Early maturity in sweet corn (Zea mays), especially for northern U.S. production areas is an important breeding objective. In northern areas, early maturing fresh market sweet corn usually commands the highest prices. Early maturing sweet corn, when planted early in the season, can escape certain diseases such as common rust (Puccinia sorghi) and maize dwarf mosaic virus and also the high temperatures of July and August (Alessi and Power, 1975; Tracy, 1999). In sweet corn production, harvestable maturity is defined by grain moisture associated with optimal flavor, tenderness, and texture (Tracy, 1999). Optimal moisture at harvest in sweet corn is between 70% and 75% (Huelsen, 1954). The growing period between germination and harvest maturity can be divided into two growth phases, vegetative, from emergence to pollen shed; and reproductive, from silk emergence to maturity (Ritchie et al., 1997). In temperate sweet corn, the length of the vegetative phase (flowering time) has a greater role in determining maturity than does the length of the reproductive phase (Huelsen, 1954). There is a relative lack of literature on the inheritance of flowering time in sweet corn, but there have been many studies in field corn. Early corn, for use as grain or silage is important in the United States. The United States leads in producing the greatest amount of early corn for grain with 24 million hectares (Troyer, 1994). Wide variability in length of the preflowering period results in the most important basis of selection for early maturity (Dessureaultt et al., 1948). Corn has a determinate growth pattern and the vegetative stage ends with the initiation of the terminal inflorescence (Kisselbach, 1949). Flowering date is also associated strongly with plant height because internode formation ceases at floral initiation. Therefore, flowering corn are usually shorter (Troyer, 1990; Troyer and Larkins, 1985). With selection for early flowering, Troyer and Larkins (1985) found that plant height decreased 23 mm/cycle.

Selection for early pollen shed moved the mean of two early populations from 69.8 to 68.0 d and 69.9 to 68.1 d in three cycles of selection for a decrease of 0.6 d/cycle (Beil, 1975). This selection program for early pollen shed had no apparent effect on the level of genetic diversity in the population (Beil, 1975).

In a selection study for early flowering on 18 adapted F2 populations, Troyer (1986) reported a decrease of 0.6 d/cycle in flowering date, 0.6% cycle in grain moisture, 2.4 cm/cycle in plant height, and 0.1 d/cycle silk delay, and a yield increase of 364 kg·ha–1 per cycle, with no effect on stalk breakage. In a similar experiment on adapted F2 populations, gain per cycle averaged a reduction of 1.2 d to flower, 1.0% grain moisture, 7.0 cm plant height, 0.1 d silk delay, and 238 kg·ha–1 yield, and an increase of 0.5 ear per 100 plants, and 3.7% stalk breakage (Troyer, 1986). In a study on selection response to early flowering for four cycles in adapted synthetics, reduction in days to flowering averaged 0.8 d/cycle, with reductions of 10 g·kg–1 grain moisture, 4.0 cm plant height, 2.7 cm ear height, 0.2 d silk delay, and 0.15 Mg·ha–1 (3%) yield, and an increase of 4% broken stalks (Troyer, 1990). The decrease in yield due to selection displayed close association with decrease in plant size, which probably reduced photosynthetic capacity (Troyer, 1990).

The rate of maturation in field corn results from complex interactions of genetic and environmental factors and is affected by the photoperiod response of corn (Troyer, 1994). Inheritance of flowering time in corn is controlled quantitatively. The genes involved act in an additive manner and heterosis complicates studying the inheritance of flowering time (Troyer, 1994). Most studies agree that more than two genes are responsible for the timing of silking and pollen shed with some evidence of partial to complete dominance and epistasis (Giesbrecht, 1960a, 1960b). On average, days to flower decreases by as much as 10% due to heterosis (Troyer, 1994). Vigor accelerates flowering time. Inbreeding decreases vigor and delays flowering time (Troyer, 1994).

