progressive acceleration of development accompanied increasing daily durations of illumination of 13-days old plants. Low light intensities were more inductive to acceleration of development than high intensities, when plants were of an age to be influenced by illumination. Light was not required for the vernalization of sprouted seeds.

Moisture during vernalization. The use of the limited moisture technique during vernalization of seeds required that the moisture content be at least 50 percent of the dry weight of the seed (Lojkin 1936). Gradual decreasing moisture percentages during cold treatments when the initial moisture percentages were 50 or 55 caused inhibition of the vernalization response; but gradual decreasing moisture percentages when the original percentages were 60 or 80 were as effective as constant percentages (ibid.). Wort (1939) found that seed vernalization of Marquis was more effective when seed moisture level was maintained at 60 percent than at 20, 30, 40 or 50%.

Gott (1961) and Weinberger (1975) stressed the importance of maintaining the percentage moisture of imbibed seeds at or above 50 percent of the dry weight of the seed during cold treatments by frequent weighings and additions of water when required. Gregory and Purvis (1952) found unlimited moisture supplied by placing seeds in

wet sand was more effective in inducing vernalization than was the limited moisture technique at 50-55% moisture supply.

Genetics of Vernalization and Cultivar Assessments

Identification of the Genes

Studies of the genetical control of the vernalization response in T. aestivum have revealed that this characteristic is controlled by a small number of genes with major effects (Qualset 1978). Pugsley (1972) in consultation with Dr. R. A. McIntosh has designated the genes controlling vernalization in wheat as belonging to Vrn series.

Although spring and winter cultivars differ by more than their vernalization requirement, studies on the genetics of vernalization have often been labelled as growth habit studies (Klaimi and Qualset 1974). McKinney and Sando (1933) viewed the spring and winter habit as being differing degrees of earliness and lateness so that upon spring planting those plants that flowered within the season were termed spring and those that did not initiate flowering were termed winter. Despite the limitation of phenological development being under control by more processes than vernalization alone, using earliness and lateness as quantifiers of vernalization response has allowed for the identification of the Vrn genes (Pugsley 1971, 1972 and Gotoh 1979).

A review by Murfet (1977) covered the genetics of flowering and vernalization with special emphasis on wheat, maize and peas.

Conventional segregation analysis. In studies of segregating generations of crosses between spring and winter or spring and spring

wheats, segregants have been classified into spring and winter types (for example Cooper 1923, Klaimi and Qualset 1974, and Gotoh 1979). However, many researchers have noted continuous variation in the spring category and split the spring segregants into classes based upon development (for example Aamodt 1923, Powers 1934, and Gotoh 1977). Dominance or partial dominance of spring over winter habit was concluded by Aamodt (1923), Cooper (1923), Gaines and Singleton (1926), Hayes and Aamodt (1927), Quisenberry (1931), Pugsley (1963, 1971) and Klaimi and Qualset (1974). The number of genes involved have ranged from one (Pugsley 1963), two (Cooper 1923, Quisenberry 1932, Pugsley 1968, Klaimi and Qualset 1974), three (Powers 1934, Pugsley 1971), to four or more (Gaines and Singleton 1926, Hayes and Aamodt 1927, Pugsley 1972, Gotoh 1977), depending on the cultivars used in the initial crosses.

Pugsley (1972) reported that the Vrn1 allele was non-responsive to cold treatment and epistatic to Vrn2. The Vrn2 and Vrn3 alleles also conferred spring habit but were responsive to cold treatments. A further allele, designated Vrn4, was found to confer spring habit in Gabo (ibid.). Pugsley developed Triple Dirk (TD) tester lines: TD (Vrn1Vrn2vrn3vrn4), TD-B (vrn1Vrn2vrn3vrn4), TD-C (vrn1vrn2vrn3-vrn4), TD-D (Vrn1vrn2vrn3vrn4), TD-E (vrn1vrn2Vrn3vrn4) and TD-F (vrn1vrn2vrn3Vrn4); and these lines have been used to assess genotypic responses and genic constitutions (Gotoh 1979, Salisbury et al. 1979, Berry et al. 1980). Gotoh (1979) found the TD-E, TD-F and TD-B genotypes to be responsive to vernalization and that winter types (vrn1vrn2vrn3vrn4) varied in their vernalization requirements. Gotoh

(1980) assessed that the vernalization requirements of winter wheats were governed by two gene differences but did not identify these genes with respect to the Vrn genes.

Aneuploid studies. Aneuploid series studies have been used to locate the chromosomes whereon the genes governing vernalization lie and to determine the multiple allelic and dosage dependent nature of the Vrn genes. By the use of chromosome substitution into Chinese Spring monosomics the following chromosomes have been identified as having major influences on growth habit or earliness:

1. 5D (Kuspira and Unrau 1957, Knott 1959, Tsunewaki and Jenkins 1961, Tsunewaki 1962, Driscoll and Jensen 1964, Boyd and Singh 1973, and others);
2. 2B (Kuspira and Unrau 1957, Tsunewaki and Jenkins 1961, Tsunewaki 1962, Boyd and Singh 1973);
3. 5A (Knott 1959, Tsunewaki and Jenkins 1961, Tsunewaki 1962, Driscoll and Jensen 1964, Boyd and Singh 1973, and others).

The Vrn1 locus has been located on 5A; and Vrn3, on 5D (Law et al. 1976, 1977, Cahalan and Law 1979, Snape et al. 1979). Increased dosages of the 5D chromosome (Vrn3) have resulted in earlier flowering and decreased vernalization response (Halloran 1967, Cahalan and Law 1979). Halloran (1976) determined single genes on each of the chromosomes 5A, 5B and 5D influenced vernalization response. However, Snape et al. (1979) educed within chromosome epistasis on 5D indicating that there may be more than one locus on this chromosome. Law et al. (1976) proposed multiple allelic series at the 5A and 5D chromosomal loci to account for the variation between substitution lines.

Assessments of Genotypes

Martinic (1973) described the requirements for a generally adapted wheat cultivar to be a spring wheat with little or no vernalization response and low sensitivity to photoperiod. He acknowledged a need in fall-planted cultivars for a control mechanism to delay flowering so that if winters were severe damage to the floral organs would not occur. Gotoh (1975) found vernalization requirements of cultivars selected from the International Winter Wheat Performance Nursery (IWWPN) varied from zero to seventy days; and within the cultivars, Rousalka and Blueboy, heterozygosity of vernalization requirement was demonstrated. Therefore, the vernalization response of winter planted cultivars was not a clear-cut requirement but was a matter of local development and adaptation. The vernalization responses of spring-planted cultivars have also been found to vary although requirements were not as great (Halloran 1975). Wall and Cartwright (1974) concluded that vernalization was an important maturity control mechanism in spring cultivars from tropical regions whereas cultivars from temperate zones had their maturity controlled by photoperiod. Marcellos and Single (1971), Levy and Peterson (1972), Syme (1973) and Ford et al. (1981) opined that the vernalization response of spring wheat cultivars was a matter of best adaptation to a local climate.

Cultivar responses. Pugsley (1971, 1972) and Gotoh (1979) have assessed cultivar responses on the basis of Vrn genes. Other researchers have assessed cultivar responses and/or requirements but have not attempted to relate their findings to the Vrn genes.

Pugsley (1971, 1972) reported the following relationships between genotype, vernalization response and spring wheat cultivars:

1. Vrn1vrn2vrn3—nil—Kolben, Thatcher, WW15, TD-D;
2. vrn1Vrn2vrn3—positive—Brown Schlanstedt, TD-B, Festiquay, Gabo;
3. vrn1vrn2Vrn3—positive—Loro, Chinese Spring, TD-E;
4. Vrn1Vrn2vrn3—nil—Triple Dirk.

Gotoh (1979) concluded that the Vrn3 allele was indigenous to Japanese spring wheat cultivars and that the vernalization response conferred by this allele could be adaptively advantageous to the growing conditions in southern Japan.

McKinney and Sando (1933), Wort (1940), Riddell and Gries (1958b), Syme (1968, 1973), Halse and Weir (1970), Marcellos and Single (1971), Levy and Peterson (1972), Derera and Ellison (1974), Wall and Cartwright (1974), Klaimi and Qualset (1974), Halloran (1975, 1977), and Ford et al. (1981) have assessed the vernalization responses of numerous spring cultivars. Despite the wide range of vernalization treatments (i.e. differences in durations, temperatures, stages, and post-cold treatment conditions of temperature and light) classification of cultivars among researchers have been fairly, although not absolutely, consistent. Those responses of interest for this thesis were the positive responses of Pitic 62 (Syme 1968, 1973, Levy and Peterson 1972, Klaimi and Qualset 1974, Wall and Cartwright 1974, Ford et al. 1981) and Cajeme 71 (Wall and Cartwright 1974). Wall and Cartwright (1974) found Yecora 70 had a slight response to their vernalization treatment. Marquis has been classified as non-respon-

sive by McKinney and Sando (1933) and Wall and Cartwright (1974) and as responsive by Wort (1939, 1940) and Levy and Peterson (1972).

Levy and Peterson (1972) and Halloran (1977) found that the vernalization requirements of spring cultivars were variable but that in most cultivars the requirements were fulfilled within four weeks of cold treatment.

Breeding programs. Gotoh (1977) felt that spring x winter hybridization programs by such international groups as CIMMYT would produce wheat lines that would differ in their vernalization requirements. Even from spring x spring crosses, Gotoh (1979) found the resulting cultivars differed in their vernalization responses.

Halloran (1977) proposed that breeders could select for increased yield by selecting for increased spikelet numbers, without drastically altering maturity. Pinthus (1967) and Rahman et al. (1978) found that a component of spikelet number was under genic control and inherited independently of vernalization response. Wall and Cartwright (1974) concluded that breeding for larger spikelet numbers by incorporation of a positive vernalization response would not be effective in temperate regions where spring temperatures would cause natural vernalization and concurrently reduction of spikelet numbers.

Levy and Peterson (1972) suggested that positive vernalization requirements in spring wheats did not serve as an adaptive advantage but were remnants of the evolutionary process reinforced by the appearance of winter types in hereditary backgrounds.

McEwan (1966) found that the influence of the parental environment on the performance of the progeny was profound and emphasized

the necessity for the use of strictly comparable seed in investigations of vernalization or photoperiodic response and in field trials for cultivar assessments and comparisons.

Hypotheses of Vernalization

History

The mechanism whereby a period of cold treatment can act posthence on a phase of development that is thereby accelerated has remained hypothetical. In reviews by Whyte (1948), Chouard (1960), Purvis (1961), and Salisbury (1963) the development of theories of vernalization have been discussed.

Chouard (1960) has outlined the requirements that a theory on the phenomenon of vernalization need encompass as:

1. Effective cold temperatures;
2. Effective cold durations;
3. Oxygen;
4. Moisture;
5. Carbohydrates to support respiration (Purvis 1947);
6. Stem or bud primary meristems (Ishihara 1961).

As well the theory must account for the duration between reception of the cold treatment and the initiation of flowering. Therefore, postulation of a stable compound or prolonged autocatalysis of the vernalized condition would be appropriate.

Early theories. Kleb's "ripeness to flower" theory encompassed the importance of temperature, light and/or darkness on phases of plant development (cited in Whyte 1948). Kleb felt that the balance between

carbon assimilation and mineral nutrition was important in bringing about ripeness (cited in Purvis 1961); and this theory led to such practices as controlling fertilizer applications and pruning to stimulate flowering (cited in Salisbury 1963).

Gassner (1918) cited in Whyte (1948) postulated that low temperatures acted as a release on flower formation and cited in Purvis (1961) that the rate of stimulation of flowering was proportional to the decreased temperature.

Tolmacev theorized that cold temperatures allowed for sufficient accumulation of products of disintegration in the "stem plasm" that stimulated fruit bearing (cited in Whyte 1948).

Cholodny (1935) presented the "Blastenin theory" to explain the effects of vernalization (cited in Purvis 1961). It was based on the premise that high concentrations of auxin developed in the embryo from the aleurone and endosperm during cold temperature treatment and that this stimulated future development (Blastenin=auxin) (cited in Whyte 1948). This theory has been discredited by the findings of Hatcher (1945), Michniewicz et al. (1978), and Reda et al. (1978), that although auxin levels increased during cold treatments of imbibed seeds this auxin had no direct role in vernalization.

The "Stadial" or "Phasic theory of development" was developed by Lysenko (cited in Whyte 1948). Lysenko postulated the existence of developmental stages each with absolute environmental requirements; however the stages were in a set order, the same in all species, absolutely irreversible, and due to irrevocable physical changes of the protoplast (cited in Whyte 1948, Chouard 1960, Purvis 1961,

Salisbury 1963). The thermic phase was inversely related to temperature (cited in Whyte 1948). As all plants passed through the thermic phase, Lysenko developed his proposals of cold treatments enhancing development and yields (cited in Lojkin 1936).

Descriptive mechanisms. Numerous descriptive formulations involving flower producing substances have been developed. Schemata have involved the production of promoters or destruction of inhibitors of the flowering process.

Van de Sande Bakhuygen (1947) proposed that an enzyme designated as "vernalase" was a product of low temperatures or the thermophase (cited in Chouard 1960, Purvis 1961). During an inter phase, promoted by warm temperatures and short days, vernalase catalyzed a reaction resulting in "vernaline" that would under appropriate concentrations be converted during the "photophase" to a "florigen" precursor.

Lang and Melchers (1947) expressed their observations of vernalization in Hyoscyamus niger (henbane) on the basis of reactions having different reaction coefficients greater than one (cited in Purvis 1961). A precursor was postulated to be converted at low temperatures to a thermolabile intermediate. This intermediate would be converted to the stable end product at normal temperatures and in the presence of oxygen (cited in Chouard 1960). At high temperatures however the intermediate was inactivated by heat devernalization (cited in Chouard 1960, Purvis 1961).

Purvis and Gregory (1952) hypothesized the existence of a precursor A that was transformed to A' during low temperatures; this reaction was reversed at high temperatures leading to devernalization.

The conversion of A' to B was proposed to procede at either low or normal temperatures accounting for the increased stability of vernalization with time and intermediate temperature treatments. The substance B could be converted to E, a vegetative hormone promoting leaf production, or to C. The product C was converted to D during appropriate photoperiodic conditions. The intermediate A' was thermolabile while the intermediate B was thermostabile. Differential temperature coefficients of the intermediate reactions greater than unity were used to explain the overall reaction (Purvis 1961).

Napp-Zinn (1937, 1957) developed a schema of the vernalization reaction in Arabidopsis thaliana var. Stockholm that involved a series of reactions with thermolabile and thermostabile intermediates (cited in Chouard 1960, Purvis 1961).

Genetic Theories

Studies have revealed that the vernalization requirement was under genetic control. There arose a need to integrate schematic mechanisms with gene control and/or products. Both Melchers (1952) and Purvis and Gregory (1952) recognized that the vernalization requirement of their respective plants of study, henbane and rye, was under genetic control (cited in Purvis 1961). Purvis and Gregory (1952) postulated that the spring form of rye was capable of bypassing the vernalization requirement by directly converting A to B independent of low temperature and the intermediate A'. Melchers, however, suggested that the spring gene could stabilize the intermediate, reverse the devernalization reaction or mediate direct formation of the final flowering product (cited in Purvis 1961).

Genome induction. The phenomenon of gibberellin induction of vernalization found by Casa et al. (1960), Weibel (1960), Pauli et al. (1962), Boldruc et al. (1970) and Kulka and Rejowski (1975) was explained by the lattermost authors as triggering metabolic changes in the plant. The mechanism of GA3 action was proposed to occur by: 1) derepression of the genome leading to biosynthesis of specific mRNA and enzymatic proteins specific to thermic induction; or 2) the direct effect of GA3 on the conformation of protein molecules involved in thermic induction (ibid.).

Tazawa et al. (1979) suggested that the effect of vernalization was due to: 1) the presence of different RNA polymerases, such as low- and high-temperature sensitive RNA polymerases; or 2) modification of chromatin structure by the low temperature so that low-temperature-specific mRNA could be synthesized.

Although vernalization has been well conceptualized the underlying process has not been irrevocably established nor a "vernalin" compound been isolated.

MATERIALS AND METHODS

General Procedures

Vernalization

The cultivars of T. aestivum used in this study were of diverse origin and agronomic importance (Table 1). All ten cultivars were assessed for their vernalization response and further study of characteristics of vernalization were carried out with selected cultivars. Except where noted cold treatments were carried out in the vernalization room that has a short day (8 hour) light regime and $4\pm1^{o}C$ temperature regime. Lighting was supplied by two white fluorescent tubes per bench.

Sterilization and germination. The grain was surface sterilized with sodium hypochlorite. The sterilization was for four minutes with a 2.5% solution of sodium hypochlorite. The four minutes had been established in a preliminary trial as effectively reducing fungal and microbial growth without seriously impairing subsequent germination. After draining the hypochlorite solution, the grain was covered with distilled water and left in room conditions for 24 hours. The water was drained after the imbibition period and the grain was placed on moist filter paper in the petri dishes for a further 24 hours in room conditions to ensure germination as indicated by the emergence of the radicle. Grain for the control or unvernalized treatment was similarly

TABLE 1. Origin, days to maturity and cultivar responses to vernalization of the ten spring wheats used in this study.

Cultivar	Origin	Days to Maturity[a]	Vernalization Response[b]
Benito	W. Canada	—	—
Cajeme 71	Mexico	—	Moderate
Fielder	W. Canada	104	—
Glenlea	W. Canada	105	—
Marquis	W. Canada	101	Little or none
Neepawa	W. Canada	100	—
Pitic 62	Mexico	106	Moderate
Prelude	Canada	—	Little or none
Sinton	W. Canada	100	—
Yecora 70	Mexico	—	Little or none

a. Based on averages from Western Wheat Co-operative Tests, 1978-79.
b. Based on Literature findings.

treated but remained in room conditions until this grain was judged to have attained the same stage of growth as the vernalized grain.

Moisture maintenance and aeration. The grain was weighed before sterilization to establish its dry weight. After imbibition, the grain was weighed to ensure 50% moisture content of the grain. The grain was then placed on moist filter paper. The moisture of the imbibed seed and moist filter paper was maintained by weighing after germination and throughout the cold treatments for replacement of moisture, lost through evaporation, with distilled water. The weighings during cold treatments took place at weekly intervals and at this same time lids were removed so that the grain might be properly aerated. The aeration was done by gentle shaking of the containers for approximately 15 seconds. For some experiments, dishes were kept in polyethylene bags and moisture contents were maintained at relatively constant levels.

Planting Procedures

For all experiments except the field planting, the germinated grain was planted in soil-filled pots. For the field planting, the germinated grain was planted in "Jiffy"$^{R.T.M.}$ pots before being transplanted to the field. Cold treatments and controls were started so that all plantings per experiment could take place at the same time; with the only exception being the experiment on plant age where germinated grain was planted prior to cold treatments. Except for the field planting of Experiment III, all experiments were carried out in growth rooms or greenhouses. Temperature and photoperiodic regimes were controlled in the growth rooms; in the greenhouses, natural daylight was supplemented and extended by fluorescent lighting.

Soil mix. The soil mix used for all experiments was 2 loam : 1 sand : 1 peat. Either 100 ml of granular 11-48-0 fertilizer was added per ten shovelsful of loam at the time of mixing or 200 ml per pot of water-soluble 20-20-20 fertilizer at 3 ml/l was applied after emergence.

Maintenance. After planting, pots were given a substantial watering to moisten the soil and prevent the seedlings from drying out. Thereafter, watering was done on a daily basis by the greenhouse staff. As required, experiments were sprayed by the greenhouse staff for the control of aphids, spider mites, powdery mildew and rust.

Statistical Procedures

A split-plot randomized design with replications was used where appropriate. Several seedlings (3-6 depending on pot size) of the same degree of growth were transplanted into pots with each pot containing plants that represented one treatment. Measurements were taken on an individual plant basis and pot means were used in the analyses.

Parameters measured. Measurements were taken on the main culm of individual plants. At two and three day intervals plants were assessed for growth stage attained and tagged. To facilitate counting of leaf number the third leaf was clipped soon after it emerged. The following parameters were measured in all or some of the experiments:

1. Days to flag leaf emergence (DFLE)—the number of days from planting to the full extension of the flag leaf (auricles visible);
2. Days to heading (DH)—the number of days from planting to full

emergence of the head (all spikelets visible above the flag leaf);

3. Days to anthesis (DA)—the number of days from planting to extension of the anthers and shedding of pollen in the central spikelets of the head;
4. Days to maturity (DM)—the number of days from planting to the last occurrence of green tissue on the spike;
5. Final leaf number (FLN)—the number of leaves of the main culm; and
6. Spikelet number (SPN)—the number of spikelets constituting the spike of the main culm.

Analyses. Experiments where more than one cultivar was used were arranged in the greenhouse or growth room with the cultivars as main plots. Cultivars were randomly arranged per replicate and treatments were randomly arranged within these main plots. Where sub-treatments were included in experiments these sub-treatments were randomly arranged within the sub-plot treatments (split-split plot design). Where feasible pots were rotated within replicates to reduce error due to location of the pots within the replicate.

Analyses of variances were performed using the General Linear Models (GLM) procedure of the Statistical Analysis System (SAS) computer programs.

Because the parameters measured were influenced by post-cold treatment conditions, correlation coefficients were determined between parameters per experiment to determine their relationships to one another. This procedure enabled detection of non-linear relationships

that could reflect differential responses to the environments of the developing plants. Assessment of the validity of using a parameter as a measure of vernalization response would then be made.

Pearson product-moment correlations and significance probabilities were calculated using individual plant measurements. Correlations were performed using the SAS procedure CORR.

Cultivar Characterization

Experiment I: Cultivar Classification

The intent of this experiment was to classify cultivars as responsive or non-responsive to vernalization treatments of 2- and 6-weeks duration. The ten cultivars—Benito, Cajeme, Fielder, Glenlea, Marquis, Neepawa, Pitic, Prelude, Sinton and Yecora—were studied.

Vernalization and planting procedures were as described under General Procedures. The grain was from a common source matured at 20+^{o}C. Germinated grain was placed in the cold room for periods of six and two weeks so that both treatments were removed concurrently. The cold treatments and controls were placed in the germination cabinet (15^{o}C) for two days prior to planting in the growth room (25/20^{o}C 16/8 h.). Five seedlings were planted per pot. The pots were arranged in a split-plot design with three replications. The main-plot treatments were cultivars and the sub-plot treatments were the vernalization treatments. Two control pots per cultivar were included in the layout; the means of these controls were used in analysis. The parameters measured were DFLE, DH, DA, FLN and SPN. Cultivar variances were tested to determine if these variances were homogeneous.

Experiment II: Cultivar Response Patterns with Extended Cold Treatments

The purpose of this experiment was to assess for the ten cultivars of Experiment I the patterns of vernalization response to extended cold treatments. Seed was from the same source as Experiment I (matured at 20+°C). The vernalization and planting procedures were as described under General Procedures.

Germinated grain was placed in the cold room at weekly intervals ranging from 1 to 9 weeks. Following completion of cold treatments, controls and cold treatments were placed in the germination cabinet (15°C) for two days prior to planting in the growth room (25/20°C 16/8 h.). Six seedlings were planted per pot. The pots were arranged in a randomized split-plot design with three replications. Two controls per cultivar were included in the layout and means of these controls were used in the analyses. The cultivars were treated as main plots; and the cold treatments (0-9 weeks) were treated as sub-plot treatments. The parameters measured were DFLE, DA, FLN and SPN.

Experiment III: Cultivar Response Patterns with Field Planting

The object of this experiment was to assess under field conditions the response patterns of the cultivars Cajeme, Fielder and Pitic. These three cultivars were selected on the basis of their performances in Experiment I. The seed was from a common source of 20+°C matured seed.

Vernalization and planting procedures were as described under General Procedures. The germinated grain was vernalized for 0, 2, 4 and 6 weeks. All treatments were concluded simultaneously and

transferred to the germination cabinet (15°C) for two days prior to planting out in "Jiffy" pots. The plants remained in the greenhouse for ten and eleven days before being transplanted with pots to the field at the University of Manitoba Field Research Stations, Winnipeg and Glenlea respectively. Plants were at the two- and three-leaf stage at the time of transplanting. Five plants per treatment were space planted in 61 cm rows. Three replicates were planted per location. To facilitate transplanting procedures cultivars and treatments were not randomized. Analysis of variance was conducted using a split-split-plot design with replicates as main plots, cultivars as sub-plots and cold treatments as sub-sub-plots. For this experiment notes on the develomental stages of jointing, flag leaf emergence, boot, heading and anthesis were taken at three-day intervals. The analyses of growth stages were based upon the date whereat 50% of the plants in the row had attained the given stage. Fertile and total tiller numbers were counted at Glenlea on Day 64.

Experiment IV: Cultivar Response Patterns with Shorter Duration Cold Treatments

The purpose of this study was to assess the responses of the three cultivars Cajeme, Pitic and Yecora to shorter duration cold treatments. The seed for these three cultivars was matured in the field.

Vernalization and planting procedures were as described under General Procedures. Germinated grain was vernalized for periods of 0, 1, 2, 4, 8, 16 and 32 days. All treatments were ended concurrently. Three plants were planted per pot and pots were left in room conditions (24°C) for two days prior to removal to the greenhouse (16/8 h.).

Pots were arranged in a split-plot design with two replicates. Cultivars were treated as main-plots and cold treatments, as sub-plots. The parameters measured for this experiment were DFLE, DH, DA, DM, FLN and SPN.

Characterization of Vernalization

Experiment V: Devernalization

The effect of warm temperature after cold and intermediate temperature treatments was studied for the cultivar Pitic (selected because of its proven vernalization response). The grain used in this study was matured at 20+°C.

Vernalization and planting procedures were as described under General Procedures. All treatments were timed so planting in the growth room (23/18°C 16/8 h.) took place on the same day. Cold exposures were for 0, 2, 4 and 6 weeks. Cold treatments were followed by 0, 1 and 3 days in the germination cabinet (15°C). These intermediate temperature treatments were followed by 0, 1, 3 and 6 days in another germination cabinet held at 25°C. Five seedlings were planted per pot. The pots were arranged in a split-plit-plot design with three replications. The main-plot treatments were the cold treatments; the sub-plot treatments, the intermediate treatments; and the sub-sub-plot treatments, the warm-temperature treatments. The parameters measured for this experiment were DFLE and DA.

Experiment VI: Stabilization

This experiment was designed to investigate the effects of duration of cold treatments and intermediate temperatures on the expression of

vernalization responses. The cultivars selected for this experiment were Cajeme, Fielder, Pitic and Yecora. Seed was bulked from growth room and greenhouse matured sources.

Vernalization and planting procedures were as described under General Procedures, except that petri dishes were placed in dark plastic bags for the duration of the cold and intermediate temperature treatments. Cold treatments were for 0, 2, 4 and 6 weeks. Intermediate temperature (15°C) treatments were for 0, 1, 3 and 6 days following the cold treatments. All treatment combinations were timed so planting in the greenhouse occurred on the same day. Five plants were planted per pot with four replicates. The conditions in the greenhouse at planting and during the next three days were very warm (20+°C at night and 40+°C during the day). The natural daylength was extended to 24 h. by continuous lighting with white fluorescent tubes. The main-plot treatments were the cultivars; the sub-plot treatments, the cold treatments; and the sub-sub-plot treatments, the intermediate temperature treatment. Parameters measured were DFLE and DA.

Experiment VII: Plant Age

This experiment was designed to determine the response to cold treatments with plant aging. Neepawa and Pitic were selected for this study as a control cultivar and a positively responsive cultivar respectively. The seed was from a common field-grown source.

Seed was sterilized and germinated as described under General Procedures. However, the grain was planted prior to cold treatments. Five plants were planted per pot and pots were held in the growth room (20/15°C 16/8 h.) until plants were of the appropriate age. All

treatments were timed for concurrent removal to the greenhouse. Cold treatments were given for 0, 2, 4 and 6 weeks to plants aged (after sowing) 0, 7, 14, 21 and 28 days. Pots were arranged in the greenhouse (continuous lighting) in a split-split-plot design with six replicates. Cultivars were treated as main-plots; plant age, as sub-plots; and cold treatments, as sub-sub-plots. The parameters measured were DFLE and DA.

Experiment VIII: Cold Temperature

The purpose of this experiment was to investigate the effect of the temperature of the cold treatment on vernalization response. The responsive cultivars Cajeme and Pitic were selected for study. The cultivar Yecora was included as a control cultivar. The seed of Cajeme and Yecora was from a common growth room source while seed of Pitic was from a field source.

Vernalization and planting procedures were as described under General Procedures. Treatments were kept in plastic bags to prevent differential moisture loss at the different temperatures of the cold treatments. The mean temperatures of the cold treatments and the standard deviations, based upon daily minimum and maximum readings, were 1.07±0.82°C, 4.93±0.74°C and 10.70±0.95°C. Cold treatments were for 0, 1, 2 and 3 weeks. All treatments were completed concurrently and placed in the germination cabinet (15°C) for two days prior to planting in the greenhouse (16/8 h.). Five plants were sown per pot with three replications. Cultivars were taken as main-plot treatments; duration of cold, as sub-plot treatments; and temperature of cold, as sub-sub-plot treatments. Parameters measured were DFLE and DA.

Experiment IX: Light

The intent of this study was to determine if vernalization responses differed when cold treatment was given in darkness or in short day (8/16 h.) conditions. Cultivars included in this experiment were Cajeme, Glenlea, Neepawa, Pitic and Yecora. All seed was from a common field source.

