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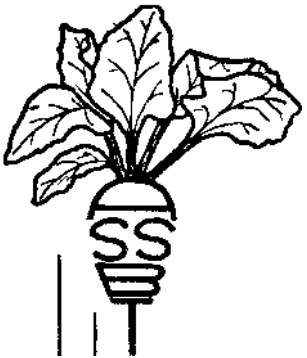

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Physiological Selection in Sugarbeet

Symposium presented at the
20th General Meetings of the
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Edited by:
Devon L. Doney

INTRODUCTION

Perhaps the most important problem facing the sugarbeet industry today is the narrow margin of profit or lack of profit in sugarbeet production. There have been numerous proposals on how to solve this problem. One of these solutions is the purpose of this symposium—that is to improve sugar production per unit land area.

Improvement in sugar production per acre over the past 30 years has not been spectacular, but there has been some major progress. In this period of time we have seen the use and misuse of commercial fertilizer, the introduction of hybrids, monogerm seed, disease resistance, and many other important contributions. As a result, root yields have increased from 12.5 tons per acre to 20.6 tons per' acre in 1977. Sharp increases in root yield were obtained in the 50's and early 70's; however, a plateauing effect occurred during the 60's and appears to be re-occurring now. Improvement in sugar production per acre has been less successful. A gradual rise occurred throughout the 40's and 50's. The 60's showed a drop in sugar production per acre, and at present we are producing only slightly more sugar per acre than we were in the late 50's and 60's. This is true in spite of significantly higher root yields. There are many factors affecting these trends, but one thing is apparent, that is, "improving sugar production is a long difficult process."

The reasons are numerous, the negative relationship between root yield and sugar percent, the expense and difficulty of testing and handling a large bulky crop, the high genotype times environmental interaction, the biannual habit of the crop, and the below-ground growth habit are a few examples.

The most difficult job for a plant breeder Is to select and exploit superior genotypes. Breeding techniques have consistently failed because of the inability of the breeder to identify and isolate superior lines per se, or line with superior combining ability.

To adequately test sugarbeet genotypes requires large field "trials. This reduces the number of genotypes that can be tested, and when testing for yield (which involves 100's of growth genes) the probability of selecting the best genotypes is reduced to almost zero. For example, an F_2 population segregating for 10 genes would have only from 1 in a thousand to 1 in a million plants carrying the best combination of those 10 genes (depending on the heterozygosity of the best combination). With these kinds of odds, it is encouraging that any significant improvements have been made.

This brings us to the purpose of this symposium, "Physiological Selection in Sugarbeet." What is physiological selection? The dictionary says that physiology is the science of the functions of living organisms; therefore, physiological selection would be a selection technique utilizing one or more fundamental functions of the plant as a selection criteria. We have seen great technological advances in the past 30 years that have added many-fold to our basic understanding of the plant and its growth processes. These growth processes can be accurately measured and controlled in the lab or greenhouse with much greater precision than the bulky field tests. To use our knowledge of these growth processes should make it possible to develop selection criteria and to more accurately and efficiently select superior genotypes.

in this symposium, we have assembled experts in a number of disciplines and have asked them to assess the possibilities of developing physiological selection criteria for use by sugarbeet breeders.

Ideotype Concepts for Sugarbeet Improvement

R. S. LOOMIS*

Received for publication April 23, 1979

The development of the beet as a sugar crop in the 18th and 19th centuries through selections among fodder beets represents one of the more successful efforts at plant improvement involving morphological and physiological traits. The simple objective was to increase the sucrose concentration to a level sufficient for effective processing while maintaining yield level. Progress was particularly rapid after Vilmorin (21) introduced juice density and polariscope measurements as estimates of sucrose concentration.

Further progress in improving yield performance since that time has come slowly. On the one hand, breeding efforts, of necessity, have focused principally on "defect elimination"—disease resistance and secondary attributes such as the monogerm trait, bolting resistance, and processing quality—and on genetic structure (male sterility, hybrid formation, and polyploidy), with only general breeding effort for yield. On the other hand, we have not yet formulated sets of characteristics which would be expected theoretically to enhance performance when combined in a single genotype in particular production systems.

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The Ideotype Concept

I will use the term "ideotype" (3) to describe the collective morphological and physiological traits of such ideal genotypes. The question before us is whether we can now define such ideotypes for sugarbeet. A logical point of departure would be to seek an increase in photosynthate supply either through alterations of the physiological processes or through manipulation of the foliage, canopy. Our own experience (7) suggests that sugarbeet has a high quantum efficiency and a high capacity for leaf photosynthesis when compared to other 0_3 plants (C_3 referring to plants carrying photorespiration and ribulose bisphosphate carboxylase as central features of their photosynthetic systems in contrast to C_4 plants such as corn). Selection for improved photosynthetic rates will be very difficult because of variations with environment and with age, as well as previous history and current status of the leaf. Unless one approaches the problem with rather sophisticated techniques and with plants grown under highly controlled conditions, there is little chance for the detection of genetic differences.

It may also be that we are already rather close to environmental (solar radiation, $C0_2$ supply and growing season) limits of production potential. Certainly the sugarbeet reveals itself as the most productive of bionass of any C_3 species (9), and C_3 plants appear to be superior to C_4 plants at middle and high latitudes with moderate levels of light and temperature (5, 9, 10).

Opportunities do exist for improvements in leaf display. Watson (22) outlined how the small size of sugarbeet embryos (relative to mature plant size), low seedling vigor, and a poor ability to grow at low temperatures combine to greatly delay the achievement of full cover. These problems remain with us today (2). But beyond full cover, it does not seem reasonable to expect to increase production more than slightly through alterations in leaf density and leaf

display since sugarbeet canopies generally possess near Ideal structure (4, 14, Loomis, and co-workers unpublished). Increasing leaf densities to a leaf-area index of 8 to 10 with very erect leaves would help, but one unit leaf area (1 ha ha^{-1}) of sugarbeet costs about 20 kg of reduced nitrogen and 800 kg of dry matter for blades and petioles. Using Penning de Vries' product value approach (17) as a basis for calculation, that corresponds to enough original gross photosynthesis (approximately 1200 kg as carbohydrate) to produce 900 kg dry weight or 4500 kg fresh weight of beet roots.

If the plant recovers significant amounts of material from senescing leaves, the ratio of 1 ha leaves/4500 kg roots would increase. It would appear that our ideal crop should have only a moderate leaf area index near the "critical" value (LAI - 4) (14). Viewing the problem in that light turns our attention from the amount of photosynthesis to the question of what that crop does with its photosynthate. My feeling is that there may be considerable room for yield improvement through selection for improved partitioning of photosynthates to sucrose storage in the root while minimizing the associated structural and maintenance costs. It is occasionally found that root sucrose equals only 30% or less of the final dry weight of the total crop.

Vilmorin's work is still viable as a model of how improvements in partitioning can be achieved. Physiological performance and morphological structure are Integrated within the plant and Vilmorin was able to identify simple selection criteria which reflected that integration. "Integration" and "simple" are the key words. The fact that our progress has slowed suggests that we must now reach deeper into our understanding of plant growth and develop in ideotype formulation to structure new combinations of traits suitable to particular cultural practices. There are three elements to that approach: identification of limiting ("pacemaker") processes or morphology at cellular and organismal levels; formulation of predictive hypotheses of how changes in such traits will quantitatively affect crop behavior; and settling on appropriate selection criteria.

The recent; literature in crop physiology provides numerous examples of disappointments in expectations because the second step, the quantitative predictions about integrated behavior, was overlooked. Several of the steps in nitrogen assimilation, "mitochondrial efficiency" and other issues have been touted as pacemaker controls over plant growth and yield. But integrative physiology studies have shown that plant behavior is insensitive to rather wide variation in such traits (e.g., Penning de Vries assessment of mitochondrial efficiency, 17).

One of the key difficulties found with such physiological hypotheses is that a single step is seldom "always limiting." Different processes limit different parts of the plant at different times. It is also clear that higher plants are rather capable in homeostasis—a deficiency in the capacity of one process or organ may be quickly balanced by an increase in the size of that system or a reduction in the size of dependent processes or organs. A simple analysis of that situation might suggest that nothing is limiting since all parts seem in balance. Clearly, advanced ideotype formulation may prove difficult and complex, requiring best efforts by physiologists, morphologists, ecologists, and geneticists. It also will require some means for formalizing the Ideotype quantitatively in terms of whole-plant and field behavior. I am convinced that the latter task requires the use of mathematical models. In some cases simple and, In others, quite advanced models with hierarcheal structure are required to handle the integrative equations. Hierarcheal models involve several levels of biological organization so that field behavior is predicted from the underlying tissue and organ level physiology and morphology. That permits one to deal quantitatively with time-varying limiting processes. In the following sections, I will develop mostly from our own work some ideas about integrative behavior, and outline what I think may be promising methods and areas for sugarbeet improvement.

A Spatial Ideotype Developed from a Simple Experiment

A key ideotype feature is the rapid and complete occupation of available space (e.g., complete light interception, efficient soil exploration), and available space depends upon plant density. The problem for the early achievement of full cover might be ameliorated through the use of higher densities. An opportunity may also exist to markedly alter the plant type to better tolerate high densities subsequently during midseason. We obtained clues on this from two experiments. In a field experiment with comparisons between high and low nitrogen supply (15), we encountered a heavy soil with high reserves of organic nitrogen which nitrified at a rate adequate to support rapid but less than maximal growth. By the end of the season, those low-nitrogen plants achieved 40 tons of roots per acre (compared to 44 tons per acre in the high-nitrogen control), although they never exceeded covering about 65% of the ground area with leaves. Aerial space was available for a 50% increase in plant population (but with nitrogen limiting, an increase in nitrogen supply also would have been necessary). The dwarfed plants also displayed a high harvest-index with over 50% of their dry matter found as root sucrose compared to 40% in the high-nitrogen plants which accomplished more photosynthesis, but partitioned much more of it to leaf growth.

Alterations in partitioning have been the objective of a number of selection efforts (Doney and Snyder, this issue) and of many growth regulator studies. Those field results pointed directly to a genotype x density solution—a dwarf, root-partitioning ideotype to be grown at high density. This was tested first by comparing a series of genotypes varying strongly in foliar development in a pot-culture experiment conducted outdoors (Loomis, previously unpublished). The vermiculite-nutrient culture (13) allowed potential growth by the noncompetitive plants with high and low levels of nitrogen. Two comparisons were obtained: among three sugarbeet inbreds; and among chard, a sugarbeet hybrid and mangel. Results are presented in Table 1 for the inbreds.

At high nitrogen, beet and sucrose production was similar for the three inbreds although weights of fresh tops varied from 620 g/pot

Table 1. Genotype-nitrogen interaction. The plants were grown outdoors at Davis, CA, in 40-g pots filled with verraiculite. Daily watering from the planting date on 5 May was with modified half-strength Hoagland solution. After an initial harvest on 15 August; (data not shown) the remaining plants were divided into two groups; one receiving the normal solution (+N) and the other chloride instead of nitrate (-N). Data are presented for the weights per pot (2 plants) at: the final harvest on 15 October; means of 8 replications.

		Fresh Basis			Dry Basis		
Treatment	Variety[1]	Living Tops	Beets	Root Sucrose	Sucrose	Tops + Beets	K[2]
		(g/pot)	(g/pot)	(%)	(g/pot)	(g/pot)	(K)
+N	NB5	2190a	3160a	11.8b	330a	840a	39
	NB4	1630b	2940a	10.7a	330a	680b	48
	NB1	820c	3170a	11.9a	360a	660b	54
-N	NB5	840c	2230b	16.4d	360a	640b	56
	NB4	290d	1680c	16.8d	280a	450c	63
	NB1	130d	2240b	14.4c	320a	510c	63

[1]NB5, nonbolting inbred with large top (F60-547); NB4, inbred with medium top (6554); and NB1, inbred with small top (5502). Supplied by J. S. McFarlane, USDA-SEA, Salinas, CA.

[2]K: coefficient of economic yield: root sucrose as a % of top + storage root dry weight.

Table 2. An estimate of potential field performance drawn from the pot-culture experimenn presented in Table 1. The diameter of the foliage on 19 October (near maximum value for +N; means of 2 observations per pot with 3 replications) was used to estimate foliage area required for two plants and assuming close spacing with no gaps or overlaps, a possible population and yield per hectare. The low-nitrogen plants are assumed to have had small foliage areas throughout the

Treatment	Variety	Foliage Area	Population	Yield	
				Fresh Beets	Sucrose
		(m^2/pot)	(plants/ha)	(kg/ha)	(kg/ha)
+N	NB5	0.42a	70400	73800	7700
	NB0	0.30b	58800	86200	9500
	Tal	0.22c	41000	124000	16000
−N	NB5	0.26b	78400	87400	14800
	NB0	0.18c	62000	96200	16000
	Tal	0.10d	40000	161000	25000

Physiological Prototype Concepts

The space-relations example presented above became complex rather quickly because the plant's plasticity to density integrates most of its physiological and morphological processes. We can simplify the problem by narrowing the discussion to particular processes, space for plant held constant.

Partitioning

The major influence of partitioning in sugarbeet appear to involve the relative capacities for leaf and root growth and the establishment of priorities for the distribution of a limited assimilate supply between these growth sinks. While the extrapolation admittedly was crude, it was on the basis that Tal was predicted to provide much larger yields of sucrose on an area basis than either NB5 or NB0.

As yet, we know little about what the controls over partitioning might be, nor is it easy to distinguish cause and effect in the observations. The number of expanding leaves and their ultimate size establishes the size of the top sink. However, leaf initiation rates, maximum leaf size, blade/petiole ratio and weight per unit blade area

for the nonleafy inbred NB1 to 2190 g/pot for NB5, and beet sucrose varied from 39 to 54 percent of the total dry weight at harvest. Top weights were reduced sharply without nitrogen. Without nitrogen, NB4 had a greater decrease in beet weight and increase in sucrose concentration than MB1 and NB5. The three genotypes thus appeared to differ markedly in the amount of reduced nitrogen which could be remobilized for further growth, and in the type of growth which was made. The key point is that NB1 did very well at either high or low nitrogen despite its sma11 size of tops and thus appeared suitable for high-density plantings.

Field experiments were attempted twice with the above inbreds and their comparison hybrids presented over a wide range of plant densities. Both experiments were failures due to the difficulty in achieving adequate stands of inbreds in flat plantings, and the hybrids differed too little in leaf-area to justify intensive study.

But even in the absence of appropriate genotypes with which to test the dwarf ideotype hypothesis in the field, we still can evaluate the concept through models. A very simple approach is illustrated in Table 2 where the largest foliage areas observed per pot (2 plants) were used to establish: a minimum estimate of the number of plants needed to fully occupy a field area with no overlap among adjacent plants (except for that between the two plants). Using the root yields obtained with water and nutrients nonlimiting (Table 1 - nitrogen limiting), a strong genotype x spacing interaction is predicted in Table 2 with marked advantage to the dwarf-foliaged genotypes at high density. The optimum field situations would be more complex with higher plant density providing some leaf overlap, root competition and with variations in time in the degree of competition and partitioning. A more complex, dynamic simulation model with sufficient structure to predict partitioning behavior under competition is needed. That can be done only with a multilevel, integrative-physiology model of the crop such as our sugarbeet simulator (6, 8). Unfortunately, the SUBGOL model is not yet sufficiently sophisticated to handle density variations (11).

are all rather plastic. Suppression of beet growth (e.g., by root cooling or grafting to chard roots) tends to increase the value of all those characteristics. The reverse response can be found in shading or crowding experiments. While those observations illustrate that roots and shoots are competitive for a limited supply of photosynthate, they tell us little about balancing mechanisms.

It could be that phloem development (transport capacity and loading and unloading ability) play a key role. For the SUBCOL model, we have retreated to a concept of "first-in-sight, first-in-right." That is, that growing leaves have a quantitative but not absolute priority for new assimilates. However, the possible growth rate of leaves is much more vulnerable to the environment than is the growth rate of roots. This is illustrated in Figure 1 where the effects of diurnal temperature in limiting the growth of leaves and storage roots as calculated in SUBCOL are presented. Roots are likely to be at optimal temperatures and water status for growth throughout the daily period, whereas leaves are subject to low night and high midday temperatures and to midday water stress. This model predicts that the thermoperiodic behavior observed in nature results from such conditions (9).