Understanding heterotic responses among germplasm sources is useful in determining the best method for introgressing germplasm with desirable traits into populations that are agronomically and

Heterosis for Flowering Time and Agronomic Traits among Early Open-pollinated Sweet Corn Cultivars

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ABSTRACT. Heterosis in corn (Zea mays L.) usually results in earlier flowering, larger plants, and increased yield. In extremely early sweet corn the effect of heterosis on flowering time may be reduced or eliminated due to developmental and physiological requirements for vegetative growth before the transition to reproductive phase. The objective of this study was to determine the level of heterosis and the combining ability for flowering time and other agronomic traits in a diallel cross of six very early open-pollinated sweet corn cultivars. The diallel was grown in 1995 and 1996. Hybrids and parents averaged over hybrids differed for silk date, plant height, ear height, 10-ear weight, ear length, and 100-kernel weight but did not differ for row number and ear width. Heterosis for silk date was significant, but the difference between parents and hybrids was very small, 0.5 day. No hybrids were earlier than the earliest parent, and average midparent heterosis was –0.8%. In contrast midparent heterosis was significant and relatively high for 100-kernel weight (10.0%), ear length (12.9%), ear height (8.6%), plant height (9.0%), and 10-ear weight (28.2%). The traits with low heterosis had very high general combining ability/specific combining ability ratios while these ratios were much smaller in traits with high heterosis. Heterosis for many of the traits, including 10-ear weight, was higher than published values. Conversely, heterosis for flowering time was small, compared to other traits in this study and to published values for silk date, indicating that this extremely early germplasm may be at or near the limit for flowering time under the photoperiod and temperatures typical of summer in Madison, Wis. (43.05°N, 89.31°W).
horticulturally acceptable (Widstrom et al., 1993). Heterosis in maize increases with increased genetic divergence of the parents but decreases when parents are extremely divergent (Moll et al., 1962, 1965).

At the University of Wisconsin-Madison we have collected a large number of open-pollinated sweet corn cultivars (Revilla and Tracy, 1995). Of these, we identified six early flowering cultivars. In Madison, the earliest of these, ‘Yukon Chief’, flowers 49 d after planting (DAP) and attains a height of only 72 cm. This is roughly one week earlier than ‘Sugar Buns’, a very early commercial sweet corn hybrid we use as an early check in our hybrid trials. We wanted to determine if hybrids among these six very early cultivars would exhibit heterosis for earliness or are approaching a limit for earliness. The objective of this study was to determine the level of heterosis and the combining ability for flowering time and other agronomic traits among the six very early cultivars.

Materials and Methods

A diallel cross (Method I of Griffing, 1956) was made with six open-pollinated sweet corn cultivars in 1994. The cultivars were ‘Yukon Chief’, ‘Golden Early Market’, ‘Dorinny’, ‘Early June’, and ‘Sweet Baby Blue’ (Revilla and Tracy, 1995), and ‘Golden Midget’ from Garden City Seed Company, Victor, Montana. Cultivars were chosen due to their earliness based on evaluation of ~50 open-pollinated cultivars (Revilla and Tracy, 1995). For each cross, pollen from 25 plants from one cultivar was bulked. This pollen was used to pollinate 25 plants from the second cultivar. This was done twice so at least 50 plants from each cultivar were used to make each cross. The resulting 15 hybrids, 15 reciprocals, and 6 parents were entries in the diallel. On 30 May 1995 and 30 May 1996 seeds from each of the hybrids and parents were planted in a Plano silt loam (fine-silty, mixed, mesic Typic Argiudolls) soil at the West Madison Agricultural Research Station. The experimental design was a randomized complete block with four replications in each year.

To reduce interplot competition, plots were four rows with data collected on the center two rows. The rows were over- planted with 30 seeds per row and thinned to a stand of 15 plants per row both years. The rows were 3.5 m long with 76 cm between rows. The final population density was 44,500 plants/ha. Weeds were controlled with 2.3 L·ha⁻¹ cyanazine, 2.3 L·ha⁻¹ alachlor, cultivation, and hand weeding.

The following traits were recorded before harvest: silk date defined as days after planting to 50% silking (DAP), plant height (from the soil to the ligule of the leaf subtending the tassel), and ear height (from the soil to the ligule of the leaf subtending the ear). Plant and ear heights of 10 plants per plot were measured. After all entries had completed dry matter accumulation (black layer formation), all ears from the center two rows were harvested and husked. From each plot, 10 representative ears were dried at 52 °C until constant weight. Numbers of rows per ear, ear length, ear diameter, 10-ear weight, and 100-kernel weight were recorded.