Vernalization and planting procedures were as described under General Procedures with the exception that germinated grain was placed on moistened paper towelling in 13x13x4 cm, clear plastic germination containers that for the dark treatment were covered with aluminum foil. Cold treatments were for 0 and 4 weeks. Upon completion of the cold treatments three plants were planted per pot with four replicates. Pots were placed in the greenhouse (16/8 h.) in a split-plot design. Main-plot treatments were cultivars; sub-plot treatments were the cold treatments. Parameters measured were DFLE, DH, DA, DM, FLN and SPN.

The photon flux density during the cold treatments at container level was 125 micro-einsteins m^{-2} sec^{-1}.

Inheritance

Experiment X: Segregation Analyses

Crosses were made between Neepawa and Pitic, Yecora and Cajeme, and Glenlea and Pitic to study segregation patterns for days to anthesis in the F2 generation. As wheat is a self-pollinated crop, cultivars were fairly homogeneous. Therefore, parental plants were designated as cultivars and crosses were made between cultivars.

Crosses. Plants were cross-pollinated by hand in the greenhouse during

the summer of 1980. Due to high temperatures of the greenhouse sterility was a problem and seed set was reduced. A standard crossing procedure was used with all crosses being bagged until maturity.

Reciprocal crosses were made between Pitic and Neepawa, and Cajeme and Yecora. The cross of Glenlea with Pitic was made in the single direction with Glenlea as the female parent. Parents were chosen on the basis of similarity of days to anthesis when vernalization responses were fulfilled.

F1 generation. The F1's, progeny of the single crosses, were grown in the greenhouse during the winter of 1980-81. The seed of the F1's was harvested in January of 1981.

F2 generation. As the F2 generation was to be planted soon after harvesting, the seed was imbibed and germination tested by placing on wet filter paper for 24 hours under room conditions. Seeds that had not germinated were subjected to three days cold treatment ($5^{o}C$) to break dormancy. The F2's were planted in pots and grown together with parents in the growthroom ($20/15^{o}C$ 16/8 h.). Days to anthesis of the main culm were measured on an individual plant basis.

F3 generation. F3 seed was harvested from the F2 plants described above. The F3's were to be grown to establish homozygosity or heterozygosity of their F2 parent. The F3's of the Neepawa-Pitic and Yecora-Cajeme crosses were planted in the greenhouse during the summer of 1981. The seed was planted in a soil-filled bench at a density of 16 seeds per 10x10 cm square (each square representing a F2 family or parental control). Due to high temperatures during the early growth

period, the Yecora-Cajeme families were stunted and sterile, so days to anthesis could not be measured. Days to anthesis were measured for the Neepawa-Pitic families; but again high temperatures subsequent to planting resulted in sterility of some early plants.

Analyses. On the basis of days to anthesis plants were classified as "spring" and "winter" types. The F2's for all crosses were fitted to expected ratios using Yates correction for continuity.

The F3's from the Neepawa-Pitic cross were classed as spring, winter and segregating spring-winter families. Chi-squared determination for goodness of fit to the expected ratio was performed, and heterogeniety of the Pitic x Neepawa and Neepawa x Pitic crosses was calculated.

RESULTS AND DISCUSSION

Cultivar Characterization

Experiment I: Cultivar Classification

Classification of the vernalization response of wheat cultivars has been based upon one or more physical manifestations of accelerated development. In this experiment five physical parameters—DFLE, DH, DA, FLN and SPN—of the main culm were measured to assess cultivar response to 0, 2 and 6 weeks of cold ($4^{\circ}C$) treatment. Comparison of response to the 2- and 6-weeks treatments with response to the control treatment was taken as an indication of vernalization response under the long-day, warm-temperature growth room conditions.

Due to heterogeneity of error between cultivars for spikelet number, the analysis of variance (ANOVA) for this parameter was divided into two groups: Group A excluded Pitic and Group B included only Pitic.

Days to flag leaf emergence, heading and anthesis and final leaf number were strongly influenced by the vernalization treatment. All five parameters measured were influenced by the cultivars. A summary of the analyses of variance is given in Table 2 (for complete ANOVA refer to Appendix 1). The cultivar x treatment interaction was highly significant for DFLE, DH, DA and FLN. The relevant mean data for the five parameters is presented in Tables 3 through 7.

TABLE 2. Summary of analyses of variance for parameters measured to classify cultivar vernalization responses.

Source of Variation	F-value DFLE	DH	DA	FLN	SPN[a]	SPN[b]
Cultivar (C)	12.58**	7.96**	18.26**	16.05**	16.58**	——
Treatment (T)	112.38**	45.62**	61.71**	26.06**	0.83	2.55
CxT	15.17**	4.12**	6.89**	3.99**	1.01	——

a. Group A.
b. Group B.
** Significant at P=0.01.

Days to flag leaf emergence. Five cultivars—Benito, Neepawa, Prelude, Sinton and Yecora—were non-responsive to the 2- and 6-weeks cold treatments as measured by DFLE (Table 3). The two-weeks treatment did not significantly affect Marquis and Glenlea; however, these two cultivars did show highly significant differences from the control with the six-weeks treatment (LSD, 1%—3.77). Three cultivars—Cajeme, Fielder and Pitic—displayed highly significant responses to both the 2- and 6-weeks treatments. For these three responsive cultivars the two-weeks treatment was intermediate between the 0- and 6-weeks treatments and the six-weeks treatments showed the greatest acceleration of DFLE.

Days to heading. The cultivar and treatment means for this parameter are presented in Table 4. Benito, Neepawa, Prelude and Sinton were non-responsive to the vernalization treatments as measured by DH. Glenlea, Marquis and Yecora had significant differences from their

TABLE 3. Effect of vernalization on days to flag leaf emergence (DFLE) of ten spring wheat cultivars exposed to 0, 2 and 6 weeks of cold treatment.

Cultivar	Cold Treatment (weeks) 0[a]	2	6	Cultivar Means[b]
		DFLE[c]		
Benito	37.50	39.70	38.40	38.53
Cajeme	45.37	36.73	31.00	37.70
Fielder	46.85	40.73	31.27	39.62
Glenlea	36.31	35.67	31.80	34.29
Marquis	38.82	37.28	32.87	36.32
Neepawa	37.28	38.10	35.93	36.98
Pitic	52.50	40.63	32.53	42.04
Prelude	31.23	31.36	31.00	31.20
Sinton	34.60	33.77	33.13	33.83
Yecora	33.67	36.17	31.00	38.61
Treatment Means[d]	39.41	36.94	32.89	

a. Weeks=0 is the mean of two unvernalized controls per replicate.
b. Significant at 1% level: LSD, 5%—2.64.
c. LSD, 5% between treatments for same cultivar--2.81; between treatments for different cultivars--3.49.
d. Significant at 1% level: LSD, 5%—0.89.

TABLE 4. Effect of vernalization on days to heading (DH) of ten spring wheat cultivars exposed to 0, 2 and 6 weeks of cold treatment.

Cultivar	Cold Treatment (weeks) 0[a]	2[c]	6	Cultivar Means[b]
		DH		
Benito	46.43	47.97	46.80	47.07
Cajeme	52.33	45.73	36.40	44.82
Fielder	54.61	51.07	38.33	48.00
Glenlea	45.89	46.00	41.00	43.81
Marquis	49.04	48.57	43.93	47.18
Neepawa	46.87	46.87	44.47	45.97
Pitic	57.00	52.42	42.47	49.83
Prelude	34.78	35.91	33.83	34.84
Sinton	44.33	43.35	43.27	43.65
Yecora	43.65	45.07	37.67	42.13
Treatment Means[d]	47.17	46.30	40.82	

a. Weeks=0 is the mean of two unvernalized controls per replicate.
b. Significant at 1% level: LSD, 5%--4.34.
c. LSD, 5% between treatments for same cultivar--4.59; between treatments for different cultivars--5.72.
d. Significant at 1% level: LSD, 5%--1.45.

controls with the six-weeks treatment, however these differences were not highly significant (LSD, 1%—6.16). Highly significant differences for six-weeks treatments were found for Cajeme, Fielder and Pitic. For the two-weeks treatment, Cajeme was the only cultivar to be significantly earlier for DH than its zero-weeks treatment.

Days to anthesis. Means for DA are given in Table 5. Benito, Glenlea, Neepawa, Prelude, Sinton and Yecora were non-responsive to the vernalization treatments as measured by DA. The two-weeks treatment for Marquis was not significantly different from the control; however, the six-weeks treatment resulted in a highly significant acceleration of anthesis (LSD, 1%—5.62). Cajeme, Fielder and Pitic were significantly accelerated by both the 2- and 6-weeks treatments, with the two-weeks treatments being intermediate to the 0- and 6-weeks treatments.

Final leaf number. There were six cultivars—Benito, Glenlea, Neepawa, Prelude, Sinton and Yecora—that were non-responsive to the vernalization treatments as measured by FLN (Table 6). Marquis was slightly responsive to the six-weeks treatment with a leaf reduction of 0.76 (LSD, 1%—1.00). Cajeme, Fielder and Pitic showed significant reductions in leaf number with both the 2- and 6-weeks treatments. Again, for these three cultivars the six-weeks treatments caused greater reductions than the two-weeks treatments.

Spikelet number. The means for spikelet number are presented in Table 7. ANOVA did not produce significant treatment effects for

TABLE 5. Effect of vernalization on days to anthesis (DA) of ten spring wheat cultivars exposed to 0, 2 and 6 weeks of cold treatment.

Cultivar	Cold Treatment (weeks) 0[a]	2[c]	6	Cultivar Means[b]
		DA		
Benito	47.63	48.97	47.47	48.02
Cajeme	53.45	44.20	37.33	45.00
Fielder	56.63	51.33	39.20	49.05
Glenlea	45.70	46.00	41.93	44.13
Marquis	50.82	49.08	44.40	48.10
Neepawa	47.69	47.87	45.00	46.73
Pitic	62.13	53.58	43.57	53.09
Prelude	35.88	37.51	34.77	36.05
Sinton	45.05	44.15	44.83	44.68
Yecora	42.75	45.71	38.60	42.35
Treatment Means[d]	48.77	46.87	41.71	

a. Weeks=0 is the mean of two unvernalized controls per replicate.
b. Significant at 1% level: LSD, 5%--3.16.
c. LSD, 5% between treatments for same cultivar—4.19; between treatments for different cultivars—4.64.
d. Significant at 1% level: LSD, 5%—1.33.

TABLE 6. Effect of vernalization on final leaf number (FLN) of ten spring wheat cultivars exposed to 0, 2 and 6 weeks of cold treatment.

Cultivar	Cold Treatment (weeks) 0[a]	2	6	Cultivar Means[b]
		FLN[c]		
Benito	7.70	8.15	7.87	7.91
Cajeme	9.21	8.13	7.07	8.14
Fielder	8.89	8.07	7.13	8.03
Glenlea	7.85	7.33	7.47	7.61
Marquis	7.83	8.25	7.07	7.72
Neepawa	7.86	7.73	7.67	7.76
Pitic	10.04	9.08	7.48	8.87
Prelude	6.43	6.38	6.33	6.38
Sinton	7.20	7.68	7.40	7.43
Yecora	7.71	7.82	7.20	7.58
Treatment Means[d]	8.07	7.91	7.27	

a. Weeks=0 is the mean of two unvernalized controls per replicate.
b. Significant at 1% level: LSD, 5%--0.46.
c. LSD, 5% between treatments for same cultivar—0.75; between treatments for different cultivars—0.76.
d. Significant at 1% level: LSD, 5%—0.24.

TABLE 7. Effect of vernalization on spikelet number (SPN) of ten spring wheat cultivars exposed to 0, 2 and 6 weeks of cold treatment.

Cultivar	Cold Treatment (weeks) 0[a]	2	6	Cultivar Means[b]
	SPN			
Group A				
Benito	11.60[c]	12.13	11.47	11.73
Cajeme	16.40	14.80	13.87	15.02
Fielder	14.34	12.80	13.87	13.67
Glenlea	12.35	14.22	13.13	13.24
Marquis	14.07	14.97	13.73	14.26
Neepawa	10.49	11.80	10.87	11.05
Prelude	14.77	13.98	14.33	14.36
Sinton	13.10	13.23	12.67	13.00
Yecora	15.64	14.13	15.00	14.92
Treatment Means[d]	13.64	13.56	13.22	
Group B				
Pitic	20.22[e]	15.61	13.78	16.54

a. Weeks=0 is the mean of two unvernalized controls per replicate.
b. Significantly different at 1% level: LSD, 5%—1.01.
c. Cultivar x treatment interaction not significant at 5% level: LSD, 5% between treatments for the same cultivar—2.14; between treatments for different cultivars—2.82.
d. Not significantly different at 5% level: LSD, 5%—0.71.
e. Treatments not significantly different at 5% level: LSD, 5%—14.13.

Group A or Group B (Table 2). The only significant effect was created by differences amongst cultivars. Therefore, although there was a trend for reduced spikelet number with the cold treatments among the responsive cultivars (especially Pitic) these reductions were not significantly different from the zero-weeks controls.

Correlation coefficients. Pearson correlation coefficients computed for the five parameters measured for this experiment using individual plant statistics are presented in Table 8. Highly significant, positive linear correlations between DFLE and DH, DFLE and DA, DFLE and FLN, DH and DA, DH and FLN, and FLN and SPN were found. However, SPN was not significantly linearly correlated with DFLE or DA and was significantly negatively correlated with DH. The breakdown of positive linear correlations between SPN and DFLE, DH or DA puts the use of spikelet number as a measure of vernalization response in question; although a positive correlation of SPN with FLN, as was reported by Pugsley (1966), was found.

There was a general agreement between the vernalization response found using DFLE, DH, DA and FLN. This agreement would be expected from the highly significant positive correlations between these parameters.

Discussion. On the basis of the results of this experiment, the ten cultivars tested for vernalization response can be classified into two groups: 1) cultivars with little or no response; and 2) cultivars with significant responses. The first group includes Benito, Glenlea, Marquis, Neepawa, Prelude, Sinton and Yecora. The second

TABLE 8. Correlation coefficients of parameters measured for ten cultivars exposed to 0, 2 and 6 weeks of cold treatment.

Parameters Correlated	Correlation Coefficient	Prob>[R] Ho: RHo=0	Number of Observations[a]
Days to flag leaf emergence with:			
Days to heading	0.85	0.0001	483
Days to anthesis	0.89	0.0001	501
Final leaf number	0.75	0.0001	530
Spikelet number	0.02	0.6049	511
Days to heading with:			
Days to anthesis	0.95	0.0001	477
Final leaf number	0.64	0.0001	487
Spiklet number	-0.13	0.0034	481
Days to anthesis with:			
Final leaf number	0.70	0.0001	507
Spikelet number	-0.02	0.6504	499
Final leaf number with:			
Spikelet number	0.24	0.0001	516

a. Of a possible 600.

group includes Cajeme, Fielder and Pitic.

The cultivars Benito, Neepawa, Prelude and Sinton were included in Group 1 because as measured by DFLE, DH, DA and FLN, these cultivars were non-responsive to either the 2 or 6 weeks of cold treatment. Of these cultivars, the response of Prelude had been previously reported by McKinney and Sando (1933) to be a delay in heading of 9 to 12 days with 67 days at $-1^{o}C$ to $7^{o}C$.

Yecora was non-responsive to either the 2- or 6-weeks cold treatment as measured by DFLE, DA and FLN. Heading time for the six-weeks treatment was accelerated but this acceleration was not highly significant. Wall and Cartwright (1974) had reported accelerated heading for Yecora with a four-weeks cold treatment, although the significance for this acceleration was not included.

The inclusion of Glenlea and Marquis in Group 1 is based upon the general findings that even where cold treatments caused highly significant reductions in the parameters measured, reductions were small. Neither of these cultivars responded to the two-weeks cold treatment. The findings in the literature for the response of Marquis are contradictory. McKinney and Sando (1933, 1935) reported that Marquis was delayed by cold treatments. Wort (1939, 1940) and Levy and Peterson (1972) reported that Marquis was accelerated by cold treatments although Wort (1940) found this acceleration was dependent on seed source and Levy and Peterson (1972) found the acceleration was not significant.

The three cultivars classified as responsive as measured by DFLE, DH, DA and FLN were Cajeme, Fielder and Pitic. Often the two-

weeks cold treatment showed significant responses but these reductions were always less than the six-weeks cold treatment. A positive response for Pitic has been reported by Syme (1968) for thirty days at 4±1.5°C, Levy and Peterson (1972) for 1-5 weeks at 1-3°C, Klaimi and Qualset (1974) for 1-8 weeks at 1°C, Wall and Cartwright (1974) for two weeks at 1°C, and Ford et al. (1981) for either 2 or 4 weeks at either 2°C or 8°C. Also reported by Wall and Cartwright (1974) was a positive response for Cajeme to two weeks at 1°C.

The classification of cultivars was independent of origin and maturity classification. The three responsive cultivars did move from being the latest cultivars tested to amongst the earliest if given six weeks of cold treatment.

Experiment II: Cultivar Response Patterns with Extended Cold Treatments

This experiment was intended to confirm the findings of Experiment I and, by increasing the number of cold treatments, to clarify the development of the vernalization response. Extension of the cold treatments beyond six weeks was done to assess if the finding by Berry et al. (1980), that cultivars carrying the Vrn1 allele had a threshold response with extended cold treatments, was a common phenomenon of cultivars classified as insensitive to vernalization treatments.

The response of the ten cultivars to 0-9 weeks of cold treatment was assessed by measuring DFLE, DA, FLN and SPN. Spikelet number was included to reassess the influence of cold treatments on this important component of yield. A summary of the analyses of variance is given in Table 9 (for a complete ANOVA refer to Appendix 2). The cultivar x treatment interactions were highly significant for all four

TABLE 9. Summary of analyses of variance for parameters measured to determine cultivar vernalization response patterns to extended cold treatments.

Source of Variation	F-value DFLE	DA	FLN	SPN
Cultivar (C)	98.83**	88.47**	49.42**	12.18**
Treatment (T)	57.48**	56.79**	47.32**	16.36**
CxT	6.88**	6.43**	5.04**	3.44**

** Significant at P=0.01

parameters. The relevant mean data was graphed by cultivar and is presented in Figures 1 through 10.

Benito. The mean DFLE and DA data for Benito are shown in Figures 1A and 1B respectively. The one-week and two-weeks cold treatments indicated a reduction in both DFLE and DA that was not highly significant. The DFLE and DA of the 3- to 7-weeks cold treatments showed no significant response to vernalization. Highly significant differences from the zero-weeks cold treatment were found for the 8- and 9-weeks cold treatments. Figures 1C and 1D show the patterns of FLN and SPN respectively. The reductions of final leaf number with the 4-, 8- and 9-weeks cold treatments were highly significant. For SPN none of the fluctuations were significantly different from the zero-weeks control. Overall Benito was relatively insensitive to the cold treatments with the significant reductions at 8 and 9 weeks being of a minor nature. These latter responses may reflect the threshold nature of the Vrn1 allele described by Berry et al. (1980).

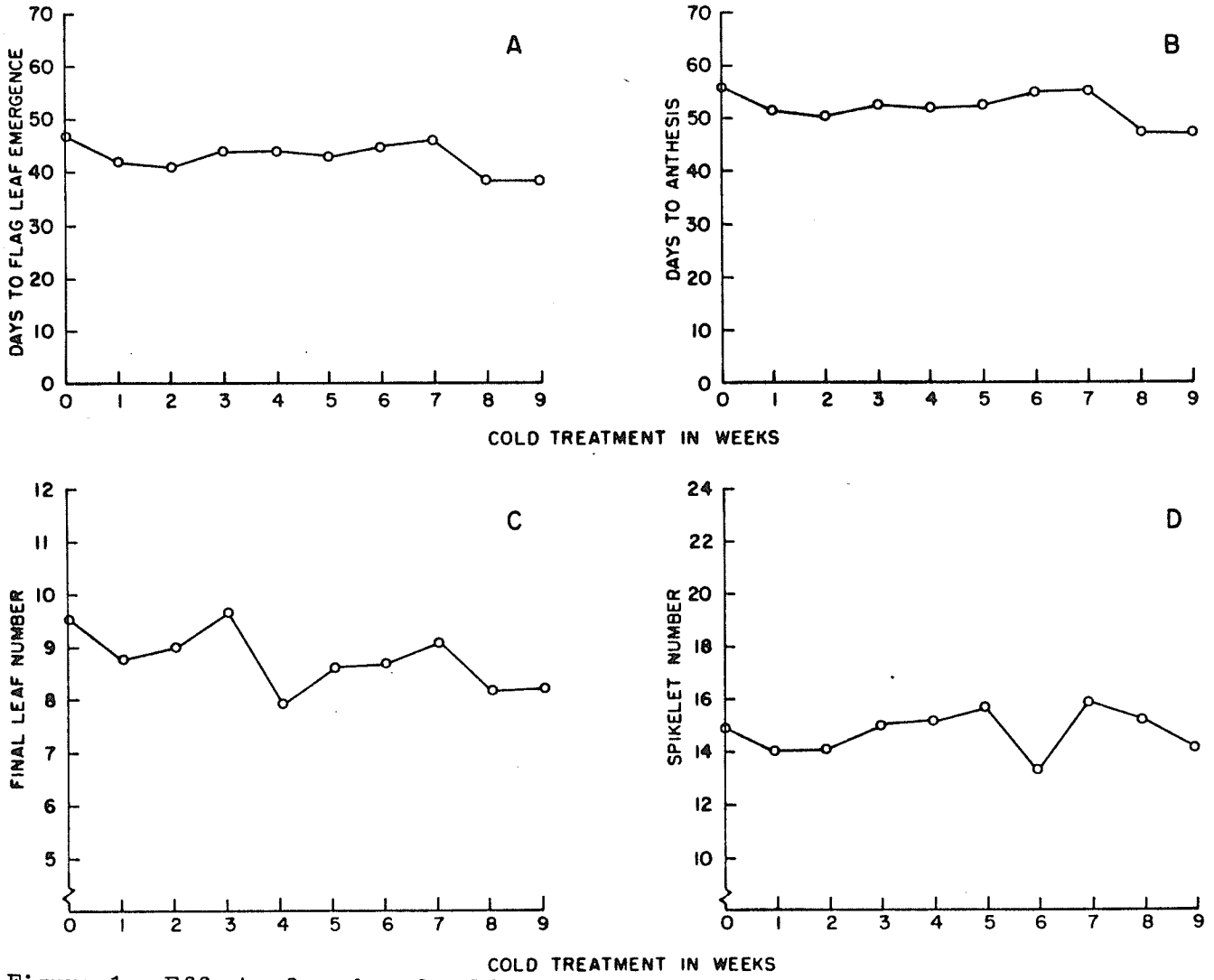

Figure 1. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Benito. (LSD: 5%, 1%--Days to Flag Leaf Emergence = 4.51, 5.96; Days to Anthesis = 5.39, 6.31; Final Leaf Number = 0.91, 1.20; Spikelet Number = 1.71, 2.26.)

Cajeme. The graphs in Figures 2A-D show the effects of cold treatment on DFLE, DA, FLN and SPN for Cajeme. Although a highly significant reduction in leaf number occurred with one week of cold treatment this reduction was not reflected in reduced spikelet numbers or days to flag leaf emergence or anthesis. For the 2- to 9-weeks cold treatments, DFLE, DA, FLN and SPN had reductions from the zero-weeks control that were highly significant. The vernalization requirement for Cajeme under the conditions of this experiment was four weeks, with longer treatments causing little or no further reductions in DFLE and DA. The perturbation of FLN and SPN at 6- and 7-weeks cold treatment respectively followed by a steady reduction of numbers with longer treatments suggested a cyclic response pattern for Cajeme.

Fielder. Figures 3A-D show that the pattern of response of Fielder under the conditions of this experiment was cyclic as measured by DFLE, DA, FLN and SPN. For DFLE, the 1- to 9-weeks cold treatments resulted in highly significant reductions from the zero-weeks control. Minima in DFLE were found with 4, 5 and 9 weeks of cold treatment. Upward fluctuations with the 6-, 7- and 8-weeks cold treatments resulted in DFLE that although significantly less than the control were higher than the minima. The pattern of response described for DFLE was reflected in the patterns for DA and FLN where for 1 to 9 weeks of cold treatment, DA and FLN were highly significantly reduced from the control but cycling occurred. Spikelet numbers were reduced by cold treatments and these reductions were highly significant with 3, 4, 5, 7 and 9 weeks of cold treatment. The fluctuations in SPN followed the same trend as for DFLE, DA and FLN. Fielder was clearly

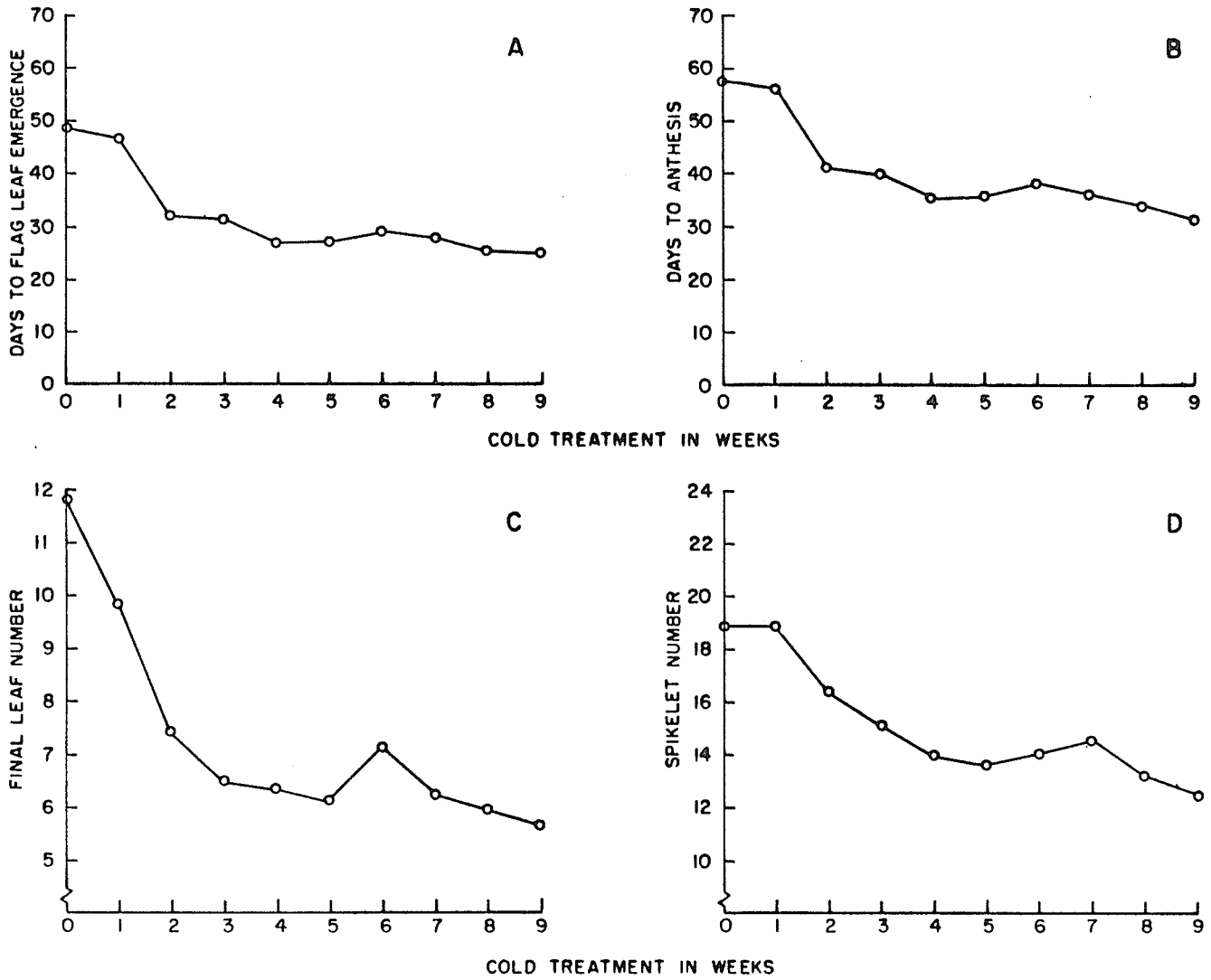

Figure 2. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Cajeme. (See Figure 1 for LSD values.)

