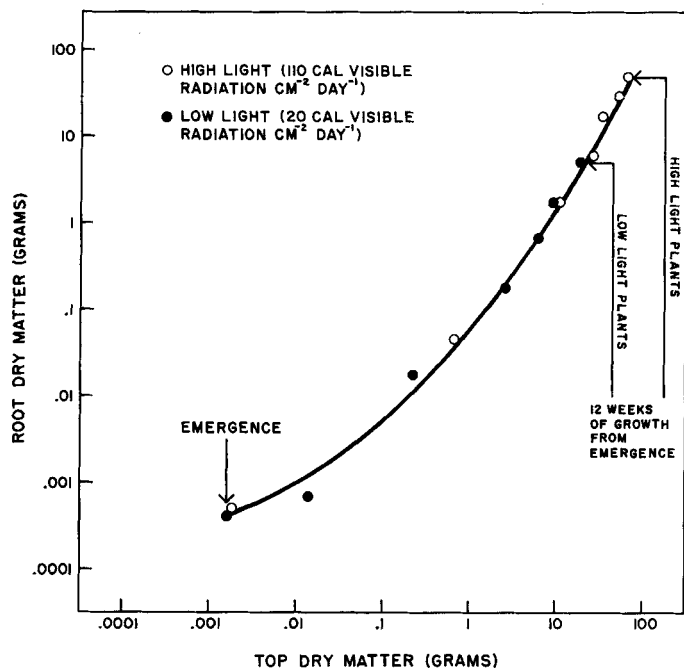
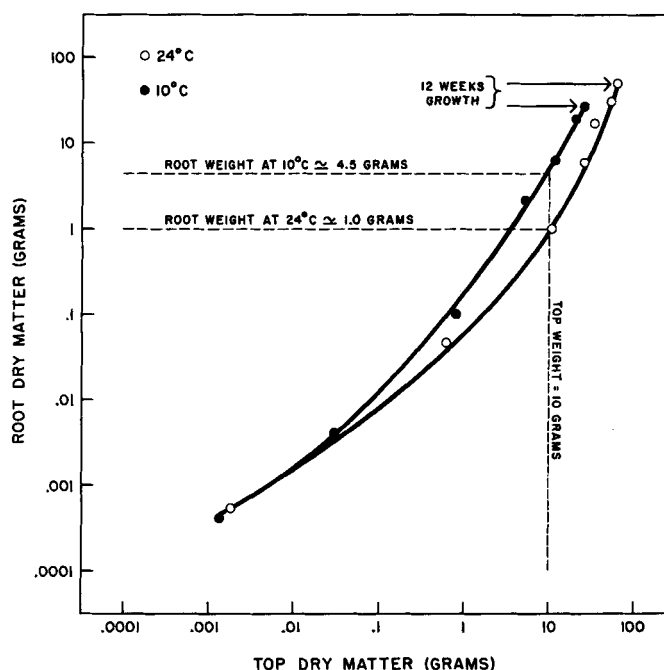


GRAPH 1. THE RELATION OF ROOT DRY MATTER TO TOP DRY MATTER FOR PLANTS CULTURED UNDER TWO LIGHT INTENSITIES AT A CONSTANT TEMPERATURE OF 24°C.



GRAPH 2. RELATION OF ROOT DRY MATTER TO TOP DRY MATTER FOR PLANTS CULTURED AT TWO TEMPERATURES, 10 AND 24°C, 110 CAL VISIBLE RADIATION CM<sup>-2</sup> DAY<sup>-1</sup> AT EACH TEMPERATURE.



# SUGAR STORAGE MECHANISMS IN BEETS

NORMAN TERRY

This article discusses environmental factors influencing the partition of sugar products between the tops and storage roots of sugar beets. Root size was found to be related in a specific way to top size. This root-to-top relationship was unaffected by changes in light intensity but was affected by change in temperature or nitrogen supply. Storage roots grew and stored sugar by the continual addition of new cells.

