

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 phytotron 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 consistently 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 growth 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

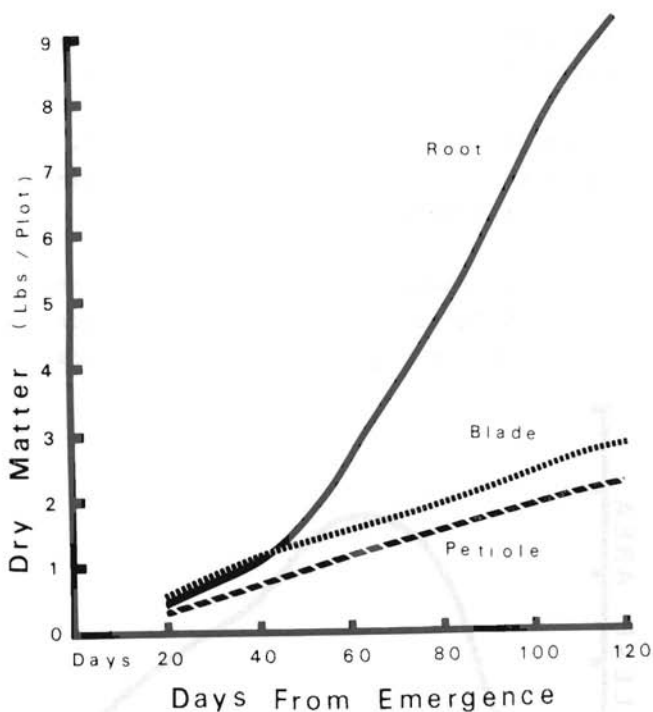


Figure 1. Seasonal accumulation of dry matter for blades, petioles, and roots of 24 genotypes. Logan, Utah. 1974.

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 the photosynthetic assimilate for a longer period.

Leaf Area

Leaf area has been one of 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. It is a typical

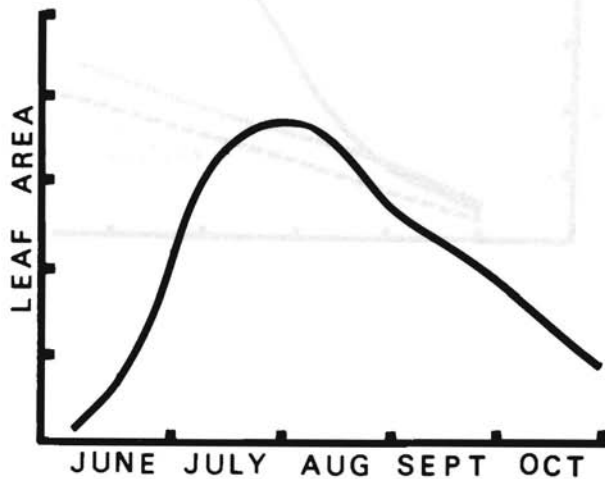


Figure 2. General pattern of seasonal changes in leaf area. See Watson (37), Campbell and Viets (4), Hodanova (15), and Storer et al. (37)..