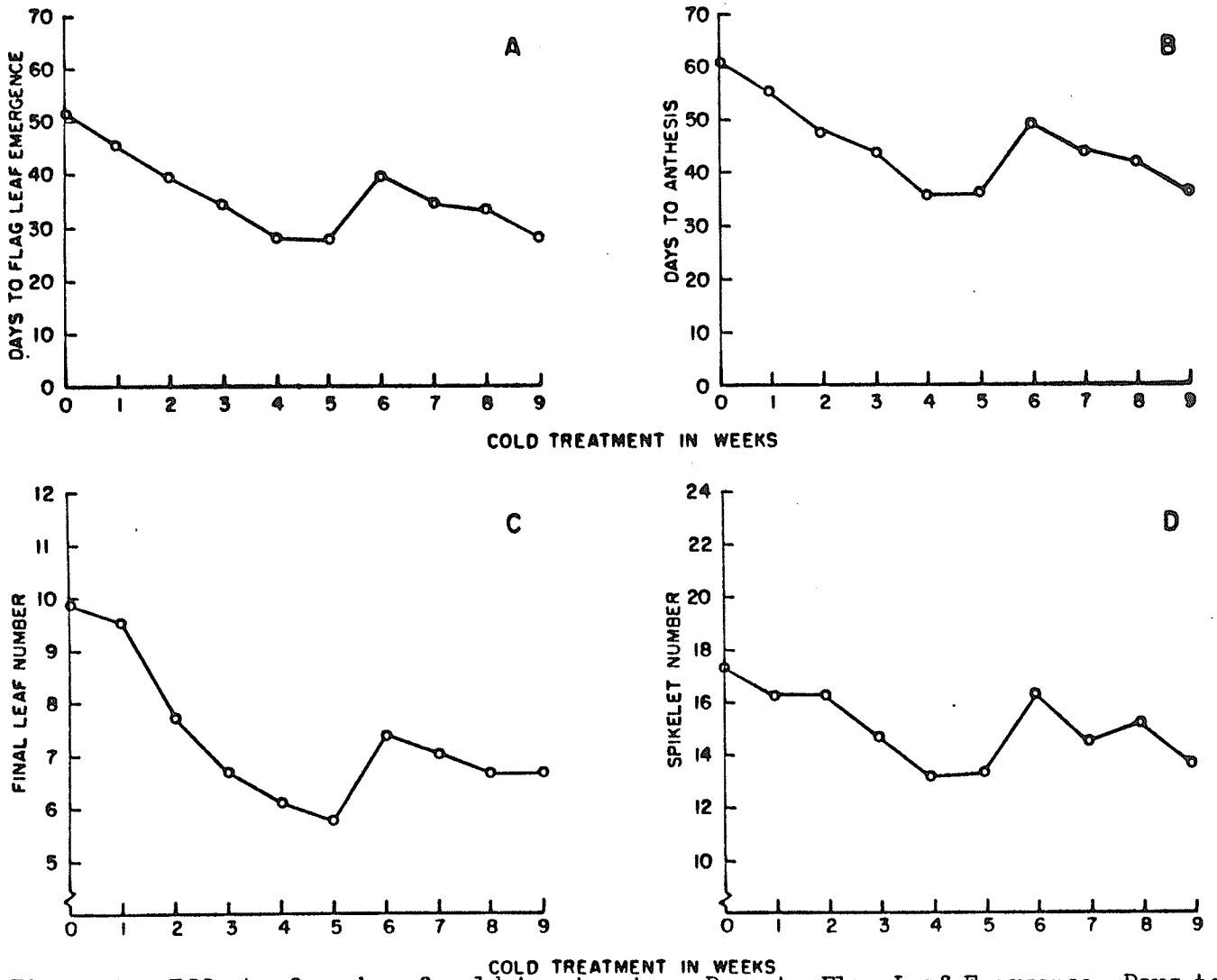

Figure 3. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Fielder. (See Figure 1 for LSD values.)

a responsive cultivar with its vernalization requirement being fulfilled with four weeks of cold treatment.

Glenlea. This cultivar was relatively insensitive to cold treatments as measured by DFLE and DA (Figures 4A and 4B). Reductions in DFLE and DA from the control were significant with 5, 8 and 9 weeks of cold treatment. Significant minima of leaf number occurred with 4, 5, 8 and 9 weeks of cold treatment (Figure 4C). Spikelet numbers were unaffected by 1 to 8 weeks of cold treatment however for the 9-weeks cold treatment SPN had a highly significant reduction from the control (Figure 4D). Glenlea was generally a non-responsive cultivar with those reductions of DFLE and DA that did occur being not highly significant except for the 8 and 9 weeks of cold treatment. The reductions in DFLE, DA, FLN and SPN with the 8- and/or 9-weeks cold treatments reflected the findings for Benito that may be part of the threshold response of Berry et al. (1980).

Marquis. Marquis was non-responsive to the 1 to 7 weeks of cold treatments as measured by DFLE and DA (Figures 5A and 5B). Differences from the zero-weeks control were highly significant for the 8- and 9-weeks cold treatments for both DFLE and DA. From Figure 5C it can be seen that FLN was relatively insensitive to cold treatments with the only highly significant difference from the control occurring with the nine-weeks cold treatment. The oscillations in spikelet number for Marquis were not significantly different from the zero-weeks cold treatment. The lack of significant response to cold treatments less than eight weeks was surprising since in Experiment I, Marquis was

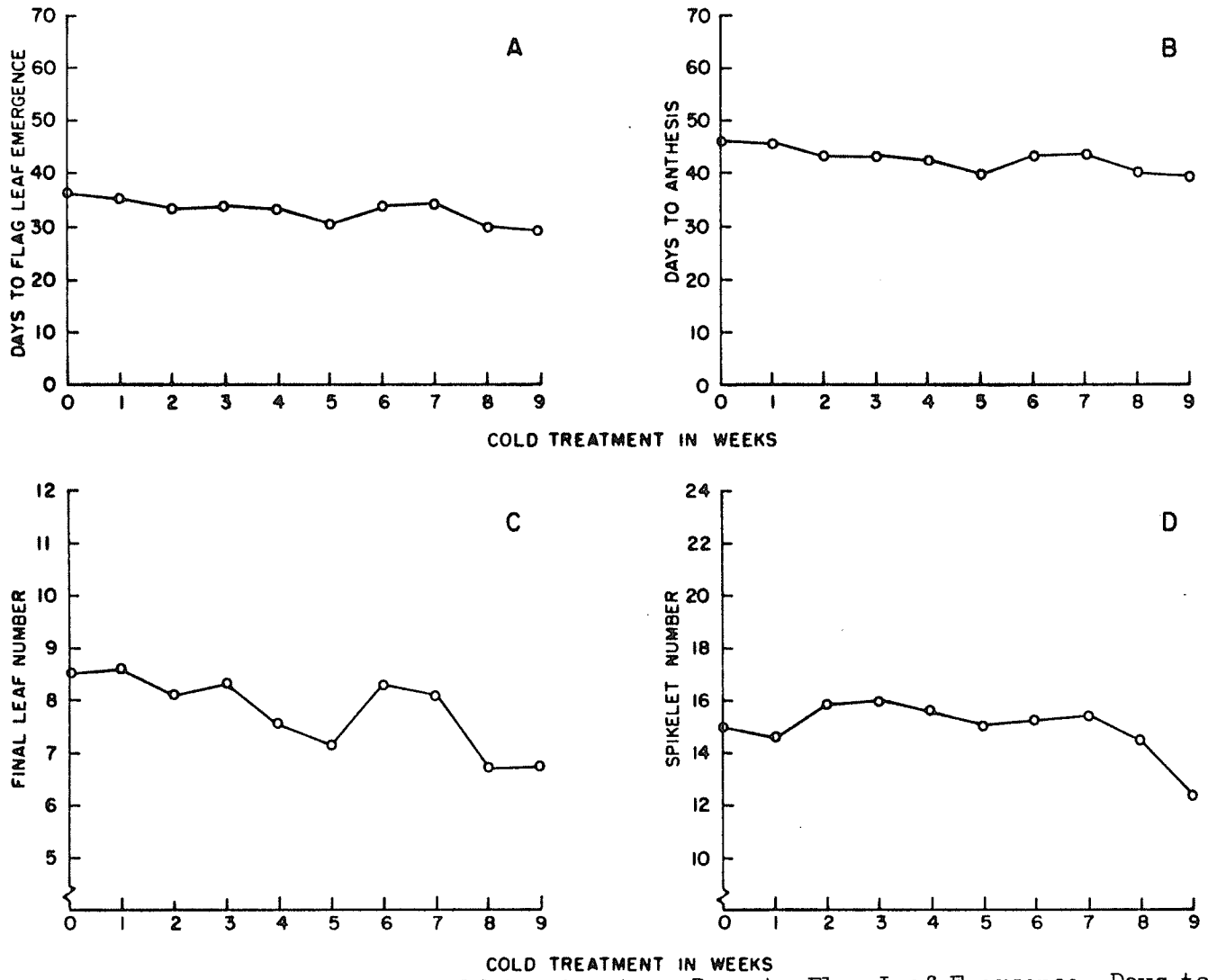

Figure 4. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Glenlea. (See Figure 1 for LSD values.)

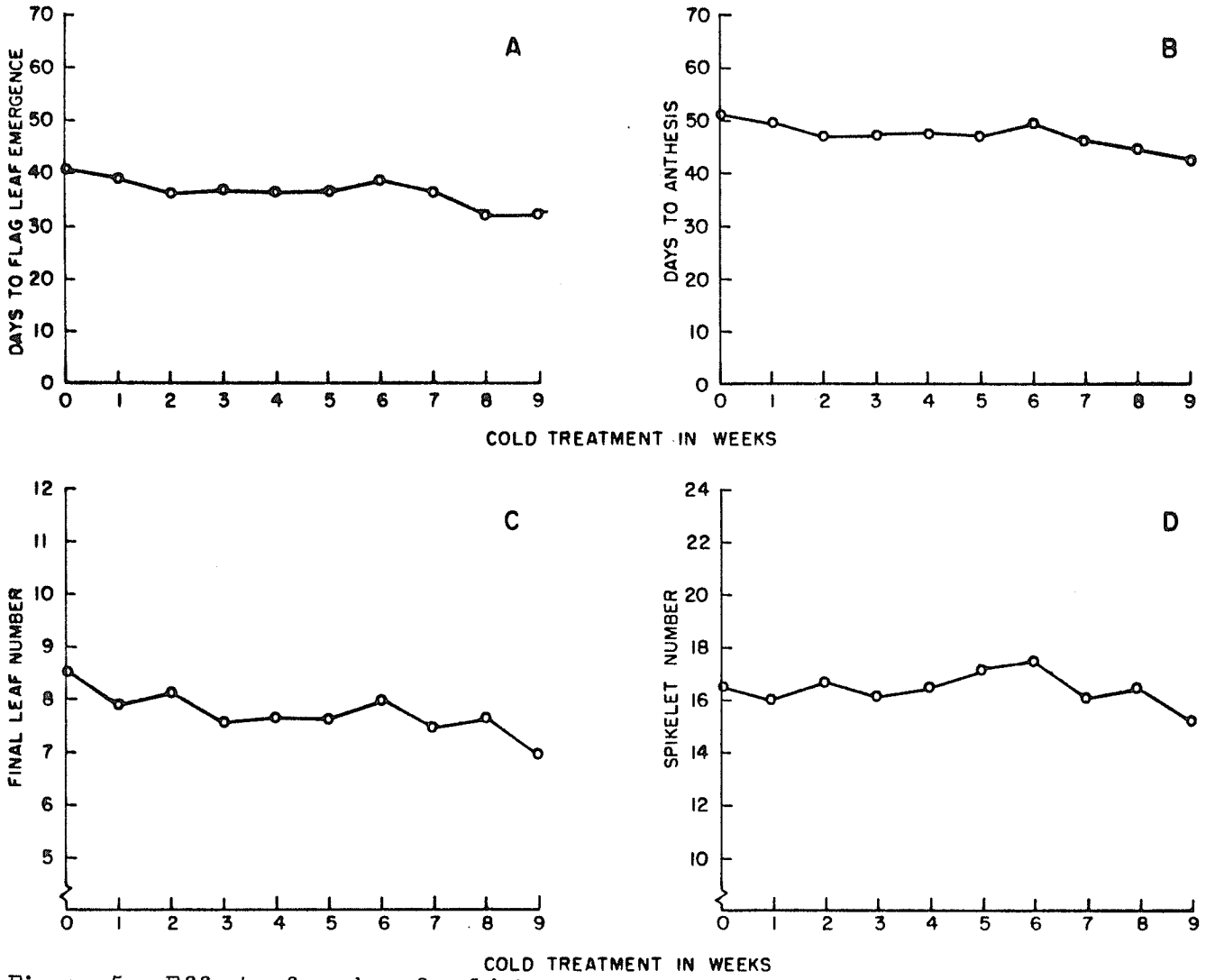

Figure 5. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Marquis. (See Figure 1 for LSD values.)

consistently responsive to the six-weeks cold treatment. However, the claim that the responses of Experiment I were of a minor nature and that Marquis be classed as a cultivar with little or no response was supported by the findings of this experiment. The significant responses with 8- and/or 9-weeks cold treatments agreed with the other non-responsive cultivars so far discussed.

Neepawa. This cultivar was significantly retarded by one week of cold treatment as measured by DFLE and DA (Figures 6A and 6B). Highly significant reductions for DFLE, DA and FLN from the control occurred with the 8- and 9-weeks cold treatments (Figures 6A-C). Spikelet number was significantly reduced from the control with 6- and 8-weeks cold treatments (Figure 6D). Neepawa was generally non-responsive to vernalization treatments of 1-7 weeks with those fluctuations that did occur being minor. However, the 8- and 9-weeks cold treatments caused marked reductions in DFLE, DA and FLN that reflected a trend among the non-responsive cultivars, Benito, Glenlea and Marquis.

Pitic. Figures 7A-D indicate the positively responsive nature of Pitic to vernalization treatments, as measured by DFLE, DA, FLN and SPN. Reductions from the control were highly significant with 2 to 9 weeks of cold treatment for DFLE, DA and FLN. For SPN, all cold treatments were highly significantly different from the control. For Pitic the vernalization requirement under the conditions of this experiment was fulfilled by five weeks of cold treatment. Vacillations at 7- or 8-weeks cold treatments followed by reductions at 8- and/or 9-weeks cold treatments would indicate a cyclic pattern of

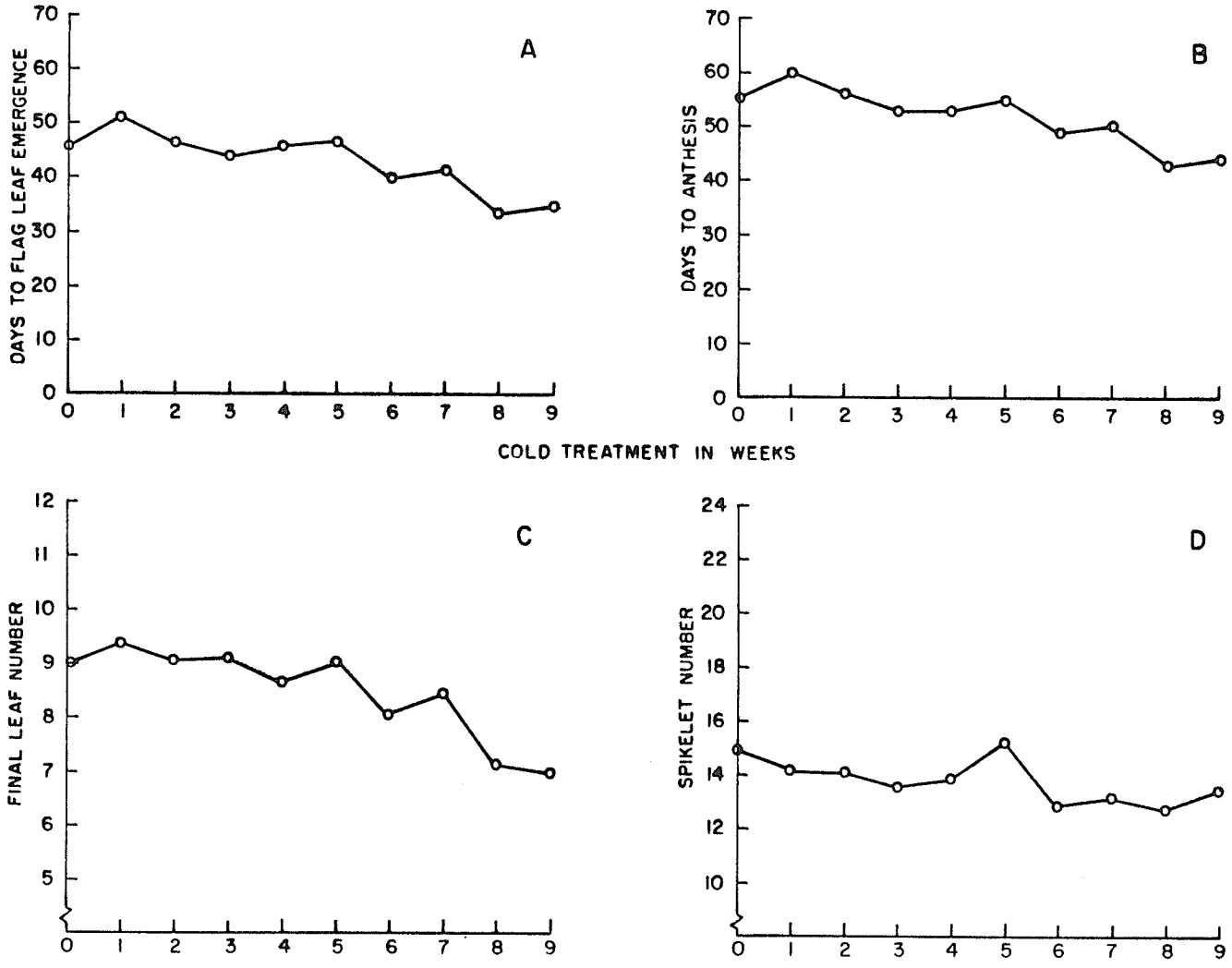

Figure 6. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Neepawa. (See Figure 1 for LSD values.)

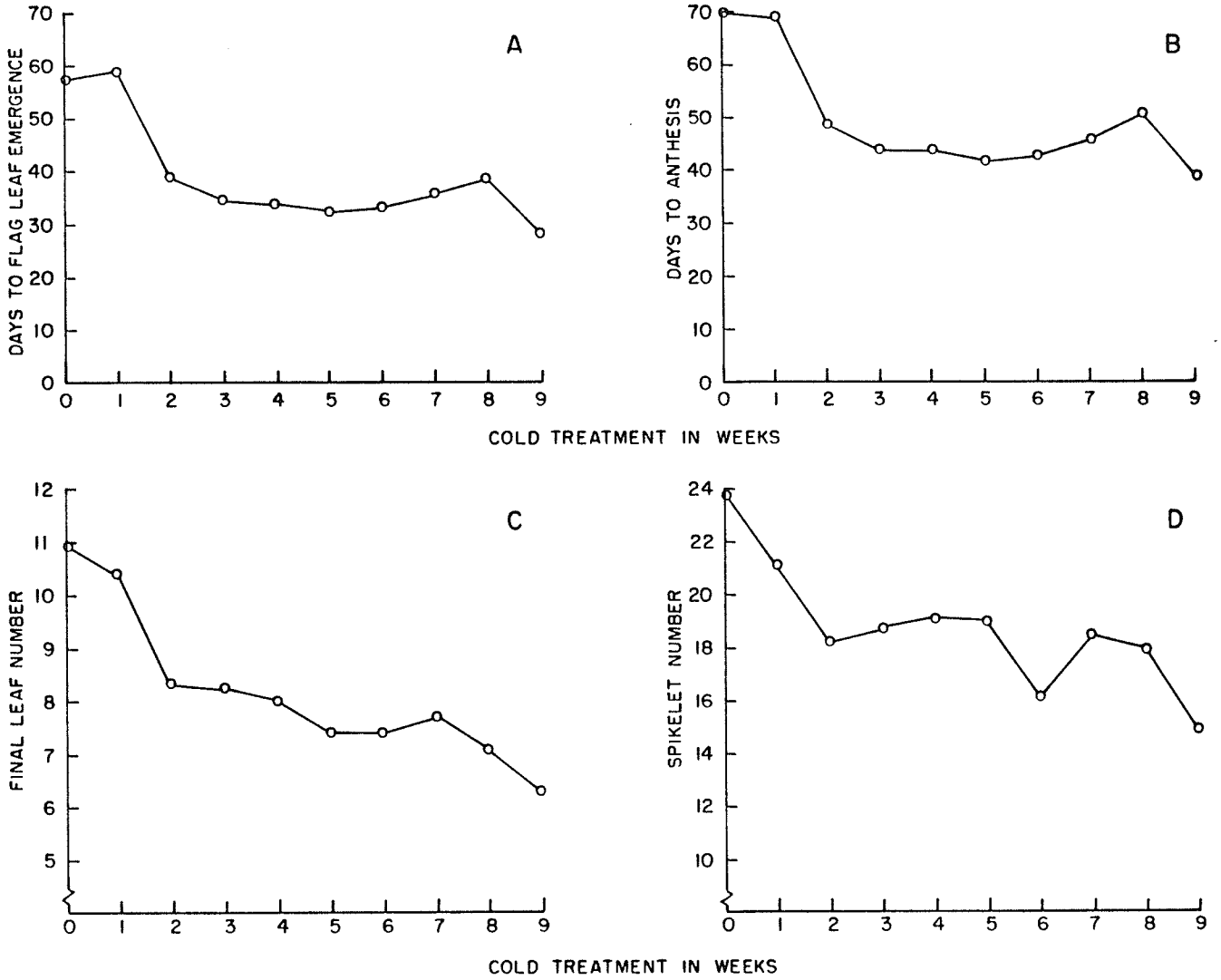

Figure 7. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Pitic. (See Figure 1 for LSD values.)

response as was found to varying degrees with Cajeme and Fielder.

Prelude. This cultivar was one of the earliest developing cultivars under investigation. From Figures 8A-D it can be seen that except for minor non-significant oscillations, Prelude was non-responsive to vernalization treatments as measured by DFLE, DA, FLN and SPN. The results of this experiment agreed with conclusions of Experiment I that Prelude was non-responsive. However, unlike the other non-responsive cultivars, there was no threshold response for Prelude with extended vernalization.

Sinton. The stability of this cultivar can be seen from Figures 9A-D. The fluctuations from the zero-weeks control for DFLE, DA, FLN and SPN were all non-significant. Sinton like Prelude was a non-responsive cultivar that had no threshold response under the conditions of this experiment.

Yecora. Figures 10A-D present the findings of the effect of cold treatment on DFLE, DA, FLN and SPN for Yecora. Significant differences from the control for DFLE occurred at 7- and 9-weeks cold treatments. The difference from the control for DA that was highly significant occurred with the eight-weeks cold treatment. Oscillations in FLN were significant with 5 and 9 weeks, and in SPN at 3, 5, 7 and 9 weeks. Yecora was relatively non-responsive but as the extended cold treatments (7-9 weeks) did cause some reductions, Yecora may be displaying the threshold response of Benito, Glenlea, Marquis and Neepawa dampened due to the earliness of Yecora.

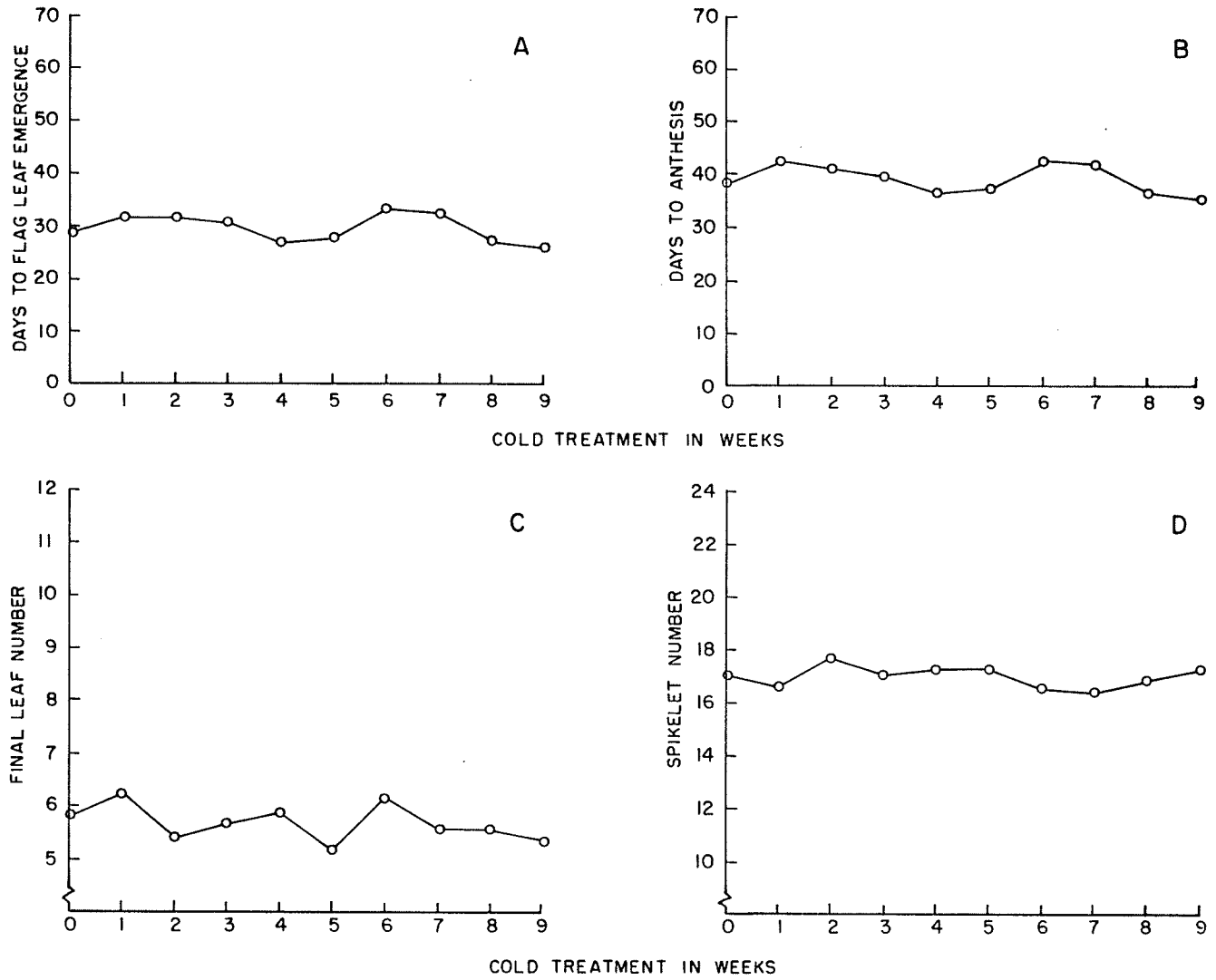

Figure 8. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Prelude. (See Figure 1 for LSD values.)

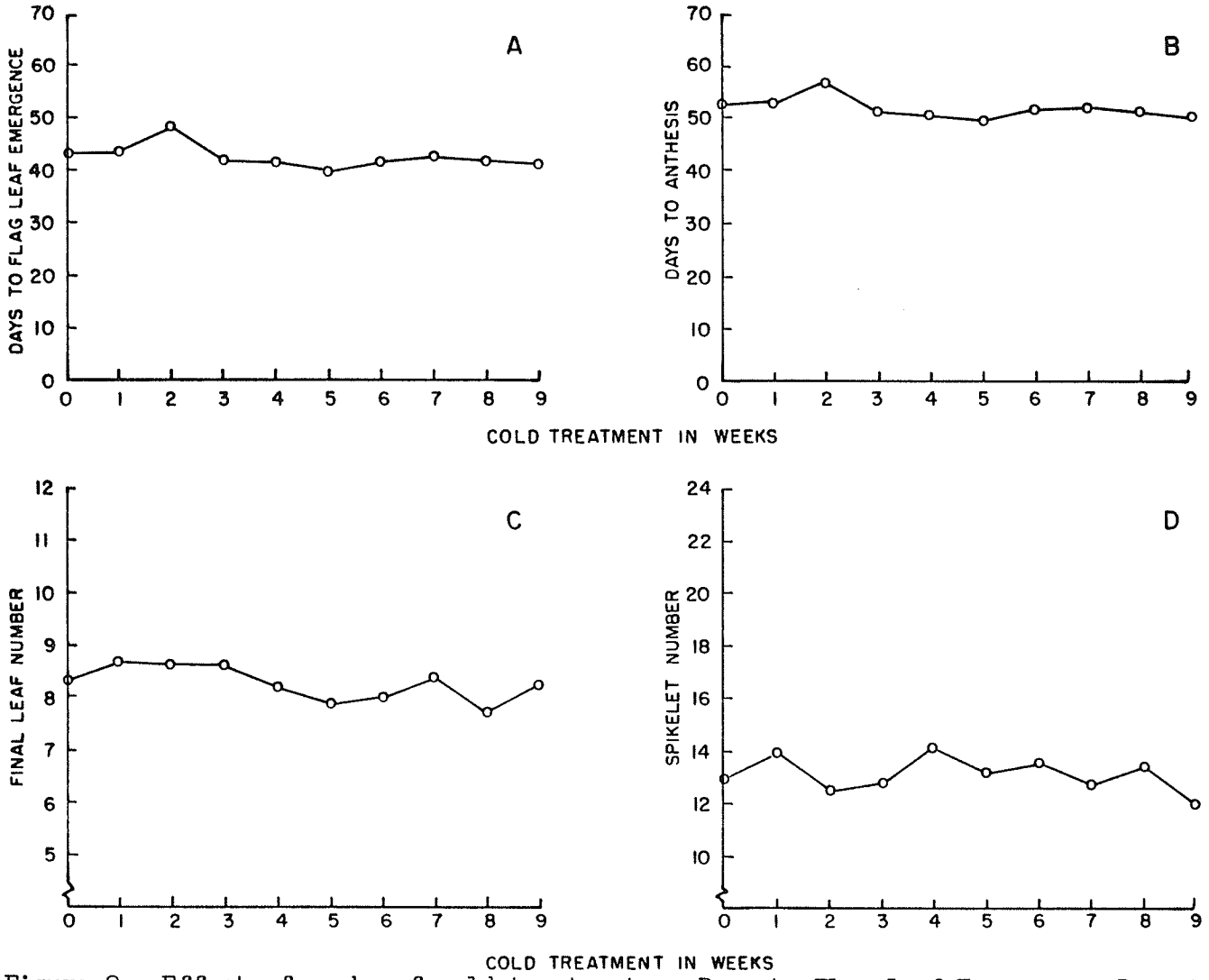

Figure 9. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Sinton. (See Figure 1 for LSD values.)

