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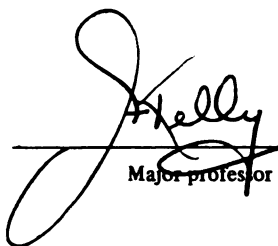
PHYSIOLOGICAL AND QUANTITATIVE DETERMINATION
OF DIFFERENTIAL SUGAR ACCUMULATION
IN CARROT (DAUCUS CAROTA L.)

presented by

Gene Edward Lester

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Horticulture



Major professor

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PHYSIOLOGICAL AND QUANTITATIVE DETERMINATION
OF DIFFERENTIAL SUGAR ACCUMULATION
IN CARROT (DAUCUS CAROTA L.)

By

Gene Edward Lester

A DISSERTATION

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ABSTRACT

PHYSIOLOGICAL AND QUANTITATIVE DETERMINATION OF DIFFERENTIAL SUGAR ACCUMULATION IN CARROT (DAUCUS CAROTA L.)

By

Gene Edward Lester

The concentration of the root sugars fructose, glucose and sucrose of carrot (Daucus carota) from different cultivars and breeding lines were determined using high pressure liquid chromatography. Over a three year study, three Michigan locations had no significant influence on sugar content, but years did differ. Genetic variation was apparent because cultivars and parental lines were consistently high or low for fructose/glucose with concomitant sucrose levels. There were no cultivars and only one parental line, 9541, that exhibited a significant difference for fructose and glucose content over all three years. However, one parental line 6000, and one hybrid cultivar, 'Spartan Fancy,' exhibited a significant difference for high sucrose and high total sugars compared to the other entries over all three years. General combining ability estimates demonstrated that parent 9541 was a strong combiner for high fructose/glucose content and parents 872 and 6000 were good combiners for sucrose from the group of

six parental lines. Based on total sugar content, parents 5986, 6000 and 9541 were good combiners in relation to other lines.

Cultivars and breeding lines of carrot with established differences in sugar accumulation capacity were studied by growth analyses to identify associations with high and low sugar content. Carrots were grown on both organic and sandy loam soils. At both locations the seasonal pattern for sugar content of high sugar accumulating lines (HSL) and low sugar accumulating lines (LSL) was similar. There was little or no association of growth indicators (dry weight accumulation, tap root dry weight and leaf area index) with high or low sugar accumulation. Differences in sugar yields were associated with mean net assimilation rate ($\overline{\text{NAR}}$), mean relative growth rate ($\overline{\text{RGR}}$) and leaf area ratio (LAR) late in the growing season. HSL had increasing $\overline{\text{NAR}}$, $\overline{\text{RGR}}$ and LAR, whereas LSL had decreasing $\overline{\text{NAR}}$ and LAR and a stabilizing $\overline{\text{RGR}}$.

In general, carrot cultivars and breeding lines producing high free sugar concentrations were distinguished from low sugar accumulating carrots by delayed physiological maturity resulting in prolonged photosynthetic activity late in the growing season.

IN MEMORIAL TO
GWEN
WHOSE LOVE AND ENCOURAGEMENT TRANSCENDS HER DEATH

ACKNOWLEDGMENTS

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SECTION I

COMPARISON OF HPLC DETERMINED ROOT SUGARS
FROM PARENTAL LINES, HYBRIDS AND
COMMERCIAL CULTIVARS OF CARROT
(DAUCUS CAROTA L.) FOR
QUALITY IMPROVEMENT

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ABSTRACT

The concentration of the root sugars fructose, glucose and sucrose of carrot (Daucus carota) from different cultivars and breeding lines were determined using high pressure liquid chromatography. Over a three year study, three Michigan locations had no significant influence on sugar content, but years did differ. Genetic variation was apparent because cultivars and parental lines were consistently high or low for fructose/glucose with concomitant sucrose levels. There were no cultivars and only one parental line, 9541, that exhibited a significant difference for fructose and glucose content over all three years. However, one parental line, 6000, and one hybrid cultivar, 'Spartan Fancy,' exhibited a significant difference for high sucrose and high total sugars compared to the other entries over all three years. General combining ability estimates demonstrated that parent 9541 was a strong combiner for high fructose/glucose content and parents 872

and 6000 were good combiners for sucrose from the group of six parental lines. Based on total sugar content, parents 5986, 6000 and 9541 were good combiners in relation to the other lines. This and other reports suggest that the sugar content of carrot roots may be enhanced through appropriate breeding procedures.

