Selecting for Taproot to Leaf Weight Ratio and its Effect on Yield and Physiology*

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Yield of sugarbeet depends upon photosynthesis and subsequent accumulation of photosynthate in the taproot (2). Both production and distribution of photosynthate are under environmental and genetic control. We have attempted to exploit genetic variation in photosynthate distribution to increase economic yield. Selection for photosynthate partitioning and root size appears to be an efficient way to increase yield.

We made selections for weight of leaves and taproot of 21-day-old sugarbeet seedings, using Taproot-Leaf Weight Ratio (TLWR) as an indicator of partitioning where:

$$\text{TLWR} = \frac{\text{Taproot + hypocotyl fresh weight}}{\text{Leaf blade fresh weight}}.$$

We found that TLWR may vary as much as three-fold among plants within a breeding line or hybrid at a given time in a given environment. We also found that mean TLWR differed by nearly two-fold among 30 unselected populations that were examined (5).

We hypothesized that yield of sugarbeet would be improved by increasing the partitioning of photosynthate into the taproot, assuming that leaf area remained adequate and other plant functions were not adversely affected.

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Growth Chamber Studies

Individual seedlings were grown in 15-cm pots in vermiculite and received an excess of complete mineral nutrient solution daily. We used fresh weights at 21 days post-emergence to identify plants of differing TLWR. The selected plants were then grown to maturity for seed production. TLWR's based on fresh weight or dry weight, are highly correlated (r = 0.98) (Figure 1); therefore, differences in TLWR do not result from differences in water content.

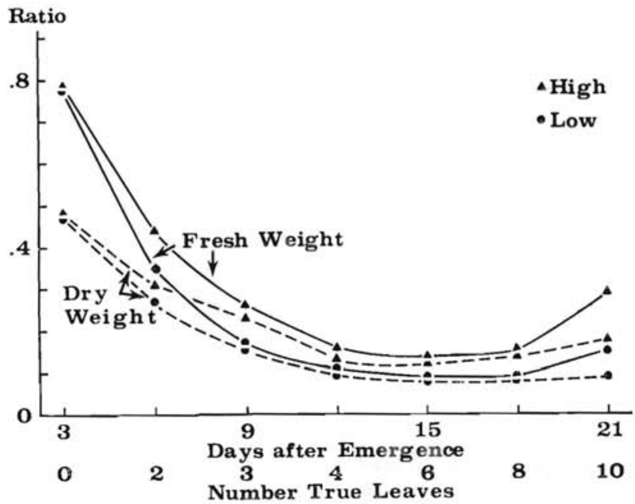

Figure 1. Relationship of TLWR calculated from fresh and from dry weight of progenies of sugarbeet selected for low and high TLWR when grown in controlled environment.

Having found considerable variation in TLWR among seedlings, we wondered whether selection for low and for high TLWR would be effective. We selected a number of seedlings of breeding line EL40 for low and for high TLWR at 21 days post-emergence. Polycrossed seed was produced from each group. Progenies of each group (Low and High TLWR) were grown in the growth chamber. TLWR was determined at 21 days post-emergence. This constituted the first cycle of selection. Out of these first-cycle progenies, another group of low-and of high- TLWR seedlings was selected for a second cycle of seed production and progeny testing. The results of these selections are summarized in Table 1. In both cycles of selection, the percentage differential between the TLWR means of the low and high progenies was about one-half of the differential between the means of the low- and the high- TLWR parents. We do not know whether progenies of other breeding lines will perform similarly to EL40.

Table 1. Effect of selection for TLWR in sugarbeet breeding line EL40 at 21 days post-emergence in the growth chamber. The 156 unselected seedlings measured had a mean TLWR of 0.151.

	Parent			Progeny		
Cycle	Number Plants Selected	Mean TLWR	Percent Differ.†	Number Plants Screened	Mean TLWR	Percent Differ.†
1 Low TLWR	11	0.123 ± 0.01		175	0.132**	
1 High TLWR	13	0.217 ± 0.02	76	217	0.179	36
2 Low TLWR	21	0.114 ± 0.01		144	0.096**	
2 High TLWR	21	0.242 ± 0.02	112	144	0.159	66

†High TLWR/Low TLWR.