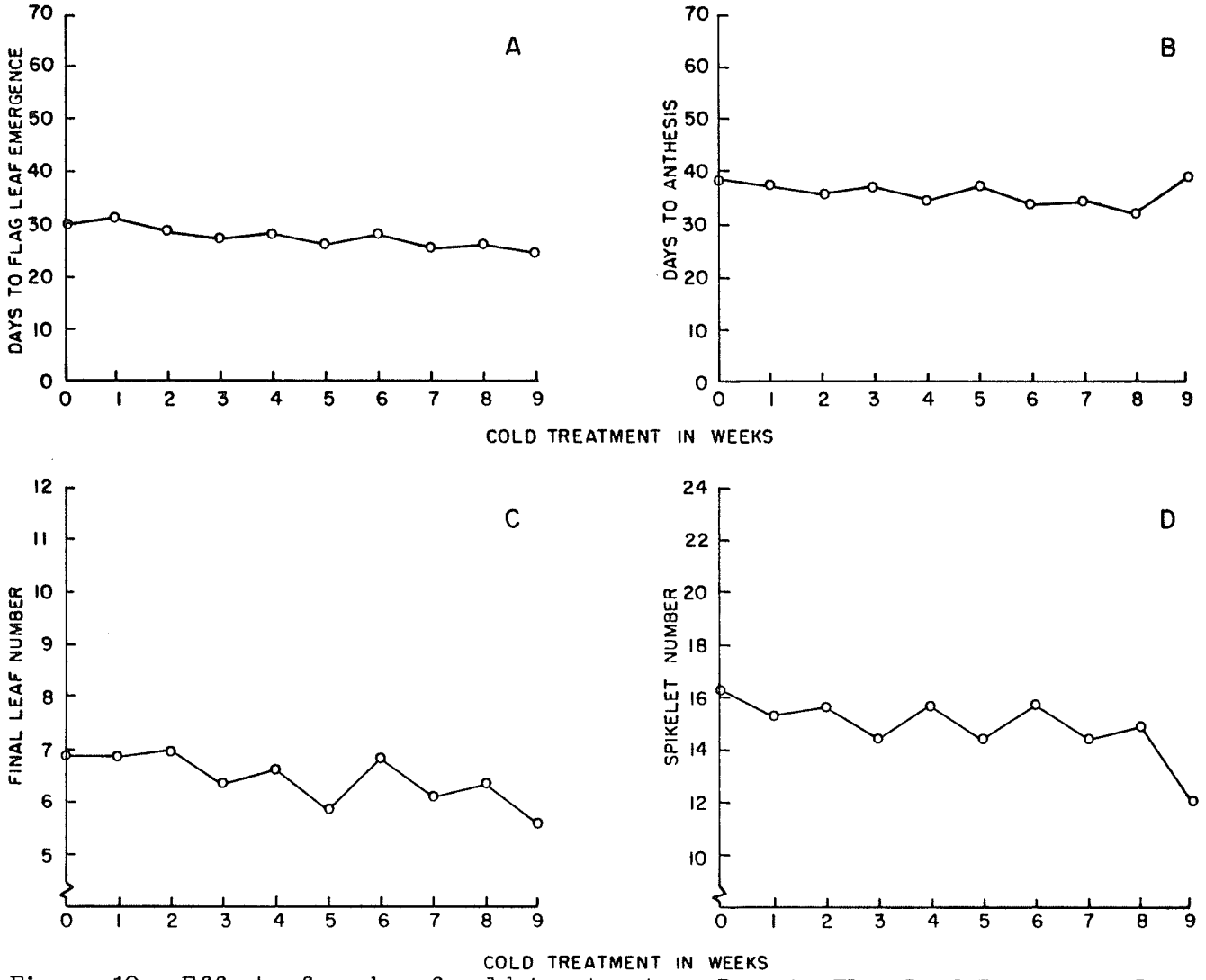

Figure 10. Effect of weeks of cold treatment on Days to Flag Leaf Emergence, Days to Anthesis, Final Leaf Number and Spikelet Number of Yecora. (See Figure 1 for LSD values.)

Correlation coefficients. Highly significant positive correlation coefficients were found between DFLE and DA, DFLE and FLN, DFLE and SPN, DA and FLN, DA and SPN, and FLN and SPN (Table 10). Unlike Experiment I, SPN was positively correlated with all of the other parameters measured in this Experiment. Although the temperature and light regimes of Experiment I and II were the same, differences between experimental conditions caused by mechanical failures, reduced lighting in Experiment II due to summer heat stress conditions and differential pest infestations and spraying did occur. Whether these differences would account for the differences in correlations between the two experiments is a matter of speculation.

Halse and Weir (1970), Pugsley (1971), Derera and Ellison (1974), Wall and Cartwright (1974) and Ford (1977) reported that spikelet number could be used to measure vernalization response; whereas Salisbury et al. (1979) and Berry et al. (1980) reported that spikelet numbers and vernalization response were non-related. Under the conditions of Experiment II, DFLE, DA, FLN and SPN all served as indicators of vernalization response.

Discussion. Although for the four parameters ANOVA produced highly significant cultivar x treatment interactions and correlations were highly significant, there was heterogeniety of response patterns within a cultivar. However, this diversity amongst parameters did not obscure general patterns of response.

The classifications of Experiment I were supported by the findings of this Experiment. Benito, Glenlea, Marquis, Neepawa, Prelude, Sinton and Yecora had little or no response to vernalization.

TABLE 10. Correlation coefficients of parameters measured for ten cultivars exposed to 0-9 weeks of cold treatment.

Parameters Correlated	Correlation Coefficient	Prob>[R] Ho: RHo=0	Number of Observations[a]
Days to flag leaf emergence with:			
Days to anthesis	0.98	0.0001	1820
Final leaf number	0.69	0.0001	1825
Spikelet number	0.40	0.0001	1836
Days to anthesis with:			
Final leaf number	0.68	0.0001	1802
Spikelet number	0.43	0.0001	1821
Final leaf number with:			
Spikelet number	0.50	0.0001	1825

a. Of a possible 1980.

Cajeme, Fielder and Pitic were positively responsive to vernalization.

The positive response patterns of Cajeme, Fielder and Pitic were characterized by: 1) a gradation of reduction with the first few weeks of cold treatment; 2) an initial plateau with four or five weeks of treatment (fulfillment of vernalization requirement); 3) a slight or marked reversal with extended cold treatments; and 4) a further downward trend with the 8- and/or 9-weeks cold treatments. Fluctuations in response patterns were reported by Derera and Ellison (1974) and Halloran (1977) for a number of spring and winter wheats.

The cultivars Prelude and Sinton were non-responsive to all of the cold durations of this experiment. This insensitivity to cold treatments was independent of the earliness of Prelude and relative lateness of Sinton; and supported the report by Levy and Peterson (1972) that vernalization response was independent of maturity classification.

Benito, Glenlea, Marquis, Neepawa, and Yecora were all found to have significant although minor responses to the extended (8-9 weeks) cold treatments. Pugsley (1971) reported that the Vrn1 allele was non-responsive to 30-days vernalization. However, Berry et al. (1980) found that extension of the cold treatment (0-11 weeks) caused genotypes with the Vrn1 allele to display a threshold response with five or more weeks of cold treatment. Therefore, the patterns found with Benito, Glenlea, Marquis, Neepawa and Yecora may be an expression of the Vrn1 allele as found in Triple Dirk. Differences from the five weeks of Berry et al. (1980) can be accounted for due to the differences in growth conditions.

Experiment III: Cultivar Response Patterns with Field Plantings

The three cultivars--Cajeme, Fielder and Pitic--classified as responsive to vernalization in Experiment I and II, were selected to study the expression of this response under field conditions. The seed was cold treated for 0, 2, 4 and 6 weeks prior to planting and subsequent field transplantings were at U. of M. Field Research Stations, Glenlea and Winnipeg. A summary of the analyses of variance is given in Table 11 (refer to Appendix 4 for complete ANOVA). Days to jointing (DJ), days to flag leaf emergence (DFLE), days to boot (DB), days to heading (DH) and days to anthesis (DA) were affected at a highly significant level by the cold treatments as was expected for this group of cultivars. Computation of an orthogonal contrast of the zero-weeks control with the 2, 4 and 6 weeks of cold treatment

TABLE 11. Summary of analyses of variance for parameters measured to classify vernalization responses of Cajeme, Fielder and Pitic with post-cold treatment field plantings.

Source of Variation	F-value DJ	DFLE	DB	DH	DA
Cultivar (C)	0.14	1.48	6.14*	8.23*	11.46**
Treatment (T)	61.52**	72.57**	145.83**	211.77**	212.79**
CxT	0.55	2.63*	2.27	0.85	0.41
Orthoganol Contrasts:					
Control vs Cold Treatments	176.38**	213.00**	392.29**	572.33**	571.16**

* Significant at P=0.05.
** Significant at P=0.01.

indicated that the control was significantly different from the cold treatment as measured by DJ, DFLE, DB, DH and DA. Only DFLE had a significant cultivar x treatment interaction. The gradual increase in the significance of cultivar effects with later developmental stages may be due to different rates of development amongst these cultivars.

Correlation coefficients were determined and are presented in Table 12. Highly significant positive correlations were found for all single combinations of the parameters DJ, DFLE, DB, DH and DA. Any differences in development rates must have been small enough not to have affected the linear relationships between the parameters measured. These results indicated that any easily delineated developmental stage from jointing to anthesis could be used to measure vernalization response.

As the effects of cold treatment was determined for all parameters to be significantly different from the control, and there were highly significant positive correlations between all parameters, only the mean data from DA has been graphically presented in Figure 11. The effect of location on DA was non-significant (Appendix 4). From the graphs of Figure 11, it can be seen that expression of vernalization response for Cajeme, Pitic and Fielder was graded. This agreed with results of Experiments I and II. As vernalization requirements of 4 or 5 weeks were determined for these cultivars in Experiment II, the levelling of response between 4 and 6 weeks of cold treatment in this Experiment would reflect a similar fulfillment of vernalization requirement. Under field conditions no reversals of cold treatment effects with 2, 4 and 6 weeks cold treatments were found.

TABLE 12. Correlation coefficients of parameters measured for three cultivars exposed to 0, 2, 4 and 6 weeks of cold treatment followed by field planting.

Parameters Correlated	Correlation Coefficient	Prob> [R] Ho: RHo=0	Number of Observations[a]
Days to jointing with:			
Days to flag leaf emergence	0.92	0.0001	71
Days to boot	0.84	0.0001	70
Days to heading	0.81	0.0001	70
Days to anthesis	0.79	0.0001	70
Days to flag leaf emergence with:			
Days to boot	0.93	0.0001	70
Days to heading	0.89	0.0001	70
Days to anthesis	0.88	0.0001	70
Days to boot with:			
Days to heading	0.97	0.0001	70
Days to anthesis	0.96	0.0001	70
Days to heading with:			
Days to anthesis	0.98	0.0001	70

a. Of a possible 72 plot assessments.

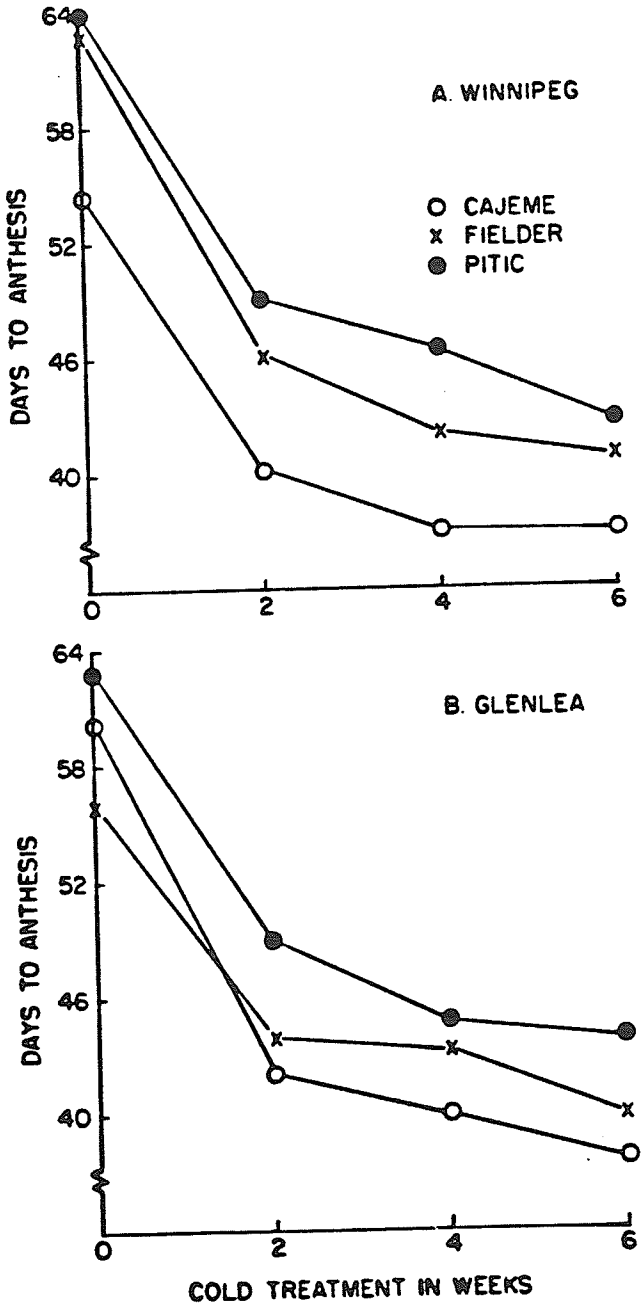

Figure 11. Effect of weeks of cold treatment on Days to Anthesis of Cajeme, Fielder and Pitic planted at two locations, (A) Winnipeg and (B) Glenlea. (LSD: 5%, 1%—Between cold treatments for the same cultivar = 2.19, 2.93; Between cold treatments for different cultivars = 28.56, 137.23.)

At the Glenlea location, fertile (FT) and total (TT) tiller numbers were counted. Cultivar x treatment interactions were not significant for either FT or TT (see Appendix 5 for complete ANOVA). The relevant mean data is presented in Table 13. Cultivars were significantly different in their fertile and total tiller numbers. However, fertile tiller number was unaffected by cold treatments whereas total tiller number was significantly reduced for all three cultivars. Reduced tiller number was found by Purvis (1934) for vernalized winter rye and by Levy and Peterson (1972) for vernalized spring wheats such as Pitic that were responsive to vernalization.

By the Feeke's scale, the tillering stage precedes the jointing stage. As all stages of jointing, flag leaf, boot, heading and anthesis were found to be advanced by cold treatments, the reduction in tiller number with cold treatments was no doubt due to the earlier termination of the tillering stage. Although tillering capacity was reduced by cold treatment, under the 1981 Glenlea field conditions it was adequate to ensure maximum utilization of tiller number as a component of yield as fertile tiller number (spike/unit area) was unaffected by vernalization treatments. Unfortunately, other yield components such as spikelet number, kernels/spike and kernel weights were not determined due to termination of this experiment by hail.

Experiment IV: Cultivar Response Patterns with Shorter Duration Cold Treatments

The last in the series of cultivar assessments was an experiment on the development of vernalization during the early period of cold treatment. Three cultivars were selected for this experiment, Cajeme

TABLE 13. Total (TT) and fertile (FT) tiller numbers for three cultivars exposed to 0, 2, 4 and 6 weeks of cold treatment with subsequent field planting at U. of M. Field Research Station, Glenlea.

Cultivar	Parameter	Weeks of Cold Treatment 0	2	4	6	Cultivar Mean
Cajeme	TT	18.57[a]	12.47	10.53	10.00	12.80[b]
	FT	8.21[c]	10.47	8.20	7.87	8.69[d]
Fielder	TT	22.80	17.20	14.67	11.47	16.53
	FT	9.20	11.60	9.07	8.07	9.48
Pitic	TT	24.50	18.13	16.00	15.73	18.05
	FT	9.70	12.07	9.93	11.60	10.93
Treatment Means						
	TT	21.72[e]	15.93	13.73	12.40	
	FT	8.97[f]	11.38	9.07	9.18	

a. LSD, 5% between treatments for the same cultivar—12.75; between treatments for different cultivars—11.47.
b. Significant at 1% level: LSD, 5%—3.21.
c. LSD, 5% between treatments for the same cultivar—8.90; between treatments for different cultivars—8.67.
d. Not significant at 5% level: LSD, 5%—4.08.
e. Significant at 1% level: LSD, 5%—7.36.
f. Not significant at 5% level: LSD, 5%—4.45.

and Pitic because of their positive vernalization responses and Yecora because of its unresponsiveness to short durations of cold treatment (Experiments I and II). The summary of analyses of variance is given in Table 14 (refer to Appendix 6 for complete ANOVA). The effects of cold treatments on the six parameters measured—DFLE, DH, DA, DM, FLN and SPN—were highly significant. Cultivar effects were significant for all parameters except SPN. Significant cultivar x treatment interactions were found for DFLE, DA and FLN. The cultivar means per treatment of each parameter were graphed versus cold treatment and are presented in Figures 12A-F. Correlation coefficients were computed for the various single combinations of parameters and are presented in Table 15.

Days to flag leaf emergence. The significant cultivar x treatment interaction for this characteristic indicated that the cultivars did

TABLE 14. Summary of analyses of variance for parameters measured for Cajeme, Pitic and Yecora to study vernalization response patterns to short-duration cold treatments.

Source of Variation	F-value					
	DFLE	DH	DA	DM	FLN	SPN
Cultivar (C)	331.59**	201.01**	290.78**	107.15**	162.20**	11.16
Treatment (T)	35.99**	15.46**	37.67**	11.99**	33.36**	7.66**
CxT	7.34**	2.16	6.77**	1.69	2.88*	2.13

* Significant at P=0.05.
** Significant at P=0.01.

not respond in the same manner to the cold treatments (Figure 12A).

The 0, 1 and 2 days of cold treatment did not significantly affect DFLE for Pitic. The cold treatments of four and more days significantly reduced DFLE from the zero-days control. The most marked drop in days occurred between the 2- and 4-days treatments followed by another marked drop between 4- and 8-days cold treatments. This pattern would suggest that: 1) the underlying mechanism for vernalization required a period of induction; and 2) after induction the process proceeded rapidly but was slowed down as the vernalization requirement was met. This sigmoid pattern of the velocity of the vernalization reaction was reported by Purvis (1948) for winter rye and Devay et al. (1976) for winter wheat.

The lag period for Cajeme was longer than for Pitic with the 1- to 8-days cold treatments being not significantly different from the unvernalized control. The increase in DFLE at four days was not significant. The decrease in DFLE from the 8-days to the 16-days cold treatment was steep and followed by a further decrease from the 16-days to 32-days treatment. Despite differences during their lag periods the development of the response was similar for Cajeme and Pitic.

As expected for the nonresponsive cultivar Yecora significant acceleration of DFLE by these short cold treatments did not occur. The increased days with the one-day treatment was not significant.

Days to heading. The non-significance of the cultivar x treatment interaction precludes the statistical comparison of the effects of cold treatment on DH by individual cultivar. The probability of the

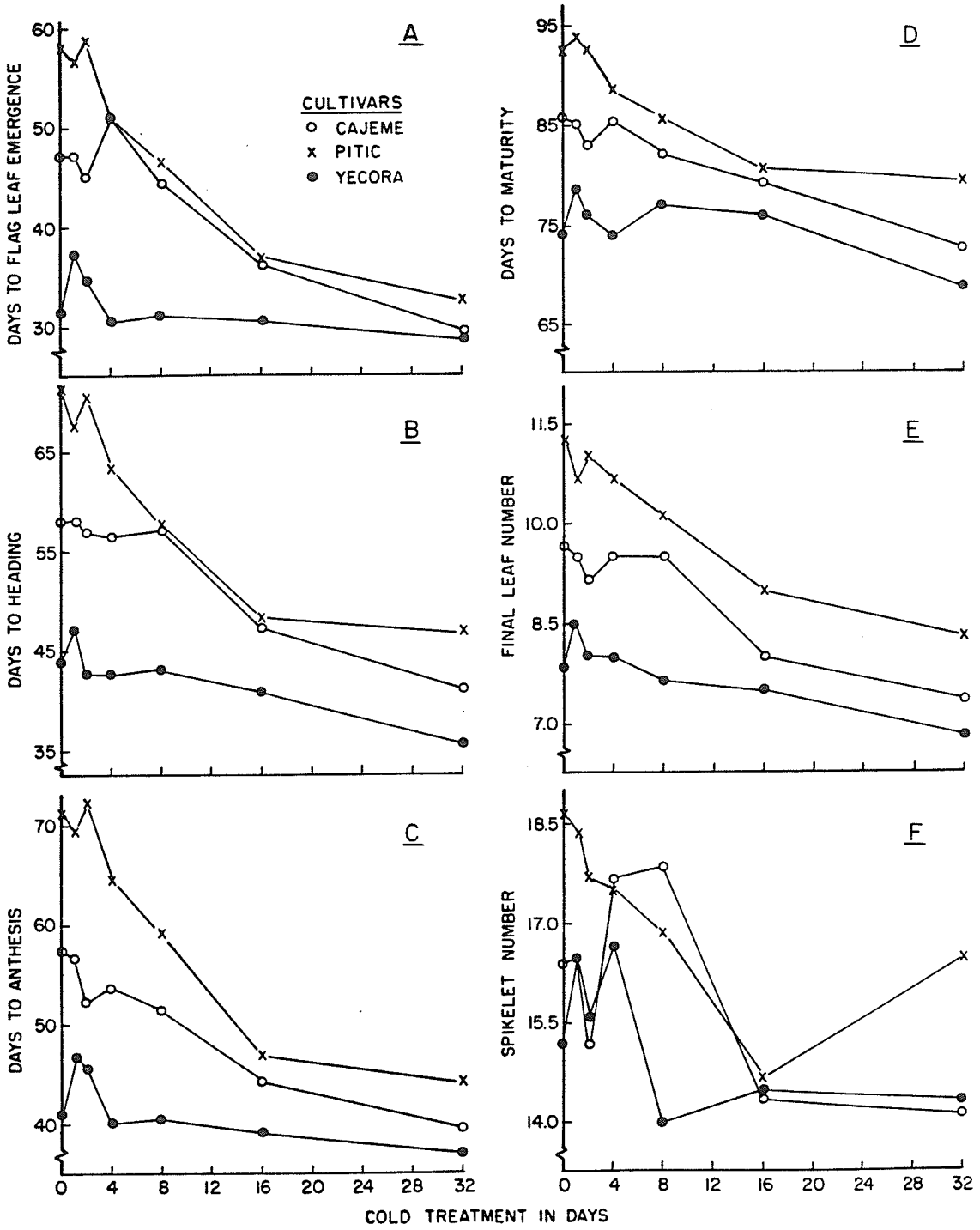

Figure 12. Effect of days of cold treatment on Days to Flag Leaf Emergence, Days to Heading, Days to Anthesis, Days to Maturity, Final Leaf Number and Spikelet Number of Cajeme, Pitic and Yecora. (LSD: 5%, 1%—(Between cold treatments for the same cultivar) Days to Flag Leaf Emergence = 5.53, 7.33; Days to Heading = 8.73, 11.96; Days to Anthesis = 5.64, 7.66; Days to Maturity = 6.12, 8.12; Final Leaf Number = 0.73, 0.99; Spikelet Number = 1.95, 2.72.)

F-value was 0.0676 indicating that there was at least a non-significant cultivar x treatment interaction. The non-significance of the interaction was due to the response of Yecora to accelerate DH with the longer cold treatments, a phenomenon previously found in Experiment I. Significant treatment and cultivar effects were found. The 16- and 32-days treatments caused significant reductions in days to heading with the greater reduction being from 8 to 16 days. From Figure 12B it can be seen that patterns for Cajeme and Pitic for DH were closely aligned to their respective patterns for DFLE.

Days to anthesis. There was a significant cultivar x treatment interaction for this characteristic and results are presented in Figure 12C. No significant differences from the unvernalized control were found for Yecora. Pitic and Cajeme, however, were accelerated by the cold treatments. For Pitic, cold treatments of 4 or more days were significantly lower than the control. As was found for DFLE, the pattern of response was sigmoid for Pitic. The lag period for Cajeme continued until the 8-days cold treatment whereafter a rapid decrease in DA occurred.

Days to maturity. The non-significance of cultivar x treatment interaction was unexpected due to the inclusion of the nonresponsive cultivar Yecora in the experiment. Reference to Figure 12D will reveal that the three cultivars were accelerated by the longer cold treatments for this parameter. Treatment and cultivar effects were highly significant. There was a gradual decline in DM with increased cold durations that was significantly different from the control at the 8-,

16- and 32-days cold treatments.

Final leaf number. Significant cultivar x treatment interaction was found. Final leaf number for Yecora was not significantly affected although perturbations with cold treatment did occur (Figure 12E). For Pitic, FLN was significantly reduced from the zero-days control with cold treatments of eight days or more. The pattern of development of the vernalization response for Pitic as measured by FLN was very similar to patterns for DFLE and DA. The FLN's of Cajeme were significantly reduced by cold treatments of 16 and 32 days. Like Pitic, the pattern of vernalization response for Cajeme as measured by FLN was similar to DFLE and DA patterns.

Spikelet number. The lack of a significant cultivar x treatment interaction was not unexpected due to the variability of the response of this characteristic in Experiments I and II. However a significant treatment effect was found with the 16- and 32-days cold treatments. From Figure 12F the variability of SPN concurrent with short cold treatments can be seen.

Correlation coefficients. The correlation coefficients determined between the parameters measured in this experiment were all positive and highly significant (Table 15). It is clear from the foregoing discussions however that not all parameters were equally effective in discerning vernalization responses.

Discussion. The effectiveness of cold durations in accelerating development can only be measured by developmental processes that may

TABLE 15. Correlation coefficients of parameters measured for three cultivars exposed to 0, 1, 2, 4, 8, 16 and 32 days of cold treatment.

Parameters Correlated	Correlation Coefficient	Prob>[R] Ho: RHo=0	Number of Observations[a]
Days to flag leaf emergence with:			
Days to heading	0.96	0.0001	144
Days to anthesis	0.98	0.0001	150
Days to maturity	0.91	0.0001	157
Final leaf number	0.93	0.0001	161
Spikelet number	0.65	0.0001	158
Days to heading with:			
Days to anthesis	0.97	0.0001	141
Days to maturity	0.91	0.0001	142
Final leaf number	0.91	0.0001	144
Spikelet number	0.69	0.0001	143
Days to anthesis with:			
Days to maturity	0.92	0.0001	148
Final leaf number	0.94	0.0001	150
Spikelet number	0.69	0.0001	149
Days to maturity with:			
Final leaf number	0.87	0.0001	157
Spikelet number	0.57	0.0001	156
Final leaf number with:			
Spikelet number	0.65	0.0001	158

a. Of a possible 162.

be differentially influenced by post-cold treatment conditions (Cooper 1956). From the results of this and previously discussed experiments the most consistent measurements of vernalization response have been DFLE, DA and FLN.

The development of the vernalization response consists of a lag period, a rapid acceleration after induction and a deacceleration with increasing fulfillment of the vernalization requirement. The results of this experiment indicated the lag period was from 2 to 8 days depending upon cultivar and parameter measured and that the vernalization process slowed between 16 and 32 days, again depending upon cultivar and parameter. Upon re-examination of the results of Experiment II for the responsive cultivars Cajeme, Fielder and Pitic, there was a general trend of response patterns that supports the conclusions of this experiment.

Riddell and Gries (1958b), Levy and Peterson (1972), and Halloran (1977) found similar patterns of vernalization velocities for the spring wheats they tested as positively responsive to vernalization.

Characterization of Vernalization

Experiment V: Devernalization

The first of the series of experiments to investigate the characteristics of the vernalization response in spring wheats was a study to determine if the vernalization phenomenon was reversible by warm temperatures. The cultivar Pitic was selected because of its proven positive vernalization response. Intermediate temperature treatments ($15^{o}C$) were interposed to determine if stability would be

increased, a phenomenon reported by Purvis and Gregory (1952) and Friend and Purvis (1963).

A summary of the analyses of variance is presented in Table 16 (refer to Appendix 7 for complete ANOVA). Significant cold-, intermediate-, and warm-temperature effects were found as well as significant cold x intermediate and cold x intermediate x warm interactions. The relevant mean data is presented for DFLE and DA in Figures 13 and 14 respectively.

Calculation of multiple correlations produced the following best three variable models for maximum R^2 improvement:

DFLE= 55.08 + (-3.53)xCold + (-0.66)xIntermediate + (0.38)xWarm (R^2=0.91);

TABLE 16. Summary of analyses of variance for parameters measured to determine the effects of post-cold treatment temperatures on the vernalization response of Pitic.