Partitioning between root and shoot also is dependent upon the capacity of the root sink, which is clearly shown in the larger size of sugarbeet leaves when grafted to chard roots (17). Older sugarbeet roots do not appear to be limited by the number of dividing and expanding storage-root cells (Rapoport, H., 20th Jcnl. Mtg., Am. Soc. Sugar Beet Technol.). Such roots are able to use far greater quantities of photosynthate than can normally be supplied. But storage-root size may be limiting in the young plant. The SUBCOL model predicts that photosynthate supply during the juvenile phase following seedling establishment can greatly exceed storage-root growth capacity (11, 12). The simulation presented in Table 3 shows that during the first 30 days after emergence only a small fraction of the crop photosynthesis could have been used by the very small storage roots. Even at 30 days where the plants had a high carbohydrate status, and the beets had a high relative growth rate of 0.30g $g^{-1}day^{-1}$ beet (compared to 0.44 potential), beet growth used

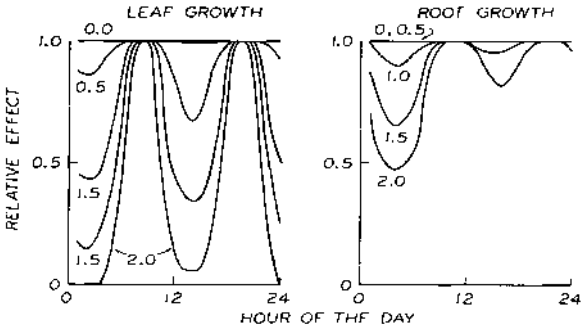


Figure 1. Relative effects of temperature with different diurnal amplitudes on the growth rate of leaves (left) and storage roots (right) as they operate in the SUBGOL simulation mode. These data are for a midseason date at Davis, CA, when mean temperatures were optimal for growth. The l.G curves are for the normal diurnal amplitude of air (17°C) and soil 7.5°C) temperatures for that date; the O.G, 0.5, 1.5, and 2.0 curves depict the effects on growth when diurnal amplitude is multiplied by those factors.

only 0.07 (7%) of Lhe daily photosynthate production. After 40 days, root-sink capacity greatly exceeded photosynthate supply, and beet growth was simulated to use between 40 and 50% of that supply. Very large leaves are produced during the juvenile period (day 20 to 35) when photosynthate supply is not limiting to leaf growth.

It appears that a larger initial storage-root size and/or growth capacity might be desirable ideotype characteristics. However, other simulations indicate that would detract from leaf-area development and would reduce root yields except over a long growing season. The effect could be offset by increased plant density (e.g., narrower

Table 3. Early growth of a sugar beet crop simulated with the SUBGOL model. The daily totals of gross photosynthesis and the accumulated beet weight and the absolute and relative beet growth rates are given in dry weight equivalent to the chemical composition of sugar. The absolute growth rate is then shown as a fraction of the daily photosynthesis. The beets achieve a very high relative growth rate of 0.30 on day 30, but they are unable to use a significant fraction of DPH until they reach a larger size, after day 40. Emergence on 16 May; Davis weather, 7 plants/m^2 .

Day from Emergence	DPH[1]	TDWB[2]	CRS[3]	CRB[4]/TDWB	CRB[5]/DPH
	($g\ m^{-2} day^{-1}$)	($g\ m^{-2}$)	($g\ m^{-2} day^{-1}$)	($g\ g^{-1} day^{-1}$)	
10	1.05	0.10	0.006	0.05	0.006
20	7.13	0.30	0.036	0.12	0.005
30	21.1	6.04	1.82	0.30	0.07
40	38.3	135	16.8	0.12	0.44
50	43.0	494	17.6	0.04	0.41
60	42.4	921	20.6	0.02	0.50

[1]Simulated daily gross photosynthesis of the crop.

[2]Simulated dry weight of beets including sugar.

[3]Daily growth rate of dry weight of beets including sugar.

[4]Simulated relative growth rate of beet. The maximum observed value is 0.44.

[5]CRB as a fraction of the total current gross photosynthesis of the crop.

rows) or by larger embryo size. Savitsky's (18) work on selection for increased embryo size merits additional effort.

Respiration

The respiration activities of higher plants can be divided into two components; one associated with the energy costs of growth (biosyntheses) and one associated with maintenance (16, 17). The current view is that biochemical pathways are more or less fixed, and growth respiration is, thus, dependent on the amount and chemical composition of synthesized materials. Highly reduced compounds, such as fats and proteins, generate more respiration than do cellulose and

and sugar storage. The most efficient sugar- beet then is one which makes a minimum expenditure for proteins (particularly in leaves) for each amount of sucrose which it stores.

Maintenance respiration is chiefly concerned with repair of proteins and membranes and with maintenance of chemical gradients. The need for such reoair seems to increase geometrically with temperature. Our crop should maintain low temperatures (complete leaf cover and freely transpiring so that net radient energy is dissipated to evaporation) and have a low percentage, of labile proteins and lipids with a low propensity to increase turnover as temperature increases. Selective turnover may be desirable since that is one way plants avoid the necessity cf having all enzymes for all systems at all times—old enzymes are hydrolyzed into the free amino-acid pool, and the new enzymes of the moment can be induced as needed. Selection for low maintenance respiration may prove difficult. McCree (16) suggests that the respiration rate of starved tissue (no growth.) is the best index, and it should be expressed per unit protoplasm (e.g., per mg protein-N) since wall material, starch and stored sugar have little or no maintenance requirements, and their weight would dilute the observed rate. Selection for low sensitivity to temperature seems particularly important.

SUBSOL simulations indicate that 30 to 40% of the seasonal gross photosynthesis of a sugar beet crop is lost to respiration (15). Growth respiration dominates in early season, but maintenance respiration becomes more important as biomass accumulates and during hot weather. Seasonal respiration is quite sensitive to assumptions about protein content and turnover rate (Table 4).

Cell Size

The integration of structure and function is seen particularly clear at the cellular level. The size of the cells comprising a tissue affects their surface/volume ratio, and, thus, the proportion of the biomass which is wall material. for the same degree of secondary wall formation (the addition of lignin and hemicellulose), small cells have more of their dry matter allocated to wall material when compared to large cells, and the walls occupy a larger fraction of the fresh

Table 4. The influence of plant composition and the maintenance requirements of biomass on the seasonal yield and respiration of a sugar beet crop. Simulated with the SUBCOL model with emergence on 1 June; 140 days of growth, 1967 Davis weather, and 7 plants/m^2. Adapted from Hunt (8).

Plant Composition[1]	Respiration factors		Production			Seasonal Respiration			Y[4]
	G_R[2]	M_R[3]	Total Crop	Tops	Beet (including sugar)	Total	R_G	R_M	
			(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	
Normal	0.25	0.005	2602	540	1830	855	435	420	0.76
High-protein	0.39	0.02	-40%	-9%	-50%	+95%	+4%	+188%	0.54
High-protein	0.39	0.005	+9%	-3%	-20%	+15%	+41	-13	0.72
Low-protein	0.13	0.002	+17%	-7%	+28%	-45	-30	-50	0.88

[1] The normal chemical composition is taken as 46% carbohydrate, 22% protein, and 16% carboxylate, excluding stored sugar. High protein is 34% protein while low-protein was 14%, balanced by changes in carbohydrate and carboxylate.

[2] G_R: Growth respiration factor (g respiration/g photosynthate used in growth) calculated from Penning de Vries (17) for the particular biomass composition.

[3] M_R: Maintenance respiration factor. The value of 0.005 is drawn from Stout and Smith (19) for normal sugarbeet; 0.02 from McCree (15) for white clovers; and 0.002 is taken as a minimum M_R for succulent, low-protein biomass. All values were varied geometrically with temperature with a Q_{10} near 2.

[4] Y: The apparent growth yield is the g biomass produced/g photosynthate used in growth and growth respiration; maintenance respiration excluded.

volume. This fact has important consequences to the behavior of the tissue. For example, the interconnected wall spaces are important avenues for transport of organic and inorganic substances between the tissue and the vascular strands which supply it (Wyse, this issue). This space is termed the apoplast (in contrast to the symplast of interconnected protoplasts) and, theoretically, we expect more apoplast and perhaps lower intratissue transport resistance with small cells. In addition, for a given density of carriers per unit area, of cell membrane (plasmalemma) , the greater surface to volume ration of such cells might allow more membrane carriers per unit of cytoplasm for the uptake of ions and organic substances.

Such a hypothesis of more rapid movement and uptake of materials by small-celled tissues does not seem to have been studied experimentally although a number of implications about the growth and development of sugarbeet roots can be drawn from it.

There has been work on the influence of cell size on the water relations of plant tissues. For example, in cotton leaves, small cells were found to be an important feature, of hardening to drought stress (1). With small cells, a smaller fraction of the plant's water content is with Ln the plasmalemma-bound osmotic space and less increase in solutes is required per unit volume of tissue for osmotic adjustment to changing water potentials.

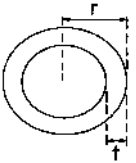
The model and the method of calculation employed in that cotton work can be applied to the question of the possible sucrose concentration in sugarbeet storage roots. Sucrose concentration is normally expressed as a percentage of fresh weight. Considering a turgid root such as we would find in well-watered soil, a percentage of weight can also be expressed as a percentage of tissue volume to the extent that volume remains constant. But within this tissue, the stored sucrose is largely confined to the osmotic space of the symplast and may be mostly within the vacuoles of that space.

The water potential of the root tissue will be in equilibrium with the. soil-water potential and, during times of the. day when transpiration gradients are small (such as just prior to dawn), we can write:

$$\psi soil = \psi root = \psi osmetic - \psi turgor;$$

where the ψ's are water-potential terms measured in bars or Joules/kg. The turgor value thus determines the amount of osmotically active solutes which can be. accumulated within the symplast. Measurements of turgor potentials for fleshy tissues like sugar-beet roots are difficult and uncertain, and we know little about, how that value may vary with variations in tissue morphology. We can assume, since turgid beets ordinarily do not split, open when the outer tissues are ruptured, that turgor pressure is maintained by the tensile strength of the walls of each cell rather than by a contrasting or binding action of just the outer cell layers. We can also assume that the tensile strength of walls is, in part, a property of wall thickness with greater strength in thicker walls.

With that background, we can now consider some of the implications of cell size on sucrose storage. A simple model for the calculation of wall and osmotic volumes is established in Figure 2. Large cells with thin walls will have a larger traction of their total volume as osmetic space suitable for sucrose, storage than will small cells and/or cells with thick walls. When such cells are packed into tissues, three types of space can be identified: osmotic, wall, and intercellular air spaces. With close-packed, round cells, the percent of air space is independent of cell size. Whether that is also true in real tissues with more complex cell shapes is unknown.



$$V = \frac{4}{3}\pi r^3$$

$$V_o = \frac{4}{3}\pi (r-t)^3$$

$$V_w = \frac{4}{3}\pi (3r^2t - 3rt^2 + t^3)$$

$$\psi_{cell} = \psi_{solute} + \psi_{turgor} = \psi_{soil}$$

Figure 2. A conceptual model for partitioning cell volume (V) into osmotic (V_o) and wall (V_w) space depending upon cell radius (R) and wall thickness (t).

In Table 5, calculations are presented for tissue-water relations in sugarbeet roots with three cell sizes and two wall thicknesses. For simplicity, these cells are assumed to be closely packed with no air spaces. It is further assumed that the tissue has a bulk density of 1.0 and that the matrix potential of the cytoplasm and the physical volume of the cytoplasmic material are zero. This permits us to predict sucrose concentration for the whole tissue on the basis of sucrose concentration in the osmotic space. Table 5 is based on 0.44 molar sucrose (a 15% solution) in that osmotic space generating ψ_{solute} = 10.6 bars (from ψ_{solute} = -RT/V). With ψ_{soil} = 0, then turgor = 10.6 bars. large, thin-walled cells are found then to yield 14.5% sucrose on a fresh weight of tissue basis, whereas small cells with thick walls yield only 12.2%. That difference is due to the change in wall volume from 3.5 to 18.7% of the whole tissue. We can only guess the extent to which smaller cells or thicker walls would increase the permissible turgor. Based on the sucrose concentrations observed in sugarbeets grown with a low supply of nitrogen or at low night temperatures, turgor pressures in the range of 13 to 15 bars seem possible.

The 30µ and 15µ radii used here are typical mean values for the parenchymatous cells in sugarbeet: and chard roots, respectively (Rapoport, 20th Genl. Mtg. , Am. Soc. Sugar Beet Technol.). There is considerable variation in cell size in the intercambial zones of sugarbeet with small cells near the vascular cambia and larger cells (r = 60µ) in midzone. The small cells presumably are immature and progress with time tO large cells. The model predicts (Table 5) that The greatest concentration of sucrose per weight of tissue would be found in midzone parenchyma. However, this is not the case with real beets where small beets have greater concentrations than large beets (13) and cambial zones greater than midzone parenchyma (20). This seems likely to be cue to the occurrence of other solutes within the osmotic space of midzone cells, thus limiting the proportion of ψ_{solute} due to sucrose. Such solutes include amino acids, organic acids, inorganic: ions and other sugars. At least Na+ and K+ (and presumably equal concentrations of anions such as Cl^- and organic acids) have been shown to vary across the intercambial zone (D. F. Cole, 20th Genl. Mtg., Am. Soc. Sugar Beet Technol.). Rough

Table 5. The potential influence of cell size and wall thickness on sucrose concentration expressed as a percent of tissue fresh weight. Calculations based on the model in Figure 1 assuming close-packed cells (0 air space) with 0.44 M (-9.8 bars) sucrose solution in the osmotic space and a tissue bulk, density of 1.0 g cm^{-3}.

Cell Radius	Wall Thickness	Volume per Cell			Cells	V_W	
		Total (V)	Osmotic (V_O)	Wall (V_W)	Liter	V	Sucrose
(μ)	(μ)	(10^{-11} ℓ)	(10^{-11} ℓ)	(10^{-10} ℓ)	(10^9)	(%)	(% f.wt.)
15	1.0	1.41	1.15	0.26	70.7	18.7	12.2
15	0.7	1.41	1.27	0.19	70.7	13.4	13.0
30	1.0	11.3	10.2	1.09	8.8	9.7	13.6
30	0.7	11.3	10.5	0.77	8.8	6.8	14.0
60	1.0	90.5	85.0	4.45	1.1	4.9	14.3
60	0.7	90.5	87.3	3.13	1.1	3.5	14.5

calculations with one of Cole's data sets indicate than Na+, K+ and their counter ions contribute -2 bar to solute in cambial zones and -4- bars in midzone parenchyra. The 2-bar difference, taken at the expense, of sucrose, would reduce tissue sucrose concentration by nearly 20%, from -10.6 bars to -8.6 bars. Another data set showed even larger differences.

One can speculate, further that the basis for such distributions may lie with [illegible] of sucrose [illegible] the apoplast with increasing distance [illegible] than occurs for Na+ and K+ with distance from the [illegible]. Midzone cells might then find little sucrose but considerable Na+ and K+ [illegible] free space as the basis for further expansion. Studies of such phenomena should include culture [illegible] juice purities are increased sharply. [illegible] attention of the need for additional study [illegible] space movement and cell expansion. Until then, further [illegible] generalizations about root anatomy and function would seem premature.

Summary

I have [illegible] approach [illegible] for [illegible] sugar beet production. [illegible] physiological [illegible] and [illegible] affecting the [illegible] photosynthate, rather than [illegible] production, since we know [illegible] about those aspects and they may offer greater opportunity for improvement.

The [illegible] are [illegible] concepts. They involve qualitative assessment of [illegible] and balances and [illegible], of necessity, involve the formulation of [illegible] calculation of potential benefit, identify [illegible] information, and define selection conditions and [illegible]. The [illegible] presented here are mostly simple ones, designed to [illegible] attention [illegible] method, and to show the value of [illegible]; but [illegible] the issues are dynamic and exceedingly complex. Those will require sophisticated, hierarchical simulation models.

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Growth Patterns in Sugarbeet Production*

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For decades the. sugarbeet plant has been studied to learn about its growth processes and how they interact with the environment to influence sucrose yield. Growth studies have also been used as a way to discover inefficiency in sugarbeet production and to develop) techniques and cultural practices that can be used to remedy such inefficiencies.

Plant physiologists have mainly used pot cultures in the greenhouse, growth chamber, or phytoiron in their sugarbeet growth experiments. Much of the research has been done with a. limited number of commercial varieties, with little attention given the effect of genotype. Agronomists have conducted field trials testing cultural practices such as the effects of fertilization, irrigation, and planting density. Sugarbeet breeders have continued to follow routine methods for the development of commercial varieties based upon their combining ability and performance for root yield, sucrose content, and pest resistance. They have censistantly struggled with the apparent inverse relationship between root yield and sucrose content. Breeders have directed little effort toward selecting a particular type of leaf canopy or internal root structure that is more efficient in partitioning of photosynthate to growth and to sucrose storage in the root. Physiologists

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and geneticists are now becoming aware of the need for team research to study the variation among genotypes and to develop principles, methods, and models for the selection and breeding of superior cultivars.

The purpose of this paper is to: 1) summarize some of the general characteristic patterns of growth and sucrose accumulation that have been observed in sugarbeet as a summer crop in a temperate region and 2) to present data we have obtained in recent years on growth and sucrose accumulation patterns in inbreds and hybrids, and the relationships that exist between inbreds and their hybrids for these characteristics.

General Growth Pattern

Early scientists such as Bouillene et al. (3) and van de Sande Bakhuyzen (31) distinguished three phases of growih in the sugarbeet: leaf formation from emergence until the end of July, "root formation or tuberization during August, and storage, or ripening, through the rest of the season. Watson and Selman (39) agreed that early growth is dominated by the foliage and later development by the root, but they were unable to distinguish a separate phase for sucrose storage in the root.