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

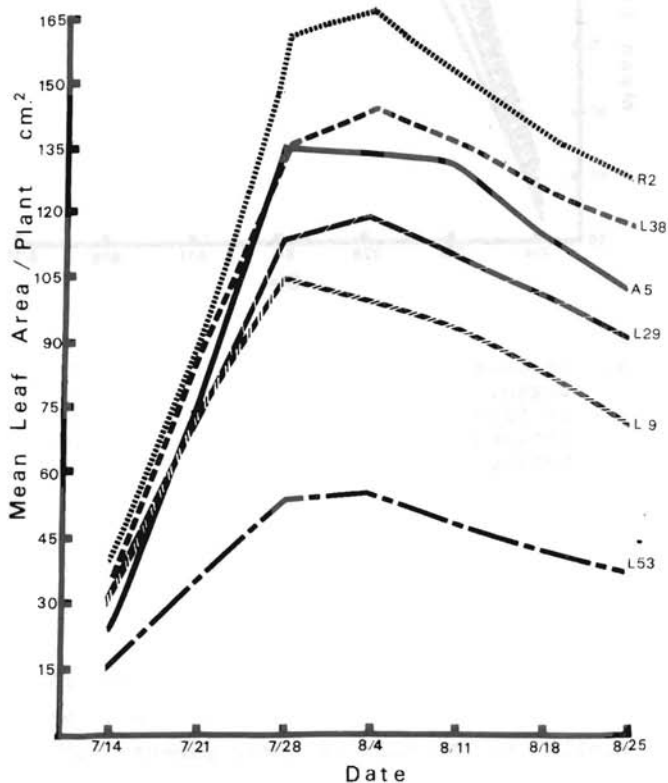


Figure 3. Seasonal pattern of leaf area for inbreds at Logan, Utah.

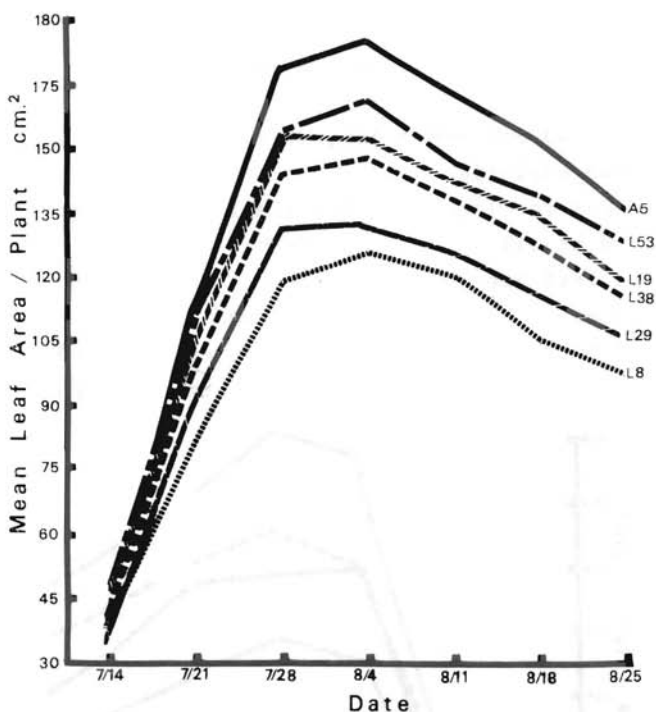


Figure 4. Seasonal pattern of leaf area for hybrids at Logan, Utah. Each curve represents the mean of five hybrids of the indicated pollen parent crossed to the same cytoplasmic male sterile female parents.

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 4 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 0.30 at harvest. Thus, meaningful relationships must be defined, and selection for leaf area should be made 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 and also delays maximum leaf canopy development until the last of August (6, 9, 33). Milford and Thorne (25) found that cold temperatures late in the growing season resulted in plants having slightly smaller leaf areas, and halving light intensity had little effect on 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 and 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 not 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 leaf placement, horizontal or erect growth habit, differences in light-absorbing capacity, and photosynthetic efficiency could all affect production. Miyaura et al. (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.