**Low and high progenies in each cycle differ at 0.01 level according to analysis of variance test.

Field Studies

Do yields of the low- and the high- TLWR populations differ in the field after a full season of growth? How does TLWR change during the growing season? We used bulked seeds from a number of second-cycle-selection plants to answer these questions. In 1976, we grew the low- and high- TLWR entries at stand densities of 17,920, 23,685, 27,550, and 32,660 plants per acre and a hybrid (SP69561-01 x 70420) x SP6922-0) at 25,470 plants per acre. Each density was replicated three times (4). In 1977, we grew low-TLWR, high-TLWR, and unselected populations of breeding line EL40 and unselected US H20 hybrid at stand densities of 14,265, 21,360, 32,585, and 49,050 plants per acre and replicated each four times.

Taproot weight and TLWR were determined on 20 plants per plot in 1976 and on 15 plants per plot in 1977. Each year 10 roots per plot were analyzed for sucrose and purity. The growing season was 170 days in 1976 and 163 in 1977.

TLWR increased with age in the field in 1976 (Figure 2) and was similar in 1977. At harvest, TLWR of the high-TLWR population was 20% greater in 1976 and 26% greater in 1977 than the low-TLWR population. Root yield of the high-TLWR population was 23% greater in 1976 (Table 2) and 22% greater in 1977 (Table 3) than the low-TLWR population.

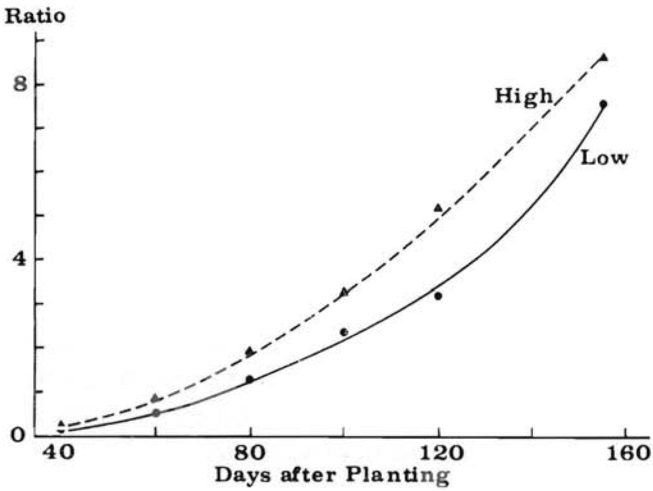

Figure 2. TLWR of low- and high- TLWR sugarbeet selections grown in the field at Beltsville, Maryland, in 1976.

Mean TLWR decreased as stand density increased (Table 3). Mean root yield per acre was significantly lower at the lowest stand density as compared to the intermediate densities (Table 3). High-TLWR plants yielded least at the low-stand density, whereas US H20 had the highest yield at medium plant densities. US H20 had greater root weight, significantly greater leaf blade weights and significantly lower TLWR than the other entries. At the two highest densities, US H20 had significantly greater leaf weight than the high-TLWR entry, but root yield did not differ. Apparently, the greater partitioning of photosynthate to the root of the high-TLWR entry offset any advantage of the greater leaf weight of US H20. These results suggested that incorporation of TLWR into breeding programs must be accompanied by appropriate management research.

Table 2. Mean yield and TLWR across all stand densities of sugarbeet grown at Beltsville, Maryland, in 1976.

Entry	TLWR	Root Yield M.T./Ha.†	Recoverable White Sugar M.T./Ha.†
EL40, Low TLWR	7.77	64.3	8.05
EL40, High TLWR	9.36*	79.1*	9.80
Hybrid	4.92	88.6‡	10.84

†Conversion factor to tons per acre, multiply by 0.446.

*Means of the high and low TLWR selections are significantly different at 0.05 level.

‡Plant spacing 71 x 25 cm only.

Sucrose and purity percentages were similar for the high-TLWR and low-TLWR populations at Beltsville in 1976. In 1977, a significant increase in sucrose percentage accompanied the 22% increase in root yield of the high-TLWR population (Table 4).

The high-TLWR population produced 35% more recoverable white sugar than the low-TLWR population and equalled that of US H20 (Table 4). Similarly selected low- and high- TLWR populations were grown in Michigan by G. J. Hogaboam in 1977. He found that root yields did not differ at the very low stand densities (9,150 to 13,625 plants per acre), but all of the high-TLWR lines had significantly higher sucrose and purity than low-TLWR lines.

