Ideotype Concepts for Sugarbeet Improvement

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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 collec-
tive 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 photo-
synthesis when compared to other C_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 tech-
niques and with plants grown under highly controlled condi-
tions, there is little chance for the detection of genetic
differences.

It may also be that we are already rather close to environ-
mental (solar radiation, CO_2 supply and growing season)
limits of production potential. Certainly the sugarbeet
reveals itself as the most productive of biomass 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 $\simeq$ 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; formu-
lation 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 mito-
chondrial efficiency, 17).

One of the key difficulties found with such physiological
hypotheses is that a single step is seldom "always limit-
ing." 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 bal-
anced by an increase in the size of that system or a reduc-
tion in the size of dependent processes or organs. A
simple analysis of that situation might suggest that noth-
ing is limiting since all parts seem in balance. Clearly,
advanced ideotype formulation may prove difficult and
complex, requiring best efforts by physiologists, morpholo-
gists, 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 sugar-
beet 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 geno-
type 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-ℓ pots filled with vermiculite. 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.

Treatment	Variety [1]	Fresh Basis			Dry Basis		K^2
		Living Tops	Beets	Root Sucrose	Sucrose	Tops + Beets	
		(g/pot)	(g/pot)	(%)	(g/pot)	(g/pot)	(K)
+N	NB5	2190a	3160a	11.8b	330a	840a	39
	NB4	1030b	2940a	10.7a	330a	680b	48
	NB1	620c	3170a	10.9a	360a	660b	54
-N	NB5	640c	2230b	16.4d	360a	640b	59
	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 experiment 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
          season.

Treatment	Variety	Foliage Area	Population	Yield Fresh Beets	Sucrose
		(m^2/pot)	(plants/ha)	(kg/ha)	(kg/ha)
+N	NB5	0.43a	46400	73300	7700
	NB4	0.34b	58600	86200	9500
	NB1	0.22a	91000	144000	16000
−N	NB5	0.25b	78400	87400	14300
	NB4	0.18c	114000	96200	16000
	NB1	0.14d	144000	161000	23100

Physiological Ideotype 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 pro-
cesses, space per plant held constant.

Partitioning

The major aspects 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
those growth sinks. While the extrapolation admittedly was crude,
it was on the basis that NB1 was predicted to provide much larger
yields of sucrose on an area basis than either NB5 or NB4.

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 concen-
tration than NB1 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 small size of tops and thus appeared suit-
able 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 competi-
tion 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 SUBCOL 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 SUBGOL 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 SUBGOL 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 (12). Older sugarbeet roots do not appear to be limited by the number of dividing and expanding storage-root cells (Rapoport, H., 20th Genl. 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 SUBGOL 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
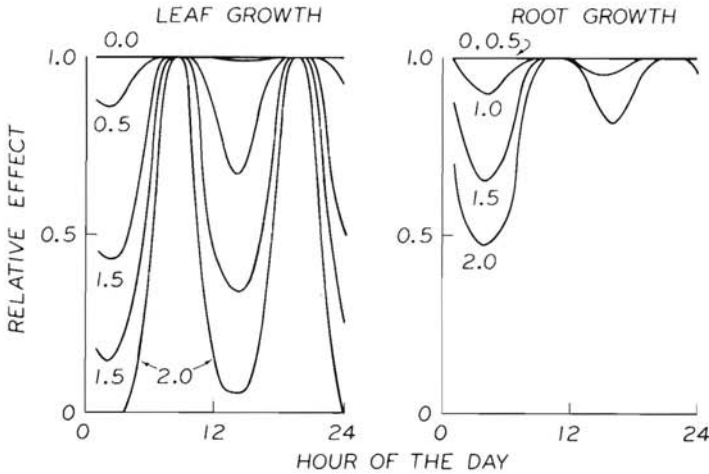
Figure 1.   Relative effects of temperature with different diurnal
             amplitudes on the growth rate of leaves (left) and storage
             roots (right) as they operate in the SUBGOL simulation
             mode.   These data are for a midseason date at Davis, CA,
             when mean temperatures were optimal for growth.   The 1.0
             curves are for the normal diurnal amplitude of air
             ($17°$ C) and soil $7.5°$ C) temperatures for that date;
             the 0.0, 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 the 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 develop-
ment 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]	GRB[3]	$\dfrac{GRB}{TDWB}$[4]	$\dfrac{GRB}{DHP}$[5]
	($g\ m^{-2}day^{-1}$)	($g\ m^{-2}$)	($g\ m^{-2}day^{-1}$)	($g\ g^{-1}day^{-1}$)	
10	1.04	0.10	0.006	0.06	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
60	43.0	494	17.6	0.04	0.41
80	41.4	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]GRB 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 repair 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 of 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.