Carrots (Daucus carota L.) are an important vegetable crop from the standpoints of crop value, food production and nutritional contribution to the human need for vitamin A (15). A 100 g portion of most commercial carrot cultivars supplies 200% of the recommended dietary allowance (RDA) of provitamin A (13, 28). Hence, an increase in the utilization of this vegetable in the human diet would be beneficial. One method for achieving increased consumption would be to improve carrot flavor. Carrot flavor is characterized by bitter, oily and sweet components in an otherwise relatively bland background (1, 12, 16, 24).

Sucrose, the major endogenous sugar, plays an important role in flavor and sweetness. Increased total sugar concentrations in the carrot results in more sweetness (6) and total sugars are negatively correlated with harsh flavor (23). The free sugars in carrot are fructose, glucose, sucrose and maltose (1, 16, 17, 18, 20). The standard sweetness rating for sucrose is 100, while fructose, glucose and maltose have relative values of 173, 74,

and 33 respectively (9, 11). The sugar content of carrot depends upon the stage of maturity (17, 18, 30), portion of the root (17, 18, 29), cultivar (6, 7, 13, 23, 29) and growing location (14). The ratio of nonreducing to reducing sugars decreases following harvest and subsequently in cold storage, but total sugar concentration remains unchanged (17, 18, 19, 29). If carrots could be selected for increased levels of sucrose and/or fructose sweeter tasting and more palatable carrot cultivars may be developed.

Previously reported methods of determining free sugars in carrot did not offer a quantitative, rapid and reproducible assay necessary to screen large numbers of individual roots in breeding and selection programs for high sugar content. Prior to the 1970s standard methods for carbohydrate analysis consisted of various coloration measuring techniques. Others were correlations between soluble solids and total sugars (19, 20, 21), relative specific gravities of individual roots in brine solution (5) and gas-liquid chromatography using volatile trimethylsilyl sugar derivatives (6). These methods suffered because they were either indirect, nonquantitative or too labor intensive. Recently developed analytical procedures using high pressure liquid chromatography (HPLC) are particularly useful because they permit rapid quantitative measurement

of soluble sugars in large numbers of carrot roots. HPLC, although very beneficial, may be too expensive for most breeding programs.

The purpose of this study was to utilize the HPLC to quantify fructose, glucose and sucrose in parental lines, hybrids and cultivars for culinary quality, and to determine if differential sugar accumulations are maintained when carrots are grown on organic soils in three different locations and years.

MATERIALS AND METHODS

All carrots (Table 1) were grown at three locations near Grant, Inlay City and Bath, MI. during 1976-1978 using standard cultural practices for organic soils (3). Carrots were planted in mid-May and harvested in mid-October for all three years. The hybrid cultivars and parental lines were recently described (4). Tops were removed at harvest. Roots were washed, surface-dried and stored at 4 C. Sample preparation was within 48 hr of harvest.

Root samples were prepared by slicing cross-sectionally to provide a 4 cm mid-section that was saved for sugar analysis. The 4 cm section was sliced into 2 mm discs; then three 50 g samples from each carrot line were selected randomly and frozen at -10 C. The samples were lyophilized in an automatic Virtis unit at a plate temperature of 60 C, a condensor temperature of -60 C and vacuum of less than 5.0 μ m. The lyophilized samples were weighed, ground through a no. 40 mesh screen in a Wiley mill, collected and capped in glass jars and stored under dry atmosphere at -10 C to prevent the loss of sugars at room temperature (6).

Sugars were determined by extracting 1 g of carrot powder with 50 ml of 80% ethanol (stirring 5 min at 98 C)

Table 1.--Carrot lines and cultivars, utilized to determine endogenous sugars of carrot roots grown in three consecutive years.