One of the major obstacles to the improvement of sugar production in sugar beets has been the lack of knowledge of the physiological and biochemical mechanisms of root development and sugar storage. Sugar is formed in plants with the help of the light energy from the sun. This energy is trapped by means of the green pigment, chlorophyll, so carbon dioxide from the atmosphere can be chemically reduced to sugar products. Partitioning of sugar products between the roots and leaves is dependent on environmental factors during plant growth, as well as on the genetic characteristics transmitted from the seed.

If we examine each of the environmental factors in turn we see that differ-

ent mechanisms are involved. The growth of the sugar beet plant may be compared with the construction of a house for which all the building materials are available but which lacks man-power or building energy for its completion: the faster that man-power is applied the faster the house is built. Thus, the faster the light energy is supplied to the leaf surface, the faster sugar is formed and the faster the plant grows—provided that temperature and nutrient supply are held at optimal levels and that light intensity is below saturation. Just as there is no change in the architectural plan of a house if it is built at a faster rate, there is also no change in the "architectural plan" of growth in terms of the propor-

tion of sugar products utilized in root or top development when a plant grows faster with more light.

### Root increase

When the dry matter of roots was plotted against the dry matter of the tops, in plants which had been cultured in a controlled environment with high or low light (see graph 1), the proportion of root increased with increases in size of tops—and high light increased the rate of growth. However, the amount of root at any top size was *not* affected by high or low light, so that although increased light speeded up the growth of the whole plant, the way in which roots were related to tops was unchanged. In other words, sugar beets do not grow by supplying sugar first for tops and then, if sufficient sugar is available, to roots for growth and sugar storage. Rather, increased sugar supply as a result of increased light, or other factors, results in a faster rate of growth of the whole plant, including faster sugar storage.

### Variations

Variations in temperature had a different effect: at 24°C—the optimum temperature for growth—the amount of root dry matter associated with a top dry weight of 10 grams, for example, was about 1 gram, compared with a root dry matter weight of 4.5 grams at 10°C (see graph 2). The rate of plant growth in-

creased with an increase in temperature from 10° to 24°C, but (unlike results with increased light), the “architectural plan” of development was also changed so that more sugar products were utilized in tops than in root growth. A similar situation resulted from variations in nitrogen supply (see graph 3). Although plants grew faster with high applied nitrogen, more of their sugar products were utilized in tops than in root development.

### Sugar yields

When considering how to agriculturally manipulate the growth of sugar beets to improve sugar yields, it is essential to remember that although additions of fertilizers such as nitrogen may increase the rate of growth of the whole plant, it may also cause the shift of more sugar products into leaves and away from roots and sugar storage. Improvement of the light reception of a crop by techniques developed by agronomists will not have this effect and can only result in improved sugar yields.

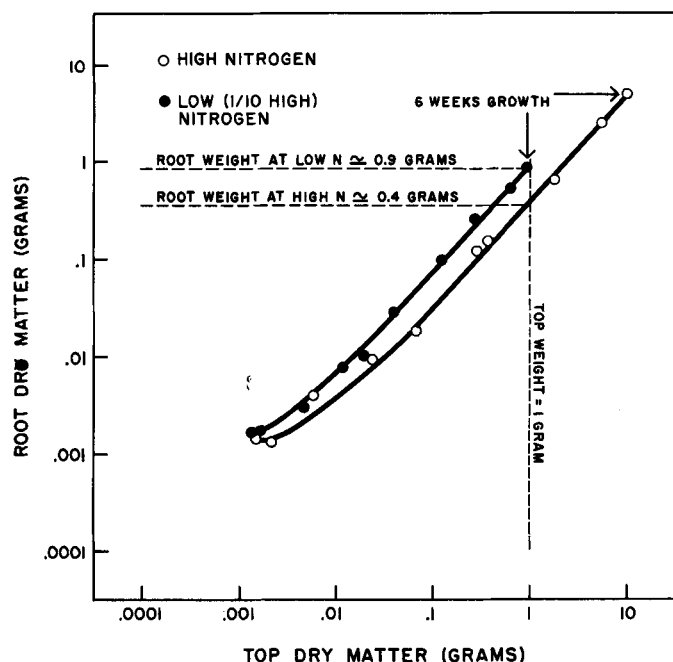
It has been shown that external environmental factors may affect top and root relationships, but what are the internal factors controlling storage root growth? How does the storage root grow and store sugar? To gain more information on these topics, the storage root was examined at the cellular level. The storage root consists of a large number of concentric meristems which form large