Leaves and petioles have the first priority for metabolic products during seasonal development of a plant as long as conditions favor vegetative growth. During the first few weeks of growth, leaves and petioles constitute the main part of the plant and account for most of the plant dry matter (34, 10, 21, 33). At about 6 weeks, the root begins to accumulate dry matter more rapidly than do petioles and leaves combined. From that point on, the root shows an accelerated linear accumulation throughout the season, while the dry matter content of blades and petioles tends to accumulate at a constant rate. This is illustrated with data from a test of 24 hybrids and inbreds grown at Logan in 1974 (Figure 1). This suggests that

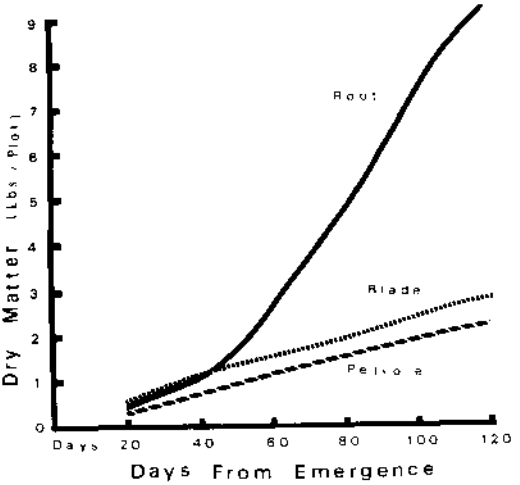

Figure 1. Seasonal accumulation of dry matter for blades, petioles, and roots of 2^{L} genotypes. Logan, Utah. 1974.

the earlier the leaf canopy develops, the better the chance for higher sucrose production because the root, rather than the foliage, receives the bulk of Lhe photosynthetic assimilate for a longer period.

Leaf Area

Leaf area has been one cf the main parameters to measure growth in plants. According to Storer et al. (33), it appears to approximate photosynthetic production as well as any measureable leaf attribute.

As early as 1947, Watson (36) observed that leaf area was a main constituent in determining sugarbeet yield. Others have substantiated that root yield was correlated with a rapidly developed, large leaf area index (LAI) (12).

Several workers (4, 14, 15, 16, 19, 21, 32, 33, 37) have noted the distinct pattern of leaf area increase and decrease during the growing season.

A typical seasonal change in leaf area in the northern hemisphere with N fertilization to maximize sucrose production is shown in Figure 2. If is a typical

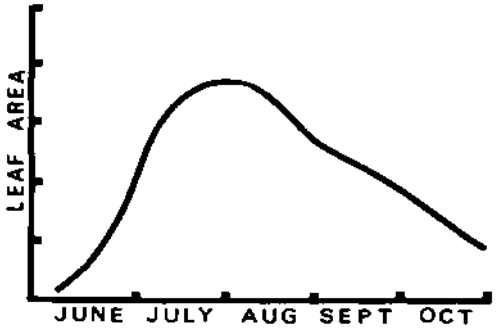

Figure 2. General pattern of seasonal changes in leaf area. See Watson (37), Campbell and Viets (4) Ilodanova (15), and Storer et al. (37).

logarithmic growth curve maximizing midway in the growing season; it then decreases because as the older leaves die, their leaf area is not entirely replaced by that of the newly formed leaves.

In the northern latitudes under normal N fertilization, plants usually reach their maximum LAI in the latter part of July or the first part of August, then decrease until

harvest. The rate of decrease in leaf area after the maximum is dependent upon nitrogen availability. With high rates of nitrogen, the leaf area does not decrease as rapidly as illustrated in Figure 2.

Goodman (14) collected data at seven locations in England, using two varieties, and found significantly different leaf areas for locations but similar seasonal growth patterns at all locations. We have observed the same general leaf area growth curves in diverse inbreds and hybrids as observed in various open-pollinated varieties studied by other scientists (Figures 3 and 4). There were differences between genotypes and between years for

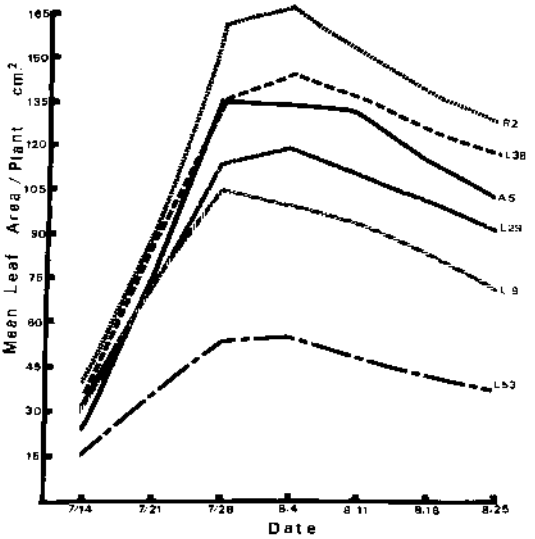

Figure 3. Seasonal pattern of leaf area for inbreds at Logan, Utah.

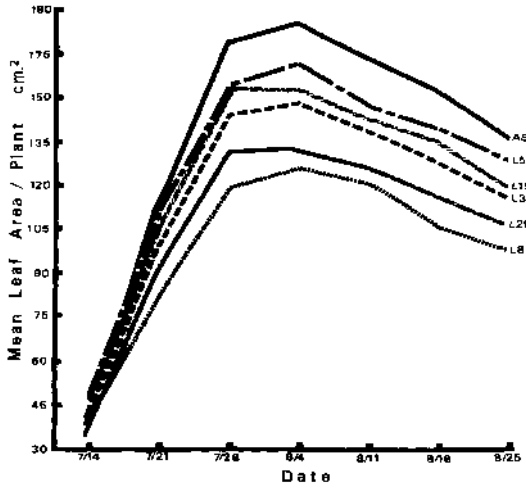

Figure 4. Seasonal pattern of leaf area for hybrids at Logan, Utah. Each curve represents the mean of five hybrids of the indicated pollen parent crossed to the same cytoplasmic male sterile-female parents.

dates when the maximum leaf area was reached, but the growth patterns remained relatively similar for all of the genotypes during different growing seasons.

Significant differences in leaf area were observed between inbreds and between hybrids. Some hybrids showed leaf growth similar to the mean of their parent inbreds. Others exhibited heterosis for leaf area. For example, L53 inbred has the smallest canopy of the inbreds we studied (Figure 3). However, in hybrid combinations, it produced large leaf areas (Figure 4). It appears that leaf area

is a multigenic character governed mainly by nonadditive genetic factors. These data and data from other unpublished experiments demonstrate that the total seasonal leaf area of a hybrid in the field cannot be accurately predicted from the leaf area of its parents.

From the literature, we would conclude that: leaf area indexes of 3 to M in August are nearly optimal for sugar-beet growth (10, 13, 14, 32, 33, 37). However, no leaf area is optimal from year-to-year (33). Goodman (14) pointed out that: an increase in root yield has been associated with an increase in LAI up to 5.5. He suggested that, beyond an LAI of 4 the added canopy may contribute to total plant dry matter yield because of the foliage, but the leaves on the average are so deficient for maintenance carbohydrate that they do not contribute to root growth and sugar accumulation.

One of the most likely ways to increase sucrose yield would be to develop varieties that reach their maximum leaf areas early in the growing season and thereafter do not surpass the LAI for optimum growth. This partitioning of assimilate to the root and the early establishment of a large sink size in the root are necessary for high sucrose yield.

In a 1976 test at Logan, leaf areas of nine inbreds gave a correlation of 0.80** with root weight at the July 21 harvest date. The correlation coefficient for leaf area and root weight of six hybrids developed from these inbreds was 0.60**. Campbell and Viets (4) reported that the correlation between LAI and root weight approached 0.90** by the end of June but dropped to 0.33 at harvest. Thus, meaningful relationships must be defined, and selection for leaf area should be mace early in the growth season while the canopy is being formed.

Leaf area is greatly influenced by environmental factors. Watson, et al. (38) reported that leaves expand more in moist years than in dry years, and that shading decreases leaf size. Nitrogen fertilizer increases leaf growth-arid also delays maximum "leaf canopy development until the last of August (6, 9, 33). Milford and Thorne (25) found that cold temperatures late in trie growing season resulted in plants having slightly smaller leaf areas, and halving light intensify had little effect en leaf area. Lenton and Milford (18) reported that increased photoperiod in controlled environments increased leaf area 47% ; however, leaves were thinner and had dry weight production similar to sugarbeets grown in a normal environment.

Leaf Number

The number of leaves on a plant continually increases in a linear manner throughout the growing season for all genotypes. We have observed similar growth patterns for both inbreds and hybrids (Figures 5 and 6). Significant differences in leaf number ana heterosis occur for this character. However, leaf number is relatively unaffected by cultural practices or environmental factors (38).

Canopy Type

The multiplicity of canopy types in sugarbeet further complicates the problem of selecting the most: efficient plants for breeding and production. Much of this variation has nor been critically studied because scientists have used commercial varieties in their growth studies, and most of our commercial varieties are quite similar in canopy type.

Foliar geometry of loaf placement:, horizontal or erect growth habit, differences in light-absorbing capacity, and photosynthetic efficiency could all affect production. Kiyaura et dl .(27) have reported that erect and horizontal canopy types are different: in their transition from one stage of development to another during the growing season.

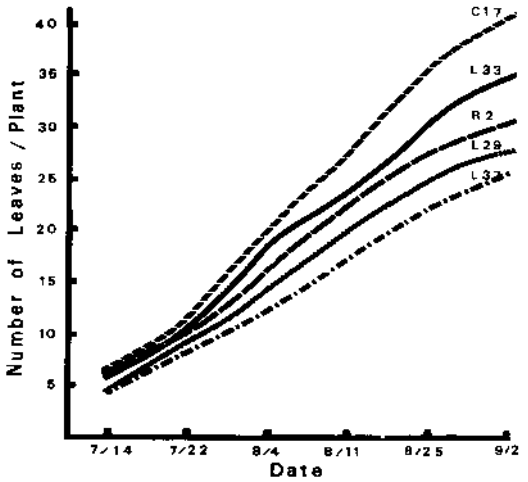

Figure 5. Seasonal pattern of leaf accretion for inbreds at Logan, Utah..

Loomis and Williams (22) reported that leaf angle distributions are quite cifferent from different strata in the canopy, and a single mean angle for each stratum would be a poor representation of canopy morphology. So far we have railed to develop reliable techniques that can be used as selection criteria for the most effective canopy type for sugarbeets. Some attempts to study Lhe effects of the canopy have been made by defoliation or decapitation of the terminal bud (5, 8, 11). These practices have resulted in decreased root yield and sucrose production. Early leaf removal stimulated the remaining leaves to increase in size at the expense of root growth; late removal of leaves also reduced sucrose

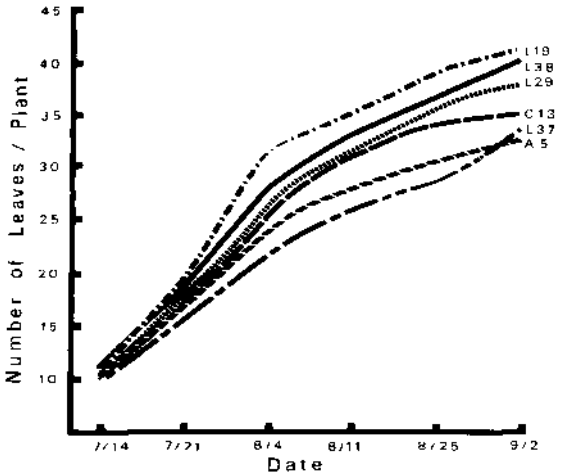

Figure 6. Seasonal pattern *of* leaf accretion for hybrids at Logan, Utah.

contort. Gerra (31) estimated that loaf removal caused a 40% decrease in cell number and a 50% decrease in the width*of* vascular rings in the root.

Plant Density

Plant density experiments have been another means of studying the partitioning of assimilate for growth. It is well established that plant density affects production (4, 5, 7, 13). Increasing plant density increases leaf growth per unit area, decreases the root/shoot ratio and root yield, and increases sugar percentage (17, 20, 24). Sucrose yields seem to be optimal at a plant population of about 30,000 plants per acre. In 1974, we compared three genotypes having different canopy structure in 8-inch, 12-inch, and 24-inch spacings in 22-inch rows in

the field. One genotype had a prostrate growth habit with leaves on, or near, the soil surface. A second genotype had an extremely erect growth habit, and the third genotype was intermediate between the ether two. The erect and semi-erect canopy types tended to be less erect in the wider spacings, but the growth habit of the prostrate genotype remained unchanged. The interaction of genotypes x density was not significant. All three canopy types gave the highest yield at the same density and had similar sucrose contents. Data from a 1976 study also demonstrated that plant density affects sugar production, but canopy types of different growth habit showed little interaction with plant density. Similar results have been observed by Loach (19).

Root-shoot ratio

The root/shoot ratio of a plant is an indication of the partitioning of assimilate between the top versus the root. This ratio follows a linear pattern during the growing season (Figure 7). Early planting increases the root/shoot ratio when low temperatures tend to limit leaf growth (13). Loach (19) demonstrated that cultivars with a larger root/shoot ratio maintained more rapid assimilation rates during the latter stages of growth. It was hypothesized that the plants were able to maintain faster rates of assimilation because they had larger roots in which to store sucrose. Some varieties with relatively large root/shoot ratios produced as much total dry matter as others with less leaf area (Watson, 37). In our experiments, the best relationship between sucrose content, or yield and root/shoot ratio, occurred only in the growing season.

Root Development

According to Arrschwager CD, the sugarbeet root is derived from a series of concentric cambia developed at a very early stage. He suggested that all of the vascular rings of the root are developed concurrently and just

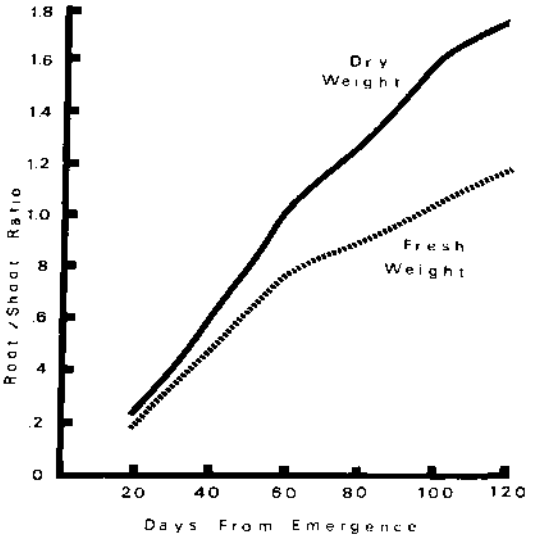

Figure 7. Root/shoot ratio of 24 genotypes.

expand with growth. Kilford (23) recently concurred that rings develop together and not sequentially. Our research atHO supports this conclusion.

The sugarbeet root begins an accelerated growth about 6 weeks after germination and continues to accumulate dry matter linearly throughout the growing season (Figure 1). Root growth occurs by both cell division and cell enlarge merit, and individual varieties may differ greatly in the proportion of each of these two processes.

Vascular Rings

It is generally assumed that high-sucrose types have many narrow vascular rings, whereas high-root-yield types show the opposite pattern. This was first suggested by Roemer (30) and Pack (2S). Pack observed a correlation of 0.30 for sucrose content and ring density and suggested that ring density could be used by breeders as a selection criterion for high-sucrose lines. Artschwager (1) noted that large ring number, high ring density, broad vascular zones, narrow parenchymal zones, well developed phloem, absence of lignification in the sugar sheath and white tissue color were all indicative of a high-sucrose content. However, he cautioned that the relative influence of these traits on sucrose can differ with the genetic material, and systematic study would bo required to define the effect for a given selection. He found no relationship with the size of the central core, nor a consistent relationship between the number of vascular bundles in the root and sucrose production. He also concluded that the shape of the root has little consistent relationship to its internal structure.

In a 1974 study at Logan, 24 inbreds and hybrids were harvested five times during the growing season, and the vascular ring numbers and ring widths determined. Well-developed ring numbers increased on the average from seven on July 28 to 11 on October 15, the date of final harvest. The relative growth rate of the rings showed that they grew in a parallel manner at quite similar rates during the season (Figure 8). Rings decreased in width from the central core outward. Ring widths were influenced by different plant densities; however, genotypes showed similar patterns of behavior. Milford and Watson (26) found that the heavier roots of nitrogen-fertilized beets had the same number of rings as roots grown with low nitrogen, but root enlargement was due to increased width of individual rings. The number of cells was not affected, but mean cell volumes were 40%

larger in the high-nitrogen plants .

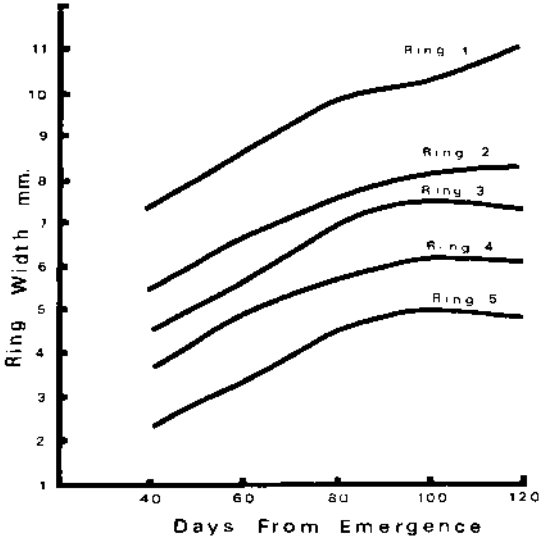

Figure 8. Seasonal change in ring width for 24 genotypes of sugarbeet at Logan, Utah. 1974.