Parental Line No./Cultivar	Line No./ Pedigree	Source
<u>Parent</u>		<u>Original Cultivar</u>
872	MSU 872	Long Chantenay
1302	MSU 1302	Danvers
5931	MSU 5931	Long Chantenay
5986	MSU 5986	Waltham HiColor
6000	MSU 6000	Empress
9541	MSU 9541	Danvers
<u>Cultivars</u>		<u>Company</u>
Danvers	Open-pollinated	Crookham
Gold Pak	Open-pollinated	Crookham
Spartan Bonus	MSU (872 x 5931) 9541	Crookham
Spartan Delite	MSU (5931 x 6000) 5986	Crookham
Spartan Fancy	MSU (5931 x 5986) 6000	Crookham
Spartan Sweet	MSU 5931 x 6000	Crookham

filtering (no. 5 Whatman paper) and rewashing the residue with an additive 25 ml hot (98 C) 80% ethanol, followed by filtration. A 2 ml sample of combined filtrate was purified by passing through a C₁₈ Sep-Pak filter (Waters Associates) prior to injection into a Waters HPLC equipped with a Waters R-401 differential refractometer. Twenty µl of Sep-Pak filtrate were injected onto a Waters C₁₈ carbohydrate HPLC analysis column with a solvent of 80:20 acetonitrile:water (v/v) at a flow rate of 3.5 ml/min. Solutions containing 1 mg/ml fructose, glucose and sucrose were used as sugar standards to determine peak retention times. An internal standard of 1 mg/ml of xylose was injected with each sample. Peak area was measured by triangulation.

Estimates of general combining ability were on progeny from a diallel cross involving six parents. Six crosses (no reciprocals) were made to determine parental effects. The diallel was analyzed according to Griffing's (10) model 1 (fixed genetic material), method 4 which restricts inferences to the parental lines used in the experiment.

RESULTS AND DISCUSSION

Samples extracted from carrot roots cochromatographed with standards fructose, glucose and sucrose (3.0, 3.5 and 5.8 min retention times respectively).

The three locations had no significant effects on sugar accumulation. Therefore, locations were combined for within year statistical comparisons of cultivars and parental lines. Significant differences ($p = .05$) in fructose and glucose concentrations of the parental lines, hybrids and cultivars occurred in different years, both sugars exhibited two- to four-fold higher concentrations in 1977 than in 1976 or 1978 (Tables 2 and 3). The reasons for the large differences among years may be explained by 1977 having averaged 380 more growing degree days (base 40) than 1976 or 1978 (25, 26, 27). This increased number of growing degree days in 1977 would permit photosynthesis and resultant increased free sugar accumulation at harvest. Sucrose content was also generally high in 1977, but the magnitude was less than that for reducing sugars. Total sugar concentrations remained more constant for a given line over all three years than reducing sugar concentrations for both parental lines and cultivars. The more stable content of total sugars over years was expected because

Table 2.--Endogenous sugar content (mg/g root fresh weight)
of carrot parental lines grown over three years
on three Michigan locations on organic soil.

Parental Line No.	1976	1977	1978	1976	1977	1978
	Fructose			Glucose		
872	5.2b ^z	6.6b	8.0a	5.6b	7.3c	8.1a
5931	5.6b	6.2b	3.0c	5.8b	7.0c	3.6c
5986	4.5b	7.5b	5.0b	4.8b	9.7b	5.6b
6000	5.4b	7.1b	3.6b	5.1b	8.0b	3.5c
9541	7.4a	14.6a	8.7a	7.8a	14.6a	9.4a
mean	5.6	8.4	5.7	5.8	9.3	6.0
	Sucrose			Total Sugars		
872	39.0a	50.6a	53.1b	49.8ab	64.6b	69.3a
5931	36.5a	42.2b	23.7d	47.9abc	55.5c	30.3b
5986	36.1a	51.5a	42.3c	45.4c	68.8a	53.0c
6000	40.4a	54.1a	64.2a	50.8a	69.3a	71.3a
9541	31.6b	38.8b	45.3c	46.8bc	68.0ab	62.4b
mean	36.7	47.4	45.7	48.1	65.2	57.2

^zMeans separated within columns by Tukey's HSD test,
5% level.

Table 3.--Endogenous sugar content (mg/g root fresh weight)
of carrot cultivars grown over three years on
Michigan locations on organic soil.

