# Maternal Inheritance of Sugar Concentration

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### ABSTRACT

**Sugar concentration in sugarbeet (*Beta vulgaris* L.) root is controlled by the additive effects of numerous polygenes; hence, the possibility of increase due to heterosis is small. High sugar content must be expressed in all cultivar components, namely male sterile lines and pollinators. Field trials showed that sugar content in the progeny obtained from crossing high sugar content (Z-type) and high yielding, low sugar lines (E-type) depends to a greater extent on the maternal rather than the paternal component. This maternal effect can be used in developing cultivar components and when determining hybrid composition.**

**Additional Key Words:** *Beta vulgaris,* heterosis, plant genetics, selection, sugarbeet

Maternal inheritance is the transmission of traits exclusively from the maternal parent of a cross or an advantage of the female parent in transferring some quantitative traits to its progeny (Kerner, 1881). Pseudogamy is a complete lack of paternal genotype contribution to the progeny and is most frequently encountered in crosses involving taxonomically distant parents (Focke, 1881; Opeña and Lo, 1978). In animals and dioecious plants, maternal effects may be related to the presence of different allosomes (sex-linked inheritance; Morgan, 1914; Zhu and Weir, 1996). The most frequent maternal inheritance mechanism is dependent upon genes located in mitochondria (mtDNA), or plastids (plDNA) (Imai, 1936). Male sterility, controlled by plasmotype and nuclear gene interactions, is the basis for commercial sugarbeet hybrid production (Owen, 1945).

The impact of maternal effects on quantitative traits is complex and the influence of plasmotype often is significant. Cytoplasm genotype (plasmotype, cytotype) may influence the expression of nuclear genes (Byers et al., 1997). In many species, the initial phases of ontogeny and embryo and/or seedling growth are dependent upon endosperm tissue, to which the maternal contribution is twice that of the paternal parent. In species without endosperm in the seed, including beet, nutritive tissue is of maternal origin (perisperm). Not only nutrients can be passed from a parent plant to seed, but also some pathogens, toxins, hormones, and enzymes. All of these may affect an offspring, becoming evident in both the juvenile period (Weis et al., 1987; Tucic and Avramov, 1996) and in further ontological stages (for a review see Górnik and Grzesik, 1998).

Kirkpatrick and Lande (1989) restricted the term 'maternal effect' to include only the expression of the traits not determined directly by genetic factors. Maternal effects of this type have been observed in morphological and chemical properties of cotton (*Gossypium* spp.) seed (Wu et al., 1995), and in protein, starch, and fat concentration in corn (*Zea mays* L.) seed (Letchworth and Lambert, 1998). Numerous examples of maternal effects have been documented in rice (*Oryza sativa* L.); they include resistance to chilling (Li et al. 1994), total protein and lysine concentration (Shi et al., 1996; Shi et al., 1998), amylose concentration (Shi et al., 1997), and seed size (Chenwu and Aihong, 1998). MacKenzie et al. (1995) observed a maternal effect for chlorsulfuron resistance in perennial ryegrass (*Lolium perenne* L.). Rossiter (1996) recognized that parents do not only serve as gene donors. Environmental factors, especially during the reproductive phase of the maternal parent, may cause a more or less permanent effect on the progeny phenotype. Thus, maternal effect (and also paternal at times) remains a special case of 'inherited environmental effects', observed  not only in animals but also in plants.