SUBGOL simulations indicate that 30 to 40% of the seasonal gross photosynthesis of a sugar beet crop is lost to respiration (16). 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 SUBGOL 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 | | | |
	G_R[2]	M_R[3]	Total Crop	Tops	Beet including sugar	Total	R_G	R_M	Y[4]
			(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	(g/m^2)	
Normal	0.25	0.005	2440	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%	−24%	+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 at 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 clover; 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 within 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:

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

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 fraction of their total volume as
osmotic 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
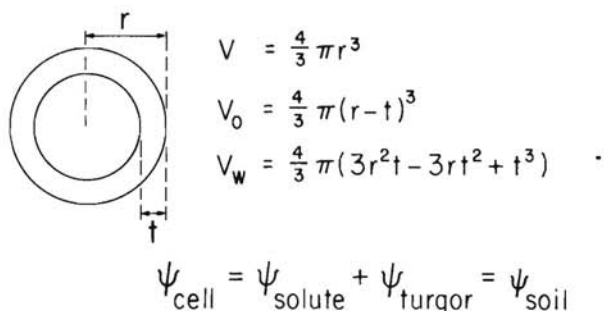also true in real tissues with more complex cell shapes is unknown.

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

$$V_0 = \frac{4}{3}\pi (r-t)^3$$

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

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

Figure 2. A conceptual model for partitioning cell volume (V) into
osmotic (V_0) 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 due 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	$\frac{V_W}{V}$	Sucrose
		Total (V)	Osmotic (V_0)	Wall (V_W)	Liter	V	
(μ)	(μ)	$(10^{-11}\ell)$	$(10^{-11}\ell)$	$(10^{-10}\ell)$	(10^9)	(%)	(% f.wt.)
15	1.0	1.41	1.15	0.26	70.7	18.7	12.2
15	0.7	1.41	1.22	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	86.0	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 that Na+, K+ and their counter ions contribute -2 bar to ψ_{solute} in cambial zones and -4 bars in midzone parenchyma. 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 lay with a more rapid depletion of sucrose from the apoplast with increasing distance from the phloem than occurs for Na+ and K+ with distance from the xylem. Midzone cells might then find little sucrose but considerable Na+ and K+ in the external free space as the basis for further expansion. Studies of such phenomena should include culture at low nitrogen where thin-juice purities are increased sharply. Such extrapolations focus our attention on the need for additional study of free-space movement and cell expansion. Until then, further effort at ideotype generalizations about root anatomy and function would seem premature.

Summary

I have taken a rather theoretical approach regarding means of formulating ideotype concepts for the improvement of sugar beet production. Emphasis was given to modeling morphological and physiological aspects affecting the fate of photosynthate, rather than to photosynthate production, since we know less about those aspects and they may offer greater opportunity for improvement.

The theoretical approach was deliberate. Ideotype concepts are systems concepts. They involve quantitative assessments of trade-offs and balances and that, of necessity, involves the formulation of models to organize our information, facilitate calculation of potential benefit, identify missing information, and define selection conditions and criteria. The models presented here are mostly simple ones, designed to focus attention on the method, and to show the value of even match-book cover models; but some of the issues are dynamic and exceedingly complex. Those will require sophisticated, hierarcheal simulation models.

LITERATURE CITED

(1) Cutler, J. M., D. W. Rains, and R. S. Loomis, 1977. The
     importance of cell size in the water relations of plants.
     Physiol. Plant. 40:255-260.

(2) Doering, E. J. 1976. Sugarbeet yield and theoretical photo-
     synthesis in the Northern Great Plains. J. Am. Soc. Sugar
     Beet Technol. 19:163-175.

(3) Donald, C. M. 1968. The breeding of crop ideotypes.
     Euphytica 17:385-403.

(4) Duncan, W. G. 1971. Leaf angle, leaf area, and canopy photo-
     synthesis. Crop Sci. 11:482-485.

