

FILLING COMPONENTS, YIELD, AND HARVEST MOISTURE
CONTENT AMONG EARLY MATURING INBRED LINES AND
HYBRIDS OF CORN (ZEA MAYS L.)

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Joseph David Anderson

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ABSTRACT

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FILLING COMPONENTS, YIELD, AND HARVEST MOISTURE AMONG EARLY MATURING
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Helgason.

The interrelationships among eleven variables related to grain filling, yield, and harvest moisture content of the grain were examined in a group of six early maturing corn inbreds and nine derived single cross hybrids in 1977. This material was grown at Winnipeg and at Carman, Manitoba, but frost prior to grain maturity at Carman prevented full use of the data obtained there. Variables examined were vegetative period duration, filling period duration, growth period duration, filling rate, kernel number, kernel weight, ear length, ear diameter, percent moisture at black layer maturity, percent moisture of the grain at harvest, and grain yield.

Grain yield of hybrids was found to be positively related to filling period duration and to kernel number, but was not related to filling rate. Moisture content of the grain at harvest was found to be positively related to filling period duration, kernel weight, and percentage moisture at the time of black layer formation. Harvest moisture was negatively related to kernel number per plant when the effects of varia-

tion in growth period duration were removed by partial correlation techniques.

Of the three filling components, yield was most closely related to filling period duration, but extending the filling period is probably not the best approach to hybrid yield improvement, since filling period duration was found to be positively related to growth period duration. Because kernel number per plant was positively related to yield and negatively related to grain moisture content, a more appropriate goal for a corn breeding program in Manitoba may be the development of hybrids that produce a large number of kernels.

Midparent trait vs. hybrid trait correlations were significant and positive for filling period duration, growth period duration, filling rate, ear length, ear diameter, and yield. Several different combinations of midparent traits could be used in multiple regression equations to explain more than 90% of the variation in hybrid yields. These results suggest that midparent-hybrid relationships in early genotypes may be stronger than those found previously in dent types in the United States Corn Belt.

1. INTRODUCTION

The average frost-free season in Manitoba is completely utilized by the currently available corn hybrids. Even with the earliest hybrids there is danger of encountering a killing frost prior to maturity, especially when planting is delayed past the middle of May. As a result, it is desirable to produce earlier hybrids in order to reduce the chance of premature death by frost. Another aim of a corn breeding program in Manitoba should be the production of hybrids that have a lower grain moisture content at harvest time in order to reduce the cost of grain drying after harvest. While it may be possible to obtain concurrent progress in both these areas, the breeding program is made much more difficult by the addition of a third essential goal - yield improvement.

Insight into the method by which yield improvement can be realized has frequently been sought through yield component analysis. The yield components traditionally examined in corn (ear number per plant, grain weight per ear, kernel weight, kernel number per ear, kernel row number, and kernel number per row) have been related to ear and kernel number and weight. Since this type of yield component analysis is primarily concerned with the division of a final yield into various segments or compartments, these yield components might well be called divisional components of yield. If the alteration of one or several of these divisional components of yield does not have an effect on the developmental process by which the final yield is obtained, then there is no reason to

expect that a yield increase will result from such an alteration. For example, an increase in kernel weight might be offset by a decrease in kernel number, or an increase in row number might occur at the expense of kernel number per row. In fact, past research has shown that yield components are generally negatively correlated with each other and poorly correlated with yield. For this reason, it seems logical to examine a set of yield components more directly related to grain filling, a developmental process which determines the final grain yield.

Grain yield per plant can be completely defined by two factors that may be called filling components of yield: (1) filling period duration, or the time between silking and physiological maturity, and (2) filling rate per plant, or the rate at which dry matter accumulates in the grain. Filling rate per plant can be further divided into filling rate per kernel and kernel number per plant.

Several studies have concluded that grain yields may be increased by extending the duration of the grain filling period, but there is also considerable reason to doubt whether substantial progress can be made toward this end in short season material without simultaneously delaying maturity. Consequently, a more reasonable approach to yield improvement in early hybrids appears to lie in increasing the rate of dry matter accumulation in the grain while maintaining the length of the filling period. Although this approach sounds appealing, past research has consistently shown no relationship between yield and filling rate calculated on a per kernel basis. Unfortunately few filling period studies to date have considered kernel number, which is required along with

filling rate per kernel and filling period duration to completely define yield per plant. Therefore, the possibility exists that the true relationship between yield and filling rate may have been obscured by an inverse relationship between filling rate and kernel number.

The purpose of this research was to examine the complete set of yield components consisting of filling period duration, filling rate, and kernel number and the relationships of these variables with grain yield, maturity, and harvest moisture content of the grain in a group of locally developed inbreds and derived single cross hybrids. Several other related variables were also examined.

2. LITERATURE REVIEW

2.1 FILLING PERIOD DURATION

Filling period duration (FPD) is the length of the period between silking and physiological maturity, which is the time of maximum accumulation of dry matter in the grain. The time of silking is easily determined, but the time that physiological maturity is attained is not so readily ascertained. One method that is commonly used involves the taking of frequent grain harvests and the prediction of the time of physiological maturity from the plot of dry matter accumulation against time. This method is laborious and the necessity for frequent destructive harvests requires that ample experimental material be available.

An easier method for determining the time of physiological maturity was found by Daynard and Duncan (1969) who showed that the formation of a black closing layer at the base of the kernel coincided with the time of maximum accumulation of dry matter in the kernel. Later research by Rench and Shaw (1971) and Carter and Poneleit (1973) confirmed this conclusion. In the last two studies, a significant loss of dry weight from the kernel was observed during or after black layer formation, which adds further support to the conclusion that black layer formation is an accurate indicator of the time of physiological maturity.

In their initial study, Daynard and Duncan (1969) found that the black layer developed rapidly with three days or less between the time that black layer development was first visible to the naked eye and the

time of its completion. However, Carter and Poneleit (1973) found that the inbreds that they examined varied both in the color of the black layer and in the time required for its development. Some lines formed a distinct black layer in three or four days while others took as long as 15 to 20 days to complete development. This may have been an effect of temperature since those lines that matured early developed the black layer rapidly, but those lines that matured late in the season, when growing degree days accumulated more slowly, generally took much longer to complete black layer development.

Daynard (1972) observed a similar effect of temperature on black layer development. In a study conducted in Ontario, he found more plant-to-plant and intra-ear variability in the date of black layer formation than had been evident in a previous study in Kentucky (Daynard and Duncan, 1969). He felt that this increased variability in Ontario was caused by cooler ambient temperatures during the period of black layer development.

Although later research indicates that Daynard and Duncan (1969) may have overstated the precision with which black layer maturity can be determined, especially in corn maturing under cool temperatures late in the season, the general consensus remains that black layer formation is a useful indicator of the time of physiological maturity in corn. Coupled with silking date, the time of black layer formation provides a relatively simple means of determining the length of the grain filling period. In this thesis, the term black layer maturity (BLM) will be used synonymously with physiological maturity.

That percentage moisture in the grain is not an adequate indicator of physiological maturity has been amply demonstrated by several workers who reported that corn genotypes show significant variation in the percentage moisture at black layer maturity (PMBLM). Studies using black layer formation as the indicator of maturity have found PMBLM to range from 15.4 to 42% (Rench and Shaw, 1971; Daynard, 1972; and Carter and Poneleit, 1973). Other studies that used maximum dry weight accumulation as the indicator of maturity found PMBLM to range from 30 to 47.5% (Shaw and Thom, 1951; Hallauer and Russell, 1962; Hillson and Penny, 1965; Gunn and Christensen, 1965; Bunting, 1972; and Gunn, 1974). While some of the variation in PMBLM may be due to differences in technique, it seems safe to conclude that grain moisture is not a reliable indicator of maturity.

In addition to genotypic effects on PMBLM, there also appears to be a substantial environmental influence. Rench and Shaw (1971) and Daynard (1972) found that early planted hybrids had lower PMBLM than the same genotypes planted at a later date. Bunting (1972) obtained similar results in an experiment in which silking dates were varied by manipulating temperatures prior to silking in the same genotype planted on the same date. He felt that early flowering plants reach maturity at a lower moisture level because they ripen under conditions of higher temperature.

Hallauer et al. (1967) analyzed extensive data obtained over three years in the Iowa Corn Yield Tests. They found that percent grain moisture at approximate physiological maturity was positively related to yield, to date of silking, and to grain moisture at harvest.

2.1.1 Environmental Effects on FPD

Shaw and Thom (1951) examined filling period duration (FPD), or the time between silking and physiological maturity, in three Iowa hybrids that varied in maturity. They found such small differences in FPD both between years and between varieties that they concluded that the date of corn maturity in Iowa could be reliably predicted by adding about 51 days to the silking date. Hallauer and Russell (1962) also found that FPD was relatively constant in the material they examined in Iowa. However, more recent research has shown ample variation among corn genotypes in the time from silking to physiological maturity as indicated either by black layer formation (Daynard and Duncan, 1969; Carter and Poneleit, 1973; Gunn, 1974; and Daynard and Kannenberg, 1976) or by the accumulation of maximum dry weight in the grain (Gunn and Christensen, 1965; Hillson and Penny, 1965; Hanway and Russell, 1969; Daynard et al., 1971; and Cross, 1975).

Unlike Shaw and Thom (1951), several researchers later found significant environmental influences on FPD. Peaslee et al. (1971) concluded that the nutrient status of the soil could affect FPD as they found an increase in FPD with both applied potassium and applied phosphorus. Breuer et al. (1976), in a growth chamber study, found that the filling period took 46% longer under 20C than under 30C. In another growth chamber study, Allison and Daynard (1979) found that FPD was decreased when either temperature or photoperiod was increased during the period before ear initiation.

This effect of temperature on FPD has been confirmed by other studies conducted in the field. Bunting (1972), in an experiment in which silking date was manipulated in plants of the same genotype and planting date, found that earlier flowering plants had shorter filling periods because they ripened under higher temperatures. He concluded that, under the conditions of his study, a one day advance in flowering would result in a two day advance in maturity. Supporting evidence for this conclusion was provided by Gunn (1974). In recent years many workers have chosen to express FPD in some form of thermal unit rather than in days (Peaslee et al., 1971; Daynard, 1972; Johnson and Tanner, 1972a and 1972b; Carter and Poneleit, 1973; and Cross, 1975).

Although reduced temperatures generally increase the number of days required in grain filling, extended periods of cool weather late in the season can shorten FPD by inducing "premature" black layer formation (Daynard, 1972). Frost, however, does not necessarily mean the end of the filling period, even though the frost may be severe enough to kill all leaf tissue. Daynard reported that grain filling can continue for two weeks or more after a killing frost, apparently at the expense of sugars accumulated previously in the stalk.

That the stalk acts as a reservoir of mobile sugars that can be utilized in grain filling was shown by Duncan et al. (1965). These workers found that kernel growth continued linearly in plants that had been completely defoliated and then covered with foil to stop photosynthesis by the stalk and husks. Kernel growth in the defoliated plants was paralleled by a decrease in dry weight of the stalks. Other studies

(Hanway and Russell, 1969, and Daynard et al., 1969) have shown that stalk dry weight reaches a maximum after silking and then declines later in the season when the rate of photosynthesis is reduced.

Daynard and Duncan (1969) speculated that the mechanism which triggered black layer development was dependent upon the flow of metabolites into the kernel with black layer formation beginning when the flow of assimilate fell below a critical level. This could occur when the kernel reached its maximum potential weight or when the supply of carbohydrates from current photosynthesis or the stalk reservoir was exhausted. Consequently, grain filling need not end with the death of leaf tissue through natural senescence or premature frost, except when the frost is severe enough to disrupt the apparatus by which assimilate is translocated to or deposited in the grain.

2.1.2 FPD and Yield

Numerous studies have shown a positive relationship between FPD and grain yield, but some of these have used a calculated effective filling period duration (EFPD) rather than the actual number of days or thermal units between silking and maturity. Hanway and Russell (1969) used the regression equation of grain dry weight on time in days to calculate the number of days required for each of their hybrids to achieve its final grain yield. The hybrids varied in EFPD (43 to 60 days), and this period was positively related to final grain yield. The reality of this relationship is questionable, however, since final grain yield was used in the calculation of EFPD and, hence, the two values are not independent.