numbers of new cells, some of which are used for storage, throughout life. Graph 4 shows that the increase in storage root dry matter was paralleled by an increase in the number of cells per root; the average cell volume, however, decreased from the high initial value found in the seedling hypocotyl (and tap root) owing to the production of many small cells after the initiation of cambia. In fact, during the entire season, the average cell volume never attained the high values of the seedling hypocotyl. There was, therefore, no stage in the growth of the storage root when a large proportion of cells underwent a phase of expansion—unlike the leaf, which expanded rapidly in size, after unfolding from the bud by means of just such an expansion of cells.

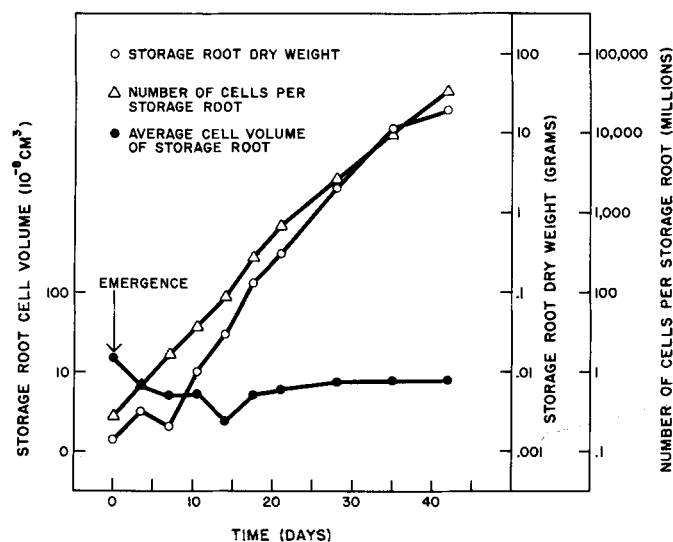
### Cell division

Cell division in beet roots may be directly related to sugar supply, because at 15° and 20°C the growth of roots, and the activity of the terminal bud in producing new leaves—both cell division processes—accelerate with time so that they eventually become greater than at the plant growth optimum of 25°. Concurrently, the sugar concentration in leaves also increases with time from less than 0.5% fresh weight to values greater than 2% fresh weight, while at 25°C sugar concentrations remain at about 0.5%. Thus, at these sub-optimal temperatures, it appears that rates of cell divi-

GRAPH 3. RELATION OF ROOT DRY MATTER TO TOP DRY MATTER FOR PLANTS CULTURED AT TWO LEVELS OF APPLIED NITROGEN—PLANTS CULTURED AT 15°C, 100 CAL VISIBLE RADIATION CM<sup>-2</sup>DAY<sup>-1</sup>.



GRAPH 4. CHANGES, WITH TIME, OF STORAGE ROOT CELL NUMBERS, CELL VOLUME, AND DRY WEIGHT—PLANTS CULTURED AT 15°C WITH 100 CAL VISIBLE RADIATION CM<sup>-2</sup>DAY<sup>-1</sup>.



sion are increased because of an increase in the availability of sugar.

### Storage

Studies in which radioactive carbon dioxide ( $^{14}\text{CO}_2$ ) was supplied to sugar beets and the subsequent distribution followed in various parts of the plant, have indicated that 60% of the radioactive sugars formed were translocated from leaves to the root within  $1\frac{1}{2}$  to 2 hours. However, it seems unlikely that these sugars were immediately located in their final storage sites because radioautographic studies have shown that as much as 72 hours may elapse before radioactive sugars have completely moved from the region adjacent to the transporting cells of the vascular ring into the tissues between the rings. Also, radioactive carbon was found to accumulate steadily in cell wall and protoplasmic materials of the storage root for 72 hours after the radioactive sugar had arrived in the roots.