Analysis of variance was performed for each of the eight traits combined across years. Years and replications within years were considered random and all other effects were fixed. SAS was used for combined analysis of variance (SAS, Cary, N.C.). For each year, heterosis, combining ability, and mean comparisons for the parents across hybrids were computed using the diallel analysis of Burow and Coors (1994). Spearman rank correlation coefficients were calculated to determine whether significant year × combination effects were due to changes in magnitude or rank (Little and Hill, 1978).

Results and Discussion

All traits differed over years. Parents did not differ for ear width, but did so for all other traits. Genotypes, combinations (parents and all hybrid combinations), and hybrids differed for all traits. Reciprocals within hybrids differed for plant height, ear height, and 100-kernel weight. The contrast, parents versus hybrids, was significant for silk date, plant height, ear height, 10-ear weight, ear length and 100-kernel weight. Though there were significant year × combination effects, rank correlations (silk date rₛ = 1.00, 10-ear weight rₛ = 0.73, row number rₛ = 0.64, 100-kernel weight rₛ = 0.86, n = 36) were high over the two years and the differences were due largely to changes in magnitude. Therefore, data averaged over years are reported.

In this study, DAP to midsilk (50% silking) were used to determine midparent heterosis for flowering time. Mean silk date of parents averaged over hybrids was 53.1 DAP. For silk date averaged over hybrids, ‘Yukon Chief’ resulted in the earliest hybrids (51.4 DAP) and ‘Golden Midget’ the latest (54.4 DAP) (Table 1). The earliest parent per se was ‘Yukon Chief’ (48.8 DAP) and the latest parent was ‘Golden Midget’ (56.2 DAP). ‘Yukon Chief’ × ‘Dorinny’ was the earliest hybrid (48.5 DAP). The latest hybrid was ‘Sweet Baby Blue’ × ‘Golden Midget’ (55.6 DAP).

For silk date over all parents, average midparent heterosis equaled –0.8%. Negative heterosis indicates earlier flowering. This is smaller than heterosis observed for silk date (~3.0%) by Revilla and Tracy (1997). Averaged over hybrids, the greatest midparent heterosis for silk date was −1.7% for ‘Early June’ and −1.0% for ‘Sweet Baby Blue’ (Table 1). ‘Yukon Chief’ averaged the least

Table 1. Mean silk date of 15 sweet corn population hybrids (above diagonal), six parent populations (on diagonal), six parent populations averaged over hybrids (left margin), percent heterosis (below diagonal), and average heterosis for each parent (bottom margin) from the Design 1 experiment grown in 2 years.

| Sweet corn population | YC | GEM | DOR | EJ | SBB | GM | Mean |
|----------------------|----|-----|-----|----|-----|----|------|
| YC                   | 48.8® | 52.0 | 48.5 | 52.2 | 51.5 | 53.0 | 51.4® |
| GEM                  | 0.7 | 54.5 | 52.7 | 53.6 | 54.4 | 55.2 | 53.6 |
| DOR                  | −3.6 | −0.8 | 51.9 | 53.0 | 51.9 | 53.7 | 52.0 |
| EJ                   | 1.0 | −1.8 | −0.6 | 54.7 | 55.1 | 54.4 | 53.7 |
| SBB                  | −1.0 | −0.9 | −3.1 | 0.2 | 55.2 | 55.6 | 53.7 |
| GM                   | 1.0 | −0.2 | −0.6 | −2.0 | −0.2 | 56.2 | 54.4 |
| Mean                 | −0.4 | −0.6 | −0.9 | −1.7 | −1.0 | −0.4 | --- |

®YC = Yukon Chief, GEM = Golden Early Market, DOR = Dorinny, EJ = Early June, SBB = Sweet Baby Blue, GM = Golden Midget.

®LSD(0.05) = 1.0 for comparisons among hybrid and parent mean silk dates.

®LSD(0.05) = 0.5 for comparisons among parent mean silk dates averaged over hybrids.
amount of heterosis for silk date (–0.4%). Though there is a great deal of literature on midparent heterosis for yield, there is relatively little on traits such as silk date. In pearl millet, midparent heterosis for earliness was reported as large as –10.8% (negative being indicative of earlier flowering) and as little as 13.7% (Chowdari et al., 1998). Castro et al. (1968) found that in genetically diverse races of maize there was –1.6% average midparent heterosis for days to flower. Widstrom et al. (1993) reported –2.7% heterosis for days to 50% pollen. In our experiment midparent heterosis for silk date was greatest in hybrids between ‘Dorinny’ x ‘Yukon Chief’ and ‘Sweet Baby Blue’ x ‘Dorinny’, –3.6% and –3.1% (Table 1). Hybrids ‘Yukon Chief’ x ‘Early June’ and ‘Yukon Chief’ x ‘Golden Midget’ exhibited the least heterosis (1.0%).