Daynard et al. (1971) used a similarly calculated EFPD and found that, for the two years of their study, 71 and 80% of the yield differences among three hybrids could be accounted for by variation in EFPD. These workers predicted that significant yield advances might be obtained by breeding for longer effective filling periods. But once again the calculated EFPD was not statistically independent of yield.

The EFPD calculated by Cross (1975) differed from the previous studies in that he determined the time required to achieve 95% of final kernel dry weight using filling rate expressed on a per kernel basis. Thus, this measure of EFPD is statistically independent of grain yield. The correlation between EFPD and yield for 21 hybrids over two years was highly significant ($r=0.81$).

Daynard and Kannenberg (1976) compared the actual filling period duration (AFPD = days from mid-silking to black layer maturity) and EFPD (based on the number of days required to achieve final kernel dry weight) and examined the relationship of both to grain yield among a large number of hybrids in Ontario. AFPD and EFPD were highly and positively correlated with each other and both were correlated with grain yield ($r=0.56$ and 0.53 respectively). Although the two measures accounted for similar proportions of variation in yield among hybrids, the authors preferred EFPD because of its freedom from semi-subjective judgements regarding the time of black layer formation.

Johnson and Tanner (1972a) divided the total grain filling period into three parts: (1) The lag period following silking in which little dry matter is accumulated, (2) the linear period of grain growth during

which most of the dry matter is deposited in the grain, and (3) the leveling off period immediately preceding black layer formation. EFPD is an approximation of the duration of the linear period and may be a more meaningful measure than AFPD, since hybrids with the same AFPD may differ in the length of the lag period and/or the length of the leveling off period. Such a case was apparently found by Daynard et al. (1971) who reported that two hybrids which did not differ in AFPD were significantly different in EFPD.

Fakorede and Mock (1978) reported the results of variety hybrid trials involving unimproved varieties and these same varieties improved by seven cycles of reciprocal recurrent selection for grain yield. In one set of hybrids, average yield improvement per cycle of selection was 5.51%, and this increase was accompanied by an increase in FPD which was obtained by an advance in silking date and a delay in maturity. A second set of variety hybrids showed similar trends but the difference in FPD between original and improved hybrids was statistically nonsignificant.

Peaslee et al. (1971) grew a single cross hybrid under varying levels of phosphorus and potassium fertilization and discovered that AFPD increased with improved nutrient conditions and that yields increased with AFPD. Since no genotypic differences were involved, this indicates that there may be a significant environmental component in the relationship between yield and filling period duration.

2.1.3 Relationships Between FPD and Other Traits

In addition to yield, other traits have been reported to be related to FPD. In hybrids, positive relationships have been found between FPD and maturity (Gunn and Christensen, 1965), between FPD and percent moisture in the grain at harvest (Cross, 1975), and between FPD and days to mid-silk (Daynard and Kannenberg, 1976). In inbreds, Carter and Poneleit (1973) reported a negative correlation between FPD and PMBLM and positive correlations between FPD and kernel weight and between FPD and the length of the vegetative period (VPD).

To summarize, research related to the filling period in corn indicates that there is substantial variation among genotypes in FPD and that FPD is affected by environmental factors, particularly temperature. Grain filling can continue from the stalk reservoir for some time after the cessation of photosynthesis. Grain yield is positively related to FPD, which suggests that yield advances might be made by breeding for an extension of FPD. However, positive correlations between FPD and maturity and between FPD and grain moisture at harvest may present problems when breeding for extended FPD in short-season areas.

2.2 FILLING RATE

Variation among corn genotypes in filling rate (FR), or the rate of dry matter accumulation in the grain, has been noted in inbreds (Carter and Poneleit, 1973) and in hybrids (Daynard and Kannenberg, 1976) when FR was expressed in units of mg/kernel/day. Cross (1975) found that a group of hybrids in North Dakota differed in FR expressed as grams/kernel/1000 thermal units. Hanway and Russell (1969) failed to

find differences among a group of hybrids in Iowa when FR was expressed as kg/ha/day. However, these hybrids did differ in kernel number per hectare, so they may well have differed in FR on a per kernel basis. Daynard et al. (1971) found differences in a group of Ontario hybrids in FR which ranged from 177 to 197 kg/ha/day.

Johnson and Tanner (1972b) examined two single cross hybrids and their inbred parents and reported that the single crosses were superior to their parents in FR (kg/ha/day) when compared both at equal population density and at equal leaf area index.

Most of the researchers who reported positive relationships between yield and FPD failed to find any significant relationship between yield and FR. Daynard et al. (1971) found that less than 16% of the yield differences among hybrids could be explained by differences in FR. Johnson and Tanner (1972b) reported that correlations between FR and yield were nonsignificant in both the inbreds and the hybrids that they examined. Daynard and Kannenberg (1976) also found that the correlation between FR and yield was not significant in a group of hybrids grown in Ontario.

Cross (1975) reported a nonsignificant correlation between yield and FR ($r=-0.06$) in a group of single crosses in North Dakota. He found, however, that the relationship became highly significant ($r=0.65$) when he used partial correlation techniques to control for variation in kernel number and in FPD. Since yield can be completely defined by FR, KN, and FPD, it is surprising that this partial correlation was not higher than 0.65.

In a study in which completely defoliated plants were wrapped with foil, Duncan et al. (1965) found that linear kernel growth continued for some time in defoliated plants but at a slightly reduced rate. The day-to-day dry weight increase of control plants (not defoliated) was observed to be positively correlated with air temperature but did not appear to be related to solar radiation. This suggests that FR is not dependent upon current photosynthesis but is determined by some factor related to translocation from the stalk reservoir or to the deposition of assimilate in the grain.

Additional evidence regarding the control of FR was provided by Tollenaar and Daynard (1978c) who reduced kernel number by bagging ears part way through pollination. FR (mg/kernel/day) in partially pollinated ears was not significantly correlated with kernel number. This seems to indicate that FR is not determined by the assimilate supply to the ear but is determined at the kernel level, either at the translocation step between cob and kernel or by processes within the kernel. In this same study, it was observed that the rate of dry matter accumulation in normally pollinated ears was faster in basal kernels than in tip kernels. The authors felt that the lower FR in tip kernels was related to a lower volume per kernel which could be associated with lower sink size strength.

More recent evidence on this question has been provided by Shannon (1978) who reported autoradiographic studies that showed that sugars were translocated to the pedicel faster than they could be unloaded and moved into the endosperm. Thus, the step limiting filling rate in corn appears to be the translocation step between cob and kernel.

2.3 KERNEL NUMBER

Kernel number per plant (KN) is the third yield component which, along with filling period duration and filling rate per kernel, completely defines yield on a per plant basis. Unfortunately, few studies that included FPD and FR have considered KN. Some researchers have calculated FR on a per unit area basis (kg/ha/day), but in this approach the effects of KN are confounded with those of FR per kernel.

Leng (1954) compared a large number of inbreds with their single cross progeny for several major yield components. He found that the hybrid exceeded its top parent (the one with the highest manifestation of the trait in question) in KN per ear in all of the 102 comparisons made. Since there was no difference between the hybrids and their top parent in kernel row number, this increase in KN per ear was due to an increase in KN per row. As the hybrids exceeded their top parents by only a small margin in kernel weight, Leng concluded that most of the increase in yield of the single crosses over their top parents was due to the increase in KN per row.

In a re-examination of data from the experiment just cited, Leng (1963) found that, in the hybrids, there was no significant relationship between kernel weight or KN/ear and yield. There was a highly significant negative correlation ($r=-0.36$) between row number and yield and a highly significant positive correlation ($r=0.35$) between KN/row and yield. These two significant correlations tend to cancel each other and may account for the lack of correlation between KN/ear and yield since

KN/ear is the product of row number and KN/row. There was a strong negative correlation ($r=-0.73$) between KN/ear and kernel weight.

Hatfield et al. (1965) grew two single crosses in Kentucky under six environments consisting of irrigated and non-irrigated plots planted in April, May, and June. Generally, KN per ear was the most closely related to yield of the four yield components examined (KN/ear, kernel weight, row number, and KN/row). In this study, both row number and KN/row were positively related to yield. Though still highly significant, the magnitude of the correlation coefficient between KN/ear and yield decreased for the irrigated experiment planted in June while the magnitude of the correlation coefficient between kernel weight and yield increased. The changes in these relationships could be attributed to low temperatures late in the filling period which prevented kernels from reaching their potential maximum weight. Again KN and kernel weight were negatively related, but this negative relationship was not so strong as the positive relationship between KN and yield, except in the June plantings.

Duncan et al. (1973) reported results from an experiment in which five hybrids were grown for two years at different planting rates, seeding dates, and locations. Since there was little variation in kernel weight, they concluded that yield differences among locations for any population and seeding date were due to differences in KN per ear at the high planting rates. At the low planting rates, yield differences were more closely related to ear number per plant.

Early et al. (1967) reduced incident sunlight during the vegetative, reproductive, and maturation stages in two hybrids in Illinois. Grain yield was reduced by shading in all growth phases, but shading for 21 days during the reproductive stage was more detrimental than shading for 54 and 63 days during the other two stages. The reduction in yields resulting from shading in the first two phases was paralleled by a reduction in KN.

A defoliation study by Egharevba et al. (1976) also showed that KN was sensitive to alterations near the time of silking. Leaf loss at ten days after mid-silking resulted in greatly reduced yields due to a reduction in KN. Yield losses resulting from defoliation 20 days or more after mid-silking were less severe and were more closely related to reduced kernel weight.

Goldsworthy et al. (1974) grew three tropical lowland varieties at three plant densities at two locations in Mexico and examined yield in terms of several yield components. There were substantial differences in yield between the two locations, which varied in altitude, and 70% of these differences could be accounted for by variation in KN per unit area. Yield differences across densities were also closely related to KN per unit area, as varying plant density had only a small effect on kernel size. The authors concluded that sink capacity was more important in limiting yield than source capacity in the material examined.

Goldsworthy and Colegrove (1974) reached similar conclusions regarding sink limitations on yield in a study involving five tropical highland varieties grown at three plant densities in Mexico. Again,

yield differences across varying plant densities were proportional to differences in KN per unit area. The effect of grain size on yield was small compared to the effect of number of grains per unit area on yield.

Yamaguchi (1974) examined 26 varieties planted at three densities in Mexico and also concluded that high yield was mainly attributable to high production of kernels per unit area. Grain yield was also positively correlated with kernel weight, but this relationship was not so strong as that between yield and KN/m^2 . KN/m^2 and kernel weight were not significantly correlated in this study. Yamaguchi concluded that, for a given variety, yield is mainly accounted for by KN and, to a lesser extent, by kernel weight.

Tollenaar and Daynard (1978d) attempted to assess the relative importance of assimilate source and reproductive sink by varying irradiance during various growth stages. Although they found a high correlation between KN and grain yield, other considerations led them to conclude that source factors were the primary limitations to grain yield, at least in short-season environments.

In summary, it seems that there is generally a positive relationship between KN and yield when KN is calculated on either a per plant or a per unit area basis. However, this positive relationship may disappear when there is a negative relationship between yield and one of the primary yield components that determine KN (KN/row and row number).

2.4 GRAIN MOISTURE CONTENT

In addition to the production of high yielding hybrids that mature consistently before frost, a secondary goal for corn breeders in short season areas should be the production of hybrids that reach a harvestable grain moisture content before harvesting is made difficult by deteriorating weather conditions. Ideally, short season hybrids should dry in the field to the lowest moisture content possible without yield loss so as to minimize the cost of artificial drying after harvest. Reduced harvest moisture content can be obtained by breeding for a fast rate of drying after maturity or by extending the time available for drying by breeding for earlier maturity. The first approach is more desirable, as breeding for earlier maturity is likely to result in decreased yields.