Research on the inheritance of sugar content in beet was initiated in 1908 by Andrilk et al. and continued by Vilmorin (1923), Stehlik (1933), Savitsky (1940), Culbertson (1942), and many others. The results of the research are not definitive, but the prevailing belief is that sugar concentration is a polygenic trait, primarily influenced by additive genetic factors that control anatomic characteristics (primarily root cell size), osmotic pressure, and metabolism related to sucrose synthesis. Only Powers et al. (1959) and, in some cases, Takebe and Izumiyama (1977) and MacLachlan (1972c) observed the presence of dominant genes and the occurrence of heterosis (or 'phenotypic dominance', according to Powers et al., 1959) for sugar content. Heritability estimates of sugar content fluctuate considerably, depending on the material investigated and the calculation method utilized. MacLachlan (1972a, 1972b, and 1972c) found heritabilities ranging from

0.19 to 0.60. Sugar content is a relatively stable trait; the coefficient of variability calculated by Savitsky (1940) ranged from 4.4 to 7.2 and was frequently ten times lower than the coefficient of variability for root weight, a trait with low heritability. A negative correlation between root weight (yield) and sugar content is commonly observed. Smith et al. (1973) reported a $-0.68$ correlation, which is inconsistent with the expression of heterosis observed in some hybrids (Powers et al., 1959; MacLachlan, 1972a). Sliwinska et al. (1999), reported that 75 to 90 % of mother roots with a higher than average sugar content produced progeny with a sugar content also higher than average.

Few papers report on the reciprocal crossing of high sugar content (Z-type) sugarbeet with high yield, low sugar (E type) genotypes. The results obtained by Savitsky (1940) from reciprocal crosses indicated the progeny produced on the Z-type parent had at least 0.4% higher sugar content than the progeny produced on the E-type parent. That clearly suggested a maternal effect. Similarly, Schlösser (1949) observed an impact of maternal cytoplasm on sugar content. According to Powers et al. (1959), sugar content in hybrids exhibiting heterosis was, in most cases, closer to the sugar content of the maternal parent; however, this pattern was not observed when the female parent had a much lower sugar content than that of the pollinator. The results obtained by Rush and Oldemeyer (in Powers et al., 1959) indicated a greater impact of the maternal component; the average differences in sugar content between hybrid progeny and the female parent and the pollen parent were 0.4 % and 0.6 %, respectively. However, more recent research (MacLachlan, 1972c) has not confirmed these observations.

The objective of this study was to examine the issue raised by these conflicting reports, and determine if a maternal effect on sugar concentration could be detected and used to enhance sugarbeet breeding efforts.

## MATERIALS AND METHODS

Roots of diploid multigerm sugarbeet representing extreme contrasts in sugar content were selected from breeding nurseries of the Kutnowska Hodowla Buraka Cukrowego (sugarbeet breeding company in Kutno, Poland) in 1995. Plants were crossed under tent insolators at the Smiłów Plant Breeding Station, southern Poland, in 1996. Twenty-eight contrastive pairs were planted under isolators and the seed harvested separately from each parent. All parents were from sources with a high degree of self-incompatibility. The absence of seed on a bagged branch of each parent indicated that all the seed produced was the result of cross-pollina-

tion. The quantity of cleaned seed fluctuated between 20 and 350 g per mother root. Germination percent (ISTA, 1985) exceeded 90% for most seed lots; however, a few samples were significantly below 80%. Ten pairs that produced insufficient viable seed for field trials were eliminated. Eighteen pairs (Table 1) were included in a 36–entry lattice design field trial with four replicates in 1997. The trial was located at the Polanowice Plant Breeding Station (central Poland) on a fertile alluvial soil and was not irrigated. The field trial was planted on April 23 with a Wintersteiger TPN plot seeder. Rows were spaced 45 cm apart. Plots were 8 m long and three rows wide. The stand after thinning was about 90,000 plants/ha. The roots were dug from each plot on October 28, washed, and weighed. Sugar percent, potassium, sodium and amino nitrogen concentration of a representative pulp sample were determined. Extractable sugar yield was calculated from these measurements and root yield.