In our studies we have significant, positive correlations of ring width with root yield and negative correlations of ring width with sucrose content. An example of these correlations is given in Table 1 for 18 hybrids grown at Logan in]976 .

Table 1. Correlation coefficients for vascular ring width with root weight and sucrose percent for 18 hybrids at three harvest dates.

Ring No.	Root Weight			Sucrose %		
	H2	H3	H4	H2	H3	H4
1[1]	0.13	0.77**	0.74**	-0.24	-0.67**	-0.30
2	0.62*	0.74**	0.80**	-0.57**	-0.69**	-0.32
3	0.71**	0.64**	0.79**	-0.63**	-0.42	-0.27
4	0.06**	0.71**	0.65**	-0.64**	-0.41	-0.15

[1] Rings were numbered from central core outward.

Cell Size and Cell Volume

Milford (23) recently made a detailed anatomical study of The vascular rings of the sugar-beet root. He found that The mean cell volume within both parenchymal and vascular zones of the roo: were larger in each successive ring from the corner outward . However, the vascular zones contained two to throe times as mny cells as The adjoining parenchyma. Cells enlarged less with each successive ring outward, expanding parenchymal cells increased six to eight times in volume and 10 to 15 times in number from June, to September. Vascular cell volume remained constant cell cell number increased 10 TO 30 times during This growth period. The parenchymal tissues had lower sucrose concentrations than the vascular zones composed of smaller cells. Water per cell and non-sucrose dry matter per cell were directly proportional to cell volume. He concluded that sugar concentrations in the root is determined on the basis of The relative proportions of the two types of tissue in the root. Pilot studies in our laboratory have also indicated that cell size is highly correlated with sucrose content. More research needs to be done to study root growth at the cellular level.

Root Diameter

Gemma (11) reported that root diameter was highly correlated with root weight: 0.82** for subarbeet, 0.84** for fodder beet, and 0.75** for chard. He observed that root diameter was also correlated wirh the number of rings in the root: 0.80** in sugarbeet, 0.52** in fodder beet, and 0.79** in chard. Pack's (29) correlation was 0.86** for root diameter and yield. At Logan, our root diameter ard yield correlations have varied from 0.60** Lo 0.80"" (See paper by D. T,. Doney in this symposium)

Sugar Accumulation

Several of our studies at Logan have demonstrated that sucrose accumulation in the root begins very early in the seedling stage of development and occurs concurrently with root growth. On a fresh weight basis, sucrose content increases in an almost linear matter during the growing season (Figure 9). Our results are supported by those of

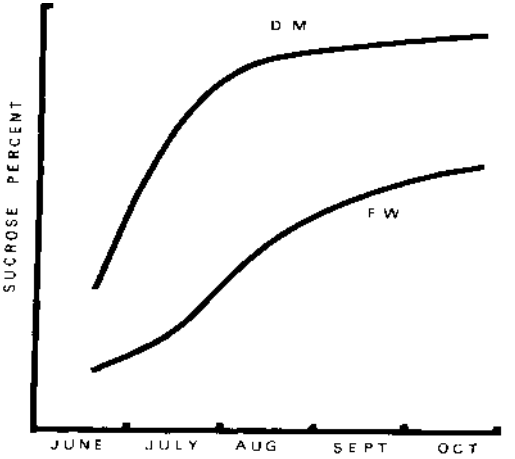

Figure 9. Seasonal changes in sucrose accumulation, fresh weight (F.W.) and dry matter (D.M.) basis.

Bergen (?), Gemma (11), Goodman (12), Follett et al. (18), Milford (23), and Watson and Selman (39). Sucrose percent of the root dry matter shows the most rapid rate of accumulation during June (Figure 9). The rate is decreased slightly in July and then remains relatively constant until harvest. This is in contrast to previous concepts (35) that sucrose does not accumulate until the root is fairly well developed, ana results from residual photosynthate not required for growth.

inbreds and hybrids follow similar linear patterns of sucrose accumulation, with the highest rate of accumulation occurring early in the season (Figures 10 and 11). Significant differences were noted between inbreds and between hybrids, and in a few cases heterosis was observed for sucrose percent. Since sucrose content is inherited mainly in an additive manner, the sucrose content of most of the hybrids was equal to Their mid-parent mean. Correlation of sucrose in inbreds with sucrose in hybrids was 0.9l**.

usually inbreds, or hybrids, high in sucrose at the beginning; of the season were also high at the end of the season. Those low in sucrose remained low during the entire growth period. The high-sucrose inbred L19 was an exception since it had a lower sucrose content than some inbreds at the first harvest in June and a more rapid rate of sugar accumulation than all other lines during the remainder of the season. This suggests that there may be different genetic and physiological mechanisms governing the amounts of photosynthate proportioned for sucrose accumulation in L19 than in other inbreds. The L53 inbred apparently receives a greater proportion of photosynthate for sucrose storage during the early stages of development, and L19 receives an increased stimulus for sucrose accumulation about 40 days after thinning. The same relationship is evident on a dry-matter basis. At the first harvest in 1976, the percent

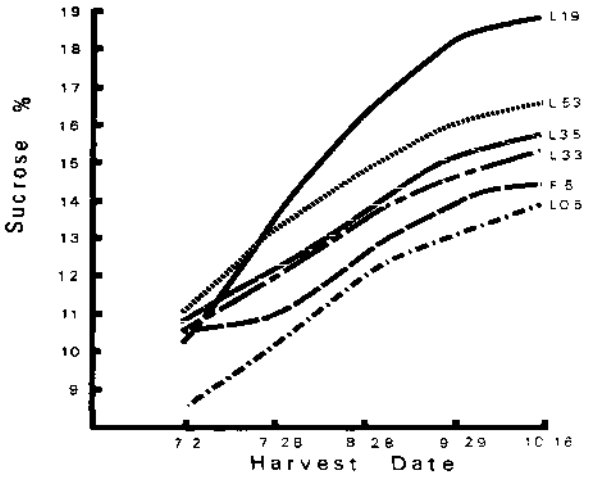

Figure 10. Seasonal change in sucrose accumulation for six inbreds, Logan, Utah. 1976. (Fresh weight basis)

dry matter[1] of L53 was 67% and of L19, 64%. At The final harvest, L19 had 2% higher sugar in the root dry matter than L53 (L53, 57% and L19, 59%). Other inbreds shown in Figure 10 averaged 60% sucrose in the dry matter for the first harvest and 55% for the final harvest. Light, soil conditions, temperature, moisture, and nitrogen could affect the control mechanisms. We need more research in these areas.

Sucrose percentage generally has a correlation of 0.7 to 0.8 with dry matter of the root. Differences in sucrose percentage on a fresh-weight basis often appear to be reflections of water content of the cells rather than sucrose per se. When sucrose content is determined on a

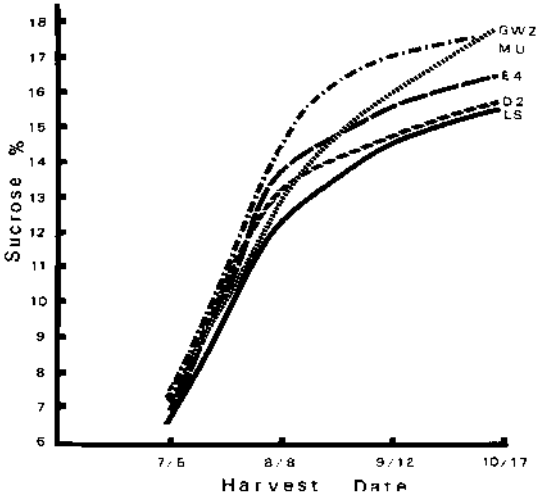

Figure 11. Seasonal change in sucrose accumulation for hybrids, Logan, Utah. 1978. (Fresh weight: basis)

dry-weight basis, there is often little difference between varieties. Bergen (2) compared a high yield with a high sucrose type variety and found that, although the varieties showed consistent significant differences on a fresh-weight basis, the differences were significant on a dry-weight basis for only the last harvest. Goodman (13) and Follett et al. (10) reported similar results.

Plant breeders generally select for high sucrose on a fresh-weight basis. More meaningful selection might result if breeders made their selections on a dry-weight basis.

Summary

There are consistent patterns of growth of leaves and roots of sugarbeets and fairly consistent patterns of sugar accumulation during the season. These may be altered by environmental factors, cultural practices, or genotypes; however, the patterns remain relatively consistent. Leaf area increases rapidly for all genotypes until the last part: of July, or first part of August (approximately 8 0 to SO days afrer emergence), and then decreases during the rest of the season. Leaf numbers, root/shoot ration, dry matter, root diameter, the number and width of vascular rings in the root, and sucrose accumulation on a fresh-weight basis have linear patterns of development. On a dry-matter basis, the pattern of sucrose accumulation is curvilinear, with the greatest rate of accumulation occuring mid-season.

Significant differences are noted between inbreds and hybrids for all growth characteristics. Heterosis occurs for some genotypes for all characters. Inbred and hybrid performance are not well related, except for additive factors such as sucrose accumulation.

Based on growth patterns, if we were to characterize an ideal beef, it would include the following:

1. Early development of maximum leaf area to LAI 3 to 4, then longer leaf duration.
2. Smaller leaf numbers and leaf orientation that favors more effective light utilization by the canopy with vertical leaves in the upper part of the canopy strata.
3. Plants with large root/shoot ratios - early in the season.
4. High sucrose percentage in the. dry matter of the root.
5. Roots in which cell multiplication dominates over cell expansion for a longer development period.
6. Large number of developed rings in the root with broad zones of vascular tissue and narrow bands of parenchyma.

Growth and sucrose accumulation patterns demonstrate that selection of genotypes for optimum sucrose production is not an easy task. No single, nor group of, growth factor(s) have yet proved to be a good index of genotype performance. However, recent studies suggest that the opportunity for improvement may be more effectively realized in the early stages of growth than we have previously supposed. Sugar-beet geneticists and physiologists need TO work as a team to develop new[7] selection techniques to identify genotypes that partition photosynthate more efficiently for plant growth and sucrose accumulation. This appears to be the most promising approach to attain new genotypes having both high yield and high sucrose content.

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Parameters Controlling Sucrose Content and Yield of Sugarbeet Roots*

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Agronomists and plant breeders working with sugarbeets have long been frustrated by the inverse relationship that exists between sucrose content and root yield. Genetic selection and agronomic practices that tend to increase yield decrease sucrose content, and those that increase sucrose content decrease yield.

In the past, plant breeders made significant gradual improvements in the potential sucrose content of commercial cultivars. In recent years, progress has slowed and we seem to have reached an Impasse. Significant progress In the production of new genotypes possessing both high yield and high sucrose will require new, innovative selection criteria. Simple selection criteria based on limited physiological factors may be the answer. Such criteria could also be used to evaluate chemical growth regulators for their ability to regulate partitioning of photosynthate to maximize yields.

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This paper will discuss partitioning of photosynthate in sugarbeet and report the results of recent investigations on the inverse relationship between sucrose content and root yield. The objective of this work was to delineate areas for needed research and to propose several physiological principles for use as a basis in efficient genetic selection.

Evidence for balanced partitioning of photosynthate between root: growth and sucrose accumulation will be presented. This partitioning is regulated in the root and it operates independently of photosynthate supply.

Sucrose is translocated to the root via the phloem, and evidence will be presented to show that it then passes into the free space between the root cells and then diffuses into the interring area. Our hypothesis is that the final sucrose content of storage parenchyma cells is regulated by length of the diffusion path and by the proportion of cells located near the vascular tissue where free-space sucrose concentrations are highest. Large cells and wide rings-are related to high yield, whereas small cells and narrow rings are related to high sucrose content.

Allocation of Photosynthate

Photosynthate is allocated to the sugarbeet root continuously throughout the growing season. The priorities for allocation proposed by Fick et al. (3) are respiration, top growth, fibrous root growth, and storage root growth including sucrose accumulation. However, the proportion of available photosynthate allocated to each sink varies continuously throughout the season depending on the relative "sink strength" of the individual plant part. This type of continuous season-long partitioning is termed "balanced" as opposed to the "phasic" partitioning that occurs in potatoes, corn, wheat, etc. (5).

The photosynthate allocated to the root Is partitioned between growth and sucrose storage. Root growth here includes both fibrous and tap roots. Snyder et al. (9) have good evidence that genetically controlled partitioning occurs between the fibrous roots and tap root and that this partitioning may be an important component of yield.

Some controversy exists concerning the pattern of partitioning between root growth and sucrose storage throughout the growing season. Based on results of greenhouse and growth chamber studies, Ulrich (10) proposed that a major portion of the photosynthate translocated to the root was allocated for root growth until late in the growing season when growth was retarded by low Temperature and nitrogen deficiency. This confirmed the previous work of Bouillene et al. (2) and van do Sande Bakhuyzen (12) who were able to distinguish three growth phases in the development of the sugarbeet plant; i.e., leaf formation, root formation, and a ripening phase. This work suggested a phasic partitioning of photosynthate for sucrose storage and assumed that the sucrose stored in the root was sucrose In excess of that utilized for growth and maintenance. In recent work by our group at Logan, we have been unable to confirm a phasic pattern for sucrose storage. Cur results confirmed those of Bergen (1), van Ginnekin (11), Milford (6), Storer et al. (8), and r'ollett et al. (4), and indicated that partitioning of photosynthate between root and shoot and partitioning between growth and sucrose accumulation within the root (Figure 1) occur continuously throughout the growing season. The results of our work and of others are summarized in figure 2. The only difference between these results and those of Ulrich is the linear increase in sucrose concentration throughout the season.

The theory that only sucrose not required for growth is available for storage (10) suggests that increasing photosynthetic rates should enhance sucrose concentrations. However, if sucrose partitioning is balanced between growth

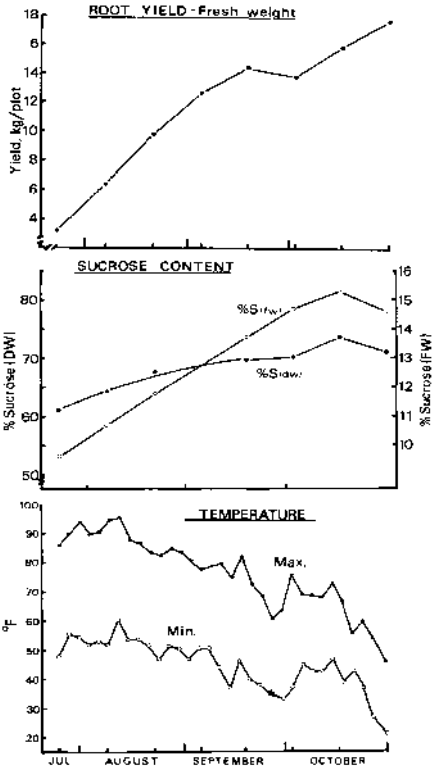


Figure 1. Seasonal growth patterns for root yield and sucrose content at Logan, Utah, in 1972. Data represents the mean of six cultivars grown in a replicated field trial and harvested at two-week intervals. Temperature data are three-day averages.

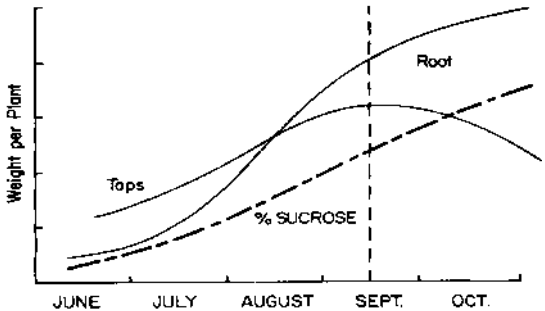


Figure 2. Seasonal pattern of root, tops, and percent: sucrose. Note linear pattern of sucrose accumulation. See Bergen (1); van Ginnekin (11); Milfcrd (6); Storer et al. (8); Pollett et al. (4).

and storage, then carbohydrate supply should increase yield but have no effect on sucrose content. Field photosynthetic rates and thus photosynthate supply can be increased by CO_2 enrichment of the air within the leaf canooy. Results of such an experiment are given in Table 1. Increasing the CO.-, level to 700 ppm increased root yield by 21%, but reduced the sucrose content from 15.4 to 15.1. Therefore, the additional photosynthate was net utilized for sucrose storage. This conclusion is confirmed by the work of Watson et al. (13) who used shading to reduce photosynthate supply. Shading reduced root dry weight yield but did not alter the sucrose to dry weight ratio. Thus translocated photosynthate was partitioned within the root between growth and sucrose storage and was independent of photosynthate supply.

These data further substantiated the hypothesis of a balanced partitioning of sucrose between storage and growth

in the sugarbeet root. This balanced partitioning concept is important to an understanding of the sucrose-yield relationship.

The discrepancy between the works of Ulrich and of Bergen (1), van Ginekin (1.1), Milford (6), Storer et al. (8), and Follet.L et al. (4) may be explained in several ways. In Ulrich's work the plants were grown in containers in nutrient: solutions. Such conditions present a physical restraint to root growth and provide much more abrupt environmental changes (temperature, nitrogen supply, etc.) than field conditions do. The more complex field environment would tend to dilute the effects of a change in any one environmental factor. Thus, the results of experiments conducted in relatively simple environments may not be transferable to the field.

Table 1. Effect of CO_2 enrichment on the sucrose content and root yield of sugarbeeLs.