Mean plant height among hybrids was 92.4 cm. When averaged over hybrids ‘Golden Early Market’ (101.1 cm) resulted in the tallest hybrids, and ‘Yukon Chief’ the shortest (85.1 cm) (Table 2). For parents, the tallest was ‘Golden Early Market’ (104.2 cm), and the shortest was ‘Sweet Baby Blue’ (62.0 cm). Among hybrids ‘Golden Early Market’ x ‘Early June’ plants were tallest (109.6 cm), and ‘Yukon Chief’ x ‘Sweet Baby Blue’ plants were shortest (76.6 cm).

Average midparent heterosis for plant height was 9.0%. This is comparable to what Revilla and Tracy (1997) found for average heterosis for plant height (7.9%). ‘Sweet Baby Blue’ had the greatest average heterosis (16.0%), and ‘Dorinny’ had the lowest (6.5%) (Table 2). The hybrids ‘Golden Midget’ x ‘Sweet Baby Blue’ and ‘Sweet Baby Blue’ x ‘Early June’ had the greatest midparent heterosis with 17.9% and 17.8%, respectively. ‘Early June’ x ‘Dorinny’ had the least heterosis for plant height (1.0%). Only 4.4% midparent heterosis for plant height was observed among insect-resistant maize populations, (Widstrom et al., 1993). Over six cycles of selection between sweet corn x tropical corn, midparent heterosis for plant height ranged from 14.3% to 21.8% (Rubino and Davis, 1990), and from inbred crosses 39.4% was observed (Zanoni and Dudley, 1989).

Mean 10-ear weight for hybrids was 449.7 g. Averaged over hybrids ‘Golden Early Market’ resulted in the heaviest 10-ear weight (532.1 g), and ‘Golden Midget’ had the lightest (413.4 g) (Table 3). While not a direct measurement of grain yield, this value for 10-ear weight exceeds those reported for grain yield in open-pollinated field corn cultivar diallels. For example, average midparent heterosis for yield in temperate synthetic cultivars equaled 11% (Hallauer and Eberhart, 1966), 14% for semi-exotic varieties (Eberhart, 1971), 20% for Caribbean populations (Moll et al., 1962), 20.1% among Spanish cultivars (Ordas, 1991), 22.5% in insect resistant corn populations (Widstrom et al., 1993), and 24.8% in genetically diverse races (Castro et al., 1968). In a similar study on heterotic patterns of full season open-pollinated sweet corn cultivars, average midparent heterosis for yield was 29.2% (Revilla and Tracy, 1997). Revilla and Tracy (1997) suggested that the sweet corn cultivars might have been more inbred than the field corn

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### Table 2. Mean plant heights of 15 sweet corn population hybrids (above diagonal), six parent populations (on diagonal), six parent populations averaged over hybrids (left margin), percent heterosis (below diagonal), and average heterosis for each parent (bottom margin) from the Design 1 experiment grown in 2 years.

| Sweet corn population | YC | GEM | DOR | EJ | SBB | GM | Mean |
|-----------------------|----|-----|-----|----|-----|----|------|
| YC                    | 72.6 | 93.4 | 85.2 | 84.4 | 76.6 | 86.1 | 85.1* |
| GEM                   | 5.6  | 104.2 | 102.2 | 109.6 | 96.2 | 104.2 | 101.1 |
| DOR                   | 5.8  | 6.1  | 88.5 | 92.1 | 86.4 | 93.2 | 91.8  |
| EJ                    | 1.3  | 10.6 | 1.0  | 94.0 | 91.9 | 95.7 | 94.7  |
| SBB                   | 13.8 | 15.8 | 14.8 | 17.8 | 62.0 | 89.0 | 88.0  |
| GM                    | 6.6  | 7.9  | 5.1  | 4.6  | 17.9 | 89.0 | 93.7  |
| Mean                  | 6.6  | 9.2  | 6.5  | 7.0  | 16.0 | 8.4  |       |

*YC = Yukon Chief, GEM = Golden Early Market, DOR = Dorinny, EJ = Early June, SBB = Sweet Baby Blue, GM = Golden Midget.