Source of Variation	F-value DFLE	DA
Cold (C)	167.54**	140.37**
Intermediate (I)	11.21**	14.85**
CxI	3.39*	5.68**
Warm (W)	8.82**	6.52**
CxW	1.36	1.44
IxW	1.81	2.18
CxIxW	2.53**	2.42**

* Significant at P=0.05.
** Significant at P=0.01.

$DA_2 = 68.08 + (-3.68)xCold + (-0.81)xIntermediate + (0.37)xWarm$ ($R^2=0.90$).

From these regression equations the following conclusions were drawn: 1) there was a 13-day difference between intercepts for flag leaf emergence and anthesis; 2) cold and intermediate temperatures hastened DFLE and DA; and 3) warm temperatures delayed DFLE and DA.

Because of the split-split plot design, comparisons were made between cold treatments at the same intermediate and warm temperature treatments, between intermediate treatments at the same cold and warm treatments and between warm treatments at the same cold and intermediate treatments.

Cold treatments. As measured by both DFLE and DA, the 2-, 4- and 6-weeks cold treatments at all intermediate, warm levels were significantly earlier than their respective zero-weeks cold treatments (Figures 13 and 14). Differences between the 2-, 4- and 6-weeks treatments were dependent on intermediate and warm temperature treatments. However, there was generally a graded response with four weeks earlier than two, and six weeks earlier than four.

Intermediate treatments. Comparison of the intermediate treatments to their respective zero-days intermediate treatments was taken as an indication of increased or decreased stability due to the intermediate treatment. Within the six-weeks cold treatments significant stabilization occurred with three-days intermediate, one-day warm as measured by DFLE and DA. The four-weeks cold treatments were stabilized by three-days intermediate at three-days warm but were significantly delayed by one-day intermediate, zero-days warm as measured by DFLE and

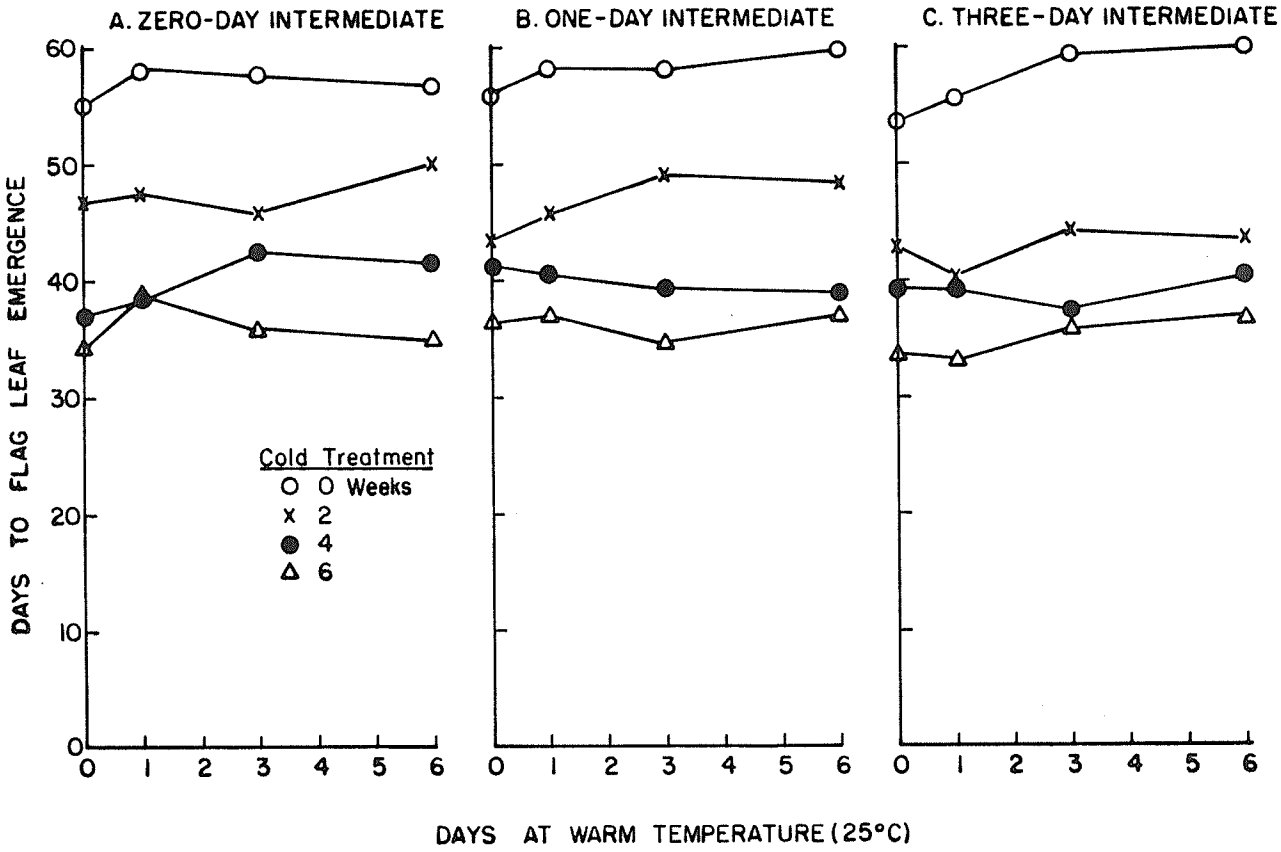

Figure 13. Effect of warm- and intermediate-temperature treatments after cold treatments on Days to Flag Leaf Emergence of Pitic. (LSD: 5%, 1%— Between warm treatments with the same cold and intermediate treatment = 3.35, 4.46; Between intermediate treatments with the same cold and warm treatment = 3.44, 4.60; Between cold treatments with the same intermediate and warm treatment = 4.12, 5.75.)

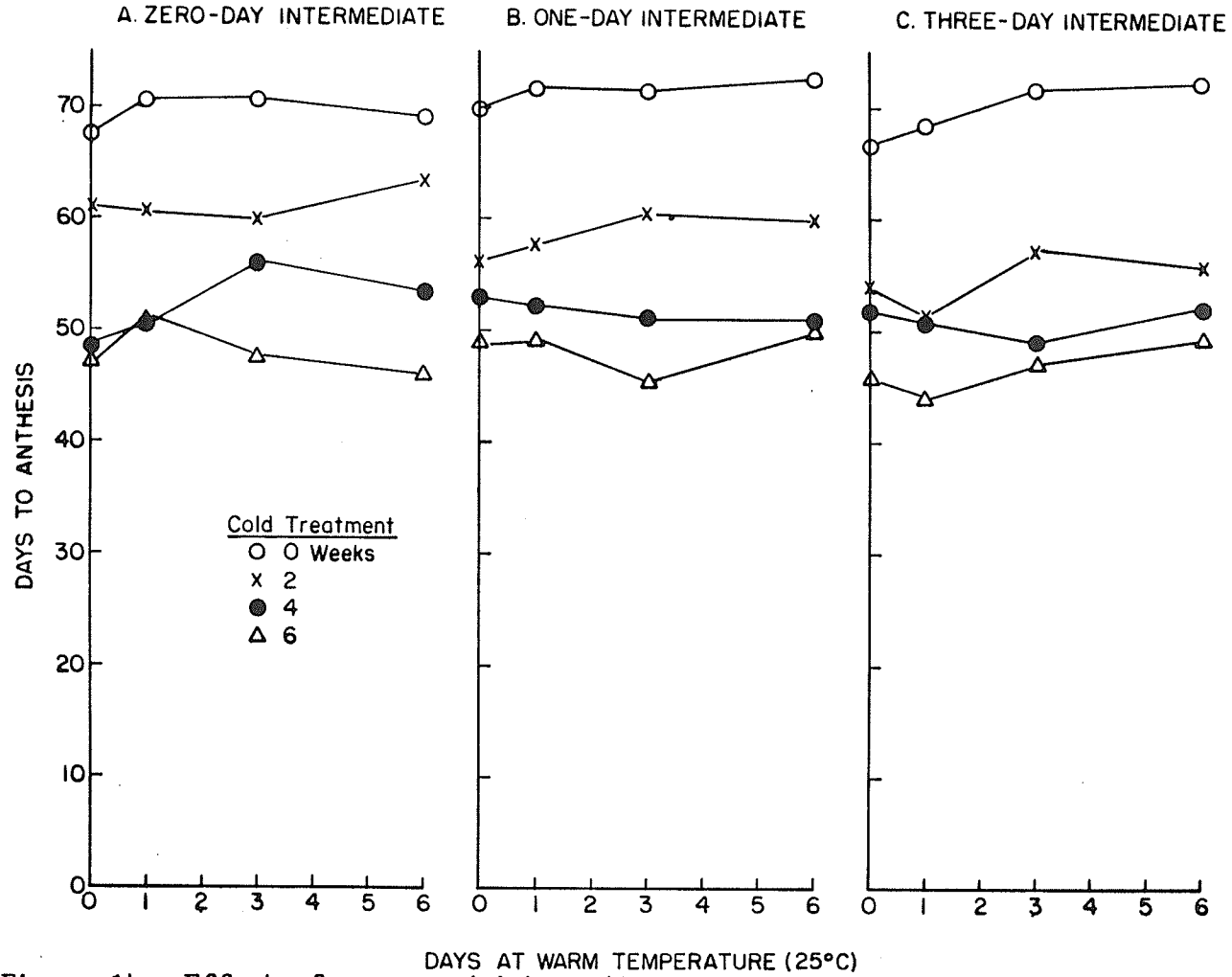

Figure 14. Effect of warm- and intermediate-temperature after cold treatments on Days to Anthesis of Pitic. (LSD: 5%, 1%—Between warm treatments with the same cold and intermediate treatment = 3.67, 4.87; Between intermediate treatments at the same cold and warm treatment = 3.72, 4.98; Between cold treatments at the same intermediate and warm treatment = 4.54, 6.37.)

DA. The two-weeks cold treatments were stabilized by three-days intermediate at 0-, 1- and 6-days warm, and by one-day intermediate when followed by zero-days warm. None of the zero-weeks, warm treatments were significantly affected by intermediate temperatures.

Warm treatments. Within cold and intermediate treatments, comparisons were made between warm treatments and their zero-days warm control to determine if the warm treatment had caused significant devernalization. Those differences which were significant as measured by DFLE and DA were considered. Warm treatments did not affect the six-weeks cold treatment at any intermediate treatment. The four-weeks cold treatments were significantly delayed by 3 and 6 days of warm temperatures only with the zero-days intermediate treatment. The two-weeks cold treatments were significantly delayed by three days of warm temperature only at the one-day intermediate level. The zero-weeks cold treatments were significantly delayed by 3 and 6 days of warm temperature only when preceded by three days at intermediate temperature.

Discussion. A small but significant amount of devernalization occurred with the extended warm-temperature treatments (3 and 6 days) when preceded by intermediate-temperature treatments at zero-weeks cold treatment. That this devernalization occurred with only the three-days intermediate treatment could reflect a depletion of respiratory substrates with extended treatments; however, the six-day period completely at warm temperatures (no intermediate treatment) showed no significant retardation. Another possibility could be that the intermediate temperatures stimulated vernalization, and the

subsequent warm temperatures caused a reversal of this stimulation that depleted substrates for development that would then need time for replacement. A slight non-significant acceleration of the zero-days warm, three-days intermediate treatment as compared to the zero-days warm, zero-days intermediate treatment would support the hypothesis that the intermediate temperatures were slightly inductive to vernalization. Friend and Purvis (1963) found that warm temperature treatments before cold treatments could significantly delay subsequent vernalization in winter rye and termed this phenomenon "predevernalization."

Purvis and Gregory (1952) found that stability to heat treatments increased with longer cold treatments. The results from this experiment for four and six weeks agreed with this finding. The six-weeks treatments were unaffected by heat treatments. The four-weeks treatments were significantly delayed by 3 and 6 days of warm treatment (no intermediate temperature treatment). Purvis and Gregory (1952) also found that intermediate temperature treatments increased the stability of partially vernalized winter rye. As the vernalization requirement for Pitic from Experiment II was five weeks, the increased stability of the four weeks cold treatments to warm treatments when these warm treatments were preceded by one or three days intermediate treatment was concurrent with Purvis's and Gregory's findings.

The relative lack of significant devernalization by the warm temperatures of the two-weeks cold treatment was unexpected as was the stabilization due to intermediate temperatures when followed by no warm treatments. From Figures 13 and 14 it can be seen that there

was a general trend for the two-weeks cold treatments to be earlier with the longer intermediate-temperature treatments. Therefore, these intermediate treatments were: 1) stabilizing the treatments lacking a warm-temperature period from devernalization by the growth room conditions (23/18°C); 2) themselves causing further vernalization of the treatments that was not reversed by subsequent treatment; or 3) a combination of these two possibilities.

The results of this experiment indicated that the inclusion of intermediate temperature treatments between the cold treatments and the subsequent growing conditions were of particular importance for partially vernalized treatments. Devernalization did occur in Pitic; however except for experimental and theoretical purposes, this phenomenon at 25°C was of minor importance compared with the influence of cold treatments.

Experiment VI: Stabilization

The second experiment in the series of characterization of vernalization was intended to establish the stable cold treatments and intermediate temperature durations necessary to ensure stability in the three responsive cultivars Cajeme, Fielder and Pitic. Yecora was included as a control cultivar. The analysis of variance produced significant cultivar, cold and intermediate effects as well as significant cultivar x cold, cold x intermediate, and cultivar x cold x intermediate interactions (Table 17, refer to Appendix 8 for complete ANOVA). Relevant mean data was graphed for the two parameters, DFLE and DA (Figures 15 and 16).

TABLE 17. Summary of analyses of variance for parameters measured to determine the effect of intermediate temperature treatments on the vernalization responses of Cajeme, Fielder, Pitic and Yecora.

Source of Variation	F-value DFLE	DA
Cultivar (C)	168.71**	99.57**
Cold (Co)	110.72**	53.15**
CxCo	13.48**	8.33**
Intermediate (I)	7.96**	4.98**
CxI	1.04	1.75
CoxI	4.17**	3.37**
CxCoxI	1.97**	2.14**

** Significant at P=0.01.

Because of the split-split plot design, comparisons were made by cultivar within cold treatments and between cold treatments at the same intermediate treatments. The correlation between DFLE and DA was highly significant at R=0.96.

Cajeme. Although intermediate-temperature treatments caused some degree of fluctuation in both DFLE and DA for the unvernalized controls, neither the upward or downward shifts were significantly different from the zero-weeks cold, zero-days intermediate treatment (Figures 15A and 16A). The intermediate-temperature treatments made no significant differences within the 2- and 4-weeks cold treatments. However, often the two-weeks treatments were not significantly different than their comparative zero-weeks control; and the stability

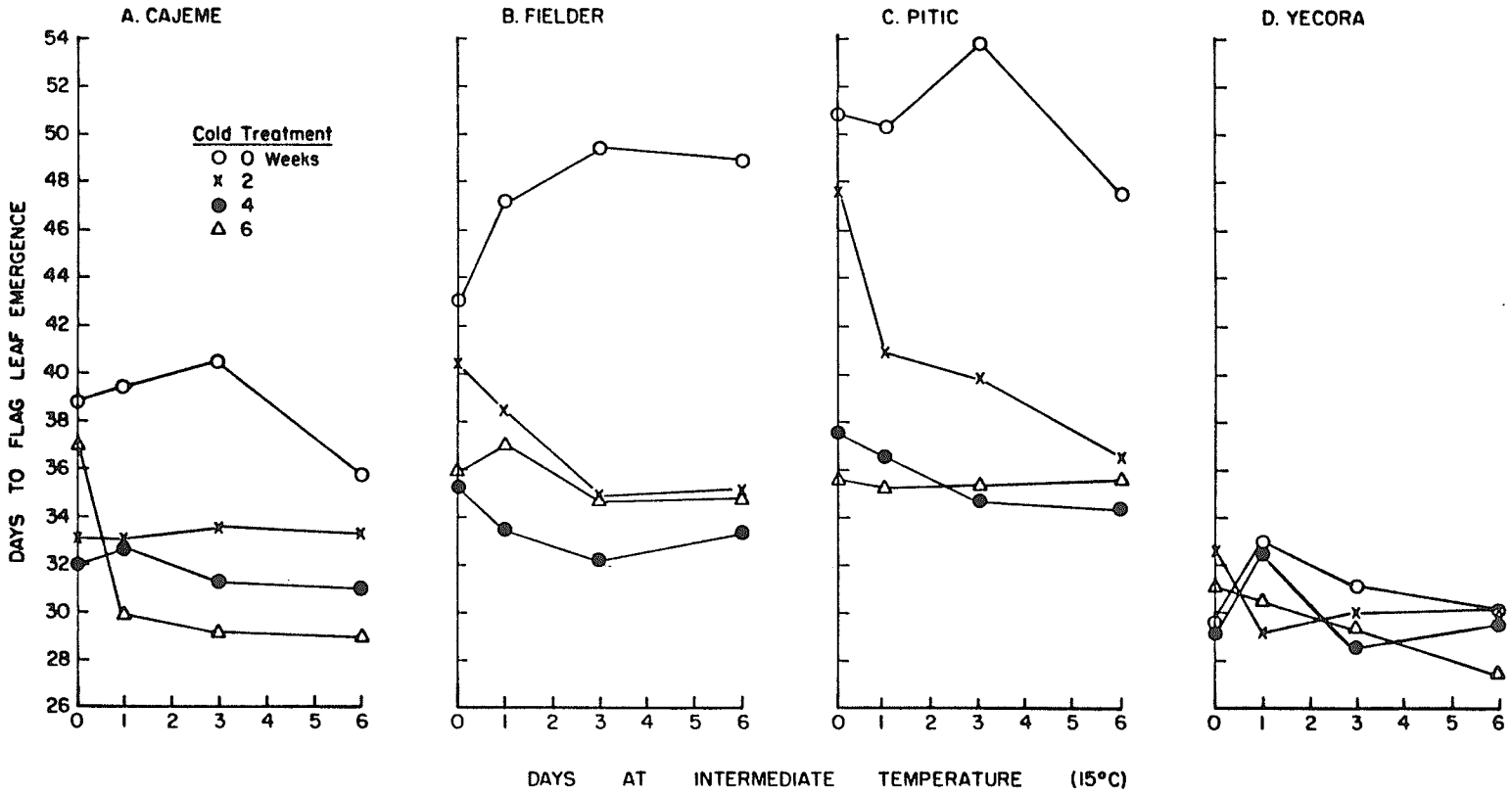

Figure 15. Effect of intermediate-temperature treatments after cold treatments on Days to Flag Leaf Emergence of Cajeme, Fielder, Pitic, and Yecora. (LSD: 5%, 1%—Between intermediate treatments for the same cold treatment and cultivar = 3.75, 4.93; Between cold treatments for the same intermediate treatment and cultivar = 3.96, 5.24.)

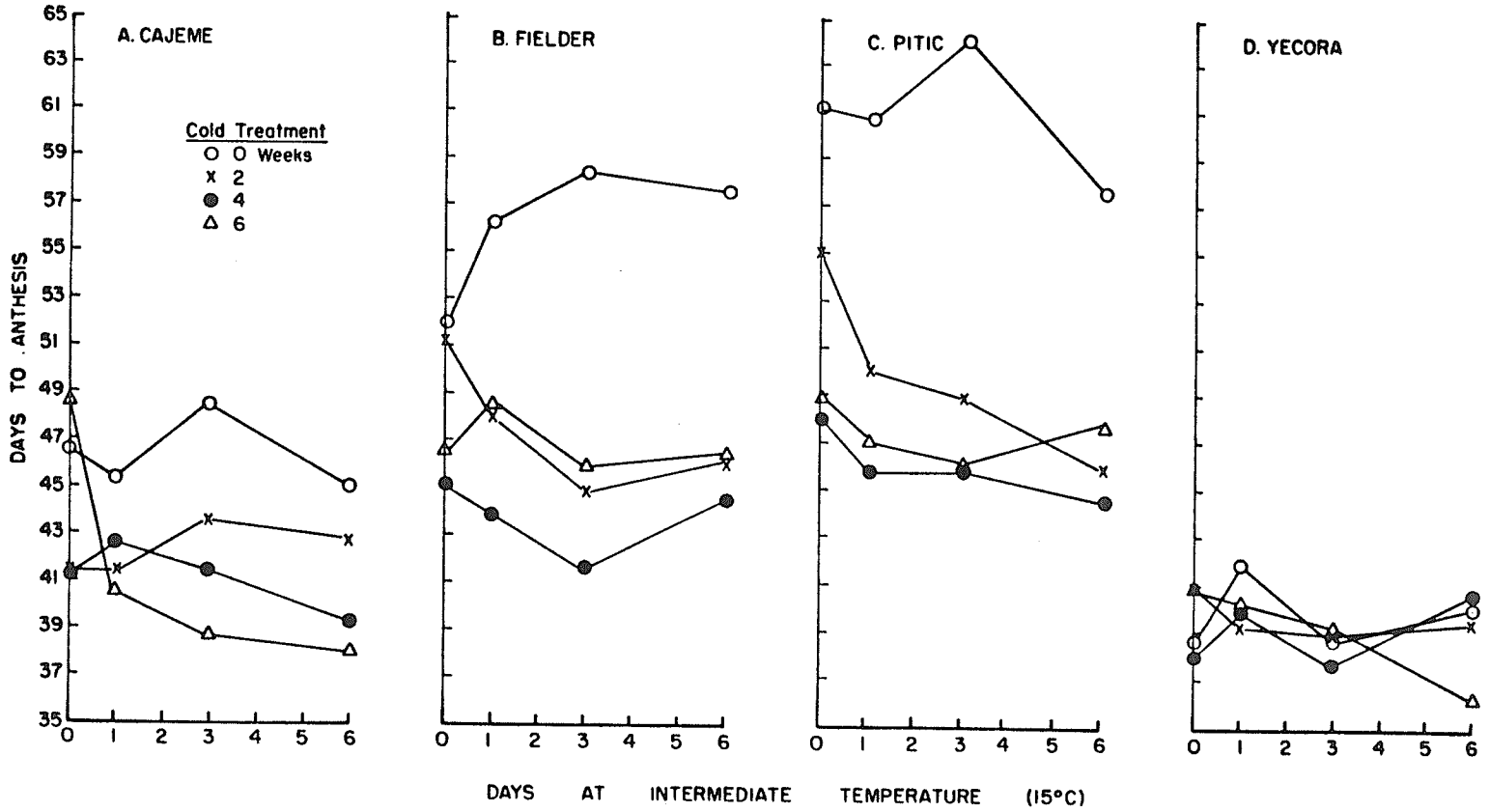

Figure 16. Effect of intermediate-temperature treatments after cold treatments on Days to Anthesis of Cajeme, Fielder, Pitic and Yecora. (LSD: 5%, 1%—Between intermediate treatments for the same cold treatment and cultivar = 4.07, 5.35; Between cold treatments for the same intermediate treatment and cultivar = 4.53, 6.00.)

of the four-weeks cold treatments were increased by the 3- and 6-days intermediate treatments. The 1-, 3- and 6-days intermediate treatments increased the stability of the six-weeks cold treatment because these treatments were among the earliest whereas the six-weeks cold, zero-days intermediate treatment was not significantly different than its comparative zero-weeks control.

Fielder. The zero-weeks cold treatments for Fielder were significantly delayed by intermediate treatments of 1, 3 and 6 days from the zero-days intermediate treatment for both DFLE and DA (Figures 15B and 16B). The two-weeks cold treatments were progressively stabilized by 1, 3 and 6 days at 15°C; the zero-days intermediate treatment was not significantly different from its comparative zero-weeks control. The 4- and 6-weeks cold treatments were not significantly differentiated by the intermediate temperature treatments, although there was a trend within the four-weeks cold treatment to be earlier with the longer intermediate-temperature treatments. The six-weeks cold treatments were consistently, although not significantly, later than the comparative four-weeks cold treatments.

Pitic. The zero-weeks cold treatments for Pitic were not significantly different from the zero-weeks cold, zero-days intermediate treatment for both DFLE and DA (Figures 15C and 16C). The two-weeks cold treatments were progressively stabilized by the intermediate temperature treatments. No significant differences were found within the 4- and 6-weeks cold treatments and all of these cold treatments were significantly earlier than their respective zero-weeks cold

controls. There was a trend within the four-weeks cold treatments of stabilization by increased intermediate-temperature treatments. The six-weeks cold treatments were slightly later than the four-weeks cold treatments but this lateness was not significant.

Yecora. The fluctuations within the cold treatments and between intermediate treatments for Yecora did not cause highly significant differences (Figures 15D and 16D). The only difference that was significant was for DA between the six-weeks cold, zero-days intermediate treatment and the six-weeks cold, six-days intermediate treatment.

Discussion. Theoretically, devernalization was of interest to early workers because it contradicted Lysenko's theory of phasic development (Purvis 1961). Practically, the degree of reversal and the conditions that prevented devernalization were of importance in evaluating the effectiveness of vernalization (Purvis and Gregory 1952, Chujo 1967).

From the results of Experiment V intermediate temperature treatments were more important than heat treatments in determining the length of development and this was concluded to be due to the fact that growth room conditions were only slightly lower (23/18°C) than the heat treatment (25°C). Friend and Purvis (1963) found both 20°C and 25°C effected devernalization.

In this experiment only the effect of the length of the cold treatment and the intermediate treatments were investigated as sources of stabilization. The hot summer greenhouse where these plants were grown would have been sufficiently warm to provide devernalizing

conditions. Yecora, the control cultivar, was relatively unaffected by cold- and intermediate-temperature treatments, and this indicated that those differences of DFLE and DA between cold- and intermediate-temperature treatments for Cajeme, Fielder and Pitic reflected vernalization and devernalization.

The partially vernalized two-weeks cold treatments for Fielder and Pitic were significantly stabilized by intermediate-temperature treatments and this stability increased with the length of the 15°C treatment. There was also a stabilizing trend within the four-weeks cold treatments for Pitic and Fielder. The observation that the six-weeks cold treatments were later than the four-weeks cold treatments, especially apparent for Fielder, reflected observations of Experiment II that six weeks of cold treatment depressed vernalization.

Cajeme, although significantly accelerated by cold treatments, did not respond to stabilizing conditions as did Fielder and Pitic. This may have been due to the fact that as compared to DFLE and DA for Cajeme from Experiment I and II, the unvernalized controls were approximately five days earlier for this experiment. Therefore, Cajeme responded to the heat conditions of this experiment by accelerating development with or without stabilization. The complete repression of the vernalization of the six-weeks treatment by lack of an intermediate temperature treatment may signify that Cajeme was more sensitive to devernalization during the depressed condition induced by the six-weeks treatment (see Experiment II).

Experiment VII: Plant Age

Neepawa and Pitic were given 0, 2, 4 and 6 weeks of cold treatment

to plants aged 0, 7, 14, 21 and 28 days before the onset of cold treatment. Neepawa was chosen as the non-responsive control cultivar and Pitic was chosen as the positively responsive cultivar.

A summary of the analyses of variance of DFLE and DA is presented in Table 18 (refer to Appendix 9 for complete ANOVA). The main, sub-plot and sub-sub-plot effects of cultivar, age and cold treatment were highly significant. The interactions of cultivar x age, cultivar x cold, age x cold and cultivar x age x cold were all significant. Relevant mean data are graphically presented for DFLE and DA in Figures 17 and 18. (Days were measured not from planting, but from placement of treatments in the greenhouse.)

TABLE 18. Summary of analyses of variance for parameters measured to determine the effect of plant age on the vernalization responses of Neepawa and Pitic.

Source of Variation	F-value DFLE	DA
Cultivar (C)	274.79**	157.79**
Age (A)	607.68**	628.47**
CxA	4.99**	2.80*
Cold (Co)	91.95**	101.59**
CxCo	54.46**	71.35**
AxCo	25.48**	30.02**
CxAxCo	20.71**	24.66**

* Significant at P=0.05.
** Significant at P=0.01.

Neepawa. From Figures 17A and 18A, it is evident that for Neepawa the plants which were cold treated at the age of 0, 21 and 28 days for 0, 2, 4 and 6 weeks were, within age groupings, nearly the same in DFLE and DA. Therefore the amount of growth and/or respiration during the cold treatments was not significantly large to accelerate or delay subsequent growth stages. The six-weeks cold treatments did significantly accelerate DFLE and DA for the 7- and 14-days old plants; while, 2- and 4-weeks cold treatments were not significantly different from their respective zero-weeks cold treatments.

Pitic. Comparison of the cold treatments of 2, 4 and 6 weeks for the 0- and 7-days old plants of Pitic with their respective zero-weeks cold control indicated that these ages were responsive to any of these cold durations (Figures 17B and 18B). The seven-days old plants gave a graded response pattern to the cold treatments; whereas, the zero-days old plants were significantly retarded by the six-weeks cold treatment as compared to the four-weeks cold treatment. The 14- and 21-days old plants also showed significant reductions in days with the longer cold treatments. The 28-days old plants were not significantly influenced by the cold treatments.