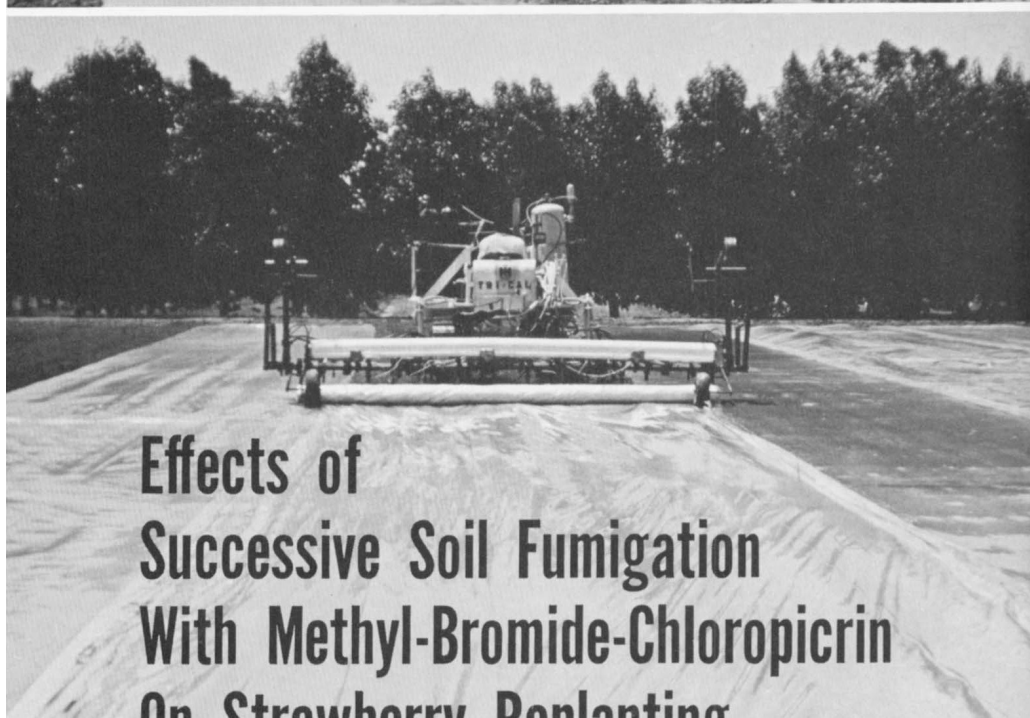
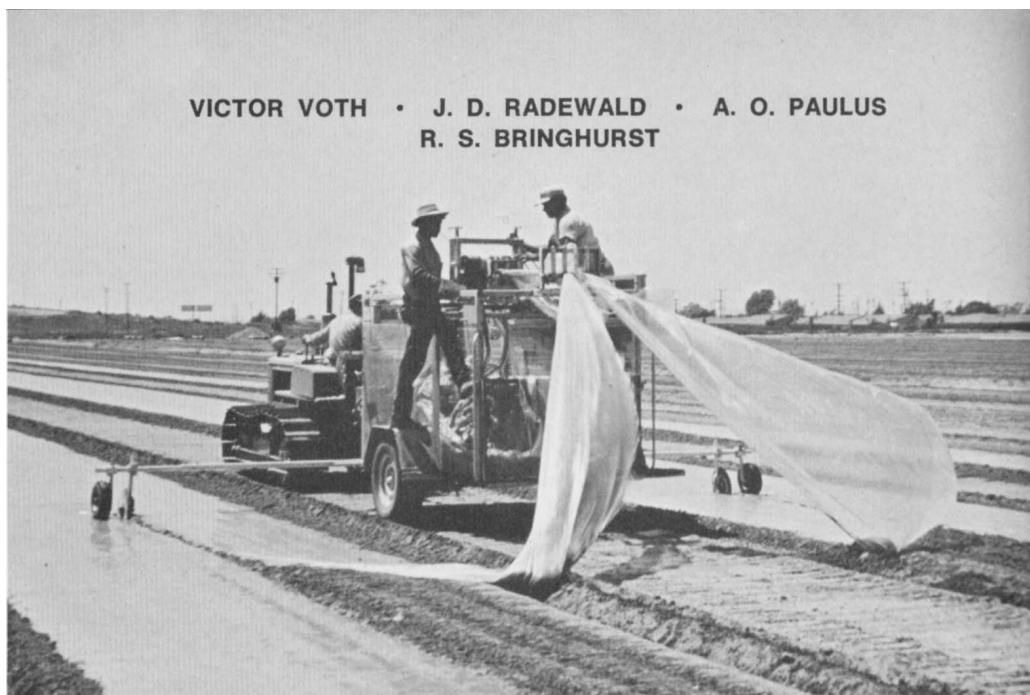
These data suggest that before newly-arrived sugar may be stored in the root, new cells must be formed which, on expansion, accumulate sugars in their vacuoles. This might explain the apparent anomaly of how sugars are moved from the leaf, against a concentration gradient, to the root where the concentration may be as high as 15% to 20%. If sugars move into young actively growing regions where the sugar utilization is high, then the sugar concentration at the site of utilization is probably diminished to a very low level.