Cultivar	1976	1977	1978	1976	1977	1978
	Fructose			Glucose		
Danvers	6.6a ²	11.1a	7.8a	6.8a	13.2a	6.6ab
Gold Pak	5.6ab	5.9d	5.9b	5.2b	5.6b	5.0c
S. Bonus	4.8bc	9.1b	7.4a	5.3b	9.8a	7.4a
S. Delite	4.7bc	10.4a	4.8bc	3.8c	11.2a	4.5d
S. Fancy	5.1ab	10.2a	4.5c	4.9bc	11.6a	5.9bc
S. Sweet	3.4c	7.7c	3.9c	3.9c	6.3b	5.7bcd
mean	5.9	9.1	5.7	5.0	9.6	5.8
	Sucrose			Total Sugars		
Danvers	23.4d	47.9b	37.9d	37.0d	72.2b	52.3c
Gold Pak	34.5c	48.0b	34.4d	45.4c	59.6c	45.4d
S. Bonus	41.6b	53.5ab	55.1bc	51.7b	72.4ab	69.9a
S. Delite	41.1b	53.3ab	60.2ab	49.6b	74.9ab	69.5a
S. Fancy	48.4a	59.3a	62.7a	58.5a	81.2a	73.1a
S. Sweet	44.7ab	53.2ab	53.4c	52.0b	67.3bc	63.0a
mean	38.9	52.5	50.6	49.0	71.3	62.2

²Means separated within columns by Tukey's HSD test,
5% level.

changes in fructose and glucose are accompanied by concomitant changes in sucrose, with resulting total sugar concentrations relatively unchanged (17, 18, 19, 29).

The parental lines over all years and pooled locations, demonstrated a greater variation in fructose, glucose, sucrose and total sugar content than the cultivars (Table 2 and 3). The high variability among parental lines, compared with variability of cultivars may be due to their unfavorable genotypic-environmental interaction (2) which would reduce the ability of the parental lines to withstand environmental stresses. Dobzhansky (8) related the reduced variability of hybrid genotypic-environmental interaction to the type of breeding system an organism exhibits. Outbreeding organisms, such as carrot, are influenced less physiologically in the heterozygous condition. Thus, hybrid carrots will exhibit greater heterozygosity than their comprising inbred parental lines. The decreased variability in sugar concentrations over years expressed by hybrids versus parental lines is supported by this concept. Parental lines exhibited various degrees of phenotypic stability by maintaining somewhat consistent rankings for sugar concentrations across all three years (Table 2). If one parental line was significantly high in either sucrose or fructose and glucose in one year, it was generally found to be high for the same sugar in other years. However, no parent maintained a year by year significant

difference from all other parental lines for both reducing and nonreducing sugars.

Parent 9541 was consistently high in fructose and glucose each year while 5931, 5986 and 6000 were consistently low and 872 was variable (Table 2). Parent 6000 was consistently high in sucrose each year and 9541 was consistently low, while 872, 5931 and 5986 were variable. Parent 6000 was also consistently high for total sugar accumulation, whereas 872 and 9541 were variable for high total sugars. Parental lines 5931 and 5986 demonstrated relatively low total sugar accumulation. Ranking the parents over years for fructose and glucose content showed 9541 to be significantly greater than all the other lines except 872 in 1978. The ranking of the parents for sucrose concentration showed 6000 to be greater than 5931 (except in 1976) and 9541. In 1978, 6000 was significantly more concentrated in sucrose than any other parental line. The ranking for total sugar accumulation demonstrated 6000 to contain the most sugar, although not always significant from other lines, while 5931 and 5986 varied across years and 872 and 9541 were intermediate.

General combining ability (GCA) in hybrid performance for sugar accumulation by 872, 1302, 5931, 5986, 6000 and 9541 over three years yielded rankings similar to the parental line study (Table 4). Parent 9541 demonstrated high GCA for fructose and glucose while 872 and 5931 were generally low. Parents 6000 and 872 were always high

Table 4.--Estimates of general combining ability effects for hybrid performance of endogenous sugars by six MSU parental lines grown in 1976, 1977 and 1978 on Michigan organic soil.