Treatment	Yield	Sucrose	Sucrose Yield
	lbs/plot	percent	lbs/plot
Control	36.2	15.4	5.6
7 C0 ppn CO_2	43.7	15.1	6.6
LSD (.35)	2.2	.34	.37

Carbon dioxide was supplied to the canopy via perforated Lubes located between the rows throughout the growing season. All plots were, surrounded (top open) by an 80 cm high clear plastic shield to help maintain the CO_2 level. CO_2 levels were determined within the canopy by gas chromatography.

The site for control of partitioning between sucrose storage and root growth is of obvious importance. The. site of control should be apparent if reciprocal grafts of roots and shoots are made between sugar and yield type plants. Such a study was conducted at Logan, Utah in 1977.

The results indicated that control of sucrose storage is located in the root (Table 2). For example, the L19 root increased the sucrose storage capabilities of Fodder tops by 35%, but the L19 top only increased the sucrose concentration in Fodder roots by 13%. Conversely, Fodder tops reduced the sucrose content of the L19 root by only 5%. However, root weight was about equally controlled by the shoot and root. Therefore, the photosynthetic capacity of the leaves and the growth potential of the root are both important for maximizing root growth, but the partitioning between growth and sucrose storage is controlled primarily in the root.

Table 2. Relative effects of root and shoot on sucrose content and root. size. Data are from grafts of L19 and fodder.

		Effect on	
		Sucrose	Yield
		percent change	
L19[1]	Scicr-	+13	-21
	Stock	+35	-25
Fodder[1]	Scion	- 5	CT*
	Stock	-30	CT

*Curly top infected

[1]L19 has a high sucrose content but low root yield. Fodder (Blanco) has a low sucrose content but a high root yield.

Lateral Movement of Sucrose

Determination of the pathway cf sucrose movement within the storage root and of the biochemical mechanism of its uptake into root storage cells may help explain the balance between growth and sucrose storage.

Before biochemical studies can be initialled, we must know the morphological pathway of sucrose movement from the

phloem cells to the storage parenchyma. Two possible pathways exisL (Figure 3). It is possible for sucrose to move

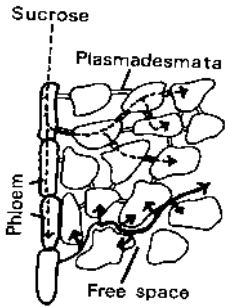


Figure 3. Diagramatic representation of possible pathways of lateral sucrose movement in the sugar-beet root. Solid line, apoplastic; dashed line, symplastic.

from the phloem directly into adjacent cells via plasmadesmata. In this case, sucrose would be actively held and actively transported at all times throughout its movement from the phloem to The interior of the vascular ring. This is an example of movement through the symplast. The second possible mechanism is movement through the apoplast or free space. In this case the phloem cells would unload sucrose directly into the free space between the parenchyma cells where it would move by diffusion away from the vascular ring. Sucrose moving via this pathway would not be actively held while in the free space and, therefore, could easily be washed out of the tissue.

Two experiments were conducted to determine which of these pathways is operable in the sugarbeet root. In Experiment 1, sugarbeet plants growing in the field were

exposed to $^{14}CO_2$ for 30 minutes. Roots were then harvested at regular intervals over a 24-hour period after exposure to the $^{14}CO_2$. At each harvest, a piece of tissue was removed from the root and CUT into 1-mm slices. Small disks (4 mm diameter) were punched out of the slices and water solubles were extracted for either 30 seconds or 6O minutes in running tap water. Then the radioactivity remaining in the tissue was determined and the percentage of activity washed out was calculated.

The results indicated that a major portion of the sucrose could be washed out immediately after translocation to the root, but, after 24 hours of uptake, the sucrose was actively held by the tissue (Table 3). This is consistent with movement in the apoplast.

In a second experiment, the inhibitory properties of glucose on sucrose uptake were utilized to substantiate the apoplastic movement theory. Glucose strongIy inhibits sucrose uptake. Previous studies in our laboratory with glucose and glucose analogs have shown the site of inhibition to be at the plasmalemma (Wyse, unpublished data). Therefore, if glucose is introduced into the free-space of a root, it should prevent sucrose uptake into the cytoplasm. This lack of uptake would leave a greater proportion of the sucrose in the free space, thus allowing a greater proportion to be washed out of the tissue.

Glucose (0.1M), sucrose (0.1M) or water were introduced through a small hole punched into the root with an 18 gauge needle. Uptake of the solutions was started 18 hours prior to $^{14}CO_2$ exposure and continued throughout a 24-hour chase period. The water soluble compounds in the area around the cavity were then extracted as described previously. Glucose significantly increased the percentage of translocated photosynthate washed out of the tissue, which is consistent with the theory of apoplastic movement of sucrose in sugarbeet root (Table 4).

Table 3. Proportion of translocated photosynthate in the free space of sugarbeet root tissue during a 24-hour chase period

Time after $^{14}CO_2$ Exposure	Percent Wash out
30 min	88
60 min	63
90 min	53
2 hr	29
4 hr	24
6 hr	15
24 hr	5

Leaves of field grown sugarbeet plants were exposed to $^{14}CO_2$ for 30 min. At regular intervals the plants were harvested and sections of root excised. Disks 1 X 4 mm were prepared. Samples of disks were washed for either 30 sec or 60 min and the. amount: of radioactivity remaining in the tissue was determined by 80% ethanol extraction. A 30 sec wash removed soluble materials from the cut cells on the surface, a 60 min wash removed soluble-materials from the free space, and 80% hot ethanol extraction removed the remaining soluble sugar,presumably that stored in the vacuole. The percent of total counts in the free space was calculated as:

$$\frac{\text{30 sec wash tissue. - 60 min wash tissue}}{\text{30 sec wash tissue}} \times 100$$

Table 4 . Effect of free space inhibitors on wash out of translocated photosynthate.

Competing Sugar	Percent Wash out
Control	27
Sucrose	34
Glucose	52

Sucrose (0.1M), glucose (0.1M), or water were introduced into the root free space via a cavity punched into the root with an 18 ga needle. The cavity was filled and connected to a reservoir via a glass capillary tube. The solutions were administered continuously 18 hours prior to $^{14}C0_2$ exposure of the leaves and during a 24-hour chase period. Extraction was as previously described in Table 3.

Since sucrose moves through the free space, a potential factor limiting sucrose accumulation may be the ability of root cells to actively move sucrose from the free space into the vacuole of the storage cells. This process is against a concentration gradient and thus requires considerable energy.

To determine if the uptake mechanism may be the limiting factor, a comparison of the mechanism in several cultivars differing greatly in yield and sucrose storage potential was made (Table 5). The. cultivars selected were Blanca (Fodder type, KWS), GWD2 (commercial hybrid, GWS), and L53XL19 (high sugar experimental hybrid). The sucrose content of the cultivars was 63, 70, 71 percent (dry weight), respectively, at the time of the experiment.

Samples of root tissue (1 X 4 mm disks) were exposed to radioactive sucrose, glucose, and fructose for 3 hours, and the rate of uptake into the vacuole of each variety determined. Labeled sugar held by the tissue after a 30-minute wash with cold tap water was assumed to be located in the vacuole. No significant differences in the rate of sucrose uptake existed in the three cultivars (Table 6.) The disks represented a constant volume of tissue; therefore, on a dry-weight basis, the fodder beet was capable of taking UP considerably more sucrose than the sugar types. These data showed no cause and effect relationship between the uptake capacity of the tissue and the sucrose concentration in that tissue. The rates of glucose and fructose uptake were much lower than that of sucrose in all varieties.

Table 5. Comparison of percent dry matter, percent sucrose (fresh weight basis), and percent sucrose (dry weight basis) of Blanca, L53XLl9, and GWD2 at harvest.

	Dry Matter	Sucrose	Sucrose
	Percent	Percent of fresh wt.	Percent of dry wt.
Blanca	15.0	9.5	63
L53XL19	24.5	17.5	71
GWD2	23.0	16.0	70

Table 6. Interaction between sucrose, glucose, and fructose during uptake into the storage cells of Blanca, L53XL19, and GWD2.

Variety	Uptake Sugar	Uptake Rate	Inhibition Sucrose	Glucose	Fructose
		µmol./3 hrs/20 disks		Percent	
GWD2	Sucrose	5.49 ± 0.33	—	81.3	59.4
	Glucose	0.55 ± 0.05	-11.4	—	- 6.8
	Fructose	0.29 ± 0.03	2.5	74.1	
L53XL19	Sucrose	5.17 ± 0.36	—	86.3	58.5
	Glucose	C.99 ± 0.01	7.7	—	2.7
	Fructose	0.88 ± 0.07	5.1	31.8	
Blanca	Sucrose	5.7? ± 0.71	—	32.5	61.4
	Glucose	0.69 ± 0.02	-15.3	—	-14.0
	Fructose	0.48 ± 0.07	12.8	63.1	

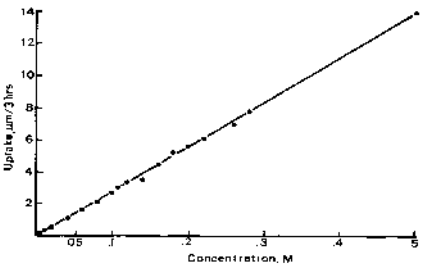
Disks were washed 30 min in running tap water before incubation. The incubation media contained the uptake sugar [0.1M, sp. act (dpm/µmol.): sucrose, 1.25 X 10^4; glucose, 1.15 X 10^4; fructose, 2.2 X 10^4] and the inhibiting sugar (0.05M) in 5 mM PO_4 buffer (pH 6.5). After a 3 hr incubation the disks were washed for 30 min in tap water before extraction in hot 80% FπOH. Radioactivity in the EπOH fraction was determined by liquid scintillation counting.

The fodder beet: was intermediate to both the sugar types and again showed a much higher rate of uptake on a dry-weight basis.

If two sugars are transported across a membrane by the same carrier-, each sugar should competitively inhibit the uptake of the other. This principle was used to determine if sucrose, glucose, and fructose were accumulaLed via the same mechanism in each variety. Glucose and fructose strongly inhibited the uptake of sucrose in all three varieties (Table 5). The similarity in the degree of inhibition would indicate that the same mechanism was operating in each case. Sucrose had little effect on the uptake of glucose and fructose. The very similar pattern of inhibition indicated a similar biochemical mechanism in each case. Therefore, the greater sucrose storing capacity of the sugar types cannot be explained on the basis of biochemical differences in the uptake mechanism.

Since sucrose moves from the phloem to the center of the vascular ring by diffusion, it is entirely possible That the rate-limiting step is the rate of diffusion. Factors such as distance and diffusive resistance could determine the relative number of cells exposed to high concentrations of sucrose in the free space. The greater the proportion of total cells exposed to adequate concentrations, the higher the sucrose content.

Figure 4. Effect of concentration on the uptake of sucrose.



Disks of sugarbeet root tissue were incubated for 3 hours in solutions containing various concentrations of sucrose. After incubation, the tissue was washed for 30 minutes in running tap water to remove free-space sugars. The tissue was then extracted with hot 80% ethanol and the concentration of labeled soluble sugars in the ethanol extract was determined by liquid scinti1lation counting.

The rate of sucrose uptake into root storage cells is directly proportional to the sucrose concentration in the free space (Figure 4). Therefore, cells nearest the sites of phloem unloading should be exposed to the highest concentrations of sucrose for longer periods of time and thus should contain the highest concentrations of sucrose.

A morphological comparison of the roots of the same cultivars used in the uptake study indicated considerable differences in ring number, ring diameter, and cell size distribution of sugar types and fodder beets. A comparison of the inter-ring area between vascular rings 3 and 4 is given in Table 7. The width of the ring was approximately 1 cm in the fodder beet and about 0.6 cm for GWD2 and about 0.4 cm for L53XL19. However, the number of cells across the ring were the same for all three cultivars. The total volume of the largest cells of the fodder type was five-fold greater than that of the high sugar hybrid, but the mean cell volume was ten-fold greater.

Table 7. Cell number, cell volume, and ring width in fodder and sugar types. Measurements are from ring 3 at final harvest.

	Ring Width	Cell Number[1]	Cell Volume Max.[2]	Cell Volume Ave.[3]
			$cm^3 \times 10^{-6}$	
Blanca	10.1	98	189.0	58.8
GWD2	5.7	67	50.5	14.6
L53XL19	4.2	67	32.8	5.9

[1]Number of cells across ring from cambium of ring 3 to cambium of ring 4.

[2]Maximum cell size at center of ring.

[3]Average cell volume for entire ring.

Therefore, the high sugar hybrid had more small cells near the vascular bundles and the low-sugar fodder beet had large cells and very wide rings. The sugar types, L53XT19 in particular, produced narrow rings and many small cells near the vascular bundles. The path of diffusion is, therefore, much shorter in the sugar types, and the sucrose passes many small cells as it diffuses into the ring. Kilford (G) found that large cells contained proportionately less sucrose and more nonsuerose soluble solids than small cells. The additional cell volume is essentially made up of water.

Diffusion Controlled Partitioning

Since sucrose moves in the free spaces by diffusion, the concentration would be highest near The unloading site of the vascular bundles. Also, since the rate of" sucrose uptake by parenchyma cells is directly proportional to the sucrose concentration in the adjacent free spaces, these parenchyma cells would contain the highest concentrations of sucrose. The proposed relationship between ceil size and free space concentration is illustrated in Figure 5. Cells furthest from the vascular area are exposed to low concentrations of sucrose in the free space and, therefore, accumulate less in

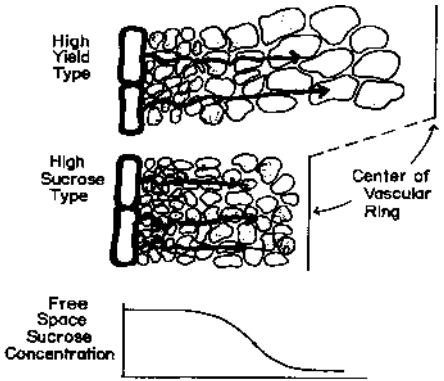


Figure 5. Diagram of diffusion-controlled partitioning of sucrose within the sugarbeet root. Note that the high sucrose root has a high proportion of its cells located in the area where free space sucrose concentrations should be highest.

their vacuoles. Roots containing a high proportion of their cells near the vascular system are roots with a high sucrose concentration. Since the capacity fcr sucrose uptake was the same in fodder beet and L53XL19 (Table 5), the factor controlling sucrose uptake apparently is not cell size per se but rather the distance of the cell from the vascular system. Cell size and/or cell: number determines this distance.

Thus agronomic practices that promote narrow rings should promote high sucrose content. For example, excessive nitrogen fertilization increases root size by cell enlargement. Marrow row spacings or high stand density decrease root size by limiting cell expansion (7). Therefore, the effects of genotype, environment, and nitrogen fertilization on sucrose concentration car. be explained by a diffusion-limited or a diffusion-controlled partitioning of photosynthate within the sugar-beet root.

If this hypothesis Is confirmed by further study, it is apparent that high yield .and high sucrose are possible only if increased yield resales from an increase in ring numbers nor freer, an enlargement of cells. Therefore, growth regulators and breeding lines should be screened, for their ability to promote proliferation of secondary cambia and to control cell enlargement.

There *are* still many other factors that may affect sucrose partitioning within the sugarbeet root. For example, we know very little about how the. phloem unloads sucrose into the free space. A sophisticated control mechanism allows part of the translocated sucrose to move in the phloem through the tap root into the fibrous root system. Given the dominant sink strength and the large, surface area of the vascular system within the tap root, this control system is indeed impressive.

The hormone relationships regulating secondary cambial development, cell division and cell expansion are not well known but appear to be crucial in the control of the sucrose-yield relationship.

Summary

1. Root yield of sugar-beet is determined by photosynthate supply and balanced partitioning of photosynthate between shoot and root. There does not appear to be conflict between the sink strength of the root and its ability to store sucrose (19). Root size is controlled both by the ability of the shoot to provide photosynthate and the growth potential of the root.
2. Photosynthate translocated to the sugarbeet root is partitioned between growth and sucrose storage. This partitioning is balanced and appears to be independent of photosynthate supply, but is influenced by environmental and genetic factors.
3. Because sucrose diffuses from the vascular tissue through the free space of the root, diffusive, resistance and length of the diffusion path may be factors controlling sucrose accumulation within the root. Narrow rings allow a large proportion of the total numbers of cells to be exposed to the high concentration of sucrose in close proximity to the phloem.
4. Research efforts should be directed toward production of large roots with an increased number of rings. This criterion should be useful in selecting superior genotypes.

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

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Yield of sugarbect depends upon photosynthesis and subsequent accumulation of photosynthate in the taproot (2). Both production and distribution of phoTosyriLhaLc 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[1] weight of leaves and taproot of 21-day-old sugarbeet seecings, 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 3C unselected populations that were examined (5).

We hypothesized that yield of sugarbeet would be improved by increasing The partitioning of photosynthate into the taproot, assurring 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 vcrmiculite 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. Tne 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 wafer[1] content.