Crane et al. (1959) found that hybrids which had been shown previously to vary in field drying rate differed in rate of drying in a forced-air dryer. Although differences existed among these hybrids in husk and shank characteristics and in ear length and circumference, these factors did not appear to be associated with drying rate. There was, however, an association between pericarp permeability and drying rate, with faster drying hybrids having the more permeable pericarps.

Hallauer and Russell (1961) examined the relationship between six weather factors and moisture loss between silking and physiological maturity in crosses among slow and fast drying inbreds. Only degree-days showed a consistent association with grain moisture loss and this correlation was not close enough to be of real predictive value. While these conclusions may be reasonable for the grain filling period, they

should not be extrapolated to include the period after maturity when we would expect drying to be more responsive to weather factors.

Gunn and Christensen (1965) examined moisture loss regressions over the period from 30 to 100 days after silking in 49 hybrids covering a wide range of maturities. No significant difference in drying rate was found among the hybrids in this test, but early hybrids had lower moisture content than late hybrids throughout the period examined.

In contrast to the above findings, Hillson and Penny (1965) found highly significant differences in moisture loss regressions from 51 to 75 days after silking in a group of 15 single cross hybrids. The inbred parents differed in their effects on the drying rates of their hybrid progeny. There was apparently no relationship between drying rate and percent moisture at 95% of final kernel dry weight.

Purdy and Crane (1967a) studied oven drying rates in a diallel involving three fast and three slow drying inbreds. Broad sense estimates of heritability for drying rate were relatively high (52 to 95%). Correlation analysis indicated that selection for faster drying would result in smaller ears, later silking, and lower percent moisture at 60 days after silking. Husked ears were used so no estimate of the effect of husks was available.

In a second study using the same material, Purdy and Crane (1967b) concluded that a fast rate of water loss was associated with thinner pericarps and with greater pericarp permeability. As kernels "killed" in potassium cyanide solution showed no change in drying rate, these

authors concluded that differences in drying rate were due to the physical structure of the pericarp and not to metabolic processes within the kernel.

Troyer and Ambrose (1971) evaluated drying rates in 150 plant introductions and in five single crosses to which various treatments had been applied. They concluded that (1) premature death speeds rate of drying, (2) ear moisture loss is from the ear rather than from other plant parts, and (3) short, loose husks of a low number are conducive to fast drying.

Hicks et al. (1976) attempted to simulate the effect of frost on drying rate by removing ears from maturing corn, subjecting the ears to freezing temperatures, and then reattaching these ears to stalks in the field. They concluded that the drying rate of treated ears was not significantly different from the drying rate of normally maturing ears.

Much of the evidence in the literature on drying in corn seems contradictory, possibly due to differences in the material studied by various researchers. While it seems safe to conclude that moisture loss from individual kernels is closely related to the physical structure of the pericarp, factors affecting drying of intact ears are much less certain. However, it does seem reasonable to expect that the rate of moisture loss will be faster from small ears that have short, loose husks.

3. MATERIALS AND METHODS

3.1 MATERIALS

Six adapted inbred lines that represented a range in silking date, maturity, and harvest moisture content were chosen for the study. These lines were in two groups of three, with each line in one group having been crossed by each line in the other group in 1976, thus giving nine single cross hybrids for the study. CK43, CK52, and CK59 were in one group and the other group consisted of CK48, CM37, and CM72. The "CK" designated lines were developed at the University of Manitoba while the "CM" designated lines were developed at the Agriculture Canada Research Station at Morden, Manitoba.

In naming the hybrids used in this study, the "CK" and "CM" designators have been omitted. Inbred numbers within hybrid names reflect the direction in which the crosses were made.

3.2 METHODS

Inbreds and hybrids were planted in 1977 in adjacent blocks on May 11 at Winnipeg and on May 24 at Carman which is located approximately 60 miles southwest of Winnipeg. The experimental design was a randomized complete block with two replications at each location. Each plot consisted of three hand-planted 5.5m rows spaced 91cm apart. Rows were double-seeded at 23cm intervals and later thinned to give a uniform plant density of 47,800 plants per hectare. A common competitor was

seeded in a single row between each three-row plot: line CK23 was used in the inbred plots and the commercial hybrid Pioneer 3994 was used in the hybrid plots. Fertilizer at a rate in excess of soil test recommendations was sidebanded after emergence in both locations (on June 2 in Carman and on June 9 in Winnipeg).

Weeds were controlled by a pre-seeding application of Eradicane at Carman and by a pre-emergence application of Gramoxone at Winnipeg. In addition, plots at both locations were cultivated once prior to silking and hand weeding was used when necessary.

Vegetative period duration (VPD), filling period duration (FPD), and growth period duration (GPD) were defined as the number of accumulated corn heat units (CHU) from planting to midsilking, from midsilking to BLM, and from planting to BLM, respectively.

Mid-silking was taken as that day on which emerged silks were observed on at least one-half of the plants in a plot. Determination of mid-silking and measurement of all other variables except harvest moisture were confined to the centre rows of the three-row plots, with end plants excluded. The remaining plants in the centre rows were allocated to various parts of the experiment as follows: plants 2 to 6 - filling rate samples, plants 7 to 14 - determination of BLM, and plants 15 to 24 - yield samples.

Sampling to determine the time of BLM was commenced when black layers were evident on tip kernels of the earliest silking lines. Ten kernels from the centre of ears from five plants per plot were examined at

one or two-day intervals. BLM was said to have been reached in a particular plot when well-formed black layers could be observed in at least six of the ten kernels on at least three of the five examined ears.

Initially, black layer determination was attempted through the use of longitudinal cross-sections as described by Rench and Shaw (1971). However, this method was judged to be unreliable because some lines took as much as ten days between the first appearance of a dark layer at the tip of the kernel and the definite appearance of a completely formed black layer, a difficulty which had been pointed out previously by Carter and Poneleit (1973). It was found that, as kernels approached BLM, the base of the kernel could be broken off to reveal the extent of black layer formation in a more complete fashion than could be obtained by the use of cross-sections. Consequently, cross-sectional examination was abandoned in favor of this method. This technique for black layer determination may have resulted in slightly longer estimates of FPD compared to those reported by other investigators. However, determinations of the relative time of BLM among the hybrids was probably more accurate than could have been obtained by using kernel cross-sections.

CHU totals for VPD, FPD, and GPD were derived from weekly cumulative totals provided by Dr. Carl Shaykewich (Soil Science Department, University of Manitoba) who used Brown's (1964) corn heat unit equation:

$$\text{CHU} = (\text{Tmin} - 40 + 4.39\text{Tmax} - 0.0256\text{Tmax}^2 - 155.18)/2.0^\dagger$$

For the Winnipeg location, daily maximum and minimum temperatures were obtained from records kept at the experimental site. For Carman, these records were obtained from the meteorological reporting station at

[†]Temperatures are in Fahrenheit degrees.

Graysville, which is located less than two miles from the experimental site. As required, daily CHU totals were estimated by interpolation from the weekly cumulative totals.

Kernel samples for the determination of filling rate (FR), or the rate of kernel dry matter accumulation, were obtained by repeated sampling of the same ears following a method outlined by Duncan and Hatfield (1964). Plants that deviated in silking date by more than two days from the mid-silking date of the plot were marked and not used for FR samples. Husks on selected ears were slit in the central section and a flap peeled back to reveal two or three rows of kernels. Starting about one inch from the butt, approximately 15 consecutive kernels were removed from a single row and placed in a vial which was then tightly sealed. The husk flap was then replaced and secured by an elastic band. Subsequent samples from the same ear were obtained by opening additional flaps in an ordered pattern around the ear leaving at least one undamaged kernel row between sampling rows. Duncan and Hatfield (1964) and Tollenaar and Daynard (1978a) found that this method of sampling did not significantly affect the growth rate of kernels remaining on the ear.

On returning to the laboratory, ten undamaged kernels were randomly selected from each vial, attached tissue was removed, and fresh weights were obtained for each 10-kernel sample. Dry weights were determined after drying to constant weight in a vacuum oven at 80C.

Kernel sampling was begun approximately one week after mid-silking and repeated through five samplings at weekly intervals with the exception of the third sample, which followed the second by two weeks. It

had become evident that five samples were the most that could be obtained from a single ear, so one week was skipped in order to extend sampling later into the filling period.

The last four sampling dates were used in the calculation of filling rates which are defined here as the sample regression coefficients of mean kernel dry weight on accumulated CHU and have the dimensions mg/kernel/CHU. The first sampling date was not used as examination of the plot of kernel dry weight against accumulated CHU revealed that most hybrids had not yet entered the linear stage of dry matter accumulation at the time this sample was taken.

Percent moisture in the grain at the time of black layer maturity (PMBLM) was determined at Winnipeg by taking kernel samples from five plants on the same day that BLM was determined for a plot. Ten kernels were removed from the central area of selected ears and weighed and dried in the same fashion as FR samples. PMBLM was then expressed as a percent of fresh weight.

Moisture content of the grain (HM) was determined by randomly harvesting five ears from one of the outside rows of each plot on October 12 at Winnipeg and on October 13 at Carman. Harvested ears were placed in plastic bags which were closed to slow moisture loss from the ears during transport to the laboratory. 10-kernel samples were taken from the central section of harvested ears and percent moisture was determined as before.

Yield samples were obtained by harvesting ten plants per plot on October 12 in Winnipeg and on October 31 at Carman. Where a plant had two ears, both were placed in a single bag so that yield and kernel number could be determined on a per plant basis. After storage for approximately ten weeks in a well ventilated drying room, randomly selected ears from five plants were measured as to length and diameter, shelled, and kernel number per plant determined using an electronic seed counter. Grain yield was also determined on a per plant basis for the same five plants. This grain was then bulked with grain from the remaining five plants to give a 10-plant yield sample.

Two 30 to 40g samples were taken from each 10-plant bulk, weighed, and then dried to constant weight in a vacuum dryer at 80C for the determination of moisture percentage of the yield samples. Analysis of variance revealed that significant differences in moisture content existed among plots, so the mean of the two moisture samples was used to convert the yield figures to a 0% moisture basis.

Table 1 provides a listing of the variables measured in this study, the abbreviations used, and the units in which they are expressed. Unless otherwise stated, FR will refer to filling rate per kernel. Times of samplings and of major developmental events are shown in Table 2 .

TABLE 1. Variables measured, abbreviations, and units

Variable	Abbreviation	Unit
Vegetative period duration	VPD	Corn heat units
Filling period duration	FPD	Corn heat units
Growth period duration	GPD	Corn heat units
Filling rate	FR	mg/kernel/CHU
Percent grain moisture at black layer maturity	PMBLM	% of fresh weight
Harvest grain moisture	HM	% of fresh weight
Kernel number	KN	per plant
Kernel weight	KW	mg/kernel
Ear length	EL	mm
Ear diameter	ED	mm
Yield		g/10 plants

TABLE 2. Timing of Events

Event	Winnipeg			Carman		
	Inbreds	Hybrids	Inbreds	Inbreds	Hybrids	Hybrids
Planting	May 11	May 11	May 24	May 24	May 24	May 24
Mid-silking	July 11-July 16	July 8-July 14	July 24-July 30	July 22-July 27		
BLM	Aug. 31-Sept. 27	Sept. 7-Sept. 28	Sept. 21-Oct. 7 ¹	Sept. 27-Oct. 7 ¹		
First FR samples	July 25	July 20	Aug. 9	Aug. 4		
Last FR samples	Aug. 29	Aug. 24	Sept. 13	Sept. 8		
HM samples	Oct. 12	Oct. 12	Oct. 13	Oct. 13		
Yield samples	Oct. 12	Oct. 12	Oct. 31	Oct. 31		

¹After the killing frost of Oct. 2.

3.3 METEOROLOGICAL INFORMATION

Temperatures were well above average in May and substantially below average in August for both locations (Table 3). The remaining months in the growing season were either at or near the long term averages. CHU totals for the period May 15 through September 30 were above average in Carman and well above average in Winnipeg. However, the later-planted plots at Carman did not benefit from the excellent growing conditions in May to the same extent as the Winnipeg plots. This would be expected to result in substantial yield and maturity advantages for the Winnipeg location.