Parental Line No.	1976	1977	1978	1976	1977	1978
	Fructose			Glucose		
872	-0.26	-0.41	-0.31	-0.27	-0.26	-0.31
1302	0.02	0.04	0.02	-0.22	-0.21	-0.26
5931	-1.16	-1.86	-1.26	0.01	-2.18	-1.41
5986	0.47	0.74	0.53	0.66	1.12	0.72
6000	-0.11	-0.18	-0.11	-0.04	-0.33	-0.06
9541	1.04	1.67	1.15	1.16	1.87	1.32
	Sucrose			Total Sugars		
872	1.20	1.55	1.42	0.66	-0.73	0.81
1302	-2.70	-3.50	-3.22	-2.94	-2.96	-3.47
5931	0.15	0.20	0.15	-2.67	-3.01	-2.52
5986	0.10	0.12	0.10	1.21	2.77	1.33
6000	1.77	2.30	2.17	1.61	3.49	2.05
9541	-0.50	-0.62	-0.62	1.71	1.39	1.83

general combiners for sucrose while 1302 and 9541 were poor. Parental lines 5986, 6000 and 9541 were relatively high general combiners for total sugars while 1302 and 5931 were poor.

Cultivar performance for sugar content generally followed a repeatable trend over all three years (Table 3). Significant differences for fructose and glucose accumulation were noticed between 'Danvers,' (high) and 'Spartan Sweet' (low) for each of the three years. The cultivar with high sucrose and total sugar content was 'Spartan Fancy' which was within the group for high sugar content all three years had high sucrose and total sugar content. An arithmetic ranking of cultivars for total sugar accumulation within each of the three years showed 'Spartan Fancy' to be greater than 'Spartan Delite,' 'Spartan Bonus' and 'Spartan Sweet' and always to be significantly greater than the standard open-pollinated cultivars 'Gold Pak' and 'Danvers.' The high levels of sucrose and total sugar for 'Spartan Fancy' relative to the other hybrids, including 'Spartan Delite' which has the same parental lines but in different order, is probably due to the strong GCA of breeding line 6000 for high sucrose and total sugars. Thus the use of 6000 as a pollen parent with strong GCA performance for sucrose and total sugars would predictably produce hybrids of a similar sugar content.

Implications on culinary quality. A negative correlation exists between reducing sugars and fiber content (7)

and between total sugars and harsh flavor (22). Parental lines 9541 and 6000 were significantly high accumulators of and exhibited strong GCA for reducing and total sugars respectively, all three years. Thus, parental lines 9541 and 6000 should produce hybrids of a similar sugar content and possibly result in high reducing sugar/low fiber or high total sugars/reduced harsh flavored carrots. It is important to emphasize that the stability that was exhibited by 6000 and 9541 for nonreducing and reducing sugars respectively does not imply a general consistency of the phenotype in varying environments. It only implies stability in one aspect of phenotype, specifically sugar. This phenotypic stability may depend on holding some aspect of morphology or physiology in a steady state while others vary. Thus, the breeder should not neglect root color, shape or type.

SUMMARY

Significant differences did exist among carrot parental lines and cultivars for fructose, glucose and sucrose concentrations. These differences among parental lines and cultivars were exhibited over three consecutive years. Specific parental lines and cultivars exhibited significantly higher concentrations of either reducing or nonreducing sugars than other lines and cultivars in a given year. However, no single parental line or cultivar exhibited a significantly higher concentration for all sugars. Therefore, it appears that selecting for high concentrations of both reducing and nonreducing sugars in a single line is not possible within this genetic material. However, heritability studies for sugar accumulation and subsequent breeding for reducing or nonreducing sugar content should be feasible.

The HPLC has proven extremely useful in detecting quantitative differences of fructose, glucose and sucrose in carrot parental lines, hybrids and cultivars. Continued utilization of HPLC should aid breeders in genetically improving carrot sugar content. Such improvements in sugar content should contribute to enhanced carrot flavor

and culinary quality, all of which will possibly promote increased carrot consumption.

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LITERATURE CITED

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APPENDIX

APPENDIX

Table A1.--Summary of raw data of fructose (mg/g root fresh weight) for growing location, carrot parental line, year and replication.