Discussion. The effectiveness of vernalization has been documented in winter wheats and fall rye to decrease with increasing plant age prior to cold treatment (Purvis 1961, Chujo 1966a). In this experiment, Pitic was responsive from just germinated seeds to 21-days old plants, with this response being greatest at ages of 0 and 7 days and less at 14 and 21 days. Gott (1957) found green plants of winter wheat were

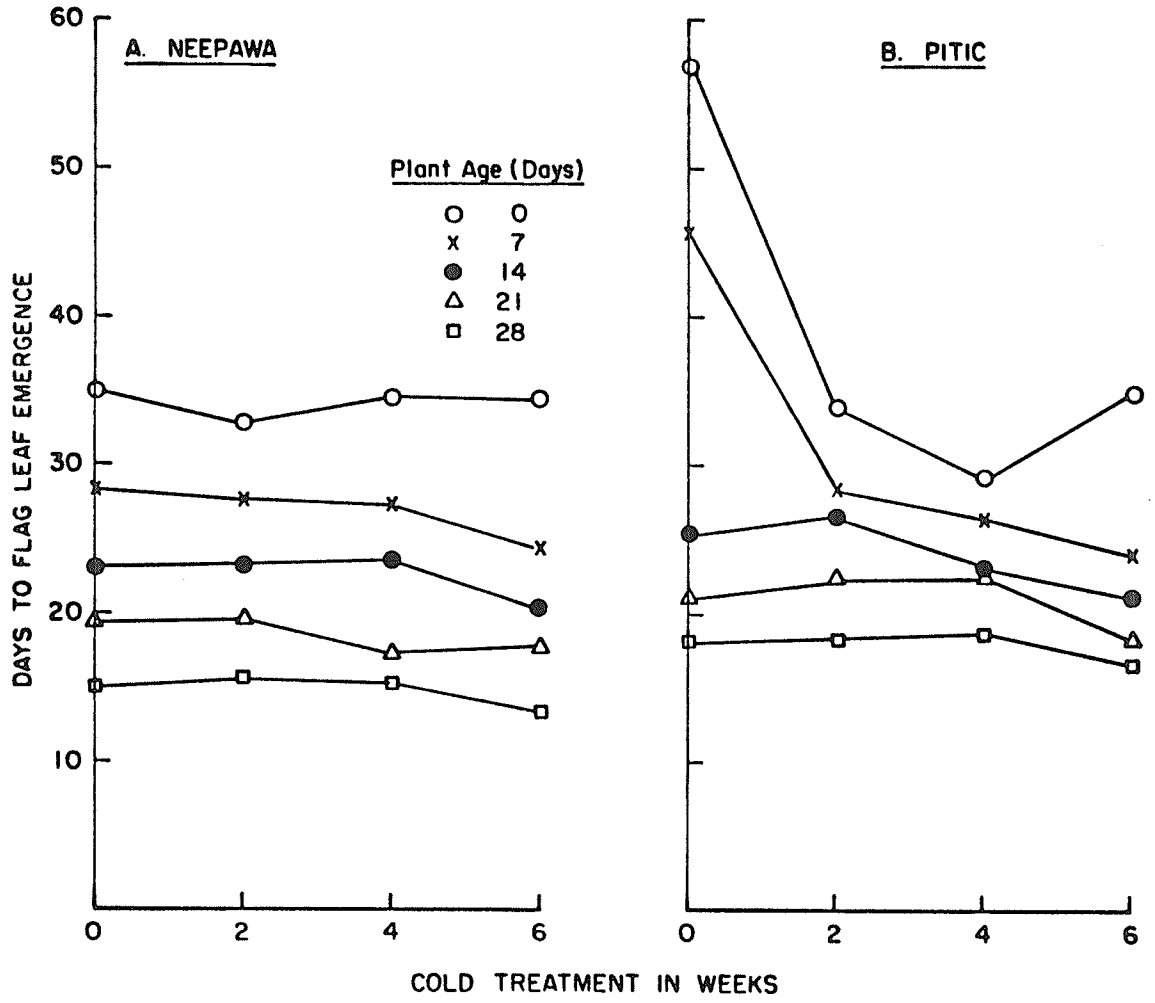

Figure 17. Effect of plant age and cold treatment on Days to Flag Leaf Emergence of Neepawa and Pitic. (LSD: 5%, 1%—Between cold treatments for same age and cultivar = 2.50, 3.30; Between ages for same cold treatment and cultivar = 2.53, 3.35.)

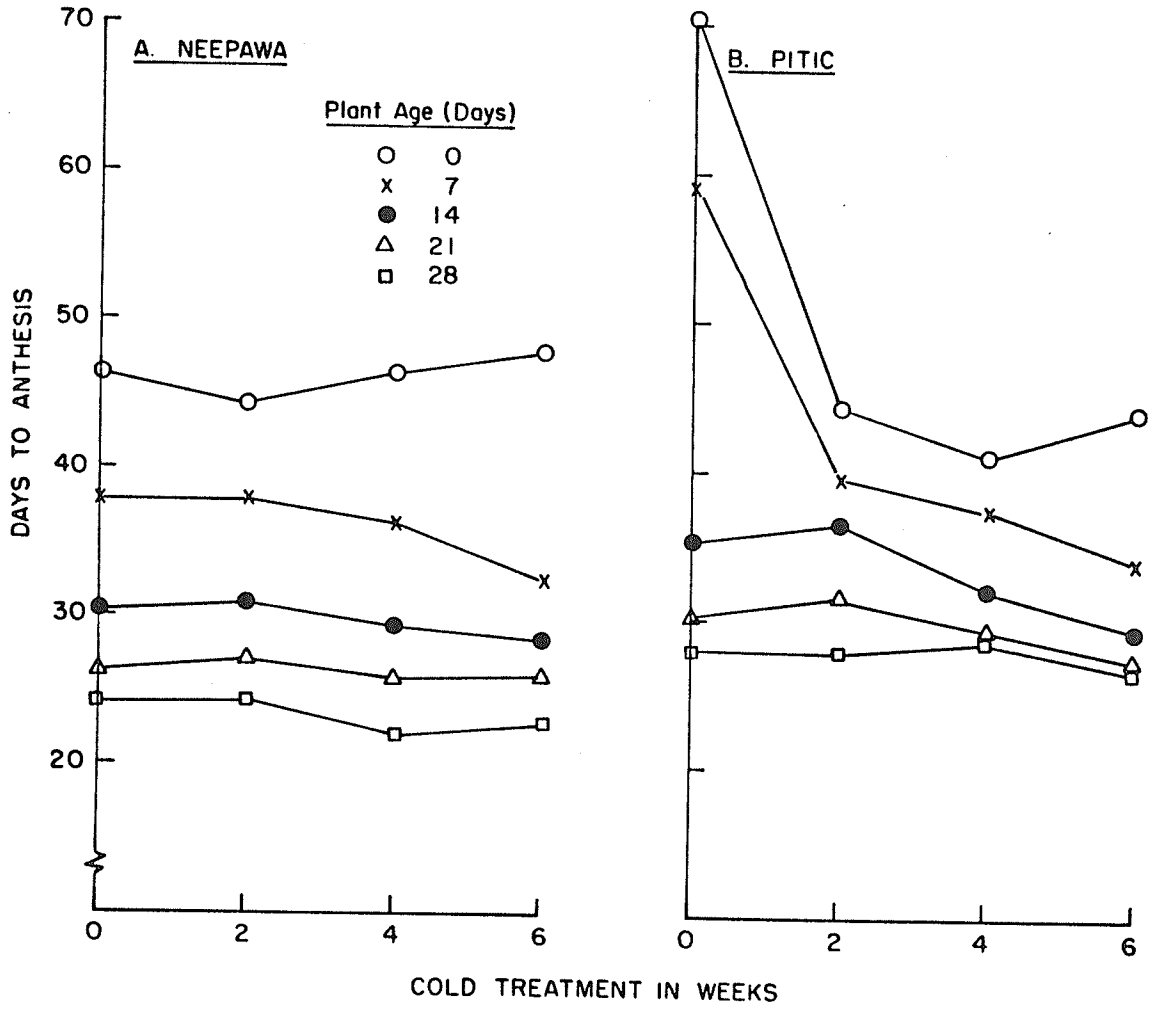

Figure 18. Effect of plant age and cold treatment on Days to Anthesis of Neepawa and Pitic. (LSD: 5%, 1%—Between cold treatments for same age and cultivar = 2.56, 3.38; Between ages for same cold treatment and cultivar = 2.67, 3.54.)

capable of responding to vernalization treatments until six-weeks old.

Gotoh (1975) reported that vernalization was proportional to the cold treatment given from the one-leaf stage. From the results of this experiment for Pitic (Figures 17B and 18B) it can be seen that the seven-days old plants showed a continuous downward gradation with extended cold treatments; and the response of the seven-days old plants was more stable than the zero-days old plants.

Salisbury et al. (1979) found that as the ratio of vernalization of imbibed seed to growing plant was decreased so that some of the cold treatment was given to growing plants there was induction of a vernalization response in cultivars with Vrn1 alleles. Pugsley (1972) found Thatcher to have the Vrn1 allele and it is possible that Thatcher types such as Neepawa, would have this allele. Therefore, the significant accelerations by six weeks of cold treatment to young growing plants of 7 and 14 days may be the expression of the vernalization response of the Vrn1 allele when cold treatment was of the growing plant. However, despite its significance, the acceleration of Neepawa was small and was of noteworthiness due to a possible allelic interpretation.

The graded response of Pitic supports the earlier findings of Experiments I, II, III and IV. The response of Neepawa was minor and supports the findings of Experiments I and II that Neepawa has little or no vernalization response.

Experiment VIII: Cold Temperature

Three temperatures of cold treatments were selected to determine if there was a difference in vernalization response induced with these

different temperatures. Although temperatures varied above and below the mean temperature in a cyclic manner due to the refrigeration mechanism of the cold room and refrigerators, the three temperature regimes were far enough apart to ensure distinct cold treatments.

Seedlings showed little growth at 1°C and while growth did occur at 5°C and 11°C it did not cause excessive elongation. All seedlings grew vigorously upon transplanting to the greenhouse, so apparently storage materials had not been exhausted to affect vernalization responses in that way.

A summary of the analyses of variance for DFLE and DA is presented in Table 19 (refer to Appendix 10 for complete ANOVA). Cultivar and weeks of cold temperature effects were highly significant as was the

TABLE 19. Summary of analyses of variance for parameters measured to determine the effect of the temperature of the cold treatment on vernalization responses of Cajeme, Pitic and Yecora.

Source of Variation	F-value DFLE	DA
Cultivar (C)	484.88**	371.61**
Weeks (W)	187.77**	145.07**
CxW	52.39**	33.04**
Temperature (T)	1.69	3.00
CxT	0.96	1.34
WxT	0.83	1.37
CxWxT	0.74	0.87

** Significant at P=0.01.

cultivar x weeks interaction. Temperature effects were not significant as were the interactions of cultivar x temperature, weeks x temperature, and cultivar x weeks x temperature. Therefore under the conditions of this experiment there was no differential response to the cold temperatures tested. Means for temperature treatments by cold treatments per cultivar are graphically presented for DFLE and DA in Figures 19 and 20 respectively.

Cajeme. The graphs of DFLE and DA in Figures 19A and 20A show that the variability within the zero-weeks control was greater than the variability within 1, 2 and 3 weeks of cold treatments. The $1^{o}C$, $5^{o}C$ and $11^{o}C$ cold treatments were equally effective in inducing vernalization response and the response increased with the duration of the cold treatments.

Pitic. Figures 19B and 20B are graphs for Pitic of DFLE and DA. The effectiveness of cold treatments showed definite trends within this cultivar. The $1^{o}C$ treatment for one week was less effective in accelerating development than the $5^{o}C$ and $11^{o}C$ cold treatments. As the length of the cold treatment was increased the differences between temperature treatments was decreased. The $5^{o}C$ treatment was in general more effective than the $1^{o}C$ or $11^{o}C$ treatments; however, the three temperatures all successfully induced vernalization responses. The $11^{o}C$ treatment induced a more graded response than the $1^{o}C$ and $5^{o}C$ treatments.

Yecora. As the control cultivar, Yecora was expected to be non-responsive to all combinations of weeks and temperatures of cold treatments.

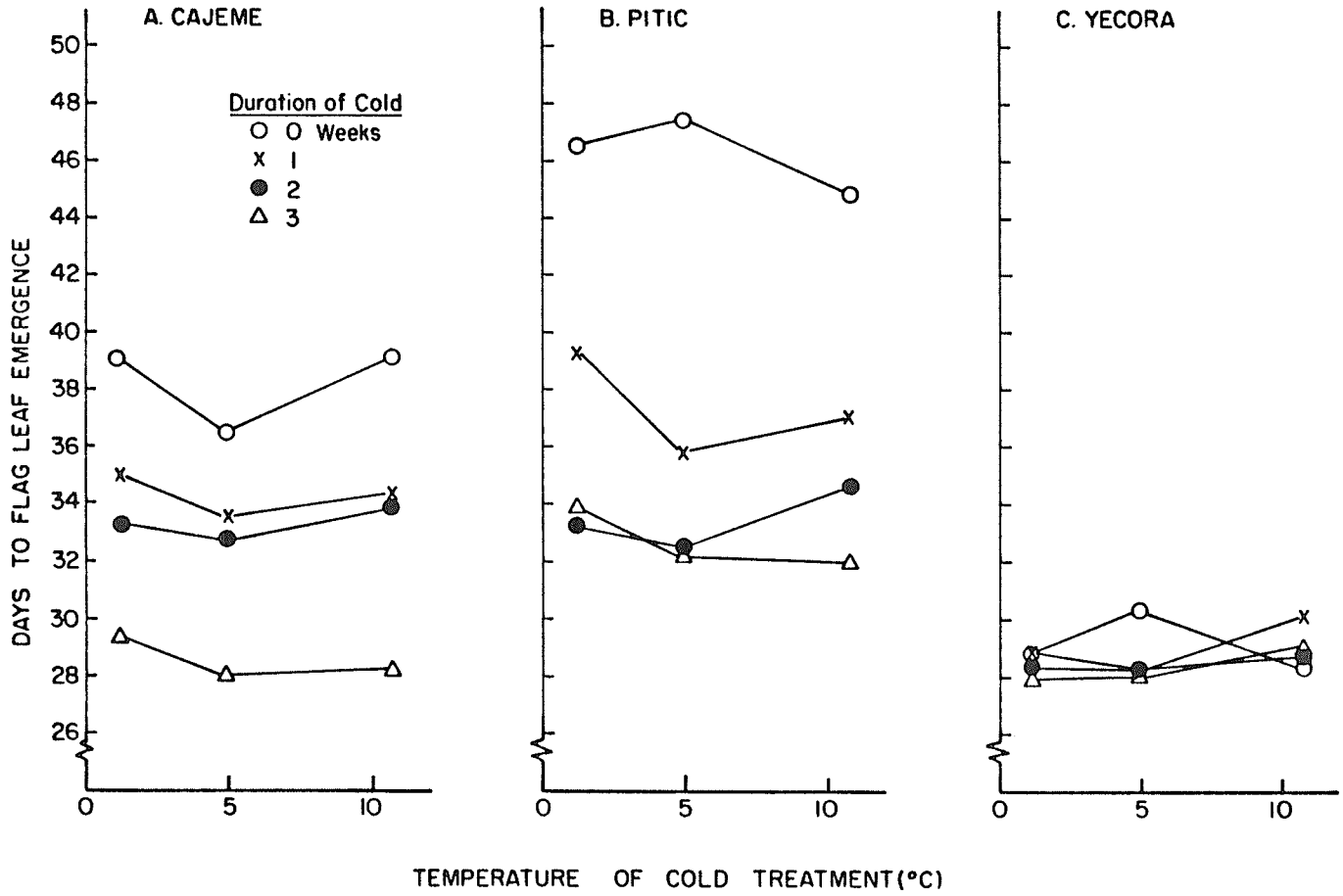

Figure 19. Effect of temperature of cold treatment on Days to Flag Leaf Emergence of Cajeme, Pitic and Yecora. (LSD: 5%, 1%—Between cold treatments with same cultivar and temperature treatment = 2.86, 3.83.)

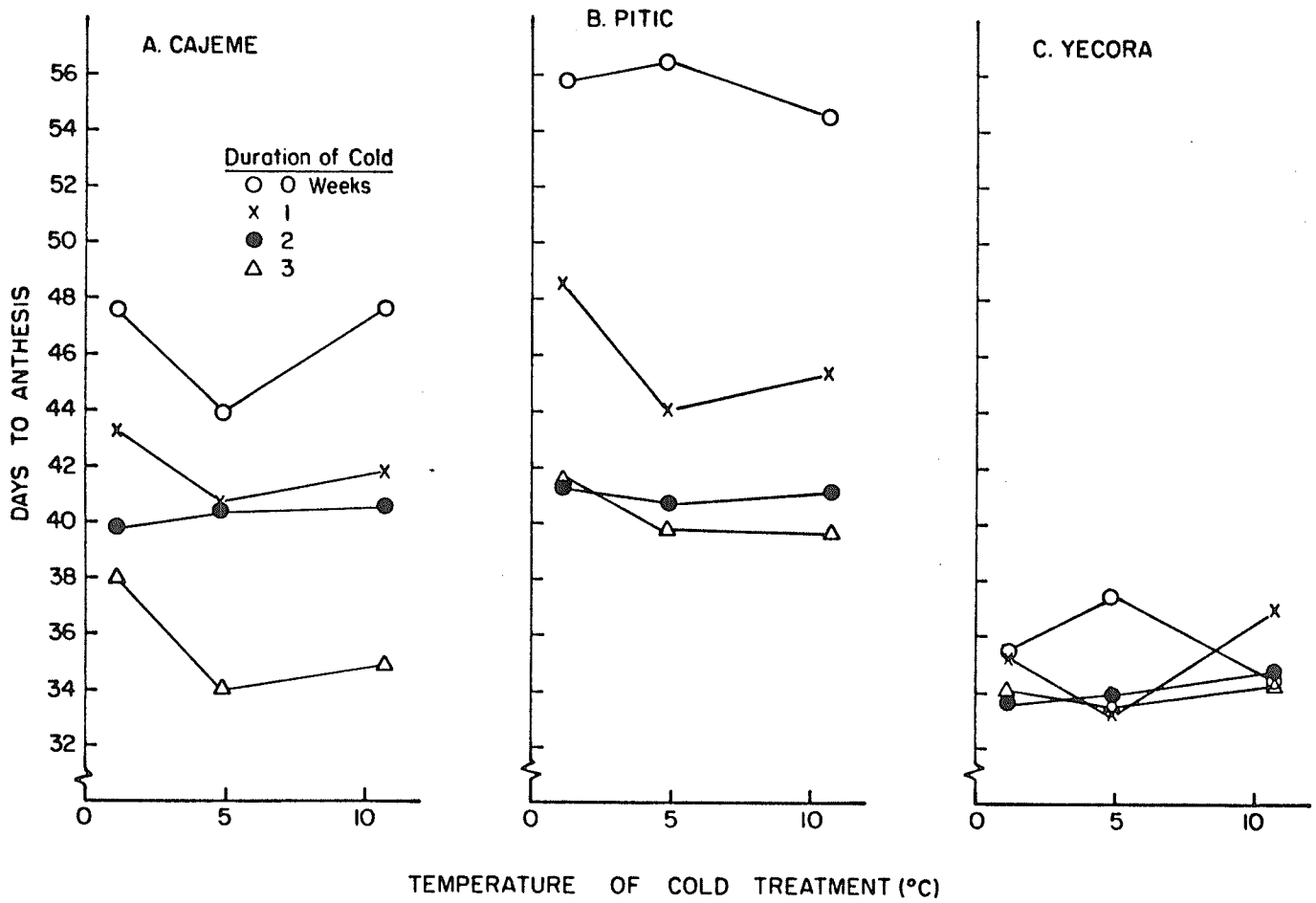

Figure 20. Effect of temperature of cold treatment on Days to Anthesis of Cajeme, Pitic and Yecora. (LSD: 5%, 1%--Between cold treatments with same cultivar and temperature treatment = 3.36, 4.51.)

From Figures 19C and 20C it can be seen that fluctuations within weeks of cold treatment did occur; as well, differences between weeks of cold treatment at the same temperature treatment did ensue. However, fluctuations and differences were minor.

Discussion. The range of operative vernalization temperatures for Cajeme and Pitic included $1^{o}C$ and $11^{o}C$. There was no detectable effect of the different temperatures on the vernalization expressed although there was a trend for the $5^{o}C$ treatments to be more effective than the $1^{o}C$ and $11^{o}C$ treatments. Inouye et al. (1964) found $5^{o}C$ and $10^{o}C$ dark treatments to be equally effective in initiating floral development in the winter wheat Konosu No. 25. Temperatures as low as $-1^{o}C$ to as high as $12^{o}C$ have been reported to effectively induce vernalization responses in winter wheats (McKinney and Sando 1933, Chujo 1966a). Cold treatments for the two spring wheats of this experiment have a broad range of effective temperatures and no optimum temperature or range of temperatures was established.

The inclusion of 1, 2 and 3 weeks of cold treatment allowed the assessment of a weeks x cold temperature treatment interaction. It was determined thereby that the equal effectiveness of the cold temperatures was not due to a differential fulfillment of the vernalization requirements at the three temperature treatments.

Experiment IX: Light

Because of the use of short day and total darkness during cold treatments, these two light conditions were tested to assess their effect on the vernalization responses of Cajeme, Glenlea, Neepawa,

Pitic and Yecora. These five cultivars were selected to include the daylength-sensitive cultivars of northern origin and less sensitive cultivars of Mexican origin.

A summary of the analyses of variance for DFLE, DA, DH, FLN, SPN and DM are presented in Table 20 (refer to Appendix 11 for complete ANOVA). Highly significant cultivar and treatment effects were found as well as significant cultivar x treatment interactions. The relevant mean data are presented in Table 21.

Comparison of the short day (L) and darkness (D) treatments with the non-vernalized control (C) were taken as an indication of vernalization response. Differences between L and D treatments thereafter were taken as an indication of differential response to vernalization in darkness and short days.

Cajeme. The four-weeks cold treatment effectively initiated the same degree of response in Cajeme whether in short days or darkness as

TABLE 20. Summary of analyses of variance for parameters measured to determine the effect of light on the vernalization responses of Cajeme, Glenlea, Neepawa, Pitic and Yecora.

Source of Variation	F-value					
	DFLE	DH	DA	DM	FLN	SPN
Cultivar (C)	54.33**	40.39**	48.34**	30.44**	59.32**	22.05**
Treatment (T)	75.87**	83.57**	68.15**	10.42**	55.29**	22.90**
CxT	21.62**	21.56**	20.60**	3.10*	16.83**	7.63**

* Significant at P=0.05.
** Significant at P=0.01.

TABLE 21. Days to flag leaf emergence (DFLE), days to heading (DH), days to anthesis (DA), final leaf number (FLN), spikelet number (SPN) and days to maturity (DM) measured for five cultivars exposed to four weeks of cold treatment in the dark (D) and in short days (L) and an unvernalized control (C).

Cultivar	Treatment	DFLE	DH	DA	FLN	SPN	DM
Cajeme	C	49.25 b	62.17 b	61.79 b	10.00 b	20.29 a	86.88 ab
	L	28.00 h	37.83 h	38.25 i	6.92 f	14.00 ef	78.83 cde
	D	31.42 gh	41.92 efgh	41.92 ghi	7.50 f	14.46 cdef	80.75 cde
Glenlea	C	37.33 ef	47.00 de	46.67 efg	8.92 de	15.58 bcde	78.00 cde
	L	33.17 fg	43.67 def	42.50 fghi	8.33 e	16.17 bcd	76.50 de
	D	37.25 ef	47.46 d	47.21 efg	8.71 de	14.83 cdef	80.50 cde
Neepawa	C	43.33 cd	54.33 c	53.21 cd	9.25 cd	13.17 f	88.33 a
	L	40.08 de	48.42 d	48.50 de	9.08 de	12.83 f	88.50 a
	D	45.79 bc	56.96 c	57.21 bc	9.83 bc	14.83 cdef	87.50 a
Pitic	C	59.67 a	73.25 a	72.75 a	12.08 a	20.63 a	91.67 a
	L	33.00 fg	43.50 defg	44.25 efgh	8.42 e	17.08 b	82.50 bc
	D	36.38 ef	46.75 de	47.42 ef	8.50 de	16.50 bc	81.56 cd
Yecora	C	30.25 gh	40.83 fgh	39.71 hi	7.50 f	15.96 bcde	79.33 cde
	L	29.54 gh	38.29 gh	39.38 hi	7.29 f	14.21 def	75.67 e
	D	29.42 gh	39.33 fgh	39.42 hi	7.08 f	13.21 f	79.67 cde

Means in the same column followed by a common letter are not significantly different by Duncan's multiple range test at the 5% level.
See Appendix 11 for ANOVA.

measured by DFLE, DH, DA, FLN, SPN and DM. Cajeme moved from the second latest or greatest to equal Yecora in earliness and reduced leaf and spikelet numbers.

Glenlea. This cultivar did not display a significant response to the four-weeks cold treatment whether in short days or darkness as measured by any of the six parameters.

Neepawa. As measured by DFLE, DA, FLN, SPN and DM, Neepawa whether vernalized in short days or darkness was not significantly different from the control. The four-week short-day treatment did accelerate days to heading. It was also noted that the short-day cold treatment was significantly earlier in DFLE, DH and DA as well as reduced in FLN than the total-darkness cold treatment.

Pitic. As measured by DFLE, DH, DA, FLN, SPN and DM, Pitic was responsive to the four-weeks cold treatments given in darkness or short days. Pitic moved from being the latest cultivar with the greatest leaf and spikelet production to being as early as, and with reduced leaf and spikelet numbers equal to, Glenlea.

Yecora. As measured by DFLE, DH, DA, FLN and DM, Yecora was non-responsive to either of the four-weeks cold treatments. A significant reduction in SPN with four-weeks cold treatment in darkness was detected, although this reduction was not significantly less than the spikelet number of the short-day cold treatment.

Correlation coefficients. Pearson's product-moment correlation coefficients were determined on individual plant statistics and are presented

TABLE 22. Correlation coefficients of parameters measured for five cultivars vernalized in short-day and dark conditions.

Parameters Correlated	Correlation Coefficient	Prob>[R] Ho: RHo=0	Number of Observations[a]
Days to flag leaf emergence with:			
Days to heading	0.97	0.0001	166
Days to anthesis	0.97	0.0001	164
Days to maturity	0.74	0.0001	157
Final leaf number	0.93	0.0001	170
Spikelet number	0.52	0.0001	162
Days to heading with:			
Days to anthesis	0.99	0.0001	163
Days to maturity	0.72	0.0001	156
Final leaf number	0.91	0.0001	166
Spikelet number	0.53	0.0001	161
Days to anthesis with:			
Days to maturity	0.73	0.0001	155
Final leaf number	0.92	0.0001	164
Spikelet number	0.56	0.0001	160
Days to maturity with:			
Final leaf number	0.69	0.0001	157
Spikelet number	0.27	0.0006	157
Final leaf number with:			
Spikelet number	0.56	0.0001	162

a. Of a possible 180.

in Table 22. Highly significant positive correlations were found between all possible single combinations of the six measured parameters—DFLE, DH, DA, DM, FLN and SPN.

Discussion. The vernalization responses of Cajeme and Pitic were unaffected by whether cold treatments were in short days or in darkness. This result agreed with the findings of McKinney and Sando (1935) and Chujo (1969) for winter wheats that vernalization of sprouted seeds was independent of light conditions during the cold treatments.

Anomalies within the non-responsive cultivars occurred with DH for Neepawa and SPN for Yecora. Despite the highly significant correlation coefficients between DA and DH or SPN for this experiment, it was concluded in Experiments I, III and IV that SPN and DH were less reliable measurements of vernalization response than DFLE, DA and FLN. Therefore, the anomalities of this experiment may be due to the general breakdown of DH and SPN as measurements of vernalization response.

Inheritance

Experiment X: Segregation Analyses

Crosses were made between Cajeme and Yecora, Pitic and Neepawa, and Glenlea and Pitic. In the first two cases reciprocal crosses were made. Classification of spring and winter type plants was made in the F2 generation. The latest frequency classes that fell outside of the latest parent were classified as winter types. The results are summarized in Table 23 and histograms of the days to anthesis of F2 plants

TABLE 23. Segregation of spring and winter type plants in the F2 generation of spring x spring crosses.

Cross	Number of Plants			χ^2 for Segregation of:[a]			Least Days to Anthesis of Winter Type
	Spring	Winter	Total	3:1	15:1	63:1	
Neepawa x Pitic	79	7	86	12.155	0.251[b] P>0.50	20.099	85
Pitic x Neepawa	62	3	65	13.338	0.083[b] P>0.50	2.204[c] P>0.10	85
Neepawa-Pitic Pooled Total	141	10	151	26.227	0.0004[b] P>0.95	21.954	85
Yecora x Cajeme	83	0	83	26.349	4.518	2.510[d] P>0.10	85
Cajeme x Yecora	93	0	93	29.681	4.859	0.635[d] P>0.10	85
Glenlea x Pitic	96	1	97	29.096	3.774	0.011[b] P>0.50	85

a. Yates correction for continuity used.
b. Fitted to ratio.
c. Fitted to the ratio, presumably due to small number of winter types.
d. Fitted to the ratio, but non-appearance of winter segregants assumed to indicate common Vrn gene.