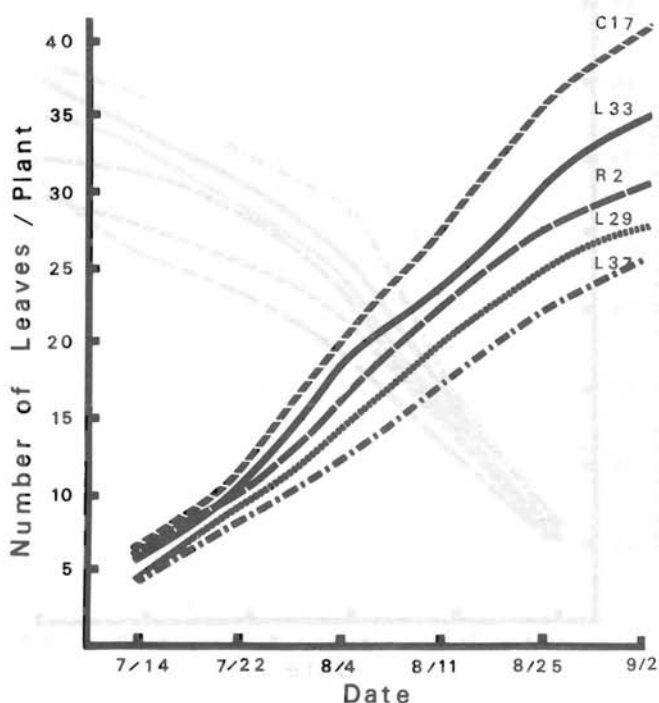


Figure 5. Seasonal pattern of leaf accretion for inbreds at Logan, Utah.

Loomis and Williams (22) reported that leaf angle distributions are quite different 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 failed to develop reliable techniques that can be used as selection criteria for the most effective canopy type for sugarbeets. Some attempts to study the 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

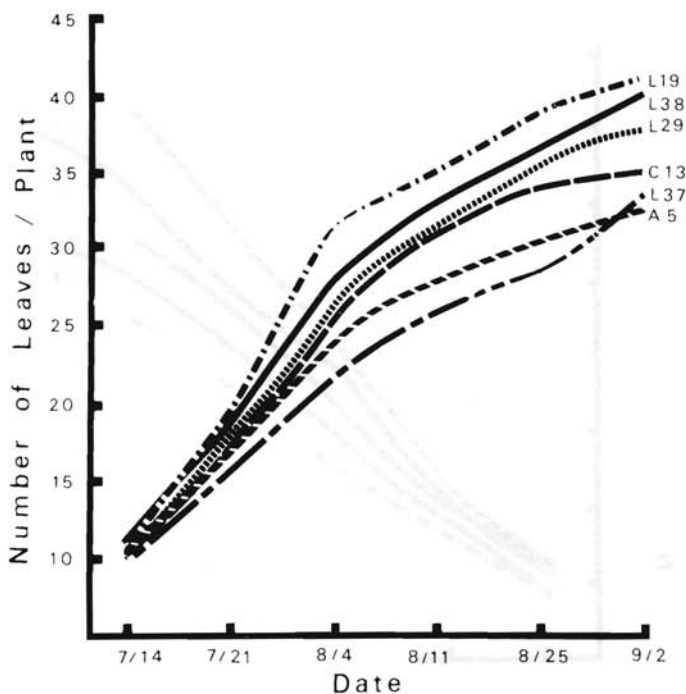


Figure 6. Seasonal pattern of leaf accretion for hybrids at Logan, Utah.

content. Gemma (11) estimated that leaf 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, 6, 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 6-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 other 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 indicator of the partitioning of assimilate to the top versus the root. This ratio follows a linear pattern during the growing season (Figure 7). Early planting increases the root/shoot ratio since lower temperatures tend to limit leaf growth (17). Loach (19) demonstrated that cultivars with a larger root/shoot ratio maintained more rapid assimilation rates during the later 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 produce 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 early in the growing season.

Root Development

According to Artschwager (1), 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