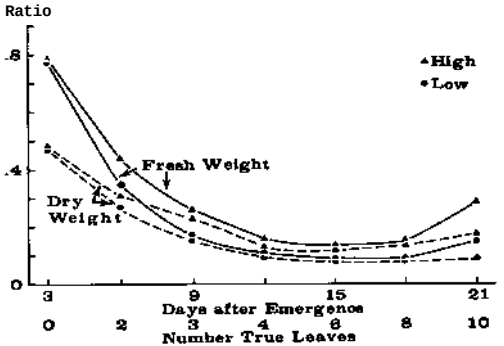

Figure 1. Relationship of TLWR calculated from fresh and from dry weight of progenies of sugarbeet selected for low and high TLWR when grown in controlled environment.

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 EL4O 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 *71* days post-emergence. This constituted the first cycle of selection. Out of these first-cycle progenies, another

grvoup of low-and of high- TLWR. seedlings was selected for a second cycle of seed production and progeny nesting. 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 arid 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		176	0.132**	
1 High TLWR	13	0.217 ± 0.02	76	217	0.179	35
2 Low TLWR	21	0.114 ± 0.01		144	0.096**	
2 High TLWR	21	0.242 ± 0.02	112	144	0.159	68

†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 SP6972-0) 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-TLVTR population.

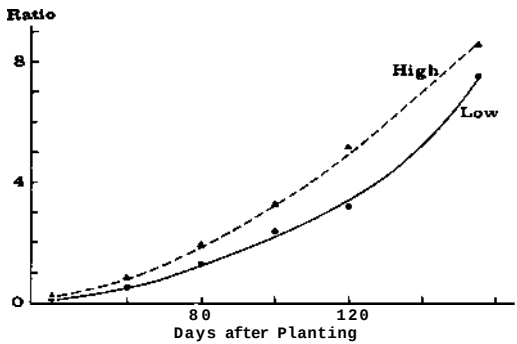

Figure 2. TLWR of low- and high- TLWR sugarbeet selections grown in the field at Beltsville, Maryland, in 1976.

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-TLV/R 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.†
TL40, Low TLWR	7.77	64.3	8.05
SL40, High TLWR	9.38*	79.1*	9.80
Hybrid	4.92	88.8‡	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.-

Entry	Stand Density				Mean
	Plants/Ha.	32,250	52,775	78,050	121,700	
	Root weight M.T. per Ha.				
EL40	Low TLWR	57.9 fg	66.1 d-g	60.6 efg	66.4 g	62.3 c
EL40	Unselected	63.1 d-g	67.2 c-f	72.5 a-d	70.1 b-e	68.3 b
EL40	High TLWR	63.9 d-g	77.2 ab	78.4 abc	77.0 abc	73.7 ab
US H20		76.- abc	80.8 a	79.4 ab	70.0 b-e	76.7 a
	Mean	65.3 b	72.9 a	72.3 a	66.4 ab	
	Leaf Blade weight M.T. per Ha.+				
EL40	Low TLWR	7.5 e	13.6 cde	9.4 de	13.1 de	9.5 b
EL40	Unselected	9.6 de	8.8 e	9.9 de	10.5 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 cde	15.1 ab	18.6 a	15.4 a
	Mean	9.7 b	11.6 ab	13.9 ab	17.4 a	
	TLWR					
EL40	Low TLWR	7.78 abc	5.32 bcd	6.41 bcd	5.90 cde	6.61 b
EL40	Unselected	6.85 bcd	7.81 abc	7.31 a-d	5.66 bcd	7..6 ab
EL40	High TLWR	8.91 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 tens per acre, multiply by C-46.

These three experiments showed that high-TLWR plants partition proportionately more photosynrhate to the taproot than low-TLVJR 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 bet-ween 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	121,700	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	92.8 a	90.5 b
EL40, Unselected	88.6 d	90.2 bcd	90.6 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	89.6 c	90.9 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	7.67 e-j	7.07 b
EL40, Unselected	8.30 hi	7.45 f-i	8.30 c-h	8.65 a-e	7.92 b
EL40, High TLWR	7.95 d-i	8.48 a-f	10.12 abc	10.70 ab	9.58 a
US H20	9.22 a-g	8.85 a-d	11.02 a	8.90 b-g	9.75 a
Mean	7.39 b	8.53 a	9.18 a	8.22 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 cur 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 tap-root and had less fibrous roots than the lew-TLWR plants.

Table 5. Dry weights of leaf blades (LEW), petioles (FW), 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	C.273 a	i.270 a	0.187 a	0.078 a	0.163 a	0.256 b
0.105 b	C.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 to-ral 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.

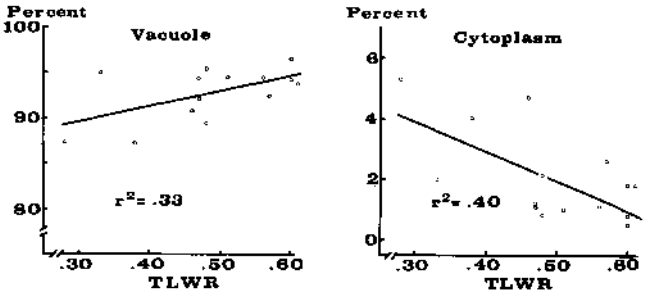

Figure 3. Relationship between sucrose distribution in sugarbeet taproot cell compartments and TLWR.

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

	Invertase Activity†	
TLWR	Acid - pH 4.5	Alkaline - pH 7.0
0.129 + 0.023	105.3 + 51.7	9 3.0 +_ 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 invortase 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 ontogonetlcally, 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[1] growth and differentiation, e.g., lateral root Initiation from the taproot.

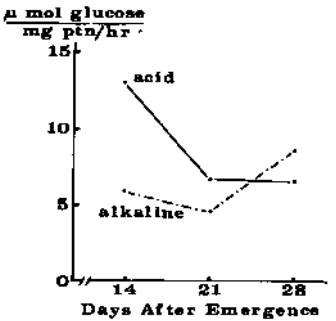

Figure 4. Relationship between in vitro acid and alkaline invertase activities and ontogenetic development of the sugarbeet taproot.

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 on fooder 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 determination 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 8% of those ranked by HDLWR.

Therefore, hypoctyl 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.
4. Most of our selection and yield studies have been done with one breeding line EL40. Determine optimum management practices (e.g.,spacing and nutrition) for lines differing in TLWR.

ACKNOWLEDGMENTS

Data for comparison of TLWR with HDLWR were supplied by G. E. Coe, AR, SEA, U.S. Department of Agriculture, Beltsville, MD.

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. Hoagboam, 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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Seedling Physiology and Sugarbeet Yield*

D. L. DONEY**

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In sugarbeet, we have a most unique crop plant: to study because of the growth phase and plant part that is of economic importance.

The physiologist likes tc divide yield into biological yield (BY) and economic yield (EY). BY is total dry matter produced in the growing season, whereas EY is the total dry matter of economic importance. In many crop plants, the EY involves the reproductive growth phase and is somewhat unrelated to the BY; however, in sugarbeet the EY involves the vegetative growth phase and is very closely related to the BY. This makes the investigation of the BY somewhat easier.

Very little differentiation takes place during the vegetative growth phase. The major differentiation between the time of germination and harvest takes place in the first few weeks of growth. Therefore, our studies of sugarbeet yield can be focused on growth and the growth processes.

Most differentiation takes place in the first 30 days of growth. Germination fakes place between 3 and 5 days after planting, depending on temperature. At about 3 days the germinating seed sends out a radicle, and by 5 days the cotyledons emerge. Growth is very slow for the next 5 to 7 days until true leaves are formed. The first true leaves begin emerging at about 10 to 12 days after planting and emerge at the rate of about 2 to 4 per week for the rest of the growing season. By the time the plants are 30 days old, they have 6 to 10 true leaves.

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The. root doesn't begin to thicken until the first true leaves are formed. When the radical first emerges from the germinating seedling, it is composed of mostly cortex material with a center core of undifferentiated merstamatic tissue. The number of cortex cells does not increase with expansion of the root, but the cells grew in size and eventually break and are sluffed off as the true root grows.

Differentiation begins immediately in the core, although it seems rather slow at first (Figure 1). In about 10 to 12 days when the first true leaves are forming, vascular material (Figure 2) can be seen in the core as well as the beginning of the primary cambial layer. This gives rise to fhe secondary cambial layer by about 18 days (Figure 3).

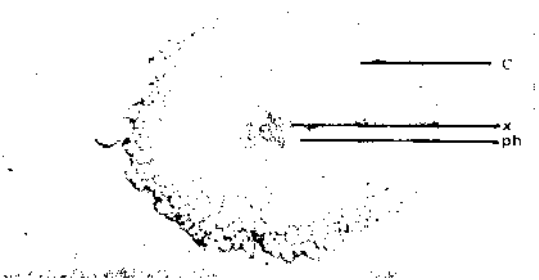

Figure 1. Cross section of 9-day old sugar-beet root. C = cortex; ph = phloem; x = xylem: x 150.

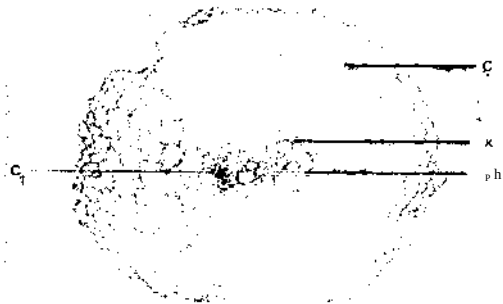

Figure 2. Cross section of 13-day-old sugarbeet root. C = cortex; ph = phloem; x = xylern; C= primary cambium; x 14 3.

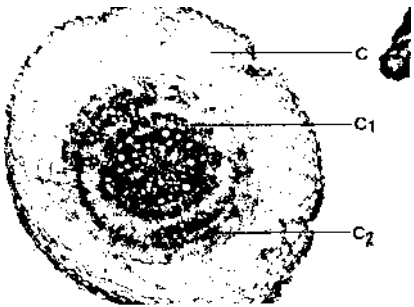

Figure 3. Cross section of 20-day-old sugarbeet root. C = cortex; ph = phloem; x = xylern; C= primary cambium; x 143.

All cell division takes place at the cambial layers from which the new cells differentiate into xylem, phloem, and storage parenchyma cells. The secondary cambial layer gives rise to the third cambial layer and so on until all the rings are formed, which occurs at about 30 to 40 days or when the root is about 1.0 to 1.5 cm in diameter (1). From then on growth is cell division and cell expansion, taking place simultaneously in ail rings. The genetic identity of a sugarbeet plant has been attained by this time. Its ring number, cell size, photosynthate partitioning, and vigor in relation to other genotypes have already been determined. This means we should be able to measure important; growth parameters in the seedling stage rather than waiting until harvest time.

Dr. Snyder reported (this issue) that he was able to select plants genet leal ly different in their partitioning of photosynthate at a rather young ago. Once the genetic relationship for partitioning of photosynthate occurs, it changes very little throughout the remainder of the growing season. For example, two inbreds (L19 and 110) differ in their partitioning, as indicated by their root/shoot ratio (Table 1).

Table 1. Root/shoot ratio of inbreds F19 and L10 from July 1 to September 8.

	Root/Shoot Ratio			
	L19	L10	L19	as % of L10
July 1	0.158	0.241		66
July 28	0.419	0.661		64
August 18	0.692	l.l25		62
September 8	0.890	1.364		65

From July 1 to September 8, the relationship between these, inbreds in root/shoot remained constant although the ratio was increasing for both.

The difference in root/shoot ratio between genotypes GWD2 and L19 is small; yet, this genetic difference can be detected in plants 10 days after planting (Figure 4). The relationship between these genotypes remains constant although the ratio changes with time. It decreases for the first 15 days, levels off between 20 and 30 days, then begins increasing and continues to increase throughout the remainder of the growing season. The leaves grow more rapidly at first until the root is about 1 cm in diameter, which is about the time all the rings are formed. Then growth of the root increases. As more meristematic tissue is formed in the root, more photosynthate is demanded for cell division and growth. However, relative genetic partitioning is determined as scon as the first true leaves begin manufacturing food.

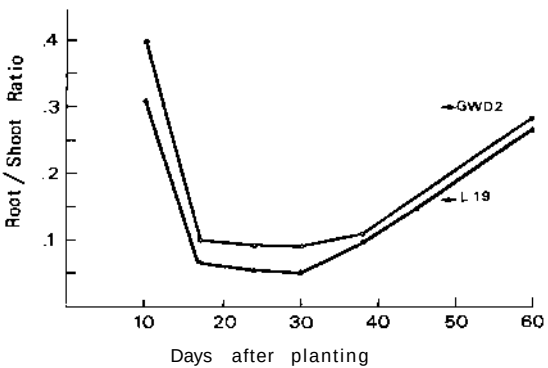

Figure 4. Root/shoot ratio of genotypes GWD2 and L19 from 10 to 60 days after planting.

The relative percent dry matter of leaves is also determined very early (Figure 5). At 10 days, genetic differences among genotypes L19, GWD2, and Blanca in percent dry matter of the leaves were already evident. These differences remained throughout the growing

season. The relative percent dry matter of the roots followed a similar pattern (Figure 6); however, genetic differences were not evident until about 15 days. The percent dry matter in the root increased more rapidly than in the leaves.

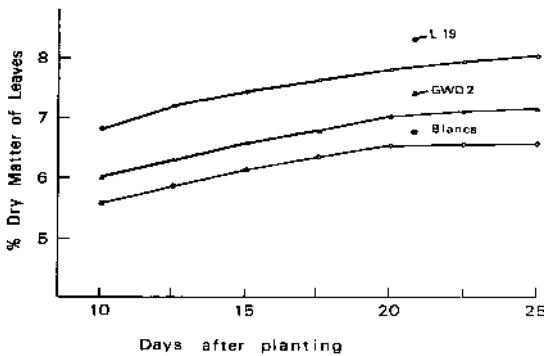

Figure 5. Percent dry matter of Leaves of genotypes L19 , GWD2 , and Blanca from 10 to 25 days after planting.

Generic: differences in root diameter are also established very early. Two genotypes, Blanca and L19, gave significant: differences as early as 5 days (Figure 7).

These results lead me to believe that we can determine the potential of a given genotype in vigor[1], growth, and sugar production at: a very young age. The keys are: 1) control of the environmental variation, and 2) knowledge of the parameters to measure.

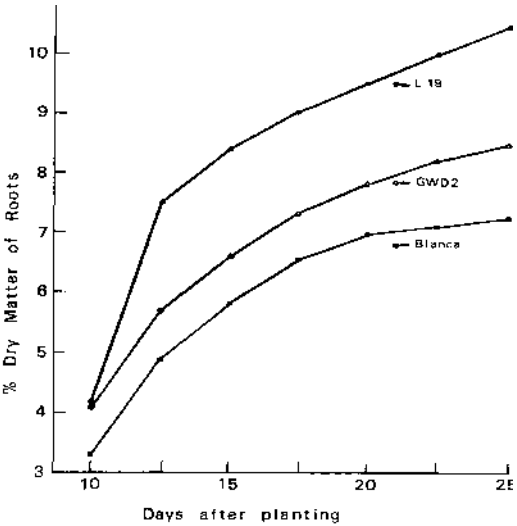

Figure 6. Percent dry matter of roots of genotypes L19, GWD2 , and Blanca from 10 to 25 days after planting.

We have found that the environmental variation for root weight is generally greater in the seedling stage Than in mature plants (Table 2). The coefficient of variation of a uniform hybrid was about 10 percent greater for seedling root yield than for root yield of nature plants.

Many workers have recognized the desirability and potential of measurement of seedling parameters. A very brief summary of some of the attempts to correlate seedling characters with yield and sugar production is given in Table 3.

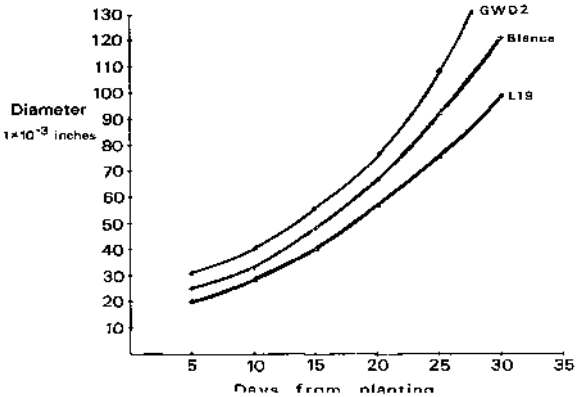

Figure 7. Root diameter of genotypes Blanca and L19 from 5 to 35 days after planting.

Pannonhalmi (14) in Hungary studied the effect of irradiation of the seed and reported a positive effect on yield. The effect cf seed size has been reported to influence yield by three workers: two from USSR (8, 13) and one from Ireland (10). The effect of germination on yield has generally given negative results (3, 6, 8, 15); only one worker (8) has reported a positive effect. All workers (5, 6, 9, 15, 18) who have studied effects of seedling root weight on yield report a positive effect on root yield. Root diameter has been shown to be highly correlated with root yield by Shimamoto of Japan (16, 17) and myself (6). One worker in Belgium (7) reported a correlation of peroxidase activity in seedlings with percent sugar, and finally a Russian (4) has reported that seed treated with ultrasonic sound germinated sooner, and the seedlings grew more rapidly than untreated seed.

Table 2. Coefficient of variation of a uniform hybrid for root weight of inature roots and 3-week-old seedlings.