Table 3. Effect of stand density on root and leaf weights and TLWR of four sugarbeet entries grown in the field at Beltsville, Maryland, in 1977.*

	Stand Density					
Entry	Plants/Ha.	32,250	52,775	78,050	121,200	Mean
	Root weight M.T. per Ha.					
EL40	Low TLWR	57.8 fg	66.1 d-g	60.6 efg	56.4 g	60.3 c
EL40	Unselected	63.1 d-g	67.1 c-f	72.5 a-d	70.1 b-e	68.3 b
EL40	High TLWR	63.9 d-g	77.2 ab	76.4 abc	77.0 abc	73.7 ab
US H20		76.4 abc	80.6 a	79.4 ab	70.0 b-e	76.7 a
	Mean	65.3 b	72.8 a	72.3 a	68.4 ab	
	Leaf blade weight M.T. per Ha.†					
EL40	Low TLWR	7.5 e	10.6 cde	9.4 de	10.1 de	9.5 b
EL40	Unselected	9.6 de	8.8 e	9.9 de	10.8 cde	9.8 b
EL40	High TLWR	7.2 e	9.8 de	9.1 de	10.4 cde	9.2 b
US H20		14.4 bc	13.4 bcd	15.1 ab	18.5 a	15.4 a
	Mean	9.7 b	10.6 ab	10.9 ab	12.4 a	
	TLWR					
EL40	Low TLWR	7.78 abc	6.32 bcd	6.41 bcd	5.90 cde	6.61 b
EL40	Unselected	6.86 bcd	7.81 abc	7.31 a-d	6.66 bcd	7.16 ab
EL40	High TLWR	9.51 a	7.89 abc	8.51 ab	7.51 a-d	8.36 a
US H20		5.46 de	6.18 cd	5.37 de	3.81 e	5.21 c
	Mean	7.40 a	7.05 a	6.90 ab	5.97 b	

*Duncan's multiple range analysis for each parameter. The set of 16 values of the interaction table were analyzed separately. Each set of four means was analyzed separately. With each set, means with the same letter do not differ significantly at the 0.05 leve.

†Conversion factor to tons per acre, multiply by 0.446.

These three experiments showed that high-TLWR plants partition proportionately more photosynthate to the taproot than low-TLWR plants, that root growth of the high-TLWR plants may be greater than that of low-TLWR plants, and that sucrose storage in high-TLWR plants is equal to or greater than that in low-TLWR plants. A positive relationship may exist between TLWR and sucrose storage. This aspect makes the TLWR approach to improvement of sugarbeet yield even more attractive than the increase in tonnage.

Table 4. Sucrose and clear juice purity percentages and recoverable white sugar by stand densities and entries of sugarbeet grown at Beltsville Maryland, in 1977.*

Entry	Plants per Hectare 32,250	52,775	78,050	121,200	Mean
Sucrose Percentage					
EL40, Low TLWR	13.7 bc	13.9 bc	14.7 abc	15.8 ab	14.5 b
EL40, Unselected	12.9 c	13.8 bc	14.2 abc	16.3 a	14.3 b
EL40, High TLWR	15.5 ab	15.5 ab	16.2 a	16.4 a	15.9 a
US H20	14.8 abc	14.8 abc	16.1 a	15.1 abc	15.2 ab
Mean	14.2 b	14.5 b	15.3 a	15.9 a	
Clear Juice Purity Percentage					
EL40, Low TLWR	88.5 d	90.0 bcd	90.6 a-d	92.9 a	90.5 b
EL40, Unselected	88.6 d	90.2 bcd	90.5 a-d	92.1 abc	90.3 b
EL40, High TLWR	90.1 bcd	89.7 cd	90.8 a-d	92.4 ab	90.8 b
US H20	90.9 a-d	91.4 abc	92.9 a	92.4 ab	91.9 a
Mean	89.5 c	90.4 bc	91.2 b	92.4 a	
Recoverable White Sugar, M.T. per Ha.†					
EL40, Low TLWR	6.08 i	7.35 ghi	7.22 ghi	7.62 e-j	7.07 b
EL40, Unselected	6.30 hi	7.45 f-i	8.30 c-h	9.65 a-e	7.92 b
EL40, High TLWR	7.95 d-i	9.48 a-f	10.18 abc	10.70 ab	9.58 a
US H20	9.22 a-g	9.85 a-d	11.02 a	8.90 b-g	9.75 a
Mean	7.39 b	8.53 a	9.18 a	9.22 a	

*Duncan's multiple range analysis for each parameter. The set of 16 values of the interaction table were analyzed separately. Each set of four means was analyzed separately. Within each set, means with the same letter do not differ significantly at the 0.05 level.

†Conversion factor to pounds per acre, multiply by 892.

These field studies indicated that selection for high TLWR has potential for increasing yields of sugarbeet. The 1977 study also demonstrated that yield and TLWR must be compared as a function of stand density, and that management practices must be developed to maximize yield.