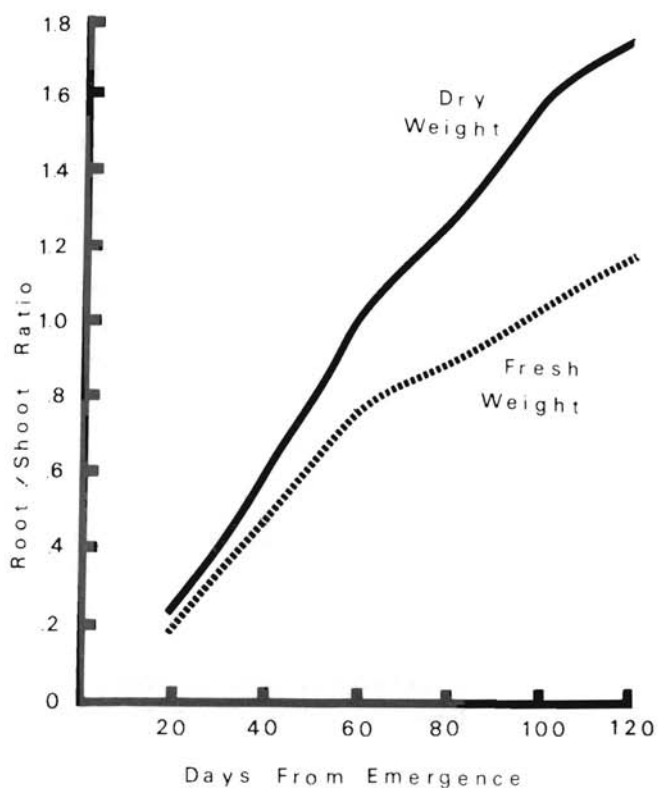


Figure 7. Root/shoot ratio of 24 genotypes.

expand with growth. Milford (23) recently concurred that rings develop together and not sequentially. Our research also 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 enlargement, 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 (28). 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 be 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.

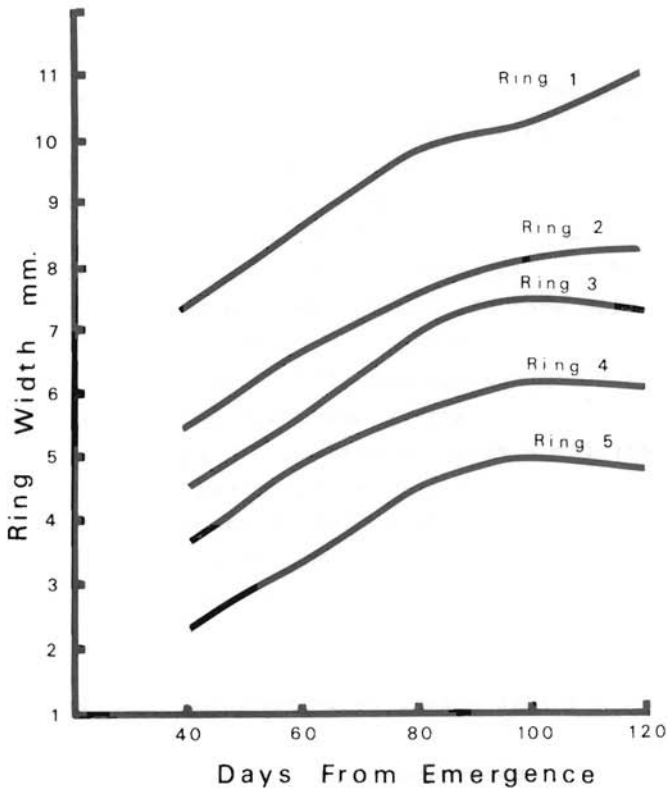


Figure 8. Seasonal change in ring width for 24 genotypes of sugarbeet at Logan, Utah, 1974.

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 1976.

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	0.66**	0.71**	0.68**	-0.64**	-0.41	-0.18

¹Rings 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 sugarbeet root. He found that the mean cell volume within both parenchymal and vascular zones of the root were larger in each successive ring from the center outward. However, the vascular zones contained two to three times as many 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 and 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 concentration 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 with 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 and yield correlations have varied from 0.60** to 0.80** (See paper by D. L. 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