Age	Measurement	CV
5 months	Root weighr	21. 5%
3 weeks	Root weight.	31.0%
3 weeks	Hypocotyl diameter	9.5%

Table 3. Seedling parameters and their influence on growth and yield.

			Influence	
Seedling Parameter	**Researcher**	**Country**	**Positive**	**Negative**
X-Irradiation on growth	Pannoriha Imi C14)	Hungary	X	
Seed size on yield	Efremov (8)	USSR	X	
	MacLachlan (10)	Ireland	X	
	Muratov (13)	USSR	X	
Seed germ, on yield	Rostel (15)	E. Germany		X
	Battle (3)	England		X
	Efreirov (8)	USSR	X	
	Doney (5)	USA		X
Seedling root wt. on yield	Kulenev (9)	Bulgaria	X	
	Rostel (15)	E. Germany	X	
	Buzanov (5)	USSR	X	
	Doney (6)	USA	X	
	Snyder (18)	USA	X	
Root diam. on yield	Shimamoto (16,17)	Japan	X	
	Doney (6)	USA	X	
Peroxidase on % sugar	Dubucq (7)	Belgium	X	
Ultrasonic sound on growth	Bulavin (4)	USSR	X	

We have studied a number of seedling characteristics in our lab. Several years ago we found that root diameter gave us a better correlation with harvest yield than the other morphological factors studied. A Japanese, worker, Shimamoto (16, 17), had earlier reported that in young plants, root diameter gave a better correlation with harvest yield than root length. One reason for this better relationship with yield is the cone shape of the sugarbeet. An increase in the diameter of a cone has a greater influence on the total volume of a cone than a similar increase in the length. We were able, to show that this relationship was true in plants as young as 3 weeks old (6). We originally measured the hypocotyl because we were saving the plants, but we have since found that better measurements can be made by pulling the plant and measuring the area of greatest expansion. A detailed description of our technique is given in Appendix I.

Over the past few years, we have conducted numerous tests to compare our hypocotyl diameter[1] rankings with the ranked yields in replicated field trials (Table ^). These comparisons gave, correlations from -0.70 to 0.91; however, most ranged from 0.60 to 0.90. Poor correlations generally resulted from poor field trials (Tests 7, 8, and 12). In Test 3, lines were not significantly different for hypocotyl diameter or harvest root yield; therefore, the correlation for Test 3 has little meaning. Entries in test 8 and 9 were identical except they were grown at different locations. Unknown residual fertilizer effects were observed in Test 8. This resulted in a very high coefficient of variation and a non-significant correlation (3.34) for root yield between these two field trials. The poor correlation for Test lb is difficult to explain. The field trial had excellent precision. The greenhouse trials were conducted to verify the hypocotyl diameter rankings and they were identical.

In general, however, relative root yield can be predicted by measuring the hypocotyl diameter of 3-week-old seedlings. Our correlations are as good or better[1] than variety trial correlations for root yield between locations.

Tabic 4. Correlations of hypocofyl diameter with harvest root yield obtained in replicated field Trials.

Year	Test	(r)	No. of Entries	Description
1973	1	0.60	18	Diallel (no inbreds)
"	2	0.70	18	Diallel
1974	3	0.10	12	O.P. lines (no difference between lines)
"	4	0.73	5	O.P. lines
"	5	0.76	19	Hybrids
1975	6	0.90	6	O.P. lines
1976	7	0.27	10	Sugar Sel. (3 reps.)
"	8	0.16	20	Hybrids
"	9	0.60	20	Hybrids (same hybrids as Test 8)
"	10	0.88	26	Diallel (inbreds included)
"	11	0.78	7	Commercial Hybrids (Ar. Orchal)
"	12	-0.70	7	Sugar Sel. (Single-row plots)
1977	13	0.50	25	Hybrids (A800)
"	14	0.74	9	Sugar Sel.
"	15	0.80	7	Hybrids (Great Western)
"	16	0.49	11	Sugar Sel.

The hypocotyl diameter selection technique was further evaluated as a selection tool in two separate experiments involving open-pollinated lines and hybrids. In the first experiment a series of lines from an open-pollinated population was screened for seedling hypocotyl diameter. Seed from those plants with hypocotyls of large diameters were pooled into Population 1006, and seed from those plants with hypocotyls of small diameters were pooled into Population 1005. These two resultant populations were tested in a replicated field trial and results are given in Figure 8. There was a 20 percent difference between the two populations in hypocotyl diameter. The large hypocotyl diameter population (1006) yielded 30 percent greater than the small hypocotyl diameter population (1005) (Figure 8). A significant decrease in sucrose percentage was observed in the large hypocotyl diameter population; however, it still produced significantly more total sucrose. The second experiment was from a group of hybrids (having a common female parent)

selected for large and small hypocotyl diameter. The large hypocotyl diameter hybrids significantly outyielded the small hypoco-yl diameter hybr.ics for both root weight and gross sucrose (Table 5). The sucrose percentage was not affected by the selection procedures.

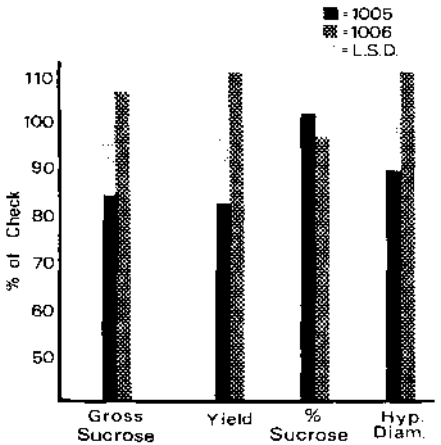

Figure 8. Gross sucrose, root yield, percent sucrose, arid hypocotyl diameter of a *large,* hypocotyl diameter population (1006) and a small liypocotyl diameter population (1005). Data are presented as a percent of a check variety.

Table 5. Gross sucrose, root yield, and percent: sucrose for hybrids selected for large and small hypocotyl diameter.

Hybrids	Gross Sucrose	Tons/ Acre	Percent Sucrose
Large hypocotyl diameter	5839	21.1	13.8
Small hypocotyl diameter	4910	17. 9	13.7
LSD at 0.05	870	2.6	0.7

If this technique is to be of value, it must be useful In a breeding program. We have, therefore, adapted it into a recurrent selection breeding program (Figure 9). This program takes only 1 year per cycle, while the conventional recurrent selection breeding method takes 3 to 4 years. Seed is space-planted in the field in July. At harvest time, about September 15, a selection is made for sucrose percentage. Selected beets are cut, in half and one half placed in the coldroom for thermal induction. At the same time, stecklings of a CMS tester are placed in the coldroom for induction. Around December 15 these half-beets and the CMS tester plants are brought from the coldroom and individually crossed. The other half-root is then thermally induced. The testcross progeny harvested from the CMS tester is then tested for hypocotyl diameter. The parents (other half) of the best progenies (largest hypocotyl diameter) are. intercrossed to produce the selection population.

In order to determine, the achieved progress in one. cycle of selection (1 year), we crossed the new[7] selection population and the parent population to the CMS tester (L53 CMS). This resulted in four test populations (Table 5). A comparison between the. parent testcross and the new population testcross indicates the effect on combining ability. Progress, per se, is indicated in the comparison between the parent and the new population.

From about 200 beefs, 17 were selected whose progenies averaged 7 percent better than the parent progeny mean. The achieved progress depends on the heritability and correlation with root yield. A heritability of LOO and a correlation of 1-00 would result ir: an increase of 7 percent in root yield (Table 6 - Predicted Yield). Based on earlier estimates (6), we would expect a 3 to 4 percent increase in root yield.

These four populations were tested in the greenhouse, for hypocotyl diameter and also in replicated field trials. The new population testcross gave a 5 percent increase in hypocotyl diameter and a 2 percent increase in root yield over the parent population testcross (Table 6). The combining ability effect was about what was expected for hypocotyl diameter but a little lower than expected for root yield.

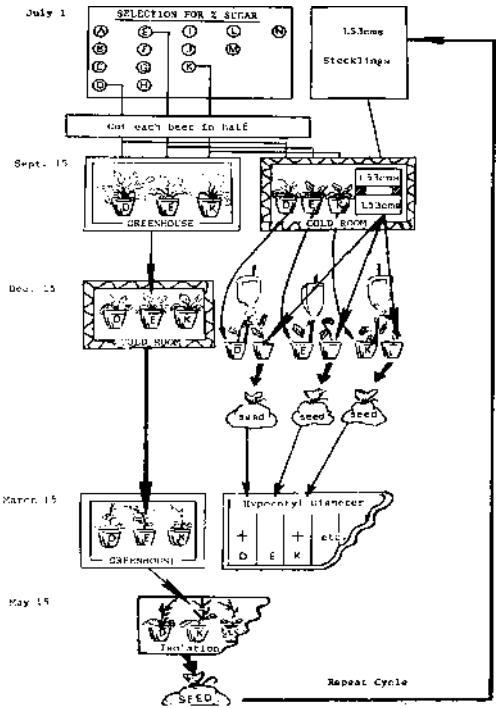

Figure 9. Flow diagram of a recurrent selection breeding method for sugarbeet using the hypocotyl diameter technique as a selection criterion for yield combining ability.

Table 6. Hypocotyl diameter and field data for parent **population** testcross, new selection population testcross, parent population and new selection population. Data are in percent of parent.

Population	Hypocotyl Diameter		Field Data		
	*Predicted Yield	Greenhouse Test	Root Yield	% Sugar	Gross Sugar
L53CMS x Parent Pop.	100	100	100	100	100
L53CMS x New Sel. Pop.	107	105	102	99	101
Parent Population		100	100	100	100
New Selection Pop.		111	110	95	104
LSD 0.05	5	4	6	3	7

*Mean hypocotyl diameter of the selected plants over the parent population mean based on hypocotyl diameter progeny tests.

The new population exceeded the parent population by 11 percent for hypocotyl diameter and 10 percent for root yield. This increase was accompanied by a significant decrease in sugar percentage. This points out the need to consider sugar concentration in any breeding program. These selections were based only on hypocotyl diameter without regard to sugar percentage. For this reason we have incorporated the sugar selection step in the recurrent selection method mentioned earlier (Figure 9). This step was added after the first cycle of selection and, at present, we haven't determined its effectiveness.

There ought to be other ways of determining sugar potential in the seedling stage. Some of the methods might be osmotic pressure, cell size, ring number, or ring width. The osmotic pressure is easily measured in the seedling stage, as is ring number and ring width. However, in a breeding program where it is necessary to evaluate a large number of plants, the feasibility of these methods is questionable.

Several workers have reported a good correlation between cell size and percent sugar (2, 12, 11); however, measurement of cell size poses a difficult problem. Counting cells in a grid or across a plane of a cross section is vary tedious and very difficult,

considering the many sizes and shapes one observes in a cross section. Cell size can also be determined by separating the cells with the use of macerating enzymes and counting repeated samples of cells. This method is rather sophisticated and time consuming. It woifLd not be practical in a breeding program. Another suggestion would be to scan for cell wall material either in a densitometer or IR analyzer from thin cross sections. We are not sure how effective or practical these methods would be.

In summary, many of the genetic differences in the growth processes are established in very young beets. Therefore, we ought to be able to improve sugar production by selecting for some of the important growth and sugar parameters in the seedling or young-plant stage. The key is to be able to control the environmental variation and to know what parameters to select.

In our greenhouse technique, we have been able to control much of the environmental variation. We have also shown that selection by use of the hypocotyl diameter of seedlings is effective in improving root yield. Some other important parameters for measurement might be photosynthaLe partitioning, root diameter, osmotic pressure, and cell size. The:re also might be other more important parameters of which we are currently unaware. At present, research in this area shows promise.

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APPENDIX I

HYPOCOTYL DIAMETER TECHNIQUE FOR PREDICTING ROOT YIELD

The key to prediction of root yield from seedling hypocotyl diameter is control of environmental variation. The more vigorous genotypes will expand in root diameter more rapidly than the less vigorous genotypes. Control of environmental variation will determine how well we can detect true genetic differences. This requires extreme care since root weight measurements of seedlings usually have a larger environmental error than those of mature plants. In our experiments, we have been able to exert excellent control for much of the environmental variation and, thus, predict the harvest root yield fairly well by the following techniques:

1. Type of Container Used. Clear plastic 185 ml vials, 45 mm diameter by 105 mm deep. These can be obtained for about 8c each. A hole is drilled into the bottom for drainage.
2. Planting. The vials are filled with vermiculite and compressed to 1 inch (25.4 mm) from the top. Two seeds are placed in the center and covered with 1 inch (25.4 mm) of vermiculite. The vermiculite is wet down very carefully, making sure to wet completely but not to overflowing.
3. Bedding. Planting takes place on Thursday. The plants begin emerging on Tuesday, and all plants that have emerged by Wednesday are saved. The remainder are discarded. We start with 36 pots per line and end up with about 30 plants per line. Because the number is not the same for all lines, we use a completely randomized design (CRD). On Wednesday, all the saved plants are placed in a moist sand bed in a CRD. The pots are spaced on 3-inch (7.62 CM) centers. A 3 ' x 29' (1 m x 6 m) bed will hold about 880 pots. Pots are thinned to one plant per pot.

   Holes for the pots are made by inverting a plastic vial, pressing it into the sand and withdrawing the sand. With moist mortar sand, this can be done rather easily and quickly. The sand is kept moist by watering two to three times a week. This maintains the root zone temperature at 20 C +_ 1.

M. Nutrient:s. Each plant receives 10 ml of nutrient solution daily (except on weekends). A diluter-disperser, adjusted to deliver[1] 2-10 m'. aliquats at each pump, is used to apply the nutrient solution. This allows two plants to be watered at a time. Using this method, 1500-1800 plants can be watered per hour.

5. Rotation. There is still about a 15-20 percent gradient in light intensity over the bed. To compensate tor this variation in light, the plants core rotated twice a week frcn front to rear and left to right.

G. Temperature. Root zone "temperature is 20 C +_ 1 and air temperature, is 24 C +_ 0.. There are greater fluctuations in air temperature in the grcehouse during the summer than in the winter; therefore, our[m] results are best in the winter months.

7. Measuremerits. Plants are measured 19 days after emergence. The best time to measure is when the hypocotyl of maize is about 7.1 inch. As the plant gets larger, the cortex of the hypocotyl splits and is unsymmetrical. Measurement is made by a spring-loaded microcaliper calibrated in 1/1000 of an inch. The plants are pulled and the largest part of the hypocotyl-taproot tissue measured (excluding the crown). Some hypocotyls are not round; therefore, all plants are measured in two directions (180°) and the average recorded.

8. Preserving Plants. If it is desirable to save individual plants, the leaves ore trimmed back and the plant repotted. Survival rate at: this stage of growth is about 80 to 90 percent. The survival rate of smaller plants is much less.

9. fVecision. A uniform hybrid is included in every test as a measure of the environmental variation and as a standard. The coefficient of variation of this standard runs between 7 and 9 percent. Significant differences are lietween *h* and 5 thousandths of an inch. Fac.h test consists of 25 lines and two checks as standards.

The more vigorous genotypes at the seedling stage are generally more vigorous throughout the. growing season and are the highest yielding.

Some New Techniques for Sugarbeet Improvement*

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From a host of recent reports and recommendations (e.g. 1, 2) has come the expectation that contemporary analytic biology will contribute to the goals and methods of agricultural research. Can molecular biology be utilized for- the solution of problems in agricultural plant biology? Will a correlation of in vitro events with the responses of crop plants in the field allow a better understanding (and perhaps more importantly, allow manipulation) of the biological processes underlying crop productivity? There are several possible responses to these questions, all of which have been expressed in one form or another during the numerous recent debates concerning the potential of increasing agricultural productivity. The first response points out that our current levels of crop productivity were achieved in the absence of a direct knowledge of molecular mechanisms, and that there is no reason to believe this knowledge would enhance productivity. A second response, the direct opposite of the first, asserts that only by a complete molecular anlaysis of the processes underlying crop productivity is there any hope of manipulating the components of yield in a rational, way. A third and more realistic response suggests that a molecular analysis will be of importance in manipulating some biological processes but will not be a panacea for all the problems of agricultural biology.

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Plant breeding is an ancient science. The origins of our current crop species are buried in prehistory; all evidence indicates that most crop species were domesticated during the Stone Age. Crop species arose from native wild species that underwent natural hybridization resulting in increased genetic variability and subsequent selection for desirable phenotypes by prehistoric peoples. Methods of reaping and sowing in the field, or methods for storage or preparation, can be effective selection screens for plants just as growth on a Petri plate is for a bacterial colony. The early plant breeders searched for, recovered, and propagated genetic variants or recombinants which displayed desirable traits under certain environmental conditions. The transformation of wild species into crop plants was accomplished in the absence of modern science, or of any knowledge of Mendelian genetics.

Contemporary plant breeders employ essentially the same strategy with great success. Their approach involves the production of populations with a broad genetic base followed by selection at the whole plant level for recombinants with desirable alterations. •Genetic manipulation is practiced without knowing the biochemical basis of the separate components which comprise the character being modified. Selection for traits such as final yield is practiced at the endpoint of the complex biological processes which produce a whole plant. Mendelism and a knowledge of genetic transmission provide a conceptual basis for what is occurring during the breeder's genetic manipulations (3).