(5) Ehleringer, J. R. 1978. Implications of quantum yield
     differences on the distribution of C_3 and C_4 grasses:
     Oecologia (Berlin) 31:255-267.

(6) Fick, G., R. S. Loomis, and W. A. Williams, 1975. Sugar Beet.
     pp. 259-295. In: L. T. Evans (ed.) Crop Physiology - Some
     Case Studies. Cambridge Univ. Press, Cambridge, U.K.

(7) Hall, A. E. and R. S. Loomis. 1972. Photosynthesis and
     respiration by healthy and beet yellows virus-infected sugar
     beets (Beta vulgaris L.). Crop Sci. 12:558-561.

(8) Hunt, W. F. 1974. Respiratory control and its prediction by
     a dynamic model of sugar beet growth. Ph.D. Diss., Univ.
     Calif., Davis. 243 p.

(9) Loomis, R. S. and P. A. Gerakis. 1975. Productivity of
     agricultural systems. pp. 145-172. In: J. P. Cooper (ed.)
     Photosynthesis and Productivity in Different Environments.
     IBP Vol. 3. Cambridge Univ. Press, Cambridge, U.K.

(10) Loomis, R. S. and E. Hg. 1978. Influences of climate on the
     photosynthetic productivity of sugar beet. pp. 259-268.
     In: D. O. Hall, J. Coomb, and T. W. Goodwin (eds.).
     Photosynthesis 77. Proc. Fourth Intl. Cong. Photosynthesis.
     The Biochemical Society, London.

(11) Loomis, R. S., E. Ng, and W. F. Hunt. 1976. Dynamics of
     development in crop production systems. pp. 269-286.
     In: R. H. Burris and C. C. Black (eds.) CO_2 Metabolism
     and the Productivity of Plants. Univ. Park Press, Baltimore, MD.

(12) Loomis, R. S. and H. Rapoport. 1977. Productivity of root crops.
     pp. 70-84. In: J. Cock, R. MacIntyre, and M. Graham (eds.).
     Proc. Fourth Symp. Intl. Soc. Tropical Root Crops (Cali,
     Colombia). Intl. Develop. Res. Centre, Ottawa, Canada

(13) Loomis, R. S. and A. Ulrich. 1962. Responses of sugar beets
     to nitrogen deficiency as influenced by plant competition.
     Crop Sci. 2:37-40.

(14) Loomis, R. S. and W. A. Williams. 1969. Productivity and
      the morphology of crop stands: patterns with leaves. pp. 27-
      47. In: J. D. Eastin et al. (eds.) Physiological Aspects of
      Crop Yield. Am. Soc. Agron., Madison, Wis.

(15) Loomis, R. S. and G. F. Worker, Jr. 1963. Responses of sugar
      beet to low soil moisture at two levels of nitrogen nutrition.
      Agron. J. 55:509-515.

(16) McCree, K. J. 1970. An equation for the rate of respiration
      of white clover plants grown under controlled conditions.
      pp. 221-229. In: I. Setlik (ed.). Prediction and
      Measurement of Photosynthetic Productivity. PUDOC,
      Wageningen, The Netherlands.

(17) Penning de Vries', F. W. T., A. H. M. Brunsting, and H. H.
      Van Laar. 1974. Products, requirements, and efficiency of
      biosynthesis: a quantitative approach. J. Theor. Bio.
      45:339-377.

(18) Savitsky, V. F. 1954. Relation between the weight of fruit
      and weight of germ in mono- and multigerm beets. Proc. Am.
      Soc. Sugar Beet Technol. 8(2):16-22.

(19) Stout, M. and C. H. Smith. 1950. Studies on the respiration
      of sugar beets as affected by bruising, mechanical harvesting,
      severing into top and bottom halves, chemical treatment,
      nutrition, and variety. Proc. Am. Soc. Sugar Beet Technol.
      6:670-679.

(20) Teranishi, R., R. L. Patterson, and H. S. Owens. 1956.
      Sampling of sugar beets for the processing laboratory.
      J. Am. Soc. Sugar Beet Technol. 9:74-77.

(21) Vilmorin, J. E. de. 1923. L' Hérédité chez la Betterave
      Cultivée. Gaughiers-Villars, Paris.

(22) Watson, D. J. 1952. The physiological basis of variation in
      yield. Adv. Agron. 4:101-145.