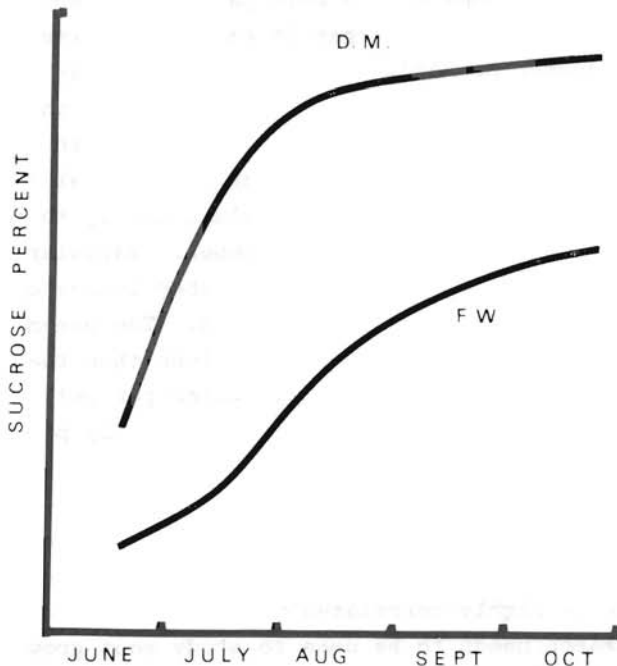


Figure 9. Seasonal changes in sucrose accumulation, fresh weight (F.W.) and dry matter (D.M.) basis.

Bergen (2), 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, and 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 0.91**.

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

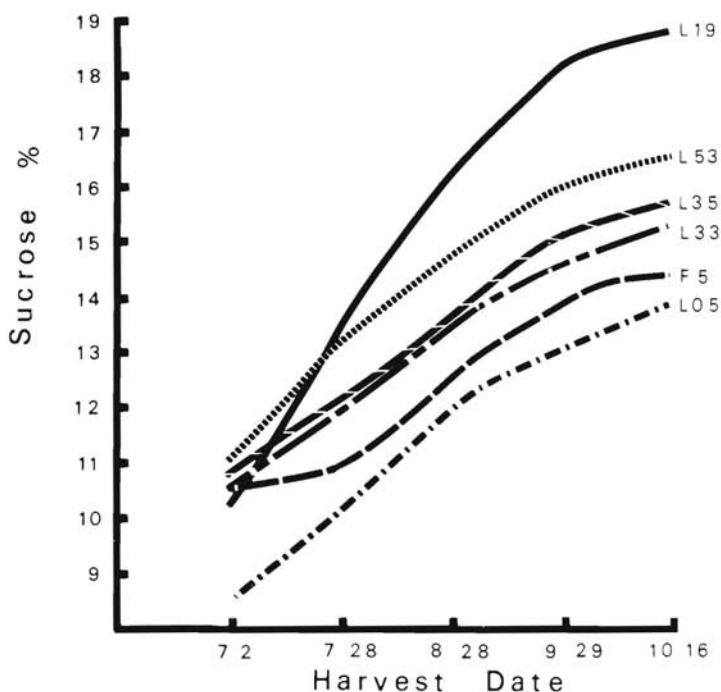


Figure 10. Seasonal change in sucrose accumulation for six inbreds, Logan, Utah, 1976. (Fresh weight basis)

dry matter 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

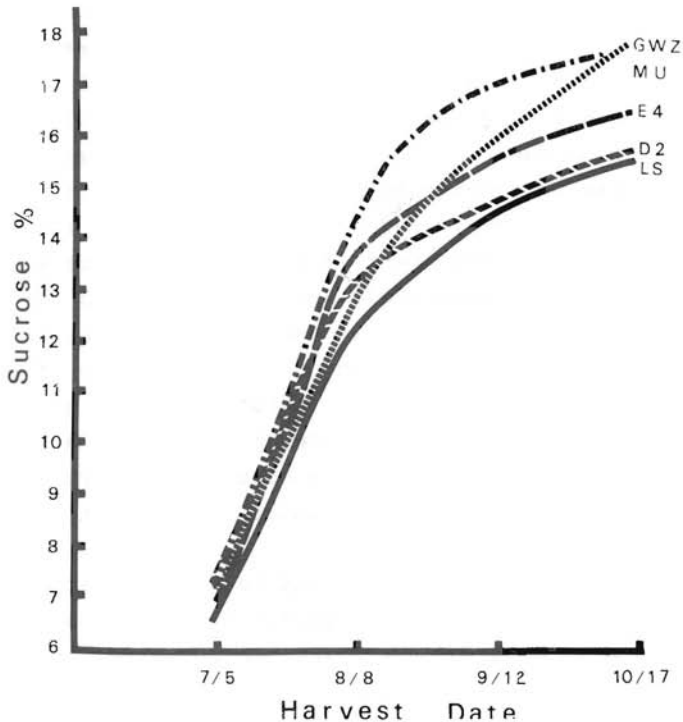


Figure 11. Seasonal change in sucrose accumulation for hybrids, Logan, Utah. 1978. (Fresh weight basis)

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 80 to 90 days after 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 occurring 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 beet, 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 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.