Precipitation was well above average during May and September at both locations. For the remaining three months, rainfall was slightly above average at Carman. At Winnipeg, rainfall was below average in June and above average during July and August. The option of irrigation was available at Winnipeg, but rainfall was judged adequate to maintain normal growth.

The first damaging fall frost (-2C) occurred on October 2 at both locations. This frost was severe enough to kill all remaining green leaf tissue.

3.4 ANALYSIS OF DATA

The data were first analyzed as four separate experiments (inbreds and hybrids in each of two locations), each consisting of a randomized complete block design with two replications. For each variable in each experiment, a two-way analysis of variance was performed based on one

TABLE 3. Meteorological information

	WINNIPEG		CARMAN	
	1977	Avg.	1977	Avg.
TEMPERATURE (mean C)				
May	18	11	19	11
June	18	17	17	17
July	20	20	20	20
August	15	19	15	19
September	13	13	13	13
PRECIPITATION (mm)				
May	153	52	144	56
June	70	81	75	72
July	109	74	73	69
August	101	71	74	63
September	112	56	151	46
CHU (May 15 to Sept. 30)	2759	2477	2502	2404

observation per plot (VPD, FPD, GPD, and yield) or on the mean of five observations per plot (FR, KN, KW, EL, ED, PMBLM, and HM).

Data combined over the two locations were analyzed according to a procedure recommended by Snedecor and Cochran (1967, pp. 375-377) for a series of identical experiments in different locations. A two-way analysis of variance was carried out on the combined data with the two classifications being lines (inbreds or hybrids) and locations. The lines, locations, and lines by locations interaction entries in the final combined analysis of variance table were obtained directly from this analysis. The final two lines in the combined analysis of variance table, blocks in locations and pooled error, are pooled values from the analyses in the individual locations. The interaction mean square was tested against the pooled error mean square. Where this interaction was significant, the main effect of lines was tested against the interaction mean square; otherwise, it was tested against the pooled mean square error. The main effect of locations was tested against the mean square for blocks in locations. An example of the combined analysis of variance for one trait is given in appendix Table 1.

The statistical analyses were performed using computer procedures found in the Statistical Package for the Social Sciences.

4. RESULTS AND DISCUSSION

4.1 COMPARISON OF LOCATIONS

The first killing frost (-2C) occurred on October 2 at both locations. Black layer maturity had occurred before the frost in all plots at Winnipeg, but at Carman black layer maturity had been reached in only four of the 18 hybrid plots and eight of the 12 inbred plots prior to October 2.

The variance ratio test for equality of experimental error variances (Snedecor and Cochran, 1967, pp. 116-117) between the two locations was performed for each trait and the results are presented in appendix Table 2 for hybrids and in appendix Table 3 for inbreds. These tests led to the conclusion that error variances were homogeneous between locations for all traits except FPD and GPD in the hybrids.

Heterogeneity of variances for FPD and GPD in the hybrids was expected as premature frost at Carman severely restricted variation for both of these traits. Although the error variances in the hybrid experiments for FPD and GPD should not be pooled, the differences between locations for these traits were of sufficient magnitude that no rigorous statistical test is required in order to conclude that the Carman means for both traits were lower than those obtained at Winnipeg.

Summaries of the results of the analyses of variance combined over locations are given in Table 4 for hybrids and in Table 5 for inbreds.

Location means for each of the traits are given in Table 6 for both inbreds and hybrids.

In the hybrid experiment, location means differed significantly for all traits except FR and KN, which are probably less likely to be affected by premature frost than most of the other traits examined. For the traits that differed, Winnipeg means were greater for all traits except PMBLM (measured in only two hybrids at Carman) and HM. Most of these differences between locations can be explained as a result of late seeding and immaturity at time of frost at Carman. Under these conditions, Carman means for FPD, GPD, KW, and yield would be expected to be less than the values obtained at Winnipeg.

HM was expected to be greater at Carman, as HM samples were taken only one day later at Carman than at Winnipeg, while plots at Carman were planted almost two weeks later than at Winnipeg. The Winnipeg plots accumulated about 400 more CHU than the Carman plots during the period from planting to harvest.

The reasons for the differences in VPD between locations are not readily apparent. Because of the delayed planting at Carman, the period from planting to milking did not cover the same set of days at the two locations. It was felt that expressing VPD in CHU would adjust for differences in environmental conditions between the two locations and the two time periods and, hence, reduce variation in VPD between the two locations. However, there were highly significant differences between locations in VPD of hybrids expressed in CHU, but no significant differences between locations when VPD was expressed in days. Although the

TABLE 4. Summary of analysis of variance combined over two locations for ten traits in nine hybrids

Trait	F-ratios		
	Hybrids	Locations	Interaction
VPD	14.73**	119.78**	1.96
FPD	1.79	134.38**	5.81**
GPD	1.59	277.59**	8.66**
FR	5.26*	1.79	4.41**
KN	11.61**	1.86	1.37
KW	4.93**	332.07**	1.44
EL	24.05**	46.75*	3.59*
ED	46.90**	39.87*	1.76
HM	1.30	97.50*	5.83**
YIELD	1.32	52.24*	2.64*

*,** significant at the 5% and 1% levels of significance, respectively.

TABLE 5. Summary of analysis of variance combined over two locations for ten traits in six inbreds

Trait	F-ratios		
	Inbreds	Locations	Interaction
VPD	10.95*	112.12**	7.65**
FPD	3.44	3053.57**	109.50**
GPD	2.71	77852.73**	110.11**
FR	16.23**	50.00*	2.36
KN	5.37*	97.24*	4.71*
KW	5.99*	301.04**	11.31**
EL	51.74**	15.79	2.41
ED	146.49**	179.70**	1.54
HM	5.66*	1378.11**	19.30**
YIELD	3.78	712.94**	7.65**

*,** significant at the 5% and 1% levels of significance, respectively.

TABLE 6. Location means for 11 traits in nine hybrids and six inbreds

Trait †	Hybrids		Inbreds	
	Winnipeg	Carman	Winnipeg	Carman
VPD	1374	1280	1439	1364
FPD	1332	1024	1250	918
GPD	2706	2304	2689	2282
FR	0.37	0.38	0.31	0.29
KN	544	535	377	306
KW	286	208	231	160
EL	175	169	140	128
ED	42.7	41.0	35.8	34.0
PMBLM	32.8	37.6 ¹	30.0	38.5 ²
HM	24.8	33.2	22.8	33.3
YIELD	1455	1025	807	443

¹Mean of two hybrids.

²Mean of four inbreds.

† Units are those shown in Table 1, p. 28.

heat unit concept has been widely accepted as a means of reducing variation in GPD between different environments, these results indicate that the heat units used here were not effective in reducing variation in VPD between locations.

Differences in mean daylength between the two locations may partially account for the failure of corn heat units to reduce the difference in VPD between the two environments. Because planting and silking were about two weeks later at Carman than at Winnipeg, the vegetative periods at the two locations did not cover the same calendar days. For the sets of days not in common to the vegetative periods in the two locations (May 11 to May 23 for Winnipeg and July 11 to July 25 for Carman), mean daylength at Carman was 0.40 hours longer than at Winnipeg (Russelo et al., 1974). Therefore, plants at Carman would have received more solar radiation per CHU accumulated than plants at Winnipeg, assuming that cloud cover did not differ between the two locations. This may explain, in part, why the mean VPD was shorter at Carman (1280 CHU) than at Winnipeg (1374 CHU).

Most of the significant hybrid by location interactions (Table 4) can be explained as resulting from premature frost and low accumulation of CHU at Carman. The latest maturing hybrids might be expected to be more affected by frost at Carman than earlier maturing hybrids for traits such as FPD, GPD, yield, HM, and EL.

As an example, consider the significant yield by location interaction. The major contributor to this interaction sum of squares was hybrid 72X59, which was the highest yielding hybrid at Winnipeg, but the

lowest yielding at Carman. Since 72X59 had the longest GPD at Winnipeg, it might be expected to suffer the greatest yield loss as a result of the premature cessation of grain filling at Carman. Conversely, an earlier maturing hybrid would be expected to suffer a proportionally lesser yield loss, as it would have lost a smaller fraction of its growth period at Carman.

Analysis of variance combined over locations showed no significant effect of hybrids for four traits: FPD, GPD, HM, and yield. For all these traits, both the location and hybrid by location effects were significant, which probably served to obscure differences that might have existed among hybrids.

In the inbred experiment, location means differed significantly for all traits except EL (Table 5). Winnipeg means exceeded Carman means for all traits except PMBLM and HM (Table 6). As in the hybrid experiment, the higher HM at Carman was an expected result of later planting at Carman. The lower Carman means for traits such as FPD, GPD, KW, ED, and yield were also an expected result of premature frost and lower accumulation of CHU at Carman.

Analysis of variance combined over locations using only the four inbreds that formed black layers before frost in both locations indicated that these inbreds at the Carman location were significantly higher in PMBLM and significantly lower in KW compared to Winnipeg (Table 7). The inbred showing the least difference between locations for these two traits was CK43, which was the earliest maturing of the six inbreds tested. These results suggest that black layer formation

TABLE 7. PMBLM and KW for inbreds that formed black layers before frost at both locations

Inbred	PMBLM [†]		KW [†]	
	Winnipeg	Carman	Winnipeg	Carman
CK43	28.7	31.8	167	154
CK52	30.3	37.2	233	154
CM37	33.6	44.4	312	219
CM72	28.0	40.6	201	125
Mean ¹	30.2	38.5	228	163
SE ²	0.58	0.36	7.8	7.4

¹Location means differ at the 1% level of significance for both PMBLM and KW.

²Standard error of the difference between two means.

[†]Units are those shown in Table 1, p. 28.

may have been precipitated "prematurely" (that is, before the kernels were completely filled) by the weeks of cool weather preceding the frost, as has been observed by Daynard (1972) in Ontario.

As in the hybrid experiment, location means for VPD differed significantly when VPD was expressed in CHU. But in the inbred experiment, this significant difference did not disappear when VPD was expressed in days. Mean VPD at Carman was two days longer but 75 CHU shorter than the Winnipeg mean. 75 CHU were approximately equal to three days during this period, so once again the difference in mean VPD between locations was greater with VPD expressed in CHU than with VPD expressed in days.

The inbred by location interactions were significant for all traits except FR, EL, and ED (Table 5), which indicates that the relative expression of most traits was not consistent between the two environments. This may be a result of late planting and "premature" formation of black layers at Carman.

There was no significant effect of inbreds for FPD, GPD, and yield in the analysis combined over locations. For these traits, location and interaction effects were highly significant, which may have masked any differences for these traits that might have been present in the inbreds examined.

In summary, premature frost and low accumulation of CHU seem to have had profound effects upon the expression of the traits examined at the Carman location. Compared to the Winnipeg means, Carman means for FPD, GPD, KW, and yield were substantially lower, while Carman means for

HM and PMBLM were higher in both inbreds and hybrids. Genotype by location interactions were significant for many traits in both inbreds and hybrids, making comparisons of genotypes using data combined over locations unprofitable. Relationships among the variables examined are also likely to be confused if data from the Carman location are used. In particular, relationships among FPD, FR, and yield are likely to be distorted since grain filling did not reach a natural conclusion at Carman. Under these conditions, FPD would be expected to be less closely related to yield and FR would be expected to be more closely related to yield compared to the relationships that might be evident under more normal conditions.

For these reasons, the discussion to follow will deal solely with data obtained at the Winnipeg location. Tables concerning the Carman experiment are presented in the appendix (Appendix Tables 5 to 8).

4.2 INBREDS AT WINNIPEG

Analysis of variance showed that differences existed among inbreds at Winnipeg at the 5% level of significance for all eleven traits examined. Inbred means for each of the traits in each of the six inbreds are given in Table 8 .