In most current breeding programs, the availability of genetic variability is not the limiting factor in crop and variety improvement. There is a wide range of genetic diversity in the surviving natural populations of most crop species. The focus of breeding efforts is centered on selecting the desirable recombinant types that emerge from any particular cross or segregation population. Currently, the assays of agronomic or horticultural utility and the subsequent selections are based on observations of whole plant phenotypes. Consequently, only major alterations can be recognized. These alterations appear as statistically significant changes in characteristics of bulk populations. Assaying at the endpoint of a

number of complex biochemical, physiological, and developmental processes hides many potentially useful recombinants in the complexity of the buffered processes producing whole plant (4).

The complexity of plant biology and of productivity is expressed in the genetics of agriculturally important traits. The majority of these traits appear to be controlled by "polygenes," and their transmission is analyzed by quantitative methods. The quantitative inheritance of these traits is a reflection of the complex biological processes which uriderly their[1] expression and of the lack of well defined genetic variants with which Lo analyze them. Quantitative inheritance is a phenomenon involving naturally occurring genetic variability and complex biological end products. There is no reason to expect that niutarits affecting these processes could not be produced once their individual components are identified, nor that the genetics and biochemistry of such traits would be any different from that found in other organisms (e.g., metabolic pathways). For the time being, however, the plant, breeder lias little choice but to use the phenotype of the endpoinL as the basis for selection. significant progress could be made in the improvement of breeding techniques if it was possible to establish reliable physiological or biochemical assays at critical points in a number of the component processes of agronomic traits. Examples of such processes are: nitrogen metabolism, photosynthesis, water relations, mineral nutrition, and tolerance to environmental stress. With these critical processes individually analyzed and assayed, genotypes demonstrating optimal performance at different steps in a process could be combined to produce a new, highly productive cultivar.

Recent advances in molecular biology have provided methods of genetic manipulations which should be applicable to the improvement of plant species. This is certainly an exciting prospect. Despite the rapid expansion of our knowledge of basic genetic and biochemical mechanisms in lower organisms, thi.s knowledge has had no direct impact on plant improvement. This lack of impact may be ascribed in large part to conceptual and experimental differences between the disciplines of molecular biology and plant breeding.

Molecular biology Is comprised of two basic elements: the reductionistic world-view of basic science and a powerful set of analytical experimental tools. One example of this approach was the use of defined genetic variants combined with precise biochemical methods to elucidate the mechanisms that regulate metabolic pathways in a variety of organisms. In contrast, plan;, improvement as currently practiced has, cf necessity, a more holistic approach. Plant breeders have to operate within difficult constraints. They have little choice In either their experimental materials or the problems which confront them. No strong correlations have been established between yield and any of the individual physiological or b.ioche:rical processes that contribute to the final product. The experimental and technological requirements of plant breeding and the constraints of the plant: system are different from those imposed by molecular biology. The question is, can the novel methods of "genetic engineering" defined in microbial systems really be applied to plant improvement?

There are several approaches to extending the techniques of molecular biology from microbial investigation to application for crop improvement: one of these Involves cellular manipulations. Cellular manipulations hold the potential for developing an experimental system for crop species suitable for more refined analytical techniques. Using single somatic cells as experimental organisms, it is possible to achieve mutant production, analysis, and hybridizations not possible using whole plants. Such techniques may permit important cellular processes to be characterized to the extent that useful, directed modification is possible.

Work focused upon the manipulation cf sugarbeet cells cultured in vitro has not been extensive. There is the current realization that such work could be productive, and that sugarbeets are an attractive species for the development of cell culture techniques. It is now possible to initiate and maintain callus cultures from various parts of the sugarbeet plant (5). From these callus cultures, it is possible to produce suspension cultures of sugarbeet cells proliferating in a liquid medium (4). Regeneration of entire sugarbeet plants from callus cultures has proved to be a

difficult goal, but it has been observed recently (5, 8). Regeneration of whole plants from single ceils has not been reported.

Although many tools of the molecular biologist are now available to the plant geneticist, seme limitations prevent their application to breeding problems, particularly to sugarbcet. The first problem with these approaches is a technical one. Regeneration of whole plants from single cells is essential for application of the technology- of in vitro genetic manipulation to higher plants. However, this s~ep lias only recently been accomplished with several major food crops, and it is not yet possible with sugar-beet. The second problem arises from the real needs of the plant breeder. In most instances, the availability of genetic variability is nor the limiting factor in crop improvement; the ability to recognize and recover useful recombinants sets the limit. Hence the production of genetic variability via cellular mutation, or hybridization, provides no uniquely useful tool at present. The third problem results from the development biology of agronomic and horticultural characters. Many agronomic traits are tissue-specific their expression is found in only one or a few tissue within the plant: and is often not found in cells cultured in vitro If a particular"' trait Is not expressed in culture, there is no reason to expect that the trait can be altered and screened for via in vitro methods. *The.* fourth problem involves the genetics of agricultural traits. Mutant selection systems and DMA manipulations allow modification of single gene rraics. Most agronomic and horticultural traits, as they are now defined, are polygenic in inheritance. Small additive, stepwise modifications would be difficult to recognize. Currently, genetic modification of crop plants, using cellular manipulations, should prove appropriate in cases where the alteration Involves single-gene traits which are not tissue-specific, and for which there are good selective techniques. These are indeed rare instances. The technology involved in these approaches will almost certainly be improved to overcome the limitations discussed above. However, at present, single-gene traits which are not tissue-specific are rare, as are appropriate selective systems. Possible examples of such traits would include disease resistance, or tolerance to ion toxicity, but the range is limited.

It would appear[1] that molecular biology is not yet directly relevant to crop improvement. The difficulty is that current efforts have attempted to transfer the experimental results directly (i.e., defined genetic manipulation) without also extending the reductionistic approach of molecular biology. The immediate need is not to find new ways to generate genetic: variability bur to find new ways to screen critically the variability already provided by nature and to identify the biochemical, physiological, and developmental components of traits which determine plant productivity. Once individual components and the rate limiting steps of Important traits are identified, designing methods of selection for altered traits are possible.

Effective, genetic manipulation of traits affecting plant productivity requires identification of the relevant metabolic processes and specific rate-limiting steps. Many such traits including drought tolerance, total yield, time of maturity and temperature tolerance are complex quantitative traits under the control of multiple genes (polygenes). The final phenotype is separated from the basic biochemical steps, the units of selection, by several levels of biological organization and environment-genotype interactions. Unfortunately, the definition of polygene and statistical methods for its analysis are not compatible with the analytical approaches of molecular genetics. Likewise, biochemical approaches have been frustrated by the complexity of quantitative traits, even when they include the analysis of divergent genotypes. Despite considerable effort, no strong correlation has yet been found between final yield and the productivity of any distinct biochemical pathway (1, 4). The problem is that any metabolic, reaction can affect the final productivity in a given environment. The question is, 'which reactions or steps actually do affect productivity?

Whatever the eventual role, of molecular biology in plant production, it is essential to begin to approach the classical holistic descriptions, or plant productivity, with reductionistic and analytical tools. In this process, a number of traditionally disparate biological disciplines can be brougnt to bear on the unique and complex problems of agricultural plant biology.

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Can We Break Present Barriers to Improvements in Sugarbeet Yields?

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I am pleased to have the opportunity to share my thoughts with you about how to increase sucrose yields from the sugarbeet crop. Although my major research emphasis has been on the physiology of cereal and legume crops, I nevertheless have worked with sugarbeets enough to know that many of the same physiological principles apply to most of our major field crops.

I want to emphasize, at the outset, that regardless of the discipline one pursues in crop research, whether it be plant breeding, management, physiology, or processing, the successes we achieve in improving sucrose yields will depend heavily on the extent and effectiveness of our ability to communicate data and ideas about our research experiences. Evidence indicates that those research groups, regardless of size, that have the most free exchange of information accomplish more than do groups with common research interests, but who guard their ideas for whatever reasons.

My research has dealt with factors of photo synthetic efficiency, water-use-efficiency, and plant growth analysis of crops. At the outset of my program, I had visions about developing simple screening procedures that could be used by plant breeders to identify and select superior lines of certain crop species. With perhaps one exception, I have had little success with the development of efficient screening techniques. Nevertheless, through the process of communicating my research results about fundamental aspects of crop growth and development, I believe I have helped my plant breeder associates improve in their "minds eye" how a more ideal plant type should appear and how it should perform under field conditions.

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The breeder needs help from other researchers because he is responsible for making the first selections from heterozygous populations after parental crosses have been made. Thus, the more informed the plant breeder is about all basic and applied aspects of the crop, the mere likely he is ro make more intelligent selections from the heterozygous populations. Obviously then, it is the responsibility of resource people, e.g. plant pathologists, crop management specialists, processor's, etc., to make sound observations about crop plants and then relay information and ideas to the plant breeder about methods to select superior plant types. Undoubtedly, the degree to which we assist: the sugarbeef breeder in making better plant selections will be reflected in the progress we. make toward increasing sucrose yields in sugarbeets.

The research topics 1 wish to address are seasonal growth patterns, morphology of plant:s and crop canopies, and endogenous physiological systems.

I will relate characteristics of some grain crops to illustrate how the sugarbeet plant and its management can be altered to improve its productivity. Although subjects such as disease resistance, pest management, tillage management, etc. play distinct roles in sugarbeet production, they will not be discussed because others can address their importance more effectively than I. I will use sugarbeets grown under irrigation as my model system since my experience with non-irrigated sugarbeet production is limited. However, many of the principles I relate will apply to both irrigated and non-irrigated production systems.

It is generally accepted that fall planted wheat has a greater potential for high yield than does spring planted wheat in most growing regions around the world. Also, in the cornbelt region of the midwestern U.S., corn planted in April will usually yield more than corn planted in May, and the corn planted in Kay will yield more than corn planted in June. Why? Because the fall wheat and the early planted corn exploit more of the growing season than do the late planted crops by developing a greater vegetative base plant. The larger vegetative base is then used to produce grain during a

longer period of time from anthesis, or heading, until physiological maturity of the seed. Thus, plant breeders have knowingly increased the effective growing season of these crops by developing winter or cold hardiness into the crops which enables the plants to survive and flourish in the environments in which they are grown. Although there are some exceptions, due to environmental interactions, there is a high and positive correlation between the duration of the grain filling period and potential for' high grain yield in wheat and corn.

I believe the principle of using a longer grain-fill-duration in cereal crops can be utilized to increase sucrose production in sugarbeets. To increase the effective season of "sucrose accumulation" in sugarbeets, plant breeders should first select for high seed viability, rapid germination rate, and vigorous seedling growth in the early spring. Since most of the sugarbeet growing regions of the midwestern and western U.S. are characterized by cool, moist springs, often with a threat of late spring frosts, it behooves us to select beet genotypes that cope with these conditions. If we can accomplish in sugarbeets what the plant breeders have done to improve corn adaptation to harsh early spring conditions, we can enhance the vegetative base that is required to produce and store sucrose in the early development of the beet crop.

Tf sugarbeet varieties were developed that could establish and grow vigorously early in the spring, the next limiting factor[1] to increasing "sucrose-fill-duration" is the length of time required for the hypocotyl and/or the storage root to initiate rapid expansion. As a corollary, I relate the stage of initial rapid root expansion in beets to anthesis, or heading, in cereal crops. Obviously, grain development begins after fertilization has taken place; if this process occurs very early and physiological maturity of the grain is later, the greater will be the opportunity to increase the number of days for grain filling. Likewise with sugarbeets; the earlier the process of sucrose storage is initiated and the longer it continues, the greater will be the chance for greater sucrose production because of an increase in the effective storage period during the growing season.

The hypocotyl test Dr. Doney described during this symposium should be of significant value as attempts are made to identify sugarbeet genotypes whose hypocotyls expand earliest in the spring.

When sugarbeet genotypes are developed that have roots expanding earlier, productivity can be further increased by selecting lines with the greatest capacity to produce photosynthate and store it as sucrose in the root of the plant. Dr. Snyder and colleagues reported on a technique that should prove useful to identify lines that partition greater amounts of their photosynthate to the root tissue. Hopefully, genotypes that shunt greater proportions of sucrose to the root in the early stages of root expansion will have the capacity to continue this favorable pattern of partitioning photosynthate throughout the growing season.

Another critical growth phase in sugarbeets occurs in the summer during the period of rapid sucrose accumulation in the root. Mid-summer daytime; temperatures often rise above optimum for the plants; therefore, either genotypes must be developed that adapt well to those conditions, or irrigation systems must be managed to minimize plant stress. Regardless of whether the crop is grown under rainfed or irrigated conditions, the less moisture and/or temperature stress they experience, the more vigorously they will grow and, thus, increase their potential for high yield.

Associated with the problems of moisture and temperature stress is the factor of nitrogen management in sugarteet production. Generally, present recommendations for nitrogen suggest relatively heavy applications during early and mid-seasons, with allowance for significant reductions in the soil $NO_{„}$-level in late summer and fall. Evidence from past research lias indicated this reduction in the level of soil N is necessary to increase the sucrose level in the storage root, thus enhancing sugar yields per unit area of land.

If present sugarbeet varieties require a "ripening off" period to increase sucrose concentration induced by reduced levels of soil N in the fall, I propose it is because our present varieties have been developed in plots using this type of nitrogen regime. I suggest that we would have beet genotypes that would grow with greater vigor for a longer period during the season and, thus, have the potential to store more sucrose if initial selections of superior sugarbeet genotypes were made under a system available whereby soil N was not significantly reduced in late summer or fall. Therefore, if plant breeders could select plants that partitioned their photosynthate more favorable to the root and with less concomitant leaf development but with more rings in the root, sucrose yields could be increased by lengthening the duration of sucrose accumulation and storage in the later summer and fall periods.

Selection of new sugarbeet varieties ~chat simultaneously increase the number of days of effective sucrose storage in the root and more favorably partition photosynthate to the root, would likely result in an increase in the leaf (source) photosynthesis of the plants as a result of increase in the carbohydrate sink in the root.

Although a sugarbeet genotype with a superior rate of leaf photosynthesis might be identified at sometime In the future, It is likely that increasing the sink strength for sucrose in the beet root will be a more efficient way to enhance total photosynthesis in the crop.

In addition to the need for research mentioned above, efforts should be made to select plant types, or management systems, that optimize photosynthetic productivity throughout the growing season. There is a great need to capitalize on Interactions with crop management systems. The need for a testing system that would provide a means to measure genotype X environment interactions led me to the development of a chamber-type, gas-exchange system for field plots CD. The system consists of plastic covered chambers that can be placed over plots early in the growing season, with four or five subsequent moves to similar plots during the season. The dynamic aspects of plant growth and development can be monitored and related to various

measurements of the plant-soil-atmosphere environment that may be recorded in addition to the photosynthetic rates and transpiration rates of the plants under study.

The field chamber system provides a basis for a holistic approach to research which will produce more complete and meaningful answers to fundamental questions we now have about crop canopy design, photosynthesis, plant water relations, light utilization, etc., and how they interact under field conditions. Results from these field chamber systems can also be used to test crop growth models such as those developed by Dr. Loomis for sugarbeet growth and development.

In conclusion, if we are to move off the sucrose yield plateau in sugarbeet production, we must seek new and innovative methods to accomplish the task. Many, if not most, yield increases that have been achieved in seed crops have been accomplished by increasing the period of effective storage of carbohydrate in the seed. Through cooperative efforts, sugarbeet researchers can focus their research on methods to lengthen the duration of sucrose accumulation in sugarbeets and, thus, break the yield barriers that currently exist.

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SUMMARY

When Watson and Crick first structurally analyzed the DNA molecule and came up with a structural arrangement of the hereditary material, it wasn't a sudden breakthrough but an integration of many pieces of information. The information had already been available for some time; it was just putting each piece and each bit of information in the right perspective. Most breakthroughs happen this way; i.e., by building piece upon piece, brick upon brick until the whole structure can be visualized.

In times past, we have witnessed numerous methods that were going to revolutionize plant breeding such as mutation breeding, quantitative genetics, nitrate reductase activity, photosynthetic efficiency, mitochrondrial complementation, etc. Each one has had something to add to our knowledge and to our set of tools in plant breeding, but none have proved to be a panacea. We must learn how to use them to build the proper structure.

The growth processes are a complicated series of functions and processes all going on at the same time interacting with each other in supply, demand, and feedback equilibrium. These papers have presented us with an overview of the growth functions that hold promise as plant breeding tools (in sugarbeets). These are by no means a list of all the functions. The growth processes have been reviewed, and only those with the greatest potential have been presented. This does not say, however, that as our' understanding of the physiology of the plant is increased there will not be additional important and useful growth processes.

As a plant breeder, I am often discouraged at the slow progress we are making. Sometimes it seems as if we are going around in circles. We select and test, and select and test, and seem to make very little improvement. There are pressures on us to more rapidly and efficiently develop higher yielding and more productive hybrids. In light of our present progress and the needs of the world today, we need to look at these new approaches very carefully. They need to be evaluated and developed to the point of practical use.

The speakers have presented us with many suggestions and questions that are thought provoking and certainly deserve our attention. Some of these suggested potential selection criteria are new and novel, while some are the refinement of old techniques. Some might be useful by themselves while, at the same time, they would be more effective combined in an index with other techniques, and some may be ineffective or too expensive or time consuming. In any event, we now have at out disposal some potentially powerful new tools. The proper development, integration, and use of these tools may be the foundation for new breakthroughs in sugarbeets.