Biochemical Studies

Sugarbeet seedlings that differed in TLWR as much as two-fold were used to probe for a biochemical basis of photosynthate partitioning and enhance our understanding of source/sink relationships.

Allometric growth analysis was used to determine the distribution of dry weight among the various seedling parts of the low- and high-TLWR populations. Although the two populations differed in TLWR, they did not differ in root-shoot ratio (Table 5). The high-TLWR plants retained relatively more dry matter in the taproot and had less fibrous roots than the low-TLWR plants.

Table 5. Dry weights of leaf blades (LBW), petioles (PW), hypocotyl (HW), taproot (TRW), fibrous roots (FRW), and relationships among these components in 21-day-old seedling progenies from parent plants selected for divergent taproot-leaf weight ratio (TLWR)*.

TLWR		Shoot			Root	
(dry basis)	Root/Shoot	LBW	PW	HW	TRW	FRW
0.196 a	0.273 a	1.270 a	0.187 a	0.078 a	0.163 a	0.256 b
0.105 b	0.285 a	1.372 a	0.164 a	0.062 b	0.084 b	0.389 a

*Each value is a mean of 12 replications. Within columns, a different letter indicates a significant difference at the 0.05 level between means by Duncan's multiple range analysis.

We investigated sucrose distribution in the taproots of seedlings differing in TLWR. At about 50 days post-emergence, the percentage of sucrose in the vacuoles (storage) increased as the TLWR increased, but decreased in the cytoplasm (Figure 3). This may explain the higher sucrose content of high-TLWR taproots in the field as compared to the low-TLWR taproots (Table 4). Distribution of sucrose in the taproots was independent of taproot fresh weight and total sucrose content (80% ethanol extractable).

Acid and alkaline invertase and sucrose synthetase are the enzymes responsible for metabolizing the sucrose imported into sugarbeet taproots. In vitro, acid invertase activity was higher in taproots of low-TLWR than in taproots of high-TLWR seedlings at 21 days post-emergence (Table 6); alkaline invertase and sucrose synthetase activities did not differ.

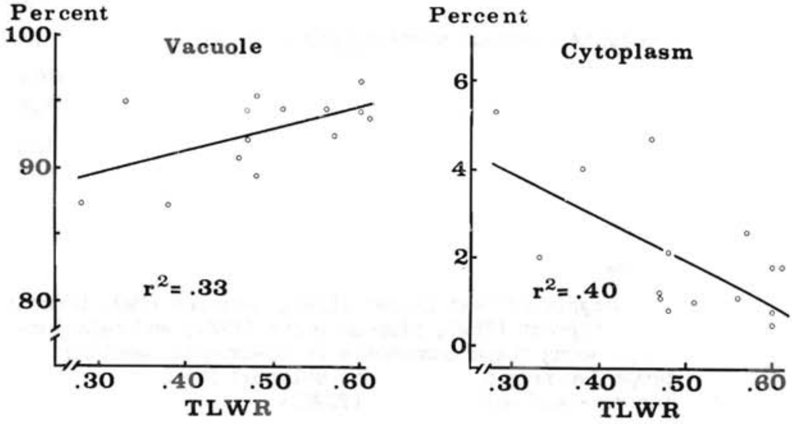

Figure 3. Relationship between sucrose distribution in sugarbeet taproot cell compartments and TLWR.

Table 6. *In vitro* acid and alkaline invertase activity in taproots of 21-day-old sugarbeet plants differing in TLWR.

	Invertase Activity†	
TLWR	Acid - pH 4.5	Alkaline - pH 7.0
0.129 ± 0.023	105.3 ± 51.7	93.0 ± 40.3
0.056 ± 0.010	222.0 ± 58.6	117.4 ± 30.4

† µmoles glucose per gram dry weight per hour.

The difference in acid invertase activity associated with TLWR did not seem to be caused by differential solubilization of the protein apparently associated with the cell walls. About 50% of the invertase activity was in the soluble fraction (3).

Acid invertase activity of taproots decreased from 14 to 28 days post-emergence, whereas alkaline invertase activity increased slightly (Figure 4). During this period, sucrose storage begins. Thus, both genetically and ontogenetically, acid invertase activity appears to be inversely related to development of the taproot as a storage organ. The enzyme may regulate cellular sucrose distribution which, in turn, influences cellular growth and differentiation, e.g., lateral root initiation from the taproot.