The results were analyzed with standard analysis of variance and regression procedures. Linear regression of sugar content in the progeny on sugar content in the mothers $(X_m)$, the fathers $(X_f)$, and the mean of both parents $(X_p)$ for each of the two groups of 18 hybrids, $Z \times E (Y_1)$ and $E \times Z$ $(Y_2)$, and for all 36 hybrids $(Y_3)$ provided estimates of heritability (Table 2). A common slope was used for both $(y_1$ and $y_2)$ groups with the intent of improving the predictive value for the sugar content of hybrids. Estimates of narrow-sense heritability coefficients, $h_n^2$, were based on regression coefficients and coefficients of determination. Additionally, multiple regression equations with sugar content of the progeny as the dependent variable and sugar content of the maternal and paternal parents as independent variables were attained. Also, correlation coefficients between sugar content and root yield were calculated for both groups of hybrids ($Z \times E$ and $E \times Z$).

## RESULTS

For sugar, K, Na, and amino N concentrations, the incomplete block design was ineffective, compared to a randomized complete block, based upon mean squares for error and the magnitudes of the LSDs. The homogeneous field conditions at the site made the division into blocks counterproductive. With the lattice design, an analysis ignoring the division into incomplete blocks is an option. A sum of squares comparing $Z \times E$ hybrids with $E \times Z$ hybrids was calculated (Table 3). This contrast was significant for sugar, indicating that, on the average, $Z \times E$ hybrids and $E \times Z$ hybrids had different sugar concentrations, hence a maternal effect. The sugar concentration of $Z \times E$ hybrids was 0.21% higher than the sugar concentration of $E \times Z$ hybrids (Table 1).

**Table 1.** Sugar content and yield of hybrids grown in 1997, and sugar content of parents, 1995.

| Parents Sugar | | Hybrids Sugar | | | Root Yield | | Sugar Yield | |
|---|---|---|---|---|---|---|---|---|
| Z-type | E-type | $Z \times E$ | $E \times Z$ | Diff.[†] | $Z \times E$ | $E \times Z$ | $Z \times E$ | $E \times Z$ |
| | | % | | | | | t / ha | |
| 22.65 | 16.16 | 19.08 | 18.46 | 0.62* | 44.78 | 45.85 | 7.53 | 7.33 |
| 23.90 | 16.98 | 19.37 | 18.95 | 0.42 | 34.10 | 37.40 | 5.93 | 6.25 |
| 22.05 | 16.04 | 18.22 | 18.52 | -0.30 | 43.88 | 39.38 | 6.94 | 6.33 |
| 23.42 | 16.35 | 19.59 | 19.39 | 0.20 | 43.65 | 36.48 | 7.55 | 6.25 |
| 22.00 | 16.37 | 18.84 | 19.03 | -0.19 | 41.98 | 41.10 | 6.95 | 6.89 |
| 22.50 | 16.45 | 18.15 | 17.96 | 0.19 | 48.05 | 49.02 | 7.50 | 7.50 |
| 21.90 | 16.36 | 18.49 | 18.50 | -0.01 | 40.75 | 39.90 | 6.53 | 6.39 |
| 21.00 | 16.09 | 18.86 | 19.03 | -0.17 | 36.10 | 42.45 | 6.02 | 7.09 |
| 21.60 | 16.58 | 19.09 | 18.35 | 0.74* | 41.18 | 40.85 | 6.95 | 6.58 |
| 21.80 | 16.96 | 19.10 | 18.89 | 0.21 | 45.58 | 42.15 | 7.55 | 6.90 |