LITERATURE CITED

- (1) Artschwager, E. 1930. A study of the structure of sugar beets in relation to sugar content and type. *J. Agr. Res.* 40:867-915.
- (2) Bergen, P. 1967. Seasonal patterns of sucrose accumulation and weight increase in sugar beets. *J. Amer. Soc. Sugar Beet Technol.* 14:538-545.
- (3) Bouillene, R., P. Kronacher, and J. DeRoubaix. 1940. Etapes morphologiques et chimiques dans le cycle végétatif de las bettarave sucriere. Publications Institut Belge pour l'Amelioration de la Bettarave. 8:87-166.
- (4) Campbell, R. E. and F. G. Viets, Jr. 1967. Yield and sugar production by sugar beets as affected by leaf area variations induced by stand density and nitrogen fertilization. *Agron. J.* 59:349-354.
- (5) Das Gupta, D. K. 1972. Developmental physiology of sugar beet: III. Effects of decapitation, defoliation, and removing part of the root and shoot on subsequent growth of the sugar beet. *J. Exp. Bot.* 23:93-102.
- (6) Draycott, A. P., M. J. Durrant, and D. J. Webb. 1974. Effects of plant density, irrigation and potassium, and sodium fertilizers on sugar beet. *J. Agric. Sci. Camb.* 82:251-259.
- (7) Draycott, A. P. and D. J. Webb. 1971. Effects of nitrogen fertilizer, plant population, and irrigation on sugarbeet: I. Yields. *J. Agric. Sci. Camb.* 76:261-267.
- (8) Dunning, R. A. and G. H. Winder. 1972. Some effects especially on yield of artificially defoliated sugarbeet. *Ann. Appl. Biol.* 70:89-98.
- (9) Farley, R. A. and A. P. Draycott. 1974. Growth and yield of sugarbeet in relation to potassium and sodium supply. *J. Sci. Food Agric.* 26:385-392.
- (10) Follett, R. F., W. R. Schmehl, and F. G. Viets, Jr. 1970. Seasonal leaf area, dry weight, and sucrose accumulation by sugarbeets. *J. Am. Soc. Sugar Beet Technol.* 16:235-253.
- (11) Gemma, T. 1971. Morphological studies in the thickening growth of sugarbeet root. *Obihiro. Zootech. Univ. Res. Bull.* (Ser. 1). 7(1):131-164.