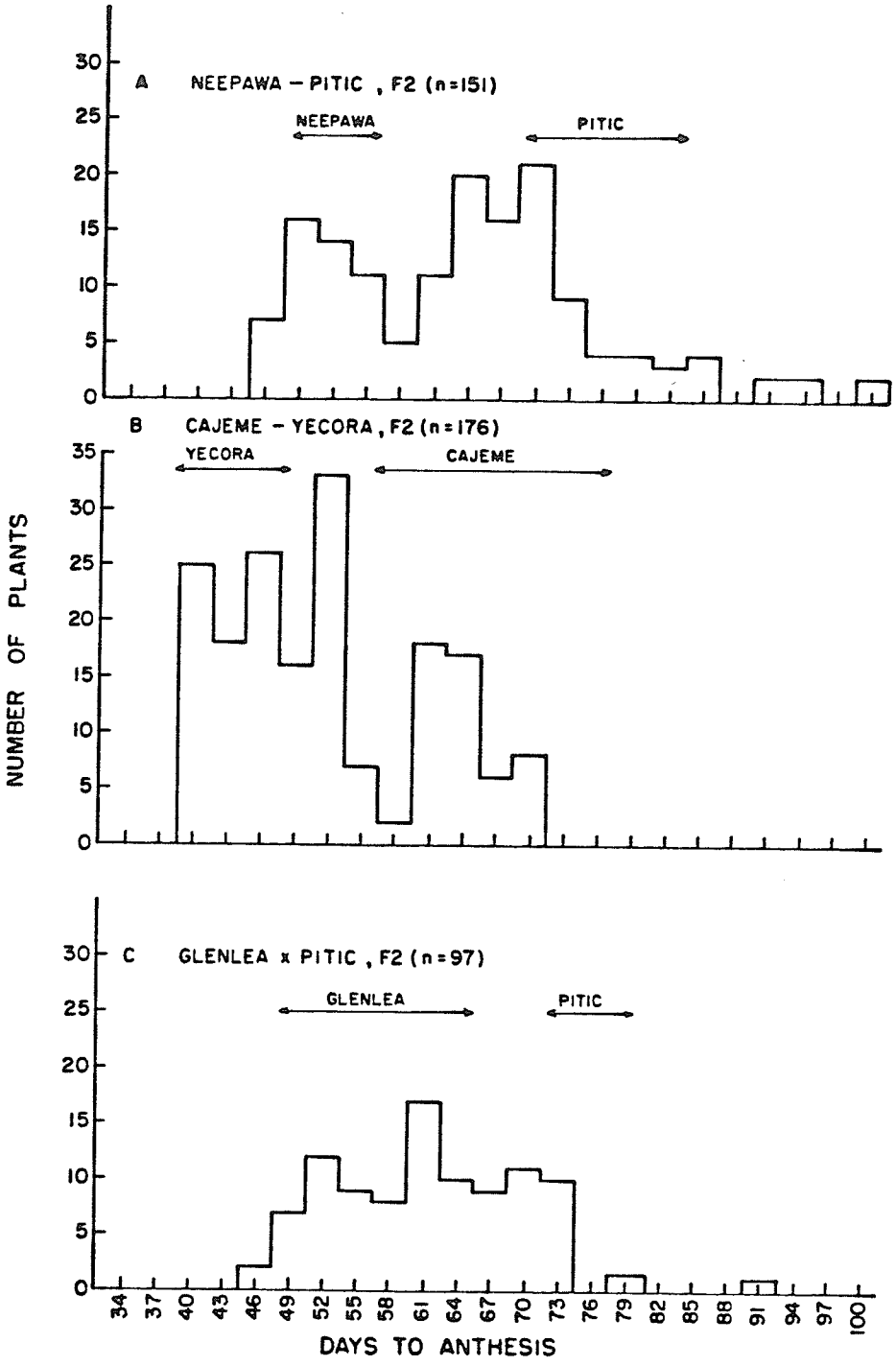

Figure 21. F2 frequency distributions for Days to Anthesis for the crosses of Neepawa–Pitic, Yecora–Cajeme, and Glenlea x Pitic. Parental range of days to anthesis indicated by arrows.

(reciprocals pooled) are presented in Figure 21.

The crosses of Yecora with Cajeme failed to segregate winter types in the F2 generation. The lack of winter segregants was taken to indicate that these two cultivars had a Vrn allele in common. The segregation of plants within the bounds of the parents and the knowledge that Yecora was non-responsive and Cajeme was responsive to vernalization would indicate that these two cultivars did differ in at least one Vrn locus. The segregation of early:late within the pooled data for the Yecora-Cajeme cross fitted a 3:1 ratio with P greater the 0.10. The skewed distribution indicated dominance of the early allele.

The Glenlea x Pitic cross produced one winter segregant in the F2 generation. The appearance of this winter segregant was taken to indicate that Glenlea and Pitic do not have the same spring Vrn allele in common. This result seemed reasonable because Pitic has a positive response whereas Glenlea has little or no vernalization response. As the results fitted a 63:1 ratio, Glenlea may differ from Pitic at three Vrn loci. Therefore, either Glenlea or Pitic may carry two dominant winter inhibitor alleles.

The Neepawa-Pitic crosses produced winter segregants in the F2 generation. The appearance of transgressive segregants indicated that Pitic and Neepawa did not have a Vrn allele in common. The segregation of 15:1 spring to winter plants would support a hypothesis that each of these spring wheats possessed one winter-inhibiting allele. The allele of Neepawa would be insensitive to vernalization while the allele possessed by Pitic would be a responsive Vrn allele.

The Neepawa-Pitic F2 generation was taken to the F3 generation to

confirm or refute the conclusions made on the basis of the F2 segregation. Segregation of spring and winter type plants was assessed in the F3 generation on the basis of days to anthesis. The results are summarized in Table 24. The demarcation between spring and winter types was advanced from 85 days used in the F2 generation to 80 days for the F3 generation. This advancement was based on the acceleration due to the hot greenhouse of parental mean days to anthesis:

	Neepawa	Pitic
F2 generation	52	74
F3 generation	39	68.

On the basis of segregation of F3 plants, F2 families were classified as spring, winter and segregating. The results of the F3 generation study fitted an expected 7:1:8, spring:winter:segregating ratio at a probability level of P greater than 0.05 (pooled data). The calculation of a heterogeneity chi-square to test if the reciprocal crosses represented a single population had a P-value greater than 0.50. There was, therefore, no evidence for heterogeneity and the conclusion that the reciprocal crosses were a homogenous population was not refuted.

Discussion. The F2 and F3 generations were grown indoors to avoid natural vernalizing conditions as were found by Klaimi and Qualset (1974). However, the 20/15°C growth room conditions during the F2 study may have caused some vernalization that would have caused the lack of destinctive spring and winter classes. The almost continuous segregation patterns of the segregating generations may be the influence of segregating modifier genes as were postulated by Kuspira and

TABLE 24. F3 segregation for growth habit in Neepawa x Pitic and Pitic x Neepawa crosses.

Cross	Number of F3 Families			χ^2 for Segregation of:	Least Days to Anthesis
	a Spring	b Winter	c Segregating	a:b:c 7:1:8	of Winter Type
Neepawa x Pitic	34	3	38	0.6571 P>0.50	80
Pitic x Neepawa	34	2	27	3.0998 P>0.10	80
Total				3.7569 (D.F.=4) P>0.10	
Pooled	68	5	65	2.7180 (D.F.=1) P>0.05	
Heterogeniety				1.0389 (D.F.=3) P>0.50	

Unrau (1957) and Gotoh (1977, 1979). The F2 generations were definitely skewed towards the earlier parent indicating partial dominance of the earlier spring allele.

Pugsley (1971, 1972) determined that the Vrn1 allele was insensitive to vernalization. However, Berry et al. (1980) found that the Vrn1 allele had a small threshold response to vernalization and the Vrn2 allele had a cumulative or graded vernalization response. The Vrn3 allele was also a responsive spring allele found by Gotoh (1979) to be indigenous to Japanese cultivars.

Because this inheritance study did not use cultivars of known Vrn genotypes, the relationship between the genes found in Pitic, Neepawa, Glenlea, Yecora and Cajeme can not be classed on the basis of the known Vrn genes. However, on the basis of the vernalization responses and segregation patterns the following genotypes were postulated:

1. Neepawa - AAbbcc;
2. Pitic - aaBBcc;
3. Glenlea - AAbbCC;
4. Yecora - AAbbCC;
5. Cajeme - aabbCC.

The A allele may be equivalent to the Vrn1 allele. The assignment to Pitic and Cajeme of different spring genes was based on the premise that Cajeme was earlier and its requirement sooner filled than Pitic (refer to Experiment II). Also, of 18 F2 plants grown from a single Cajeme x Pitic cross, a single winter segregant appeared.

The yielding of winter segregants from spring x spring crosses may arise whenever non-responsive x responsive spring cultivars are

crossed. This possibility requires that selections of segregating generations take place under conditions where fulfillment or partial fulfillment of vernalization requirements does not occur. The use of winter wheats in spring wheat breeding programs should require only the maintenance of a single non-responsive gene such as that found in Neepawa; and winter wheats have been assessed by researchers such as Pinthus (1967) as potential sources of higher yield for spring wheats.

GENERAL DISCUSSION

The implications for breeding programs of variable vernalization responses within spring wheats are multifold. Proper assessments must be made of introductions and parental materials—especially those of exotic origin; and the vernalization responses that are acceptable for proper adaptation and dependability must be considered.

Cajeme, Fielder and Pitic are established late spring cultivars, but when their vernalization requirements are partially or fully met these cultivars become as early as or earlier than the well-adapted western Canadian cultivars such as Neepawa and Sinton (Experiments I and II). In the field, Experiment III, these three responsive cultivars reached anthesis in early and mid-July with cold treatments as short as two weeks. The non-vernalized controls however, did not reach anthesis until late July or early August. Clearly, when partial or complete natural vernalization would occur during a field assessment of these cultivars, they would be behaving as normal well-adapted cultivars. It was found that vernalization responses developed very rapidly after induction in responsive spring cultivars (Experiment IV). Should cool springs occur during the testing years, these cultivars could be considered eligible for recommendation and licensing. However, in subsequent years, warm springs especially with late plantings could lead to responsive cultivars being sources of crop failure.

Another source of concern with responsive spring cultivars is cool temperatures during grain filling that can cause on-plant vernalization of the grain (Riddell and Gries 1958b). Seed from a common source that was already vernalized would then under a wide range of early spring conditions be uniformly early again leading to possible recommendation of responsive cultivars.

The use of vernalization responsive wheats as parents in breeding programs can result in segregating generations producing early through late material. So long as selections in early generations are made in non-inductive environments, culling of late material should remove vernalization responsive segregants from the population. Because the spring allele Vrn1 has dominant or partially dominant epistasis over the winter alleles (vrn) and the responsive spring alleles (Vrn2, Vrn3, Vrn4), the removal of late segregants would not remove potentially valuable spring material where vernalization responses are undesirable.

The continuous segregation for date of anthesis found in Experiment X indicated that despite the small number of genes controlling vernalization response, there may exist many modifier genes influencing development. In crosses of spring parents that differ by one or more spring alleles, such as the crosses of Experiment X, the delineation between material that is responsive to vernalization and that which is not may be obscured by the action of these modifier genes.

The classification of the vernalization requirements may be broad such as described by Martinic (1973) or narrow, Gotoh (1976, cited in Gotoh 1979). The spring wheats assessed in this study were simply classed as responsive and non-reponsive with the latter being

denoted as stable or as having threshold responses with extended cold treatments (Experiment I and II). This broad classification seemed adequate to cover the material under study. If however, the vernalization alleles can be demonstrated to give precise responses, then a narrow classification system to assess genotypic constitution would be valid. Although, Gotoh's classification system does give a more precise knowledge of the material, it does require a greater input of both material, space requirements and man-hours.

From the results of the experiments to characterize vernalization in spring wheats general recommendations can be made concerning assessment techniques that will minimize material handled and maximize accuracy of assessments.

A vernalization treatment of four weeks is recommended. Halloran (1977) found most of the spring wheats that he tested had their vernalization requirements satisfied with four weeks of cold treatment. From Experiment II, Figures 2, 3 and 7, it may be seen that the responsive spring cultivars assessed were fulfilled or nearly fulfilled by the four weeks cold treatments. Although longer or shorter durations of cold treatments can cause detectable responses, four points must be considered. The first point is the sensitivity of partially vernalized treatments to devernalization, although this may be overcome by intermediate ($15^{o}C$) treatments (Experiments V and VI). The second point is that cold treatments of two weeks or less may not induce a detectable difference from unvernalized controls (Experiments I, IV and VI). The third point is that longer durations may cause no greater response than the four weeks treatment and may reflect a

depressed state of vernalization (Experiment II and VI). The fourth point is that longer durations (i.e. 8 and 9 weeks) may initiate the threshold response of cultivars that are basically insensitive to vernalization, that although of genotypic importance is of minor significance to cultivar classification. Comparison of four-weeks cold treated plants to unvernalized control plants should give an accurate indication of vernalization response.

Stability of vernalization response may be increased by intermediate ($15^{o}C$) treatments (Experiments V and VI). Admittedly, devernalization was not a serious problem with the four weeks treatment for Pitic, Experiment V, in that the response remained significantly earlier than the unvernalized controls. However, the one and three day intermediate treatments did increase stability. In combination with the results of Experiment VI the general recommendation is for a three-day period of intermediate treatment following the cold treatment.

Vernalization of grain and plant is possible and both procedures were used in Experiments for this thesis. The application of cold treatments to green plants was recommended by Gotoh (1975) and Salisbury et al. (1979) as this treatment better portrayed the response as it would be induced under field conditions. However cold treatment of potted plants has a limiting effect on the number of cultivars being assessed, due to the space requirements. The cold treatment of germinated grain is advocated as being the more practical method if large numbers of cultivars are being assessed for vernalization response.

If cold treatments are to be given as seed treatment several recommendations can be made. Light during the cold treatment is not necessary although when cold treatments were given in short day conditions considerably less etiolation occurred (Experiment IX). Surface sterilization is advised to prevent microbial and fungal contamination of containers. Plastic bags can be used to prevent excessive moisture loss.

The temperature of the cold treatment was not found to affect significantly induction of vernalization response (Experiment VIII). Temperatures from 1°C to 11°C can be suggested as cold treatments although 5°C is recommended as being slightly more effective.

After cold treatments, plants may be grown in the field, the greenhouse or the growth room. As was found in Experiment III, vernalization responses due to cold treatment prior to transplanting can be differentiated from unvernalized controls under field conditions. Though field planting in Experiment III involved a planting and a transplanting procedure, where growthroom space is limited and manpower is available, field assessments are advocated. The two procedures allow material to be held in non-inductive conditions until the chance of natural vernalization of controls is past while still allowing the material to be of an age that corresponds to natural planting procedures.

Continuous or long day conditions prevent the compounding of photoperiod responses with vernalization responses. Recommended temperatures for post-cold treatment growth are 20°C to 25°C to maximize rate of development without reducing differences to

non-significance. With four weeks of cold treatment and three days of intermediate treatment there should be little devernalization occurring within the 20°C to 25°C range of temperatures.

On the basis of the results of Experiments I, II, IV and IX, days to flag leaf emergence, days to anthesis and final leaf number are recommended as measurements of vernalization response with greenhouse and growth room pot-planted material. Field space planting resulted in a large number of tillers that made accurate leaf counts difficult especially in the unvernalized series. Therefore only DFLE and DA are recommended with field studies; other stages may be assessed but are more subject to variability as researchers may differ in their delineations between developmental stages.

The final recommendation is that the grain used in the assessment procedure be of known unvernalized origin.

As a physiological process the underlying mechanism for vernalization has remained in obscurity. That spring cultivars are capable of vernalization responses and that the spring form with greater insensitivity to vernalization is dominant to the responsive alleles must be incorporated into the schemata on the mechanism of vernalization. The depressed vernalization with cold treatments of 6 to 8 weeks needs also to be included in the general theory of vernalization.

The vernalization response in spring cultivars has many of the characteristics of vernalization in winter cultivars. The response is sigmoid, developing rapidly after induction until completion of the vernalization requirement (Experiment IV). The response may be in part reversed by high temperatures, and this reversal takes place

after partial vernalization fulfillment (Experiment V). The response can be stabilized by periods at neutral temperature (Experiments V and VI). And the response decreases as plants age (Experiment VII). The reaction or reactions that constitute the phases of development of the vernalization response need still to be clarified.

SUMMARY AND CONCLUSION

Cultivar Characterization

Experiment I: Cultivar Classification

Ten cultivars, of spring habit, diverse origin and varying agronomic value, were grown in a growth room after exposure to 0, 2 and 6 weeks of cold treatments. Five parameters of growth were measured to estimate the vernalization responses of these ten cultivars and to define the inter-relationships of these parameters by correlation procedures.

The ten cultivars were classified into two groups on the basis of their general performance. The first group had little or no vernalization response and included Benito, Glenlea, Marquis, Neepawa, Prelude, Sinton and Yecora. The second group were definitely responsive to the vernalization treatments and included Cajeme, Fielder and Pitic.

The days to flag leaf emergence, heading, anthesis and final leaf number were positively correlated in single combinations. Spikelet number was positively correlated to final leaf number but not to the other three parameters.

Experiment II: Cultivar Response Patterns with Extended Cold Treatments

The ten cultivars of Experiment I were reassessed under growth

room conditions for response to cold treatments of one to nine weeks duration. Four parameters were measured to estimate the vernalization response and to determine the correlation of these characteristics.

Three patterns of response to these extended cold treatments were found. The first pattern was complete stability and insensitivity to the cold treatments and was characteristic of Prelude and Sinton. The second pattern was of insensitivity to all but the longest (8 and 9 weeks) durations of cold treatments whereat a small but definite vernalization response occurred. This second pattern was characteristic of the typically non-responsive cultivars Benito, Glenlea, Marquis, Neepawa and Yecora. The third pattern was the irregular cumulative or graded responses of Cajeme, Fielder and Pitic. This third pattern showed slight or pronounced depression of the vernalization response with 6 to 8 weeks of cold treatments; followed by a recovery with the 7 to 9 weeks of cold treatments that was to or beyond the fully vernalized state that occurred at 4 or 5 weeks.

Days to flag leaf emergence, days to anthesis, final leaf number and spikelet number were positively correlated with one another. This result indicated that there was a general trend for premature termination of these characteristics with positive responses to vernalization.

Experiment III: Cultivar Response Patterns with Field Planting

The three responsive cultivars Cajeme, Fielder and Pitic were planted in the field at two locations, after 0, 2, 4 and 6 weeks of vernalization treatment. The growth stages of jointing, boot, flag

leaf emergence, heading and anthesis were assessed. As well, at the Glenlea location fertile and total tiller numbers were counted.

Evaluation of the growth stages indicated that the 2, 4 and 6 weeks cold treatments effectively induced advancement of all the growth stages and this advancement was expressed under the natural environmental conditions of both locations.

Days to anthesis displayed a graded response for each of the cultivars with a levelling of response between the 4- and 6-weeks treatments.

Fertile tiller number was unaffected by the cold treatments. However, total tiller numbers were markedly reduced, concurrent with the fulfillment of the vernalization response. This reduction purported premature termination of normal tiller production with vernalization. The fertile tiller numbers indicated that this yield component was maximized under these field conditions even with vernalization fulfillment.

Experiment IV: Cultivar Response Patterns with Shorter Duration Cold Treatments

The pattern of vernalization responses of Cajeme, Pitic and Yecora to 0, 1, 2, 4, 8, 16 and 32 days of cold treatments was assessed under greenhouse conditions. Six parameters were measured to quantify vernalization responses and to educe relationships for these traits.

Yecora was not responsive to the vernalization treatments; although for some parameters, longer cold durations (16 and 32 days) did tend to reduce measurements.

The response patterns for Cajeme and Pitic were noticeably similar although Pitic remained later and more productive than Cajeme. An initial lag period occurred that lasted from two to eight days. Vernalization proceeded rapidly thereafter with a decline in rate of acceleration between 16 and 32 days. The lag period was attributed to a necessity for an induction period and the decline to the completion of the vernalization requirement.

Days to flag leaf emergence, days to heading, days to anthesis, days to maturity, final leaf number and spikelet number were all positively correlated. However, on the basis of the results of this and previous experiments it was concluded that days to flag leaf emergence, days to anthesis and final leaf number were the most consistent and accurate measurements of vernalization responses in spring wheats.

Characterization of Vernalization

Experiment V: Devernalization

Warm temperatures subsequent to cold treatments are able to cause reversal of the vernalization induced in winter wheats and rye. This devernalization is prevented by longer cold treatments or intermediate (neutral) temperature treatments. Pitic was studied to assess devernalization by warm temperature and the stabilization created by the duration of cold and intermediate treatments.

Regression analysis revealed that cold, intermediate and warm treatments could account for much of the variability in days to flag leaf emergence and anthesis. Cold and intermediate treatments

advanced development whereas warm treatments delayed development.

Assessments were made of cold x intermediate x warm interactions. The six-weeks cold treatment was relatively stable, being neither delayed nor accelerated by warm- and intermediate-temperature treatments. The four-weeks treatments were devernalized by 3 or 6 days at warm temperature but this devernalization was prevented by 1 or 3 days of intermediate temperature. The two-weeks treatments were concluded to be the most sensitive to devernalizing conditions with stability increasing with length of the intermediate treatment.

Experiment VI: Stabilization

The duration of intermediate temperature (15°C) necessary to stabilize vernalization responses was assessed for Cajeme, Fielder, Pitic and Yecora.

Pitic and Fielder were significantly stabilized by intermediate treatments of 1 to 6 days following two weeks of cold treatment. There was a trend within the four weeks cold treatments for greater stability with the longer intermediate temperatures; but the six-weeks cold treatments were unaffected by intermediate treatments. Only the six-weeks cold treatments of Cajeme was significantly stabilized by 1 to 6 days of intermediate treatment. Yecora was non-responsive to cold and intermediate treatments.

It was concluded that 1, 3 and 6 days of intermediate treatment increased stability when the grain was partially vernalized and that although 1, 3 and 6 days at 15°C effectively induced stabilization the three-day treatment was generally the most favourable duration.

Experiment VII: Plant Age

Vernalization response is known to decrease with plant age in winter wheats and rye. In this study the effect of age on the vernalization responses of Pitic and Neepawa was ascertained.

Neepawa at ages 0, 7, 14, 21 and 28 days was non-responsive to all but the six-weeks cold treatment at ages 7 and 14 days. Pitic was responsive to cold treatments of 2, 4 and 6 weeks at ages 0 and 7 days. As ages increased from 14 to 28 days responses for Pitic decreased to non-significance for even the six-weeks cold treatments.

It was concluded that at ages 0 and 7 days vernalization response was optimal and this maximization was due in part to greater stability of the seven-days age group.

Experiment VIII: Cold Temperature

Three temperatures of cold treatment—1°C, 5°C and 11°C—were selected for study of this environmental characteristic on the vernalization responses of Cajeme, Pitic and Yecora.

The vernalization responses of Cajeme and Pitic induced by 1, 2 and 3 weeks of cold treatment were not significantly affected by the temperature of the cold treatment. Yecora was non-responsive to the 1, 2 and 3 weeks of cold treatment at any of the three temperatures.

The spring cultivars Cajeme and Pitic have a wide range of inductive temperatures and as measured by days to flag leaf emergence and anthesis 1°C, 5°C and 11°C were equally effective vernalization temperatures.

Experiment IX: Light

The effects of short days and darkness during the sprouted-seed

vernalization of Cajeme, Glenlea, Neepawa, Pitic and Yecora were assessed under greenhouse conditions by the measurement of days to flag leaf emergence, days to heading, days to anthesis, days to maturity, final leaf number and spikelet number.

Darkness or short days did not affect the vernalization response induced in Cajeme and Pitic by four weeks of cold treatment. Glenlea, Neepawa and Yecora were relatively non-responsive to either the dark or short-day cold treatments.

Inheritance

Experiment X: Segregation Analyses

On the basis of F2 segregation for days to anthesis, the number of gene differences governing vernalization response were determined for Yecora-Cajeme, Glenlea-Pitic and Neepawa-Pitic crosses.

Yecora and Cajeme were assumed to have a Vrn gene in common due to lack of winter segregants. The F2 frequency distribution fitted a 3:1 ratio of early to late segregants indicating that these two cultivars may differ at one locus, governing vernalization response.

Glenlea and Pitic produced a winter segregant indicating that these cultivars had no Vrn gene in common. The 63:1 ratio indicated a three gene difference between these two cultivars.

Neepawa and Pitic produced winter segregants indicating that these cultivars do not have a common winter-inhibiting gene. The data fit a 15:1 spring to winter ratio denoting a two-gene difference. The Neepawa-Pitic crosses were advanced to the F3 generation to determine

homozygosity and heterozygosity of their F2 parent. The data from the F3's supported the two gene difference found in the F2 generation.

Conclusion

1. Variability of vernalization responses and requirements was found within the selected group of spring wheat cultivars.
2. Expression of vernalization responses was dependent on duration of the cold treatment, the post-cold treatment temperature conditions and the age of the plant when receiving the cold treatment. Light and temperature conditions during the cold treatment within the bounds tested in this study did not greatly affect vernalization response.
3. Within the spring cultivars there were found graded-cyclic and threshold response patterns; as well cultivars were found that were insensitive to all of the cold durations used.
4. The spring cultivars crossed differed by one to three Vrn genes. The earliest non-responsive spring gene was partially dominant to the responsive spring genes and the winter genes. The inheritance of vernalization response was not influenced by maternal inheritance. And modifier genes influencing days to anthesis were suggested.
5. The greatest asset of the vernalization responsive material was its high tiller and spikelet numbers, which would give these cultivars a yield advantage when their vernalization requirements were not met and growing seasons were long enough to permit proper maturation. The fulfillment of vernalization requirement in these

cultivars would lead to depressed yield; while late maturity in short growing seasons would prevent proper seed set and filling. Increased instability of maturation and yield was introduced with spring cultivars with graded vernalization response. Selection and assessment procedures need to meet this problem.

Recommendations

1. The assessment and classification of vernalization responses of cultivars to be used in breeding programs should be carried out using a standardized procedure.

   Evaluations may be performed in the growth room or the field so long as attempts are made to avoid natural vernalizing conditions. Breeding programs that involve the use of vernalization responsive cultivars should be designed so that the undesirable responses can be discarded during early generations of selection.

2. Further investigation should be made to identify the Vrn alleles present in given cultivars. The identification would involve the use of cultivars of known genotype. The use of winter-habit cultivars of vrn1vrn2vrn3vrn4 genic constitution could be used to quantify the number of Vrn genes found in a spring cultivar.

3. The effect of vernalization on yield components should be further assessed to delineate between responses that are liabilities and those that are assets. Those components of yield that can be inherited independently from vernalization response should be determined.

4. The effects of diurnal temperature variations on the induction of

vernalization responses in spring wheats should be assessed to better understand the development of the response under natural (field) conditions.

5. To improve evaluations of vernalization and devernalization, inductive vernalizing temperatures, neutral temperatures and devernalizing temperatures should be delineated.

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APPENDICES

APPENDIX 1. Analysis of variance for parameters used to measure vernalization response of ten cultivars exposed to 0, 2 and 6 weeks of cold treatment, Experiment I.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	2	34.12	17.06	2.41	0.1180
Cultivar (C)	9	800.89	88.99	12.58	0.0001
RxC (Error a)	18	127.35	7.08		
Treatment (T)	2	648.27	324.14	112.38	0.0001
CxT	18	787.71	43.76	15.17	0.0001
RxCxT (Error b)	36	103.83	2.88		
				C.V.=4.67%	
Total	85	2,502.18			
2) Days to heading					
Replicate (R)	2	92.61	46.31	2.41	0.1182
Cultivar (C)	9	1,376.35	152.93	7.96	0.0001
RxC (Error a)	18	345.79	19.21		
Treatment (T)	2	702.39	351.20	45.62	0.0001
CxT	18	570.42	31.69	4.12	0.0001
RxCxT (Error b)	36	277.19	7.698		
				C.V.=6.21%	
Total	85	3,364.69			
3) Days to anthesis					
Replicate (R)	2	90.80	45.40	4.46	0.0267
Cultivar (C)	9	1,671.29	185.70	18.26	0.0001

Cont'd.

APPENDIX 1. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
3) Days to anthesis (Cont'd.)					
RxC (Error a)	18	183.07	10.17		
Treatment (T)	2	793.63	396.82	61.71	0.0001
CxT	18	797.37	44.30	6.89	0.0001
RxCxT (Error b)	37	237.94	6.43		
				C.V.=5.54%	
Total	86	3,774.09			
4) Final leaf number					
Replicate (R)	2	0.24	0.12	0.55	0.5874
Cultivar (C)	9	31.82	3.54	16.05	0.0001
RxC (Error a)	18	3.97	0.22		
Treatment (T)	2	10.69	5.35	26.06	0.0001
CxT	18	14.71	0.82	3.99	0.0002
RxCxT (Error b)	37	7.58	0.205		
				C.V.=5.85%	
Total	86	69.01			
5) Spikelet number[a]					
Group A (excluding Pitic)					
Replicate (R)	2	2.78	1.39	1.36	0.2858
Cultivar (C)	8	135.93	16.99	16.58	0.0001
RxC (Error a)	16	16.40	1.03		

Cont'd.

APPENDIX 1. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
5) Spikelet number (Cont'd.)					
Treatment (T)	2	2.78	1.38	0.83	0.4449
CxT	16	26.90	1.68	1.01	0.4701
RxCxT (Error b)	36	60.00	1.67		
				C.V.=9.58%	
Total	80	244.77			
Group B (Pitic)					
Replicate (R)	2	2.06	1.03	0.08	0.9250
Treatment (T)	2	66.06	33.03	2.55	0.1934
RxT (Error)	4	51.86	12.96		
				C.V.=21.78%	
Total	8	119.98			

a. Heterogeneous cultivar errors. Cultivars divided into two groups on the basis of error terms calculated to be similar at t_q 0.001.