### Table 3. Mean 10-ear weights of 15 sweet corn population hybrids (above diagonal), six parent populations per se (on diagonal), six parent populations averaged over hybrids (left margin), percent heterosis (below diagonal), and average heterosis for each parent (bottom margin) from the Design 1 experiment grown in 2 years.

| Sweet corn population | YC | GEM | DOR | EJ | SBB | GM | Mean |
|-----------------------|----|-----|-----|----|-----|----|------|
| YC                    | 279.1 | 521.1 | 410.8 | 405.6 | 381.9 | 373.8 | 418.6* |
| GEM                   | 21.5 | 578.9 | 560.1 | 561.1 | 518.1 | 499.9 | 532.1 |
| DOR                   | 22.1 | 15.2 | 393.6 | 483.0 | 422.5 | 399.1 | 455.1 |
| EJ                    | 25.0 | 18.7 | 27.1 | 366.1 | 414.8 | 382.0 | 449.3 |
| SBB                   | 48.7 | 27.4 | 34.4 | 38.1 | 234.5 | 423.5 | 429.9 |
| GM                    | 33.2 | 16.1 | 18.1 | 17.8 | 59.5 | 282.1 | 413.4 |
| Mean                  | 30.1 | 19.8 | 23.4 | 25.4 | 41.6 | 41.6 | 30.0  |

*YC = Yukon Chief, GEM = Golden Early Market, DOR = Dorinny, EJ = Early June, SBB = Sweet Baby Blue, GM = Golden Midget.

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cultivars of other studies. In tropical maize germplasm, the greatest average midparent heterosis for yield reported was 17.2%, 20.2% in transition and midaltitude maize germplasm (Vasal et al., 1992b), and 23.7% in subtropical maize germplasm.

'Sweet Baby Blue' had the greatest average heterosis for 10-ear weight (41.6%) (Table 3), and 'Golden Early Market' had the smallest average midparent heterosis (19.8%). 'Golden Midget' x 'Sweet Baby Blue' x 'Sweet Baby Blue' x 'Yukon Chief' had the greatest heterosis for 10-ear weight (59.5% and 48.7%, respectively). These values are much greater than many of the field corn values reported. 'Golden Early Market' had the lowest heterosis when crossed to 'Dorinny' and 'Golden Midget' at 15.2% and 16.1%, respectively.

Mean ear height among hybrids was 34.8 cm. Averaged over hybrids 'Golden Early Market' had the greatest ear height (39.5 cm), and 'Yukon Chief' the lowest (30.3 cm) (Table 4). Average midparent heterosis for ear height was 8.6%. Among insect-resistant populations, midparent heterosis for ear height was 3.7% (Widstrom et al., 1993), 5% in semi-exotic varieties (Eberhart, 1971), 11.5% to 23.9% among six cycles of selection in sweet corn x tropical maize (Rubino and Davis, 1990), and 49.1% among inbreds (Zanoni and Dudley, 1989). 'Sweet Baby Blue' x 'Yukon Chief' had the greatest average midparent heterosis at 16.8% (Table 4). 'Dorinny' had the smallest midparent heterosis for ear height (2.7%).

Mean row number over hybrids was 9.3 rows. The greatest row number averaged over hybrids was in 'Golden Early Market' hybrids (10.2 rows) (Table 4). The lowest was in 'Golden Midget' and 'Sweet Baby Blue' hybrids (9.0 rows). Average midparent heterosis for row number equaled –0.8%. 'Early June' had the greatest average midparent heterosis at 1.0% and 'Yukon Chief' had the smallest (–1.7%). Over six cycles of selection in sweet corn x tropical maize testcross, mean midparent heterosis ranged from –0.6% to 3.3% (Rubino and Davis, 1990), comparable to values in our study.