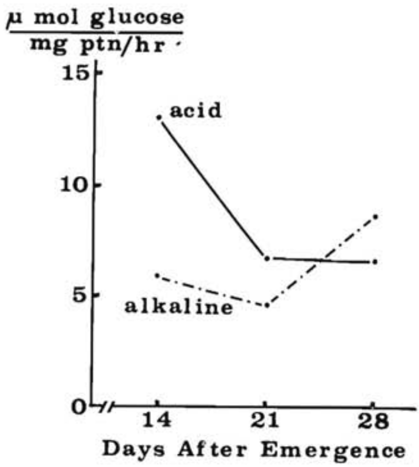

Figure 4. Relationship between in vitro acid and alkaline invertase activities and ontogenetic development of the sugarbeet taproot.

Procedures for Selection for TLWR

All of our selections for TLWR in the growth chamber were made at 21 days post-emergence. Those seedlings usually had 9 to 12 true leaves under our growing conditions (14-hour photoperiod, 3,000 to 4,000 foor candles, 27° C day and 16° C night). The number of leaves produced was related to both inherent vigor and environment. Larger seedlings survived better after measurement of TLWR. Survival also varied with cultivar.

TLWR changed with the age of the plant (Figures 1 and 2). The differential between low- and high- TLWR plants appeared as early as the third and fourth true leaf stage, but differences were not identifiable with certainty because the plants were too small. Environment also influenced TLWR; as light intensity decreased, TLWR of the seedlings decreased. For six cultivars, we found no cultivar by light interaction. Growing conditions such as pot size, mineral nutrition, and water supply also influence growth and TLWR. Thus, in selection for TLWR among sugarbeet plants, age must be identical and environments similar.

We have minimized variations in the determination of TLWR with the following procedures.

1. Discard petioles. Petioles constitute at least 15 percent of the leaf weight, but their photosynthetic contribution per unit weight is much less than blades. Furthermore, the ratio of petiole weight to leaf weight can vary two-fold at 21 days post-emergence.
2. Discard the fibrous or feeder roots. Not only is the weight of the fibrous roots appreciable, but nine-fold variations in the ratio of fibrous root weight to taproot plus hypocotyl weight can be found among 21-day-old seedlings.
3. Retain the same quantity of leaf tissue (small leaves) on each seedling for determinations of taproot + hypocotyl fresh weight.
4. Weigh leaf blades and roots immediately.

Can the TLWR-selection procedure be simplified? Determination of leaf blade fresh weight is essential and cannot be simplified. Taproot-hypocotyl fresh weight is the most accurate parameter to establish the relationship between leaf blades and taproots. However, hypocotyl diameter also relates to root weight. Doney and Theurer (1) found a good correlation between hypocotyl diameter of 21-day-old seedlings and taproot weight after a full season's growth. We have used G. E. Coe's data for two of his breeding lines to compare TLWR with Hypocotyl Diameter Leaf Weight Ratio (HDLWR). This new ratio was calculated by substituting hypocotyl diameter for taproot-hypocotyl weight. We then determined correlation coefficients for two entries (df for entry 1 = 178; for entry 2 = 232).

Correlation	Correlation Coefficient for	
	Entry 1	Entry 2
Hypocotyl diam. vs taproot-hypocotyl fresh wt.	0.87	0.88
TLWR vs. HDLWR	0.46	0.38

Hypocotyl diameter and taproot-hypocotyl fresh weight correlated well, but TLWR and HDLWR correlated poorly. Further, in the top 20% of plants ranked by TLWR, we found only 6% of those ranked by HDLWR. Therefore, hypocotyl diameter is not acceptable parameter for selection for TLWR but may be useful in selection for root size.

In the future we need to work in the following areas:

1. Continue to evaluate and verify the validity of TLWR as a selection criterion, continue inheritance studies of TLWR, and simultaneously select for high TLWR and taproot size.
2. Determine how the sugarbeet plant controls the partitioning of photosynthate to the various plant parts. We plan to cross both chard and mangel with sugarbeet, which should give us a greater range than we have at present of genetically controlled TLWR's for use in additional biochemical studies.
3. Produce a hybrid in which both the pollinator and the CMS female lines have been selected primarily for high TLWR. Most of our selection and yield studies have been done with one breeding line, EL40.
4. Determine optimum management practices (e.g., spacing and nutrition) for lines differing in TLWR.

ACKNOWLEDGMENTS

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Sugar and purity analyses were made by M. G. Frakes, Michigan Sugar Laboratory, Saginaw, MI.

The sugar and yield data for a number of low- and high- TLWR lines grown near Saginaw, MI, were supplied by G. J. Hogaboam, FR, SEA, U.S. Department of Agriculture, East Lansing, MI. He also made the crosses using female clones in Table 2.

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