- (12) Goodman, P. J. 1963. Some effects of different soils on composition and growth of sugar beet. *J. Sci. Fd. Agric.* 14:196-203.
- (13) Goodman, P. J. 1966. Effect of varying plant populations on growth and yield of sugar beet. *Agric. Prog.* 41:89-107.
- (14) Goodman, P. J. 1968. Physiological analysis of the effects of different soils on sugar beet crops in different years. *J. Appl. Ecol.* 5:339-357.
- (15) Hodanova, D. 1972. Structure and development of sugar beet canopy: I. Leaf Area - leaf angle relations. *Photosynthetica* 6:401-409.
- (16) Humphries, E. C. and S. A. W. French. 1969. Photosynthesis in sugar beet depends on root growth. *Planta* 88:87-90.
- (17) Ivins, J. D. and P. M. Bremner. 1966. Growth studies with the sugar beet crop. *Agric. Prog.* 41:77-83.
- (18) Lenton, J. R. and G. F. J. Milford. 1977. Effects of photoperiod and applied gibberellin on leaf growth in sugar beet. *J. Sci. Food Agric.* 27:796.
- (19) Loach, K. 1970. Analysis of differences in yield between six sugar-beet varieties. *Ann. Appl. Biol.* 66:217-223.
- (20) Loomis, R. S. and A. Ulrich. 1962. Responses of sugar beets to nitrogen deficiency as influenced by plant competition. *Crop. Sci.* 2:37-40.
- (21) Loomis, R. S. and A. Ulrich and N. Terry. 1971. Environmental factors. p. 19-48. In: R. T. Johnson, J. T. Alexander, R. E. Rush, and G. R. Hawkes (eds.), Advances in sugarbeet production: Principles and practices. Iowa State University Press, Ames, Iowa.
- (22) Loomis, R. S. and W. A. Williams. 1969. Productivity and the morphology of crop stands: Patterns with leaves. pp. 27-48. In: J. D. Eastin, F. A. Haskins, C. Y. Sullivan, and C. H. M. van Banvel (eds.). Physiological aspects of crop yield. Amer. Soc. Agron., Madison, Wisconsin.
- (23) Milford, G. F. J. 1973. The growth and development of the storage root of sugar beet. *Ann. Appl. Biol.* 75:427-438.
- (24) Milford, G. F. J. 1976. Sugar concentration in sugarbeet; varietal differences and the effects of soil type and planting density on the size of root cells. *Ann. Appl. Biol.* 83:251-257.

- (25) Milford, G. F. J. and G. N. Thorne. 1973. The effect of light and temperature late in the season on the growth of sugar-beet. *Ann. Appl. Biol.* 75:419-425.
- (26) Milford, G. F. J. and D. J. Watson. 1971. The effect of nitrogen on the growth and sugar content of sugar-beet. *Ann. Bot.* 35:287-300.
- (27) Miyaura, J., C Tsuda, and S. Hosakawa. 1972. Statistical analysis of physiological and morphological characters of sugar beet varieties. Basic study on application of principle component analysis for classification of sugar beet varieties (Jap.) *Univ. Fac. Agr. Mem.* 8(3):277-278. (Eng. summary).
- (28) Pack, D. A. 1927. Ring density of sugarbeets as a character for selection. *Am. J. Bot.* 14:238-245.
- (29) Pack, D. A. 1930. Selection characters as correlated with percentage of sucrose, weight and sucrose content of sugar beets. *J. Agr. Res.* 40:523-546.
- (30) Roemer, F. 1927. *Handbuch des Zuckerrübenbaues.* P. Parey, Berlin.
- (31) Sande Bakhuyzen, H. L. van de. 1949. Growth and production of sugar beets. *Verslagen van Landbouwkundige Onderzoekingen.* 55:1-227.
- (32) Scott, R. K. and P. M. Bremner. 1966. The effects on growth, development, and yield of sugar beet of extension of the growth period by transplantation. *J. Agr. Sci. Camb.* 66:379-388.
- (33) Storer, K. R., W. R. Schmehl, and R. J. Hecker. 1973. Growth analysis studies of sugarbeet. *Colo. Agr. Exp. Sta. Tech. Bull.* 118. 69 p.
- (34) Terry, N. 1968. Developmental physiology of the sugar beet. I. The influence of light and temperature on growth. *J. Exp. Bot.* 19:795-811.
- (35) Ulrich, A. 1952. The influence of temperature and light factors on the growth and development of sugar beets in controlled climatic environments. *Agron. J.* 44:66-73.
- (36) Watson, D. J. 1947. Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. *Ann. Bot. N.S.* 11:41-76.
- (37) Watson, D. J. 1952. The physiological basis of variation in yield. *Adv. Agron.* 4:101-145.

- (38) Watson, D. J., T. Motomatsu, K. Loach, and G. F. J. Milford. 1972. Effects of shading and seasonal differences in weather on the growth, sugar content and sugar yield of sugarbeet crops. *Ann. Appl. Biol.* 71:159-185.
- (39) Watson, D. J. and I. W. Selman. 1938. A comparative physiological study of sugar-beet and mangold with respect to growth and sugar accumulation. II. Changes in sugar content. *Ann. Bot. N.S.* 2:827-246.