Inbreds CM72 and CK52 were high yielding, CK43, CK48, and CM37 were low yielding, and CK59 was intermediate between these two groups. The highest yielding inbred, CM72, was also highest in KN but was lowest in FR. CK52, which did not differ significantly in yield from CM72, was intermediate in KN and in the highest group in FR, so these two inbreds



TABLE 8. Inbred means for 11 traits in six inbreds grown at Winnipeg

INBRED	VPD [†]	FPD	GPD	FR	KN	KW	EL	ED	PMBLM	HM	YIELD
CK43	1429b ¹	1009a	2438a	0.30a	431bc	167a	157c	28.5a	28.7a	15.6a	693a
CK52	1416ab	1252c	2668b	0.36b	422bc	233bc	174d	31.2b	30.3a	24.8d	926b
CK59	1416ab	1394d	2811d	0.30a	342ab	262c	110a	40.0c	31.0a	25.8d	823ab
CK48	1478c	1268c	2745c	0.28a	308ab	212b	113a	37.5c	28.6a	22.7c	730a
CM37	1392a	1396d	2788d	0.37b	260a	312d	137b	37.6c	33.6a	27.9e	735a
CM72	1502c	1183b	2686b	0.26a	501c	201b	148bc	40.1c	28.0a	19.8b	937b
Mean	1439	1250	2689	0.31	377	231	140	35.8	30.0	22.8	807
SE ²	9.5	11.6	9.5	0.01	37.2	12.0	5.0	0.77	1.12	0.75	42.4
F-ratio ³	39.2**	310.1**	403.4**	18.6**	11.6**	35.5**	49.6**	75.9**	6.9*	70.3**	12.3**

¹Means in the same column that are followed by the same letter do not differ at the 5% level of significance as determined by the Student-Newman-Keuls procedure.

²Standard error of the difference between two means.

³From the analysis of variance: $F = MS(\text{inbreds})/MSE$

*,** significant at the 5% and 1% levels of significance, respectively.

[†]Units are those shown in Table 1, p.28.

appear to have achieved their high yield by different routes. They also differed in ear shape, with CM72 having the largest ED and CK52 the longest EL.

The lowest yielding inbred, CK43, was also the earliest in maturity (GPD). The inbred with the longest GPD, CK59, was intermediate in yield. CM37 was the earliest to silk (VPD) while CM72 was the latest. Maturity relationships were reversed for these two inbreds in FPD, however, with CM37 having the longest filling period and CM72 the second shortest.

In moisture content, CK59 had the highest PMBLM and CM72 the lowest. The earliest inbred, CK43, had the lowest HM and also the smallest KW. The inbred with the largest KW, CM37, had the highest HM.

In judging the inbreds per se, CM72 has the virtues of high yield and low moisture at BLM and at harvest, but it was the latest to silk. CK52 had high yield but was also relatively high in HM. Although low in yield, CK43 was lowest in HM and the earliest to mature and might make an excellent donor parent in an earliness conversion program. CM 37 was the earliest to silk, but it was late in maturity and had the highest HM.

4.3 CORRELATIONS AMONG INBRED TRAITS

None of the traits examined in this experiment were significantly correlated with yield (Table 9). The correlation between KN and yield was relatively large in magnitude and just short of significance ($r=0.55$).

TABLE 9. Simple correlations for 11 variables in six inbreds grown at Winnipeg

	FPD	GPD	FR	KN	KW	EL	ED	PMBLM	HM	YIELD
VPD	-.37	-.08	-.81**	.49	-.59*	-.09	.34	-.79**	-.48	.30
FPD		.95**	.42	-.66*	.89**	-.54	.66*	.68*	.95**	.12
GPD			.19	-.55	.77**	-.61*	.82**	.47	.87**	.23
FR				-.44	.65*	.35	-.31	.82**	.62*	-.05
KN					-.70*	.57	-.23	-.63*	-.64*	.55
KW						-.31	.46	.82**	.93**	.03
EL							-.68*	-.10	-.32	.34
ED								.10	.48	.25
PMBLM									.72**	-.21
HM										.17

*,** significant at the 5% and 1% levels of significance, respectively.

Of the maturity components, FPD and GPD were highly correlated ($r=0.95$), but there was no significant relationship between VPD and either FPD or GPD. Variation in VPD was relatively restricted compared to variation in FPD (Table 8), so most of the variation in time to maturity can be accounted for by differences in FPD.

Because of the close relationship between FPD and GPD, it is difficult to say whether relationships observed in the inbreds were a specific effect of the length of grain filling or a general effect of overall maturity. Similar patterns were observed, with both FPD and GPD being closely and positively related to KW, ED, and HM. GPD was negatively related to EL with a similar but nonsignificant trend between EL and FPD. FPD was negatively correlated with KN, and this correlation with GPD was just short of significance. GPD did not appear to be too closely related to PMBLM, although the correlation between FPD and PMBLM was significant and positive.

In general, the inbreds in this study that were late in maturing also had long filling periods and larger but fewer kernels on short ears of relatively large diameter. Inbreds with long filling periods tended to have higher moisture content both at maturity and at harvest.

Relationships between VPD and the other traits were generally in contrast to those observed with FPD. In particular, VPD was negatively related to both KW and PMBLM and showed no relationship to either of the two ear size variables. There was a negative relationship between VPD and FR, which is somewhat surprising as we might expect that inbreds which devoted a longer time to vegetative growth might be able to fill

kernels at a faster rate. The observed relationship may be due to kernel size factors, since inbreds with a longer VPD tended to have more and smaller kernels which might be expected to accumulate dry matter at a slower rate on a per kernel basis.

Filling rate was, in fact, observed to be positively related to KW. The correlation between FR and KN was negative but nonsignificant. The two kernel variables, KN and KW, were negatively correlated, as were the two ear variables, ED and EL.

The two grain moisture variables, PMBLM and HM, were also significantly and positively correlated. As was the case with FPD and GPD, the two moisture variables showed similar patterns of relationships with the other variables in that both were positively correlated with FPD, FR, and KW and both were negatively correlated with KN. However, only PMBLM was significantly correlated with VPD (negative) and only HM was significantly correlated with GPD (positive).

In the inbreds examined in this study, high grain moisture at maturity and at harvest tended to be associated with a fast filling rate and a long filling period duration and with fewer kernels of a larger size. The combination of a high rate and a long duration of grain filling might be expected to lead to high yield, but neither of the two moisture variables were significantly related to yield. This may be due to their negative relationships with kernel number, which would tend to offset the positive effects of high FR and FPD.

4.4 HYBRIDS AT WINNIPEG

Analysis of variance showed that hybrids differed at the 5% level of significance for all traits except KW, PMBLM, and yield. Hybrid means along with mean comparisons are given in Table 10 for 11 traits in nine hybrids grown at Winnipeg.

Since the difference in mean yields between the lowest (43X48) and the highest (72X59) yielding hybrids was more than 30%, further analyses were performed in an attempt to determine why the initial analysis of variance showed no differences among hybrid yields. The analyses of variance for hybrid yield at Winnipeg by all methods are presented in appendix Table 4.

The application of Tukey's test for non-additivity to the 10-plant yield data indicated a significant hybrid by block interaction in the Winnipeg experiment. Since the method by which yield samples were taken permitted analysis either as a single 10-plant determination per plot or as two 5-plant determinations per plot, yield data were re-examined on the basis of two 5-plant determinations per plot. This method of analysis allowed the removal of a hybrid by block interaction sum of squares from the error sum of squares. Subsequent testing of the main effects of hybrids and of the hybrid by block interaction against this reduced sampling error indicated highly significant yield differences among hybrids and a highly significant hybrid by block interaction. However, testing the main effects of hybrids against the mean square for interaction, which is required if we assume a random effects model for blocks, again leads to the conclusion that there are no significant yield differences among hybrids at Winnipeg.

TABLE 10. Hybrid means for 11 traits in nine hybrids grown at Winnipeg

HYBRID	VPD [†]	FPD	GPD	FR	KN	KW	EL	ED	PMBLM	HM	YIELD
43X48	1367ab ¹	1223a	2590a	0.35ab	478a	273a	158b	40.5b	34.7a	24.2bcd	1211a
43X37	1355ab	1247a	2602a	0.39cd	454a	288a	185c	38.0a	35.0a	25.0cde	1285a
43X72	1441c	1236a	2677ab	0.36bc	527ab	286a	180c	40.0b	30.0a	22.9bc	1350a
52X48	1392abc	1299ab	2691ab	0.39cd	565abc	294a	186c	44.5de	32.3a	27.1de	1533a
37X52	1392abc	1392bc	2784b	0.42d	537ab	310a	201d	41.6bc	33.6a	27.5de	1578a
72X52	1355ab	1265a	2620a	0.39cd	627bc	262a	190c	42.7cd	30.9a	20.7a	1521a
48X59	1342ab	1425c	2768b	0.34ab	535ab	290a	146a	44.4de	30.2a	23.7bcd	1504a
37X59	1317a	1490c	2807b	0.35ab	521ab	314a	162b	46.2e	35.9a	28.5e	1520a
72X59	1404bc	1414bc	2818b	0.32a	655c	258a	164b	46.1e	32.2a	23.8bcd	1592a
Mean	1374	1332	2706	0.37	544	286	175	42.7	32.8	24.8	1455
SE ²	20.3	49.7	38.9	0.01	34.6	16.1	3.3	0.76	1.92	1.13	111.6
F-ratio ³	6.7**	7.9**	10.8**	21.7**	6.9**	2.9	58.8**	28.2**	2.5	9.7**	3.0

¹Means in the same column that are followed by the same letter do not differ at the 5% level of significance as determined by the Student-Newman-Keuls procedure.

²Standard error of the difference between two means.

³From the analysis of variance: $F = MS(\text{hybrids})/MSE$.

*,** significant at the 5% and 1% levels of significance, respectively.

[†]Units are those shown in Table 1, p. 28.

It appears that the hybrid by block interaction has obscured whatever yield differences might have existed among the hybrids. Examination of plot yields reveals that a large part of the interaction sum of squares came from two hybrids, 43X37 and 43X72, which differed substantially between the two blocks. If these two hybrids are deleted and analysis of variance performed on the remaining seven hybrids, then the effects of blocks and of interaction lose their significance and the main effect of hybrids becomes highly significant (appendix Table 4).

It is impossible to state with any certainty why the yields of 43X37 and 43X72 in block two were depressed to such an extent relative to their counterparts in block one. However, the two low yielding plots were in the same row in the field, so it is possible that they suffered some accident such as jamming of the fertilizer distributor or root damage during cultivation which was not detected at the time.

In summary, it appears that there were real yield differences among the hybrids tested, but these yield differences were hidden by the interaction which resulted from exceptional circumstances in two of the test plots. Hybrid 43X48 appears to be lower in yield than the other hybrids tested. Hybrids 43X37 and 43X72 may also be lower in yield than the remaining six hybrids, but this is difficult to determine in view of the rather large differences between the two replicates of these hybrids. The results of mean separation procedures for yield of Winnipeg hybrids based on two 5-plant subsamples per plot are presented in Table 11. According to this analysis, there are two main yield groups: a higher yielding group consisting of those hybrids without CK43 as a

TABLE 11. Yield differences in hybrids at Winnipeg

Hybrid	Mean 5-plant yield (g)
72X59	796a ¹
37X52	789a
52X48	767a
72X52	760a
37X59	760a
48X59	752a
43X72	675b
43X37	643bc
43X48	606c
SE	19.1

¹Means followed by the same letter do not differ at the 5% level of significance as determined by the Student-Newman-Keuls procedure.

parent and a lower yielding group consisting of the three hybrids having CK43 as one parent.

All of the CK43 hybrids were in the lowest groups for FPD, GPD, KN, and ED (Table 10) which may account, in part, for their low yields. Conversely, the highest yielding hybrid, 72X59, was in the highest groups for these same traits, which suggests that there may be a positive relationship between these traits and yield.

It is of interest to note that hybrids which did not differ significantly in GPD did differ in the way that this growth period was divided into vegetative and filling components. Hybrid 43X72 is representative of the lowest yielding group (CK43 progeny) in which VPD exceeded FPD. In the two highest yielding hybrids (37X52 and 72X59), VPD and FPD were approximately equal. Yields were intermediate in the case of the two hybrids (37X59 and 48X59) in which FPD exceeded VPD.