APPENDIX 2. Analysis of variance of parameters used in measuring vernalization response of ten cultivars exposed to 0-9 weeks of cold treatment, Experiment II.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	2	235.31	117.66	12.42	0.0004
Cultivar (C)	9	8,429.66	939.63	98.83	0.0001
RxC (Error a)	18	170.58	9.48		
Treatment (T)	9	4,068.59	452.07	57.48	0.0001
CxT	81	4,383.78	54.12	6.88	0.0001
RxCxT (Error b)	180	1,415.53	7.86		
				C.V.=7.74%	
Total	299	18,703.45			
2) Days to anthesis					
Replicate (R)	2	273.42	136.71	12.00	0.0005
Cultivar (C)	9	9,068.14	1,007.57	88.47	0.0001
RxC (Error a)	18	205.01	11.39		
Treatment (T)	9	4,508.92	500.99	56.79	0.0001
CxT	81	4,594.60	56.72	6.43	0.0001
RxCxT (Error b)	180	1,587.84	8.82		
				C.V.=6.48%	
Total	299	20,237.93			
3) Final Leaf Number					
Replicate (R)	2	2.84	1.42	2.62	0.1000

Cont'd.

APPENDIX 2. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
3) Final Leaf Number (Cont'd.)					
Cultivar (C)	9	240.69	26.74	49.42	0.0001
RxC (Error a)	18	9.74	0.54		
Treatment (T)	9	136.81	15.20	47.32	0.0001
CxT	81	131.11	1.62	5.04	0.0001
RxCxT (Error b)	180	57.83	0.32		
				C.V.=7.44%	
Total	299	579.03			
4) Spikelet number					
Replicate (R)	2	0.73	0.37	0.06	0.9460
Cultivar (C)	9	713.43	79.27	12.18	0.0001
RxC (Error a)	18	117.19	6.51		
Treatment (T)	9	165.73	18.41	16.36	0.0001
CxT	81	313.54	3.87	3.44	0.0001
RxCxT (Error b)	180	202.61	1.13		
				C.V.=6.88%	
Total	299	1,513.23			

APPENDIX 3. Photographs were taken of ten cultivars exposed to 0-9 weeks of cold treatment. Pots 1-9 refer to the length of the cold treatment. Pots 10 and 11 refer to unvernalized controls.

Photographs of Cajeme, Fielder, Glenlea, Pitic, Prelude and Yecora were taken 39 days after planting. Photographs of Benito, Marquis, Neepawa and Sinton were taken 46 days after planting.

Plants were from Rep 2 of Experiment II, with the exception of Prelude that were from Rep 1 of Experiment II.

Photographs are arranged in alphabetical order according to cultivar names.


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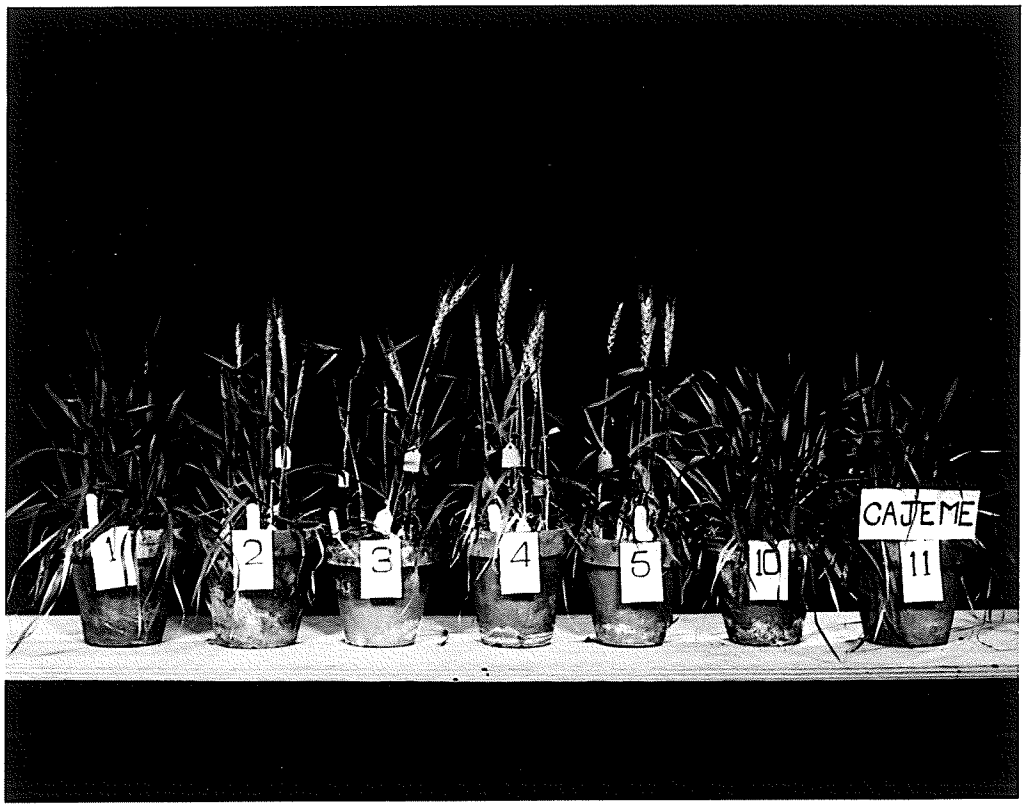
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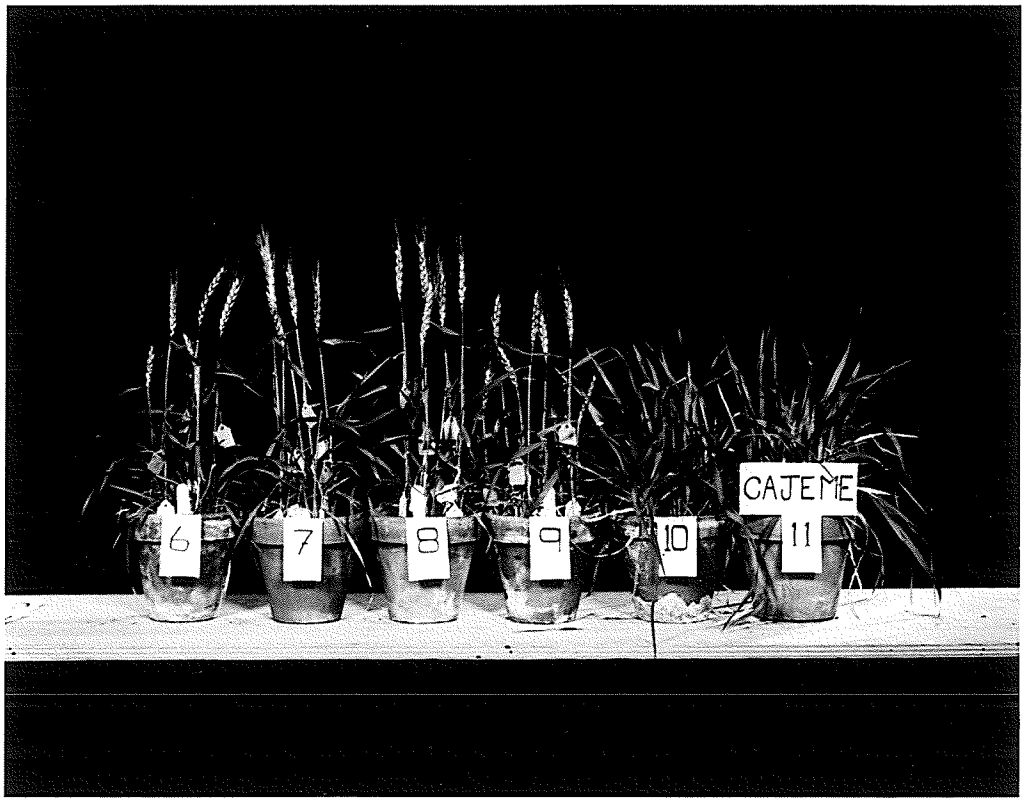
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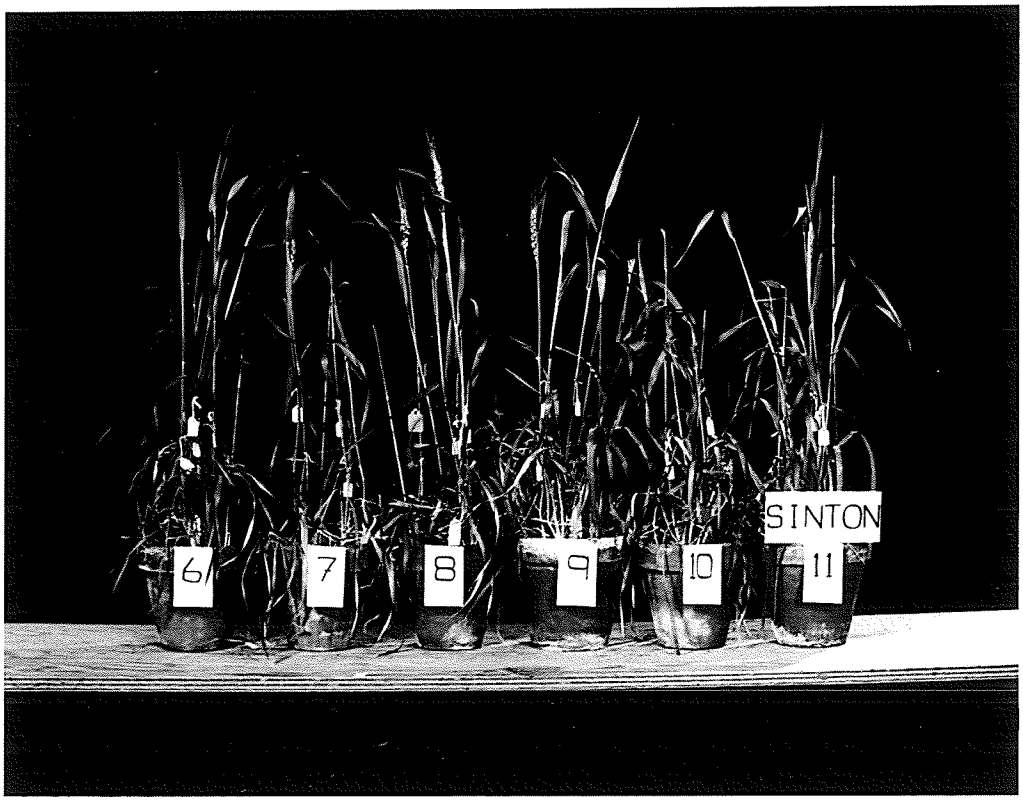
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APPENDIX 4. Analysis of variance of parameters used to measure the vernalization response of Cajeme, Fielder and Pitic exposed to 0, 2, 4 and 6 weeks of cold treatment with subsequent field plantings at University of Manitoba Field Research Stations, Glenlea and Winnipeg, Experiment III.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to jointing					
Location (L)	1	184.17	184.17	139.31	0.0071
Replicate (R)	2	0.37	0.19	0.14	0.8786
LxR (Error a)	2	2.64	1.32		
Cultivar (C)	2	0.94	0.47	0.14	0.8703
RxC	4	7.36	1.84	0.55	0.7043
LxRxC (Error b)	6	19.91	3.32		
Treatment (T)	3	593.65	197.88	61.52	0.0001
CxT	6	10.63	1.77	0.55	0.7649
RxT	6	0.76	0.13	0.04	0.9997
RxCxT	12	5.84	0.49	0.15	0.9993
LxRxCxT (Error c)	26	83.63	3.22		
				C.V.=4.89%	
Total	70	909.89			
2) Days to flag leaf emergence					
Location (L)	1	158.12	158.12	23.34	0.0403
Replicate (R)	2	30.26	15.13	2.23	0.3093
LxR (Error a)	2	13.55	6.78		
Cultivar (C)	2	41.35	20.68	1.48	0.2998

Cont'd.

APPENDIX 4. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
2) Days to flag leaf emergence (Cont'd.)					
RxC	4	27.09	6.77	0.49	0.7474
LxRxC (Error b)	6	83.66	13.94		
Treatment (T)	3	1,844.38	614.79	72.57	0.0001
CxT	6	133.53	22.26	2.63	0.0398
RxT	6	48.69	8.12	0.96	0.4722
RxCxT	12	12.90	1.08	0.13	0.9997
LxRxCxT (Error c)	26	220.25	8.47		
				C.V.=7.65%	
Total	70	2,613.77			
3) Days to boot					
Location (L)	1	46.97	46.97	3.77	0.1916
Replicate (R)	2	24.74	12.37	0.99	0.5016
LxR (Error a)	2	24.90	12.45		
Cultivar (C)	2	258.99	129.50	6.14	0.0354
RxC	4	12.62	3.16	0.15	0.9565
LxRxC (Error b)	6	126.64	21.11		
Treatment (T)	3	3,851.36	1,283.79	145.83	0.0001
CxT	6	119.87	19.98	2.27	0.0693
RxT	6	91.46	15.24	1.73	0.1550
RxCxT	12	19.65	1.64	0.19	0.9980

Cont'd.

APPENDIX 4. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
3) Days to boot (Cont'd.)					
LxRxCxT (Error c)	25	220.08	8.80		
				C.V.=7.26%	
Total	69	4,797.27			
4) Days to heading					
Location (L)	1	15.01	15.01	1.07	0.4095
Replicate (R)	2	14.84	7.42	0.53	0.6539
LxR (Error a)	2	28.03	14.02		
Cultivar (C)	2	339.70	169.85	8.23	0.0191
RxC	4	34.41	8.60	0.42	0.7918
LxRxC (Error b)	6	123.79	20.63		
Treatment (T)	3	3,771.60	1,257.20	211.77	0.0001
CxT	6	30.43	5.07	0.85	0.5412
RxT	6	84.25	14.04	2.37	0.0601
RxCxT	12	34.72	2.89	0.49	0.9031
LxRxCxT (Error c)	25	148.42	5.94		
				C.V.=5.69%	
Total	69	4,625.20			
5) Days to anthesis					
Location (L)	1	11.95	11.95	1.07	0.4103
Replicate (R)	2	10.33	5.17	0.46	0.6844

Cont'd.

APPENDIX 4. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
5) Days to anthesis (Cont'd.)					
LxR (Error a)	2	22.42	11.21		
Cultivar (C)	2	514.04	107.02	11.46	0.0089
RxC	4	17.73	4.43	0.20	0.9307
LxRxC (Error b)	6	134.56	22.43		
Treatment (T)	3	3,886.56	1,295.52	212.79	0.0001
CxT	6	15.07	2.51	0.41	0.8636
RxT	6	34.10	5.68	0.93	0.4636
RxCxT	12	20.40	1.70	0.28	0.9877
LxRxCxT (Error c)	25	152.21	6.09		
				C.V.=5.30%	
Total	69	4,819.37			

APPENDIX 5. Analysis of variance of tiller numbers of Cajeme, Fielder and Pitic exposed to 0, 2, 4 and 6 weeks of cold treatment with subsequent field planting at U. of M. Field Research Station, Glenlea, Experiment III.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Total tiller number					
Replicate (R)	2	357.88	178.94	22.27	0.0068
Cultivar (C)	2	836.05	418.03	52.03	0.0014
RxC (Error a)	4	32.13	8.03		
Treatment (T)	3	2,155.91	718.64	13.01	0.0001
CxT	6	67.55	11.26	0.20	0.9711
RxCxT (Error b)	18	994.08	55.23		
Total	35	4,443.61			
2) Fertile tiller number					
Replicate (R)	2	249.71	124.86	9.64	0.0295
Cultivar (C)	2	141.41	70.71	5.46	0.0719
RxC (Error a)	4	51.81	12.95		
Treatment (T)	3	172.99	57.66	2.14	0.1307
CxT	6	53.30	8.88	0.33	0.9125
RxCxT (Error b)	18	484.96	26.94		
Total	35	1,154.18			

APPENDIX 6. Analysis of variance of different parameters used in measuring vernalization response of three cultivars exposed to 0, 1, 2, 4, 8, 16 and 32 days of cold treatment, Experiment IV.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	1	8.10	8.10	2.68	0.2430
Cultivar (C)	2	2,001.45	1,000.73	331.59	0.0030
RxC (Error a)	2	6.04	3.02		
Treatment (T)	6	1,495.26	249.21	35.99	0.0001
CxT	12	610.19	50.85	7.34	0.0001
RxCxT (Error b)	18	124.63	69.15		
				C.V.=6.38%	
Total	41	4,245.67			
2) Days to heading					
Replicate (R)	1	4.72	4.72	0.81	0.4641
Cultivar (C)	2	2,353.46	1,176.73	201.01	0.0050
RxC	2	11.71	5.86		
Treatment (T)	6	1,600.96	266.83	15.46	0.0001
CxT	12	447.76	37.31	2.16	0.0676
RxCxT (Error b)	18	310.62	17.26		
				C.V.=7.96%	
Total	41	4,729.22			
3) Days to anthesis					
Replicate (R)	1	13.53	13.53	2.80	0.2362

Cont'd.

APPENDIX 6. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
3) Days to anthesis (Cont'd.)					
Cultivar (C)	2	2,810.37	1,405.19	290.78	0.0034
RxC (Error a)	2	9.66	4.83		
Treatment (T)	6	1,603.44	267.24	37.67	0.0001
CxT	12	576.55	48.05	6.77	0.0003
RxCxT (Error b)	16	113.51	7.09		
				C.V.=5.23%	
Total	39	5,127.07			
4) Days to maturity					
Replicate (R)	1	0.70	0.70	0.13	0.7524
Cultivar (C)	2	1,146.17	573.09	107.15	0.0092
RxC (Error a)	2	10.70	5.35		
Treatment (T)	6	610.93	101.82	11.99	0.0001
CxT	12	172.13	14.34	1.69	0.1528
RxCxT (Error b)	18	152.90	8.49		
				C.V.=3.57%	
Total	41	2,093.52			
5) Final leaf number					
Replicate (R)	1	0.005	0.005	0.04	0.8569
Cultivar (C)	2	40.25	20.13	168.20	0.0059
RxC (Error a)	2	0.24	0.12		

Cont'd.

APPENDIX 6. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
5) Final leaf number (Cont'd)					
Treatment (T)	6	23.46	3.91	33.36	0.0001
CxT	12	4.05	0.34	2.88	0.0210
RxCxT (Error b)	18	2.11	0.12		
				C.V.=3.82%	
Total	41	70.11			
6) Spikelet number					
Replicate (R)	1	7.42	7.42	6.38	0.1275
Cultivar (C)	2	25.95	12.98	11.16	0.0825
RxC (Error a)	2	2.33	1.17		
Treatment (T)	6	39.48	6.58	7.66	0.0003
CxT	12	21.92	1.83	2.13	0.0720
RxCxT (Error b)	18	15.47	0.86		
				C.V.=5.74%	
Total	41	112.56			

APPENDIX 7. Analysis of variance of parameters measured for Pitic exposed to 0, 2, 4 and 6 weeks of cold treatment with subsequent intermediate-temperature treatments of 0, 1 and 3 days and warm temperature treatments of 0, 1, 3 and 6 days, Experiment V.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	2	37.87	18.94	0.99	0.4260
Cold (C)	3	9,643.84	3,214.61	167.54	0.0001
RxC (Error a)	6	115.86	19.31		
Intermediate (I)	2	99.86	49.93	11.21	0.0009
CxI	6	90.52	15.09	3.39	0.0237
RxCxI (Error b)	16	71.26	4.45		
Warm (W)	3	112.57	37.52	8.82	0.0001
CxW	9	52.27	5.81	1.36	0.2198
IxW	6	46.15	7.69	1.81	0.1097
CxIxW	18	193.97	10.78	2.53	0.0029
RxCxIxW (Error c)	72	306.45	4.26	C.V.=4.63%	
Total	143	10,769.88			
2) Days to anthesis					
Replicate (R)	2	114.15	57.08	2.30	0.1815
Cold (C)	3	10,456.81	3,485.60	140.37	0.0001
RxC (Error a)	6	148.99	24.83		
Intermediate (I)	2	148.15	74.08	14.85	0.0002

Cont'd.

APPENDIX 7. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
2) Days to anthesis (Cont'd.)					
CxI	6	170.08	28.35	5.68	0.0025
RxCxI (Error b)	16	79.83	4.99		
Warm (W)	3	99.31	33.10	6.52	0.0007
CxW	9	65.73	7.30	1.44	0.1877
IxW	6	66.40	11.07	2.18	0.0548
CxIxW	18	221.20	12.29	2.42	0.0043
RxCxIxW (Error c)	72	365.67	5.08		
				C.V.=3.96%	
Total	143	11,936.32			

APPENDIX 8. Analysis of variance for days to flag leaf emergence and anthesis measured for Cajeme, Fielder, Pitic and Yecora exposed to 0, 2, 4 and 6 weeks of cold treatment followed by 0, 1, 3 and 6 days at intermediate temperature, Experiment VI.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	3	214.72	71.57	8.27	0.0059
Cultivar (C)	3	4,379.02	1,459.67	168.71	0.0001
RxC (Error a)	9	77.87	8.65		
Cold (Co)	3	3,322.11	1,107.37	110.72	0.0001
CxCo	9	1,213.68	134.85	13.48	0.0001
RxCxCo (Error b)	36	360.05	10.00		
Intermediate (I)	3	172.02	57.34	7.96	0.0001
CxI	9	67.22	7.47	1.04	0.4136
CoxI	9	270.21	30.02	4.17	0.0001
CxCoxI	27	383.22	14.19	1.97	0.0060
RxCxCoxI (Error c)	140	1,007.94	7.20	C.V.=7.49%	
Total	251	11,468.06			
2) Days to anthesis					
Replicate (R)	3	260.57	86.86	4.83	0.0285
Cultivar (C)	3	5,367.22	1,789.07	99.57	0.0001
RxC (Error a)	9	161.71	17.67		
Cold (Co)	3	2,510.00	836.67	53.15	0.0001

Cont'd.

APPENDIX 8. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
2) Days to anthesis (Cont'd.)					
CxCo	9	1,180.16	131.13	8.33	0.0001
RxCxCo (Error b)	36	566.72	15.74		
Intermediate (I)	3	126.81	42.27	4.98	0.0027
CxI	9	133.31	14.81	1.75	0.0836
CoxI	9	257.06	28.56	3.37	0.0010
CxCoxI	27	489.74	18.14	2.14	0.0023
RxCxCoxI (Error c)	141	1,196.27	8.48	C.V.=6.39%	
Total	252	12,249.58			

APPENDIX 9. Analysis of variance of days to flag leaf emergence and anthesis for Neepawa and Pitic exposed to 0, 2, 4 and 6 weeks of cold treatment at ages 0, 7, 14, 21 and 28 days, Experiment VII.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	5	115.14	23.03	12.39	0.0076
Cultivar (C)	1	510.63	510.63	274.79	0.0001
RxC (Error a)	5	9.29	1.86		
Age (A)	4	12,185.72	3,046.43	607.68	0.0001
CxA	4	100.03	25.01	4.99	0.0023
RxCxA (Error b)	40	200.53	5.01		
Cold (Co)	3	1,326.60	442.20	91.95	0.0001
CxCo	3	785.73	261.91	54.46	0.0001
AxCo	12	1,470.55	122.55	25.48	0.0001
CxAxCo	12	1,195.06	99.59	20.71	0.0001
RxCxAxCo (Error c)	148	711.72	4.81		
				C.V.=8.83%	
Total	237	18,610.98			
2) Days to anthesis					
Replicate (R)	5	142.16	28.43	4.48	0.0628
Cultivar (C)	1	1,008.14	1,008.14	158.79	0.0001
RxC (Error a)	5	31.74	6.35		
Age (A)	4	16,298.61	4,074.65	628.47	0.0001
CxA	4	72.61	18.15	2.80	0.0386

Cont'd.

APPENDIX 9. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
2) Days to anthesis (Cont'd.)					
RxCxA (Error b)	40	259.34	6.48		
Cold (Co)	3	1,526.15	512.05	101.59	0.0001
CxCo	3	1,078.87	359.62	71.35	0.0001
AxCo	12	1,815.46	151.29	30.02	0.0001
CxAxCo	12	1,491.75	124.31	24.66	0.0001
RxCxAxCo (Error c)	147	740.90	5.04	C.V.=6.52%	
Total	236	24,475.73			

APPENDIX 10. Analysis of variance of days to flag leaf emergence and anthesis for Cajeme, Pitic and Yecora exposed to 0, 1, 2 and 3 weeks of cold treatments at 1.1°C, 4.9°C and 10.7°C, Experiment VIII.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	2	1.70	0.85	0.60	0.5909
Cultivar (C)	2	1,369.97	684.99	484.88	0.0001
RxC (Error a)	4	5.65	1.41		
Weeks (W)	3	927.34	309.11	187.77	0.0001
CxW	6	517.54	86.26	52.39	0.0001
RxCxW (Error b)	18	29.63	1.65		
Temperature (T)	2	12.33	6.17	1.69	0.1954
CxT	4	14.05	3.51	0.96	0.4368
WxT	6	18.17	3.03	0.83	0.5526
CxWxT	12	32.33	2.69	0.74	0.7070
RxCxWxT (Error c)	47	171.44	3.65		
				C.V.=5.74%	
Total	106	3,100.15			
2) Days to anthesis					
Replicate (R)	2	10.19	5.10	1.72	0.2897
Cultivar (C)	2	2,206.72	1,103.36	371.61	0.0001
RxC (Error a)	4	11.88	2.97		
Weeks (W)	3	1,258.11	419.37	145.07	0.0001
CxW	6	573.02	95.50	33.04	0.0001

Cont'd.

APPENDIX 10. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
2) Days to anthesis (Cont'd.)					
RxCxW (Error b)	18	52.04	2.89		
Temperature (T)	2	28.22	14.11	3.00	0.0593
CxT	4	25.16	6.29	1.34	0.2696
WxT	6	38.59	6.43	1.37	0.2468
CxWxT	12	49.14	4.10	0.87	0.5802
RxCxWxT (Error c)	47	220.84	4.70		
				C.V.=5.36%	
Total	106	4,473.90			

APPENDIX 11. Analysis of variance of parameters used to measure vernalization responses of five cultivars exposed to four weeks of cold treatment under short day or dark conditions and to zero weeks of cold treatment for controls, Experiment IX.

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
1) Days to flag leaf emergence					
Replicate (R)	3	20.95	6.98	1.01	0.4241
Cultivar (C)	4	1,509.57	377.39	54.33	0.0001
RxC (Error a)	12	83.36	6.95		
Treatment (T)	2	1,327.57	663.79	75.87	0.0001
CxT	8	1,513.38	189.17	21.62	0.0001
RxCxT (Error b)	30	262.48	8.75		
				C.V.=7.87%	
Total	59	4,717.30			
2) Days to heading					
Replicate (R)	3	37.33	12.51	1.15	0.3686
Cultivar (C)	4	1,756.87	439.22	40.39	0.0001
RxC (Error a)	12	130.48	10.87		
Treatment (T)	2	1,815.57	907.79	83.57	0.0001
CxT	8	1,873.86	234.23	21.56	0.0001
RxCxT (Error b)	30	325.88	10.86		
				C.V.=6.85%	
Total	59	5,940.19			
3) Days to anthesis					
Replicate (R)	3	46.04	15.35	1.65	0.2310

Cont'd.

APPENDIX 11. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
3) Days to anthesis (Cont'd.)					
Cultivar (C)	4	1,802.53	450.63	48.34	0.0001
RxC (Error a)	12	111.86	9.32		
Treatment (T)	2	1,557.57	778.79	68.15	0.0001
CxT	8	1,883.43	235.43	20.60	0.0001
RxCxT (Error b)	30	342.83	11.43		
				C.V.=7.04%	
Total	59	5,744.27			
4) Days to maturity					
Replicate (R)	3	9.96	3.32	0.44	0.7264
Cultivar (C)	4	912.21	228.05	30.44	0.0001
RxC (Error a)	12	89.90	7.49		
Treatment (T)	2	198.38	99.19	10.42	0.0004
CxT	8	236.31	29.54	3.10	0.0117
RxCxT (Error b)	29	275.98	9.52		
				C.V.=3.74%	
Total	58	1,722.74			
5) Final leaf number					
Replicate (R)	3	0.63	0.21	1.07	0.3973
Cultivar (C)	4	44.20	11.05	59.32	0.0001
RxC (Error a)	12	2.35	0.20		

Cont'd.

APPENDIX 11. (Continued)

Source of Variation	D.F.	S.S.	M.S.	F-ratio	Pr>F
5) Final leaf number (Cont'd.)					
Treatment (T)	2	26.52	13.26	55.29	0.0001
CxT	8	32.29	4.04	16.83	0.0001
RxCxT (Error b)	30	7.19	0.24		
				C.V.=5.68%	
Total	59	113.19			
6) Spikelet number					
Replicate (R)	3	27.35	9.12	5.69	0.0117
Cultivar (C)	4	141.40	35.35	22.05	0.0001
RxC (Error a)	12	19.24	1.60		
Treatment (T)	2	71.39	35.69	22.90	0.0001
CxT	8	95.17	11.89	7.63	0.0001
RxCxT (Error b)	30	46.76	1.56		
				C.V.=8.01%	
Total	59	401.31			