Mean ear length for hybrids was 13.1 cm. Averaged over hybrids, 'Golden Early Market' resulted in the longest ears (13.9 cm) and 'Yukon Chief' the shortest (12.4 cm) (Table 4). Average midparent heterosis for ear length was 12.9%. 'Sweet Baby Blue' had the greatest average midparent heterosis (21.6%) (Table 4). 'Golden Early Market' and 'Dorinny' had the smallest midparent heterosis for ear length (9.5%). Over six cycles of selection in sweet corn x tropical maize study, mean midparent heterosis for ear length ranged from 14.4% to 44.7% (Rubino and Davis, 1990), and in pearl millet, it ranged from –10.4% to 46.8% (Chowdari et al., 1998).

Mean ear width for hybrids was 3.5 cm. When averaged over hybrids 'Golden Early Market' had the widest ears (3.8 cm) and 'Yukon Chief' the narrowest ears (3.4 cm). Average midparent heterosis for ear width was 3.1%. 'Sweet Baby Blue' had the greatest average heterosis (7.6%), and 'Yukon Chief' had the least (–2.5%) (Table 4). In pearl millet, midparent heterosis for ear width ranged from –3.5% to 29.5% (Chowdari et al., 1998).

Mean 100-kernel weight for hybrids was 19.0 g. When averaged over hybrids, 'Dorinny' had the heaviest kernels (20.9 g) and 'Sweet
Baby Blue’ had the lightest (17.5 g) (Table 4). Average midparent heterosis for 100-kernel weight was 10.0%. ‘Sweet Baby Blue’ had the greatest average midparent heterosis (12.4%), and ‘Yukon Chief’ had the smallest (7.8%) (Table 4).

Among parents, ‘Golden Early Market’ had the largest means for most of the traits. ‘Golden Early Market’ produced the greatest means averaged over hybrids for six of the eight traits analyzed. Also for six of the eight traits this cultivar exhibited the greatest means among parents. For seven of eight traits, the hybrid that exhibited the greatest means among hybrids included ‘Golden Early Market’ as a parent. The 10-ear weight of ‘Golden Early Market’ exceeded the next closest parent by 185 g. ‘Golden Early Market’ performed well per se, and in hybrids but exhibited low heterosis because parent means were high. In contrast, ‘Golden Midget’ performed poorly. For four of the eight traits ‘Golden Midget’ had the smallest means averaged over hybrids. ‘Sweet Baby Blue’ exhibited the lowest means for six of the eight traits analyzed.

These six populations are maintained as open-pollinated varieties, however ‘Sweet Baby Blue’ may be more inbred than the other populations. ‘Sweet Baby Blue’ had small means for plant height, ear height, 10-ear weight, ear width, and 100-kernel weight but had the largest midparent heterosis for plant height, ear height, 10-ear weight, ear length, width, and 100-kernel weight. Inbreeding would explain the high heterosis displayed in ‘Sweet Baby Blue’ hybrids and the low per se performance.

General combining ability (GCA) was significant for all eight traits (Table 5). This corresponds to other experiments (Widstrom et al., 1992a, 1992b, 1993) where GCA effects for corn cultivars are often significant in breeding experiments. Specific combining ability (SCA) was also significant for all eight traits (Table 5). This is in contrast to the research done on open-pollinated corn cultivars where SCA is rarely of great importance (Vasal et al., 1992a, 1992b, 1993; Widstrom et al., 1993). While SCA was significant for all traits, the GCA mean squares were ~30 to 40 times the SCA mean squares for silk date, row number and 100-kernel weight indicating that the SCA is relatively unimportant for these traits (Table 5).

There were small significant differences for silk dates between the parents and the hybrids (Table 6). Over all hybrids in this study we observed heterosis for silk date. Average silk date for hybrids (53.1 DAP) was earlier than average silk date for parents (53.6 DAP). However no hybrids were earlier than the earliest parent. Compared to the other traits with significant differences between parents and hybrids, the difference for silk date between the parental and hybrid means and heterosis were very small. There was no significant difference between parents and hybrids for row number and ear width. There were significant differences between hybrids and parents for plant height, ear height, 10-ear weight, ear length, and 100-kernel weight along with significant heterosis for these traits.

While heterosis for silk date was significant, the magnitude was smaller than observed in other studies and for the other heterotic traits in this study such as 10-ear weight and plant height. None of the hybrids were earlier than ‘Yukon Chief’ indicating that ‘Yukon Chief’ may be near the limit for earliness imposed by developmental or physiological constraints.

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