This variation in the way in which GPD was divided into vegetative and filling components suggests that it may be possible to extend FPD at the expense of VPD in material similar to that examined here. Although data obtained in this experiment are not sufficient to predict an optimum ratio of VPD to FPD, it appears that it may not be wise to produce hybrids in which FPD exceeds VPD by a substantial margin.

Although hybrids did not differ significantly in PMBLM, there was significant variation in HM ranging from a low of 20.7% to a high of 28.5%. Hence, this must have been due either to variation in the time to BLM or in the rate of grain drying after BLM. Both high and low HM

were observed within the high yield group, which suggests that it should be possible to produce hybrids that have both high yield and low grain moisture at harvest.

4.5 CORRELATIONS AMONG HYBRID TRAITS

4.5.1 Correlations With Yield

Of the three filling components, yield was significantly and positively correlated with FPD and with KN, but the correlation with FR did not differ significantly from zero (Table 12). The correlation between FPD and KN was not significant, so it should be theoretically possible to increase yield by increasing either or both of these traits.

Although GPD was the most closely correlated with yield of all the traits examined, no increase in GPD is practical as the average growing season is completely utilized by currently available hybrids. In fact, it may be desirable to hasten maturity even more in order to further reduce the risk of yield losses due to premature frost. Hybrid 72X59, for example, was the latest to mature and had the highest yield at Winnipeg, where it accumulated 2818 CHU from planting to black layer maturity (Table 10), which is an exceptional number of CHU for Manitoba. At Carman, where later planting resulted in the accumulation of about 500 fewer CHU, 72X59 did not mature before frost and was the lowest yielding hybrid. So, although 72X59 may have the highest yield potential of the hybrids tested, it would not be acceptable as a commercial variety because of its susceptibility to yield losses resulting from frost prior to grain maturity.

TABLE 12. Simple correlations for 11 variables in nine hybrids grown at Winnipeg

	FPD	GPD	FR	KN	KW	EL	ED	PMBLM	HM	YIELD
VPD	-.43	-.07	-.00	.16	-.26	.31	-.26	-.22	-.17	-.16
FPD		.93**	.25	.24	.51*	-.27	.72**	-.03	.48*	.72**
GPD			-.27	.33	.45	-.17	.69**	-.13	.46	.73**
FR				-.18	.36	.84**	-.42	.02	.17	.09
KN					-.48*	.07	.63**	-.46	-.38	.67**
KW						.20	.02	.17	.75**	.26
EL							-.40	-.01	.10	.19
ED								-.13	.22	.66**
PMBLM									.55*	-.40
HM										.15

*,** significant at the 5% and 1% levels of significance respectively.

Increasing FPD may not be a practical means of achieving yield increases in Manitoba either, as FPD was closely correlated to GPD (Table 12). In fact, both FPD and GPD show the same general pattern of relationships with the other variables in this study, making it difficult to differentiate between the effects of filling period and the effects of overall maturity.

If the risk of yield loss due to premature frost is not to be increased, FPD can be extended only at the expense of VPD. That this may be difficult is indicated by previous studies that have found VPD and FPD to be positively correlated (Gunn and Christensen, 1965; Carter and Poneleit, 1973; and Daynard and Kannenberg, 1976). In the material examined in this study, however, the correlation between VPD and FPD was negative and just short of significance ($r=-0.43$). The reason for this apparent conflict may well lie in the fact that the range of maturities examined here was more restricted (2590 to 2818 CHU) than in the previous studies. As the range of maturity in the material examined decreases, one would expect the strength of the relationship between VPD and FPD to weaken and even become negative when all material in the study was of the same maturity. Cross (1975) found no significant relationship between VPD and FPD ($r=0.13$) in a group of 21 early hybrids in North Dakota.

Shortening VPD may have an adverse effect on yield as several studies have provided indications that sink capacity is determined, at least in part, by current photosynthesis or assimilate supply around the time of silking (Early, et al., 1967; Prine, 1971; Egharevba, et al., 1976;

Tollenaar, 1977; and Tollenaar and Daynard, 1978b) and, indirectly, by the amount of vegetative growth which has occurred prior to silking. However, VPD was not significantly correlated with yield or with any factor related to sink size (KN, KW, EL, ED) in this study, nor was VPD significantly related to GPD (Table 12). Consequently, it may be possible to achieve limited yield advances in short-season hybrids by breeding for longer filling periods and shorter time to silking.

Of the two ear factors, ED was positively and significantly correlated with yield, FPD, GPD, and KN so the possibility exists that the significant correlation between ED and yield results from the relationship between ED and these other variables that are also positively related to yield. In fact, when partial correlation analysis was used to control for variation in either GPD, FPD, or KN, the correlation between ED and yield became nonsignificant. The other ear factor, EL, was significantly related only to FR, with the longer ears tending to have faster filling rates.

The two kernel factors, KN and KW, were significantly and negatively correlated. This relationship was not so strong as the relationship between KN and yield (-0.48 vs 0.67), so it seems likely that gains made by increasing KN will not be completely offset by losses due to a decrease in KW. A reduction in KW may actually be beneficial, as KW was positively correlated with FPD and HM. Thus, a breeding program that attempts to improve yield by increasing KN may also produce beneficial effects on maturity and grain moisture content at harvest by virtue of the negative relationship between KN and KW.

Another factor which should be discussed in relation to yield is FR. Where climatic restraints preclude extensive manipulation of FPD, it seems reasonable for a corn breeding program to aim at the production of hybrids that accumulate dry matter in the grain at the fastest rate possible. However, findings here agree with previous conclusions (Carter and Poneleit, 1973; Cross, 1975; and Daynard and Kannenberg, 1976) that FR expressed on a per kernel basis is not significantly related to grain yield ($r=0.09$). Since it seems reasonable to expect that FR per kernel would be negatively related to KN, the partial correlation coefficient between FR and yield, with KN held constant, was calculated. This partial coefficient was larger ($r=0.28$) than the simple coefficient but was still well short of significance. It appears, then, that little is to be gained by selecting for faster FR, at least in the material examined in this study.

In summary, it appears that yield advances might be obtained by breeding for increased FPD or KN, but not by breeding for increased FR. Since climatic conditions require that any extension of FPD be at the expense of VPD, only limited yield increases are likely to be obtained by breeding for longer FPD. As grain yield per plant can be completely defined by the rate and duration of dry matter accumulation in the grain, the logical approach to breeding for yield improvement in material similar to that examined here lies in increasing the rate of grain dry matter accumulation per plant. This can be achieved by increasing either of the two components of FR per plant, FR per kernel and KN per plant, provided that gains made in one component are not offset by losses in the other. In this experiment, the correlation between FR and

KN was not significantly different from zero ($r=-0.18$), which suggests that it may be possible to increase FR per plant by increasing either or both of FR per kernel and KN. Correlations obtained in the Winnipeg experiment indicate that increasing KN is the best approach to increasing FR per plant and, hence, to increasing yield.

Recent research has suggested that the control on FR is determined by kernel factors (Tollenaar and Daynard, 1978c) or by the efficiency of translocation into the kernel (Shannon, 1978), rather than by factors related to the production or translocation of photosynthate to the ear. This may account for the lack of correlation between FR and KN. If FR were determined by a limited supply of photosynthate or by inefficient translocation of photosynthate into the ear, then the division of this limited supply of photosynthate among more kernels should result in a negative relationship between FR and KN. If, on the other hand, excess photosynthate is available for grain filling throughout much of the filling period, as has been suggested by studies that show that the stalk acts as a reservoir of mobile carbohydrate (Duncan, *et al.*, 1965 and Daynard, 1972), then it seems probable that an increase in KN need not be accompanied by a substantial decrease in FR.

Increasing FR per plant, in itself, need not necessarily result in a yield increase but might simply lead to earlier depletion of stalk reserves and to earlier maturity. However, both Kiesselbach (1948) and Moss (1962) found that removal of the ear or the prevention of pollination resulted in reduced photosynthetic rates, which suggests that some type of feedback inhibition of photosynthesis may be operative in corn.

Support for this theory has been provided by Knievel and McKee (1978), who found that reduced sink capacity was limiting photosynthetic rates in an experiment where hand pollination was used to produce plants bearing 1/2, 1, and 2 ears. Consequently, an increase in FR per plant might, through early reduction of stalk reserves and a consequent lessening of feedback inhibition, lead to increased yields through increased photosynthesis during the grain filling period.

4.5.2 Correlations With Grain Moisture Content

In the Winnipeg hybrid experiment, grain moisture at harvest was significantly and positively correlated with KW, PMBLM, and FPD. The correlation between HM and GPD was just short of significance, and the correlation between HM and KN was negative but nonsignificant (Table 12, p. 54).

Although the simple correlation between PMBLM and HM was statistically significant, the coefficient of determination (R^2) was only 30%, which means that a large proportion of the variation in HM could not be accounted for by variation in percent moisture at BLM. At least a part of the remaining variation in HM might be accounted for by variation in the duration or rate of moisture loss following maturity.

Since hybrids varied in the number of days between black layer maturity and the date on which HM was measured, it was felt that the time of maturity might be obscuring relationships between HM and some of the other variables. Consequently, partial correlation analysis was used to examine the relationships between HM and the other variables with GPD held constant (Table 13).

TABLE 13. Simple and partial correlations between HM and ten variables in nine hybrids grown at Winnipeg

Trait	Simple r	Partial r (GPD held constant)
VPD	-.017	-.016
FPD	0.47*	0.16
GPD	0.46	--
FR	0.17	0.34
KN	-0.38	-0.63**
KW	0.75**	0.69**
EL	0.10	0.20
ED	0.22	-0.15
PMBLM	0.55*	0.69**
YIELD	0.15	-0.31

*,** significant at the 5% and 1% levels of significance respectively.

The correlations between HM and KW and between HM and PMBLM remained significant, and the correlation between HM and KN changed to highly significant ($r=-0.63$) when GPD was held constant. The partial correlation between HM and FPD was nonsignificant, which suggests that the closeness of the relationship between FPD and HM might have been due to the relationship between FPD and GPD, rather than to any direct effect of FPD on HM. HM was not significantly related to either of the ear size factors by either simple or partial correlation analysis.

The relationships between HM and KW and HM and KN are probably due to simple physical factors. Since small kernels have a larger surface area per unit mass from which water can be lost, hybrids with a large number of small kernels might be expected to lose moisture after maturity at a faster rate than hybrids having a smaller number of larger kernels. Thus, a breeding program that attempted to achieve yield increases through an increase in KN would probably also have beneficial effects on HM.

Since PMBLM can be readily determined by taking kernel samples at the time that black layer maturity is ascertained, it might also be appropriate to attempt to reduce PMBLM as one means of reducing HM in hybrids developed for this area. In the Winnipeg hybrid experiment, PMBLM was significantly related only to HM (Table 12). Though nonsignificant, the correlation between PMBLM and KN was substantial ($r=-0.46$), so attempts to increase KN might be complemented by attempts to reduce PMBLM.

In short-season areas, hybrids with high moisture content at harvest are often associated with late maturity and high yield potential. Therefore, it is of interest to note that there was no significant relationship between yield and HM in this experiment, which indicates that the connection between high moisture and high yield is not absolute. In fact, the highest yielding hybrid at Winnipeg, 72X59, was in the lowest group for HM (Table 10, p. 49) and had a lower HM than other hybrids of lower yield and earlier maturity. Although the data obtained in this experiment was not sufficient to permit firm conclusions regarding drying rates, this does suggest that there were differences among the hybrids examined in the rate of moisture loss after physiological maturity. The extent of these differences in drying rates of early hybrids and the bases for such differences should be investigated further.

4.6 INBRED-HYBRID RELATIONS

Mean values for the traits measured in the inbreds and in their hybrid progeny are given in Table 14 . Compared to the inbreds, the hybrids had shorter vegetative periods but longer filling periods. The difference in growth period duration between the two groups was negligible. Hybrid means exceeded inbred means for the other traits examined. Percent heterosis (defined here as the difference between inbred means and their progeny hybrid means expressed as a percent of the inbred mean) was greatest for yield, which suggests that grain yield is more affected by heterosis than the other traits measured.