Now

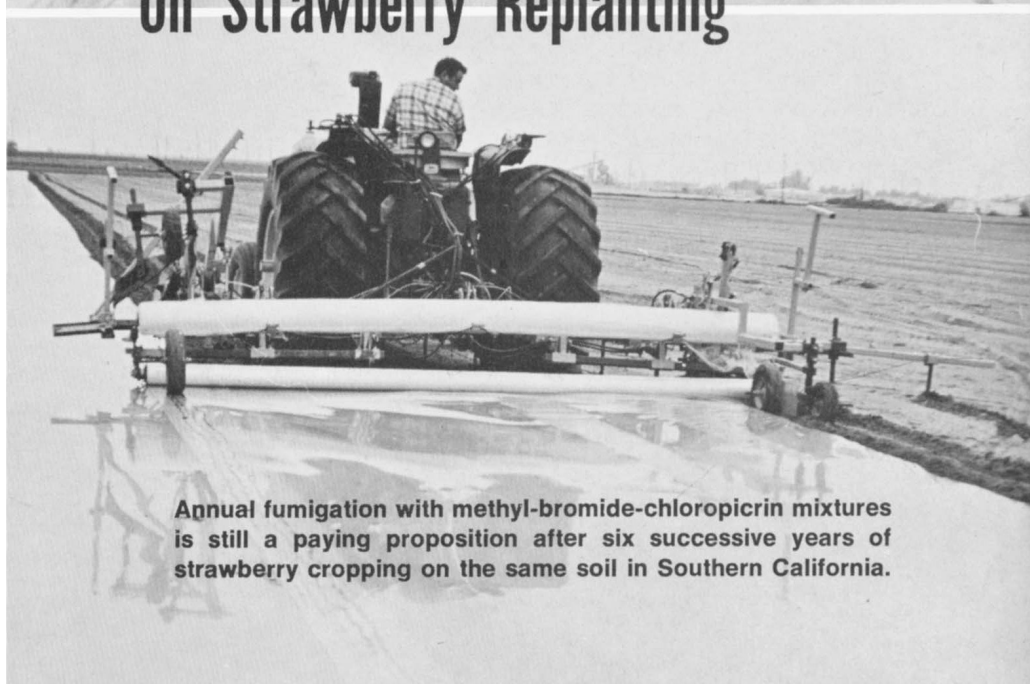
Thus, the evidence suggests that sugar storage in beets is brought about by the continuous addition of new cells which accumulate sugars on enlargement. It seems unlikely that much sugar storage will be accomplished in beet roots if conditions are unfavorable for cell division. It is clear that there is a substantial internal control over root development because of the strong dependence of root size on top size during growth, but the top-to-root relationship, as determined by internal factors, may also be modified to a considerable extent by environmental factors, particularly temperature. How the internal control (from the genotype) over cell division in the root is mediated warrants further study.

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## Effects of Successive Soil Fumigation With Methyl-Bromide-Chloropicrin On Strawberry Replanting



Annual fumigation with methyl-bromide-chloropicrin mixtures is still a paying proposition after six successive years of strawberry cropping on the same soil in Southern California.