**Table 1 (continued).** Sugar content and yield of hybrids grown in 1997, and sugar content of parents, 1995.

| Parents Sugar | | Hybrids | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Sugar | | | Root Yield | | Sugar Yield | |
| Z-type | E-type | Z × E | E × Z | Diff.† | Z × E | E × Z | Z × E | E × Z |
| % | | | | | t / ha | | | |
| 23.00 | 16.24 | 18.33 | 18.07 | 0.26 | 46.85 | 42.75 | 7.47 | 6.71 |
| 20.30 | 16.54 | 18.58 | 19.07 | -0.49 | 35.02 | 45.63 | 5.71 | 7.60 |
| 21.20 | 16.10 | 19.39 | 18.92 | 0.47 | 42.62 | 40.68 | 7.30 | 6.75 |
| 22.00 | 16.36 | 18.95 | 19.06 | -0.11 | 41.12 | 42.40 | 6.84 | 7.14 |
| 21.55 | 16.68 | 19.39 | 18.91 | 0.48 | 42.35 | 41.72 | 7.35 | 6.98 |
| 21.42 | 16.50 | 19.28 | 18.48 | 0.80* | 40.48 | 43.58 | 6.92 | 6.98 |
| 20.85 | 16.23 | 19.11 | 18.80 | 0.31 | 42.42 | 41.32 | 7.09 | 6.81 |
| 23.90 | 16.98 | 19.30 | 19.05 | 0.28 | 36.95 | 40.15 | 6.32 | 6.72 |
| Means: | | | | | | | | |
| 22.06 | 16.04 | 18.96 | 18.75 | 0.21* | 41.55 | 41.82 | 6.91 | 6.84 |

* difference is significant at $\alpha$ = 0.05 level

† (Z × E) − (E × Z)

**Table 2.** Regression of sugar content of progeny on the sugar content of mothers $(X_m)$, fathers $(X_f)$ and the average of the two parents $(X_p)$ for hybrid groups $Z \times E$ $(Y_1)$, $E \times Z$ $(Y_2)$, and for all the hybrids $(Y_3)$.

| Independent variable | Regression equation | $R^2$ | $h_n^2$ | Standard deviation for $h_n^2$ |
|---|---|---|---|---|
| $X_m$ | $Y_1=15.71+0.143X_m$ <br> $Y_2=16.38+0.143X_m$ | 0.095 | 0.286 | 0.218 |
| | $Y_3=18.13+0.0348X_m$ | 0.057 | 0.070 | 0.055 |
| $X_f$ | $Y_1=18.50+0.035X_f$ <br> $Y_2=18.22+0.035X_f$ | 0.037 | 0.070 | 0.224 |
| | $Y_3=19.26-0.023X_f$ | 0.025 | — | — |
| $X_p$ | $Y_1=16.07+0.145X_p$ <br> $Y_2=15.91+0.145X_p$ | 0.072 | 0.145 | 0.141 |
| | $Y_3=15.99+0.145X_p$ | 0.040 | 0.145 | 0.140 |
| $X_m, X_f$ | $Y_1=15.67+0.142X_m+0.004X_f$ <br> $Y_2=16.31+0.142X_m+0.004X_f$ | 0.095 | — | — |
| | $Y_3=15.99+0.088X_m+0.058X_f$ | 0.081 | — | — |

**Table 3.** Analysis of variance for sugar, K, Na, and amino N concentration and root yield, 1997.

| Traits | Mean square | | | | F | |
|---|---|---|---|---|---|---|
| | | | Contrast | | | Contrast |
| | Replicates | Hybrids | (Z×E - E×Z) | Error | Hybrids | (Z×E - E×Z) |
| Sugar | 0.2175 | 0.6954 | 1.799 | 0.1598 | 4.35** | 11.26** |
| Root Yield | 514.00 | 1539.32 | 0.0646 | 15.571 | 2.82** | <1 |
| K | 6.2867 | 0.4608 | 0.5407 | 0.1173 | 3.83** | 4.61* |
| Na | 0.3100 | 0.0557 | 0.0075 | 0.0088 | 6.80** | <1 |
| Amino N | 25.4987 | 0.5999 | 0.0109 | 0.1683 | 3.56** | <1 |
| Extractable sucrose yield | 9.6465 | 0.993 | 0.1725 | 0.4318 | 2.30** | <1 |
| Degrees of freedom | 3 | 35 | 1 | 105 | 35 and 105 | 1 and 105 |