Of the three filling components, percent heterosis was greater for KN than for FPD or FR. In fact, percent heterosis was higher for KN

TABLE 14. Mean values of 11 traits in six inbreds and their hybrid progeny

Trait		Inbred						Mean	% Het. ¹
		CK43	CK52	CK59	CK48	CM37	CM72		
VPD	I	1429	1416	1416	1478	1392	1502	1439	-4.5
	H	1388	1380	1354	1367	1355	1400	1374	
FPD	I	1009	1252	1394	1268	1396	1183	1250	6.2
	H	1235	1319	1443	1316	1376	1305	1332	
GPD	I	2438	2668	2811	2745	2788	2686	2689	0.6
	H	2623	2698	2792	2679	2731	2704	2706	
FR	I	0.30	0.36	0.30	0.28	0.37	0.26	0.31	19.4
	H	0.37	0.40	0.34	0.36	0.39	0.36	0.37	
KN	I	431	422	342	308	260	501	377	44.3
	H	486	576	570	526	504	603	544	
KW	I	167	233	261	212	312	201	231	23.8
	H	282	289	287	286	304	269	286	
EL	I	157	174	110	113	137	148	140	25.0
	H	174	192	157	163	183	178	175	
ED	I	28.5	31.2	40.0	37.5	37.6	40.1	35.8	19.3
	H	39.5	42.9	45.6	43.1	41.9	42.9	42.7	
PMBLM	I	28.7	30.3	31.0	28.6	33.6	28.0	30.0	9.3
	H	33.2	32.3	32.8	32.4	34.8	31.0	32.8	
HM	I	15.6	24.8	25.8	22.7	27.9	19.8	22.8	21.4
	H	24.0	25.1	25.3	25.0	30.3	22.5	24.8	
YIELD	I	693	926	823	730	735	937	807	80.3
	H	1282	1544	1539	1416	1461	1488	1455	

¹Percent heterosis defined as the difference between inbred and progeny means expressed as a percent of the inbred mean.

I=inbred mean

H=mean of the three hybrid progeny of that inbred

than for any of the other traits except yield. This may mean that the increase in kernel number was the most important factor in explaining the yield advantage of hybrids over the inbreds in this study.

Hybrids exceeded inbreds for both moisture traits, but the percent difference was greater at harvest than at grain maturity. Of the ear size factors, hybrids showed a greater increase in ear length than in diameter, relative to the inbreds.

In some instances, inbred and progeny means did not follow the general trends. One example involves CM37 whose progeny means were less for FPD and for KW than those obtained in the inbred. CM37 was highest among the inbreds for both these traits, but the same level of performance was not maintained in its hybrids.

The effects of specific inbreds when used in hybrid combinations can only be assessed with difficulty in this study, since the inbreds were crossed in partial rather than in complete diallel. For example, CK52 and CK59 produced the highest yielding hybrid progeny and CK43 the lowest, while the remainder were intermediate (Table 14). It must be remembered, however, that neither CK52 nor CK59 were crossed with CK43, but the remaining lines were crossed with CK43. If CK43 tends to produce low yielding hybrid progeny, as appears to be the case, then this method of testing would tend to depress the mean progeny yields of CK48, CM37, and CM72 relative to CK52 and CK59. This sort of bias may also be present in relation to the other traits studied. Keeping this restriction in mind, some conclusions are justifiable regarding the effects of inbreds when used in hybrid combination.

The CM72 progeny were lowest in PMBLM and in HM, even though both the inbred and its hybrids were of average maturity. CK43, on the other hand, produced the earliest progeny and had the lowest PMBLM and HM as an inbred, but its hybrids had higher moisture levels than the CM72 progeny. It appears that the desirable moisture loss pattern of CM72 carried over into its hybrids, but this was not the case with CK43. A similar situation existed in these two inbreds with regard to kernel number: The high KN of CM72 was reflected in its hybrids, but CK43, which ranked second highest in KN, produced hybrids with the fewest kernels.

The CM37 progeny and the inbred itself were highest in both moisture traits and in kernel weight. The low kernel number of this inbred was also reflected in its hybrids.

In the maturity components, CK59 produced hybrids with the longest FPD and GPD and CK43 produced hybrids with the shortest FPD and GPD. These rankings were consistent with the performance of the inbreds. The long VPD of CM72 and the short VPD of CM37 were expressed in the hybrids of these inbreds.

In regard to other traits, CK59 hybrids produced ears that were shortest but with the greatest diameter. CK52 progeny were high in ear length and in filling rate.

Simple correlation coefficients between the same traits of hybrids and midparents (the mean of the two inbred parents of a specific hybrid) are given in Table 15 . The correlations obtained were consistently

TABLE 15. Simple correlations between hybrids
and means of their inbred parents (midparents)

Trait	Correlation coefficients	
	Trait vs. trait	Trait vs. yield
VPD	0.49	-0.11
FPD	0.93**	0.74*
GPD	0.81**	0.81**
FR	0.78*	0.24
KN	0.52	-0.05
KW	0.65	0.57
EL	0.91**	-0.10
ED	0.85**	0.66
PMBLM	0.64	0.33
HM	0.65	0.72*
YIELD	0.73*	0.73*

*,** significant at the 5% and 1% levels of significance, respectively.

positive and relatively large in magnitude. This contrasts with the findings of Gama and Hallauer (1977) who found that the inbred-hybrid correlations for several traits were statistically significant but were consistently low (the largest R^2 was less than 0.16). Correlations obtained in this experiment suggest that, for some traits, a large proportion of the variation in hybrid traits can be explained by variation in midparent values. Coefficients of determination (R^2) for FPD, EL, ED, GPD, FR, and yield were 0.87, 0.84, 0.73, 0.66, 0.61, and 0.53 respectively.

Simple correlations between midparent traits and hybrid yields were significant and positive for FPD, GPD, HM, and yield (Table 15). Unfortunately, climatic restraints preclude much alteration in the first three traits in a breeding program in Manitoba and variation in inbred yields explains only 53% of the variation in hybrid yields.

The results of multiple linear regression of hybrid yields on 11 midparent traits at Winnipeg are presented in Table 16. Several different combinations of midparent traits can be used to explain more than 90% of the variation in hybrid yields. GPD enters the regression equation first when all 11 variables are available for entry and FPD enters first when GPD is excluded. Midparent yield is the next most important variable in explaining hybrid yields when used in combination with either GPD or FPD (equations 1 and 2).

Both midparent GPD and HM have positive regression coefficients in a regression equation that predicts hybrid yields. However, midparent GPD and HM are positively related to the same traits in the hybrids, so

TABLE 16. Multiple linear regression of hybrid yield and harvest moisture content on 11 midparent traits at Winnipeg

Variables forced	Variables excluded	Regression equation ^a	F-ratio	R ²
None	None	(1) $Hy^b = -2250 + 1.07GPD + 1.04My^c$	41.3**	0.93
None	GPD	(2) $Hy = -667 + 0.92FPD + 1.22My$	49.2**	0.94
GPD, HM	None	(3) $Hy = -1570 + 0.70GPD + 11.75HM + 1.09My$	29.8**	0.95
GPD, HM	My	(4) $Hy = -2506 + 0.95GPD + 32.95HM + 1.72KN$	27.7**	0.94
None	None	(5) $HHM^d = 25.0 - 0.25KN + 29.14FR$	6.5*	0.68

^aVariables were added to the regression equation only if they contributed at least 2% to explained variation in hybrid yield (except forced HM).

^bHybrid yield.

^cMidparent yield.

^dHybrid grain moisture content at harvest.

*, ** Regression significant at the 5% and 1% levels of significance, respectively.

it would not be desirable to increase either of these traits under Manitoba conditions. Therefore, GPD and HM were forced into the regression equation first in order to examine the relationships between other midparent variables and hybrid yields when midparent GPD and HM were held constant.

Under these conditions, midparent yield enters the regression equation after GPD and HM, contributing 29% to explained variation in hybrid yields and having a regression coefficient of 1.09 (equation 3). If midparent yield is excluded, KN enters after GPD and HM, contributing 29% to explained variation in hybrid yields with a regression coefficient of 1.72 (equation 4). Consequently, under the conditions of this experiment and in breeding material similar to that examined, we might be able to increase hybrid yields by selecting inbred parents that are higher yielding or have more kernels per plant, without increasing either GPD or HM.

Since a secondary aim of a corn breeding program in Manitoba might be to decrease harvest moisture content of the grain, HM of hybrids was also regressed against 11 midparent traits (equation 5). This equation indicates that we might reduce HM in hybrids by selecting inbred parents with increased KN and reduced FR.

The results presented here differ substantially from those of Gama and Hallauer (1977) who examined 160 unselected lines from Iowa Stiff Stalk Synthetic and 320 single-cross hybrids derived by crossing within 20 sets of eight inbreds in a pattern similar to that used in this research. These workers found the multiple correlation coefficient

between hybrid yields and six midparent traits to be 0.21 ($R^2=0.04$), which is in marked contrast to the findings here, where several different combinations of midparent traits produce coefficients of determination in excess of 0.90.

Various reasons may be suggested to account for these different results. Of the traits examined here, only VPD, EL, ED, and yield were included in the research of Gama and Hallauer. Inbreds and hybrids were grown in the same environment in this experiment, whereas Gama and Hallauer grew their inbreds and hybrids in different environments, which would tend to minimize the environmental component of the inbred-hybrid correlations. Also, average yield heterosis was greater in the material examined by Gama and Hallauer (229%) than in the material examined here (80%), and it may be that inbred-hybrid correlations decrease with increasing heterosis.

In their analysis of individual sets consisting of eight inbreds and 16 derived hybrids, Gama and Hallauer encountered several sets in which consistently high inbred trait vs. hybrid trait correlations were obtained similar to those obtained in this experiment. They also encountered several sets in which consistently negative correlations were obtained. Consequently, these authors caution that misleading conclusions may be drawn when small sample sizes are used. Thus, it may be that the results obtained here are representative only of the genotypes examined. However, the possibility exists that the association between inbred and hybrid traits in early genotypes is closer than has been suspected.

Jorgenson and Brewbaker (1927) found midparent-hybrid correlations intermediate between those reported here and those of Gama and Hallauer. In their experiment, trait vs. trait correlations were 0.50 for yield, 0.58 for EL, and 0.63 for ED. The multiple correlation coefficient of yield on five midparent traits was 0.61. The ten inbreds examined by Jorgenson and Brewbaker were all derived from the same variety (Silver King White Dent), which suggests the possibility that midparent-hybrid correlations may be higher among lines that are closely related. Inbreds suitable for use on the northern fringe of the corn growing region, such as those examined in this research, have been rigorously selected for early maturity and, for this reason, may also be rather closely related.

Nilsson-Leissner (1927) also calculated midparent-hybrid correlations in a group of inbreds that included both dent and flint types. While the yield vs. yield correlation in the dents ($r=0.19$) was similar to that found by Gama and Hallauer, the same correlation in the flints ($r=0.74$) was almost identical to that found in this research. Nilsson-Leissner's multiple correlation between yield and five midparent traits was also quite high in his flint material ($r=0.82$). If midparent-hybrid correlations in flint material are in fact stronger than in dents, then midparent-hybrid relationships in early genotypes may also be strong by virtue of the substantial flint ancestry common in early genotypes.

5. SUMMARY AND CONCLUSIONS

The killing frost which occurred at Carman prior to grain maturity in many plots severely restricted variation in grain filling and growth period duration and resulted in substantially reduced yields at Carman. Since yield potentials for many genotypes were not realized at Carman, the data obtained at that location was felt to be of little value in assessing the relative importance of the traits examined in determining final grain yield.

A comparison of kernel weights and of percent moistures at black layer maturity between the two locations in some of the inbreds led to the conclusion that black layer formation had been induced "prematurely" by the cool weather in the weeks preceding frost at Carman. Because this can occur, it is important that researchers accurately determine whether physiological maturity has been reached, especially in studies dealing with the relationship between yield and other plant characters. An example of the dangers of not adequately considering maturity factors can be found in the work of Schuster et al. (1979) who reported an extensive study in Europe using inbreds and hybrids that varied widely in maturity. Because they obtained a negative correlation between grain yield and the length of the vegetative period, they concluded that early hybrids outyield late hybrids in many cases. However, an examination of their data reveals that grain moisture content at harvest ranged from 24.2% to 46%. We can only speculate from the data available to us, but

it seems likely that a substantial number of their plots did not reach normal physiological maturity prior to harvest or to frost. In this case, we would expect that later maturing genotypes would suffer greater yield losses than those that were able to realize their yield potential more completely. While a negative relationship between VPD and yield might be expected under the conditions of this experiment, we should not conclude that this is generally the case in corn. In fact, we might expect to find the opposite relationship if the same genotypes were grown in an environment that allowed all plots to mature normally.

Black layer formation seems to be an adequate indicator of maturity in plants maturing under favorable environmental conditions. Under low temperature conditions, however, the formation of black layers does not necessarily mean that the kernels have reached their maximum potential size. Researchers working in corn in short-season areas should be aware of this limitation on the use of black layer formation as an indicator of physiological maturity.

Of the traits examined, hybrid yield was most closely related to GPD which should not be extended beyond current levels in this environment. Of the three filling components of yield (FPD, FR, and KN), FPD was most closely related to yield, but it would be difficult to extend FPD because of the close correlation between FPD and GPD. It may be possible to maintain GPD at present levels while extending FPD at the expense of VPD, but yield advances obtained in this fashion will probably be relatively minor.

Since there is little room for manipulation of FPD, major yield advances must be achieved by increasing FR per plant, which is defined by FR per kernel and KN per plant. Of these two traits, only KN was significantly correlated with yield in the material examined in this experiment. The correlation between KN and FR was not significantly different from zero, so increases in KN should not be offset by decreases in FR.

It is proposed that an increase in FR per plant will lead to increased assimilation through a decrease in feedback inhibition on photosynthesis during the filling period. Further experimentation would be desirable to determine the validity of this proposal.

Moisture content of the grain at harvest was negatively related to KN when GPD was held constant. Thus, a breeding program that attempted to achieve yield increases through an increase in KN would probably also produce beneficial effects on HM.

Data presented here indicates that a substantial proportion of variation in several hybrid traits can be explained by variation in corresponding midparent traits in the material examined. In addition, a large proportion of variation in hybrid yields can be explained by several different combinations of midparent variables. This is in contradiction to most conclusions of other researchers who worked primarily with dent genotypes adapted to the Corn Belt in the United States. The possibility that midparent-hybrid relationships are closer in early genotypes deserves more extensive investigation.

Multiple linear regression of hybrid yields on midparent traits indicates that yield advances might be obtained by selecting inbred parents that are either high yielding or have a large number of kernels. Since the harvest moisture content of hybrids is negatively related to KN in both hybrids and midparents, the most appropriate goal for a corn breeding program in Manitoba, using material of the type examined here, appears to be the development of inbreds and hybrids having a large number of kernels.

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7. APPENDIX

APPENDIX TABLE 1. An example of analysis of variance combined over two locations

(a) Analysis of variance for VPD of Winnipeg hybrids

Source	df	MS	F
Hybrids	8	2748.52	6.67**
Blocks	1	33.62	0.08
Error	8	411.85	
Total	17		

(b) Analysis of variance for VPD of Carman hybrids

Source	df	MS	F
Hybrids	8	2051.82	12.56**
Blocks	1	1285.43	7.87*
Error	8	163.41	
Total	17		

(c) Analysis of variance for VPD in hybrids combined over two locations

Source	df	MS	F
Hybrids(H)	8	4236.73 ¹	14.73**
Locations(L)	1	78993.00 ²	119.78**
Interaction (HXL)	8	563.45	1.96
Blocks in locations	2	659.50 ³	
Pooled error	16	287.63 ³	
Total	35		

¹Tested against pooled error.

²Tested against blocks in locations.

³Pooled values from analyses in the two locations.

*,** significant at the 5% and 1% levels of significance, respectively.

APPENDIX TABLE 2. Variance ratio tests for equality of experimental error variances between two locations for ten traits in nine hybrids

Trait	Mean square errors			F ¹
	Winnipeg	Carman	Pooled	
VPD	411.85	163.41	287.63	2.52
FPD	2473.28	135.19	1304.24	18.29**
GPD	1515.18	6.50	760.84	233.21**
FR	0.09 ²	0.25 ²	0.17 ²	2.78
KN	1198.33	481.73	840.03	2.49
KW	259.22	357.73	308.48	1.38
EL	10.98	19.58	15.28	1.78
ED	0.58	0.57	0.57	1.02
HM	1.28	2.66	1.97	2.08
YIELD	12450.54	5713.01	9081.77	2.18

¹F-ratio obtained by dividing the smaller mean square into the larger.

** mean squares differ at the 1% level of significance.

²X 10⁻³

APPENDIX TABLE 3. Variance ratio tests for equality of experimental error variances between two locations for ten traits in six inbreds

Trait	Mean square errors			F ¹
	Winnipeg	Carman	Pooled	
VPD	90.75	59.08	74.91	1.54
FPD	135.41	56.14	95.78	2.41
GPD	90.61	102.70	96.65	1.13
FR	0.02 ²	0.14 ²	0.08 ²	7.00
KN	1380.59	1100.71	1240.65	1.25
KW	143.80	35.14	89.47	4.09
EL	25.48	46.00	35.74	1.80
ED	0.60	0.51	0.55	1.18
HM	0.57	1.76	1.16	3.10
YIELD	1793.86	340.28	1067.07	5.27

¹F-ratios obtained by dividing the smaller mean squares into the larger.

²X 10⁻²

APPENDIX TABLE 4. Analysis of variance for yield of Winnipeg hybrids

(a) One 10-plant yield observation per plot.

Source	df	SS	MS	F	F _{.05}
Hybrids	8	300730.8	37591.3	3.02	3.44
Blocks	1	57155.8	57155.8	4.59	5.32
Error	8	99607.2	12450.9		
(Non-additivity)	(1)	(47509.3)	(47509.3)	(6.38*)	(5.59)
(Remainder)	(7)	(52097.9)	(7442.6)		
Total	17	457493.8			

(b) Two 5-plant yield subsamples per plot.

Hybrids	8	150368.8	18796.1	12.83** (3.02) ¹	2.51 (3.44)
Blocks	1	28555.4	28555.4	19.49** (4.59) ¹	4.41 (5.32)
Hybrids X blocks	8	49815.6	6227.0	4.25**	2.51
Error	18	26379.0	1465.5		
Total	35	255118.7			

(c) One 10-plant yield observation per plot with hybrids 43X37 and 43X72 omitted.

Hybrids	6	199238.7	33206.5	18.75**	4.28
Blocks	1	5261.3	5261.3	2.97	5.99
Error	6	10626.8	1771.1		
(Non-additivity)	(1)	(3018.4)	(3018.4)	(1.98)	(6.61)
(Remainder)	(5)	(7608.4)	(1521.7)		
Total	13	215126.8			

¹Main effects of hybrids and blocks tested against interaction mean square. All other F-ratios result from tests against mean square error (or mean square remainder for Tukey's test).

*,** Significant at the 5% and 1% levels of significance, respectively.

APPENDIX TABLE 5. Inbred means for 11 traits in six inbreds grown at Carman

INBRED	VPD	FPD	GPD	FR	KN	KW	EL	ED	PMBLM	HM	YIELD
CK43	1364b ¹	853a	2217a	0.29ab	242a	154b	144bc	28.4a	31.8	20.5	338a
CK52	1364b	898b	2262b	0.31ab	306a	154b	154c	28.9a	37.2	33.5c	470c
CK59	1364b	948c	2312cd	0.29ab	245a	158b	112a	37.5b	--	39.0de	362ab
CK48	1406c	916b	2322d	0.20a	283a	149b	107a	35.4b	--	41.1e	400b
CM37	1290a	994d	2284bc	0.41b	252a	219c	123ab	36.5b	44.4	35.6cd	518d
CM72	1396c	901b	2296cd	0.22a	511b	125a	125ab	37.6b	40.6	29.9b	571e
Mean	1364	918	2282	0.29	306	160	128	34.0	38.5	33.3	443
SE ²	7.7	7.5	10.1	0.04	33.2	5.8	6.8	0.71	--	1.33	18.4
F-ratio ³	55.7**	82.4**	28.4**	8.0*	19.3**	55.8**	14.6**	71.6**	--	62.3**	49.5**

¹Means in the same column that are followed by the same letter do not differ at the 5% level of significance as determined by the Student-Newman-Keuls procedure.

²Standard error of the difference between two means.

³From the analysis of variance: F = MS(inbreds)/MSE

*,** significant at the 5% and 1% levels of significance, respectively.

APPENDIX TABLE 6. Hybrid means for 11 traits in nine hybrids grown at Carman

HYBRID	VPD	FPD	GPD	FR	KN	KW	EL	ED	PMBLM	HM	YIELD
43X48	1280abc ¹	1032bc	2312c	0.40bc	484a	228b	159b	39.5b	--	30.2ab	1035a
43X37	1247ab	1011ab	2258a	0.42c	481a	211ab	175c	37.1a	39.6	35.2ab	951a
43X72	1322cd	990a	2312c	0.36b	528ab	204ab	179c	38.9b	--	34.2ab	973a
52X48	1290bc	1021abc	2312c	0.37bc	539ab	225b	180c	41.5bc	--	35.1ab	1121a
37X52	1257ab	1054cd	2312c	0.40bc	542ab	225b	199d	40.2b	--	35.3ab	1128a
72X52	1280abc	1012ab	2291b	0.41bc	563ab	206ab	184c	40.4b	35.6	29.9ab	1083a
48X59	1280abc	1042bcd	2322d	0.38bc	528ab	217b	148ab	44.2d	--	33.1ab	1074a
37X59	1235a	1071d	2306c	0.39bc	551ab	210ab	152ab	44.0d	--	29.4a	1029a
72X59	1332d	982a	2314c	0.29a	596b	147a	142a	43.0bc	--	36.2b	829a
Mean	1280	1024	2304	0.38	535	208	169	41.0	37.6	33.2	1025
SE ²	12.8	11.6	2.5	0.02	21.9	18.9	4.4	0.75	--	1.63	75.6
F-ratio ³	12.6**	12.6**	112.7**	11.1**	5.4*	3.4	37.2**	20.3**	--	5.3*	3.2

¹ Means in the same column that are followed by the same letter do not differ at the 5% level of significance as determined by the Student-Newman-Keuls procedure.

² Standard error of the difference between two means.

³ From the analysis of variance: $F = MS(\text{hybrids})/MSE$

*,** significant at the 5% and 1% levels of significance, respectively.

APPENDIX TABLE 7. Simple correlations for ten variables in six inbreds grown at Carman

	FPD	GPD	FR	KN	KW	EL	ED	HM	YIELD
VPD	-.64*	.26	-.92**	.46	-.92**	-.15	-.01	.03	-.17
FPD		.58*	.54	-.22	.74**	-.51	.66*	.67*	.33
GPD			-.29	.20	-.04	-.80**	.83**	.87**	.23
FR				-.41	.80**	.32	-.05	-.06	.13
KN					-.60*	.03	.34	-.15	.73**
KW						-.08	.08	.20	.07
EL							-.80**	-.66*	.04
ED								.58*	.39
HM									.07

*,** significant at the 5% and 1% levels of significance, respectively.

APPENDIX TABLE 8. Simple correlations for ten variables in nine hybrids grown at Carman

	FPD	GPD	FR	KN	KW	EL	ED	HM	YIELD
VPD	-.83**	.43	-.75**	.39	-.58*	-.19	.04	.46	-.45
FPD		.14	.53*	-.18	.58*	.40	.34	-.50*	.57*
GPD			-.49*	.39	-.08	-.28	.63**	-.00	.13
FR				-.52*	.69**	.54*	-.42	-.48*	.57*
KN					-.63*	-.13	.57*	.10	-.17
KW						.47*	-.18	-.37	.85**
EL							-.58*	.11	.53*
ED								-.18	.11
HM									-.38

*,** significant at the 5% and 1% levels of significance, respectively.