*, ** significant at $\alpha$ = 0.05 and 0.01, respectively

The average sugar contents of the parental components and hybrids are presented in Table 1. The LSD for comparisons of hybrid types ($Z \times E$ versus $E \times Z$) within a cross is 0.56. Twelve positive differences were observed ($Z \times E - E \times Z$), three were significant. On the other hand, only six non-significant negative differences were observed. A similar analysis was performed for root yield and the concentration of K, Na, and amino N (Table 3). The contrast between $Z \times E$ and $E \times Z$ hybrids was statistically significant for potassium only. The average difference ($Z \times E - E \times Z$) ) was -0.123, indicating that $E \times Z$ hybrids generally had higher potassium concentrations than $Z \times E$ hybrids.

Regression of sugar concentration of progeny on sugar concentration of the parents (Ubysz-Borucka et al., 1985) provided estimates of the heritability of sugar content. The difference between the regression coefficients for mothers and fathers is a measure of the relative influence of maternal and paternal parents on sugar concentration in progenies. All these regressions were non-significant at standard significance levels, $\alpha = 0.01$ and $\alpha = 0.05$. However, they were significant at a significance level of $\alpha = 0.20$. Nevertheless, they suggested a greater maternal than paternal impact on sugar content. The progeny-mother heritability coefficient was 0.286, compared with a progeny-father heritability coefficient of 0.070. Furthermore, the multiple regression coefficient for sugar content in mothers was substantially higher than the coefficient for fathers; 0.142 and 0.004, respectively.

The correlation between sucrose concentration and root yield for $Z \times E$ hybrids was much lower than the correlation coefficient for the reciprocal, $E \times Z$, hybrids ($-0.170$ and $-0.501$, respectively). This suggested that when the maternal parent of a hybrid is a high sugar genotype (Z-type), the negative relationship between the primary traits determining sugar yield is less of a problem to breeders.

## DISCUSSION

A basic method currently applied in sugarbeet cultivar development is heterosis breeding. Most of the authors quoted earlier agree that heterosis for sugar yield largely depends upon hybrid vigor for root yield because genetic variability in root yield is primarily determined by dominant genetic effects. However, sugar content is controlled by additive genetic variability and it is commonly accepted that the sugar concentration of the progeny will be intermediate to that of the parents (assuming that both parents have the same ploidy level, 2x or 4x). It is self-evident that in triploids from $2x \times 4x$ crosses, the tetraploid parent contribution will be predominant. The heterosis observed by Powers et al. (1959) was ques-

tioned by Smith et al. (1973), who observed neither dominant gene effects nor heterosis for sugar content. Similarly, the results presented by MacLachlan (1972c), who in some cases observed heterosis in sugar content, may be questionable in view of the limited genotypes sampled. Also, heterozygotic populations were crossed, a practice that is atypical for heterosis breeding, and the sugar content of the parental populations was very low. However, the results reported by Doney (1983), results reported here, data presented by other authors, and the observations of applied breeders, indicate a prevalence of additive genes in sugar content inheritance, whereas variability in root yield is controlled, in part, by non-additive genes, making heterosis breeding effective. As a result, combining high yield with high quality requires intensive selection for high sugar content and, simultaneously, an expansive testing program to capitalize on heterosis for root yield. Ideal hybrids will have the small-cell root tissue, characteristic of high sucrose cultivars and, at the same time, a rapid cell division rate to increase root weight (Doney, 1983).

The present results confirm the observations of Savitsky (1940) and Schlösser (1949) and suggest that the maternal parent has a greater impact than the pollinator on sugar concentration in the progeny. Sucrose content is the primary quality trait determining the value of sugarbeet, but it is worth noting that a maternal effect was observed in the inheritance of potassium concentration, as well. With respect to heterosis breeding this suggests that selection for high sucrose and low potassium concentration should be emphasized in the development of the CMS parent, whereas improving the root yield of a hybrid depends mainly on the combining ability of the specific parental lines.

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