Location	Parental Line	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	872	5.5	5.7	-	-	7.9	8.5
	5931	5.3	5.3	-	-	3.4	3.4
	5986	5.4	5.4	-	-	5.1	5.3
	6000	4.6	5.0	-	-	4.0	4.0
	9541	7.6	8.0	-	-	8.3	8.9
Imlay City	872	5.1	5.1	7.7	7.7	-	-
	5931	4.4	4.4	6.1	6.5	-	-
	5986	4.1	4.3	7.9	8.1	-	-
	6000	6.5	6.5	6.7	6.7	-	-
	9541	7.1	7.1	12.2	12.4	-	-
Grant	872	4.7	5.1	5.4	5.8	7.8	8.0
	5931	6.7	7.3	6.2	6.2	2.6	2.6
	5986	3.7	4.3	6.9	7.1	4.8	4.8
	6000	4.5	5.1	7.5	7.7	3.1	3.3
	9541	7.2	7.2	17.2	16.8	8.9	8.9

Table A2.--Summary of raw data of glucose (mg/g root fresh weight) for growing location, carrot parental line, year and replication.

Location	Parental Line	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	872	5.5	5.9	-	-	8.6	8.9
	5931	5.9	6.3	-	-	4.1	4.5
	5986	5.8	5.8	-	-	4.8	5.6
	6000	3.8	3.2	-	-	3.8	4.4
	9541	7.2	7.2	-	-	8.8	8.6
Imlay City	872	5.8	6.2	7.5	8.2	-	-
	5931	4.1	4.5	6.7	7.1	-	-
	5986	4.4	4.4	8.0	8.0	-	-
	6000	6.4	6.8	8.4	8.8	-	-
	9541	7.0	7.4	12.9	13.3	-	-
Grant	872	4.8	5.2	6.6	6.8	7.4	7.8
	5931	7.1	7.1	7.2	7.2	2.7	3.1
	5986	4.1	4.1	9.7	9.9	6.0	6.2
	6000	4.8	4.4	7.3	7.5	3.0	3.0
	9541	8.9	9.3	16.6	15.6	9.7	9.5

Table A3.--Summary of raw data of sucrose (mg/g root fresh weight) for growing location, carrot parental line, year and replication.

Location	Parental Line	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	872	35.0	37.0	-	-	53.1	51.3
	5931	38.6	42.6	-	-	24.6	26.8
	5986	34.3	34.3	-	-	43.3	43.3
	6000	37.8	43.0	-	-	66.2	60.2
	9541	33.0	33.0	-	-	47.8	41.2
Imlay City	872	40.4	40.4	51.0	51.0	-	-
	5931	29.0	33.4	42.9	40.7	-	-
	5986	35.3	41.9	49.9	49.9	-	-
	6000	37.6	43.6	49.7	52.7	-	-
	9541	30.4	30.4	42.7	42.7	-	-
Grant	872	38.3	42.7	48.1	52.5	54.0	54.2
	5931	36.7	38.7	41.6	43.8	20.5	22.9
	5986	34.2	36.4	53.2	53.2	41.2	41.6
	6000	40.6	40.6	56.0	58.0	62.0	68.2
	9541	29.2	33.6	31.6	38.2	45.0	47.2

Table A4.--Summary of raw data of total sugar (mg/g fresh weight) for growing location, carrot parental line, year and replication.

Location	Parental Line	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	872	46.0	48.6	-	-	67.6	70.7
	5931	49.8	54.6	-	-	32.4	34.7
	5986	45.5	45.5	-	-	53.2	54.2
	6000	45.4	51.2	-	-	68.0	74.6
	9541	47.8	48.2	-	-	58.3	67.3
Imlay City	872	51.3	51.7	66.2	67.0	-	-
	5931	37.5	42.3	53.5	56.8	-	-
	5986	43.8	50.6	65.8	66.0	-	-
	6000	50.5	56.9	64.8	68.2	-	-
	9541	44.5	44.9	67.9	68.4	-	-
Grant	872	47.8	53.0	60.1	65.1	69.2	70.1
	5931	50.5	53.1	55.0	57.2	25.8	28.6
	5986	42.0	44.8	69.8	70.2	52.0	52.6
	6000	49.5	50.5	70.8	73.2	68.1	74.5
	9541	45.3	50.1	64.4	71.6	63.0	65.8

Table A5.--Summary of analysis of variance of fructose raw data for carrots by replications, years, parental lines and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	.680	.264	.609
Year	2	52.362	20.339	.001
Parental Line	4	54.767	21.273	.001
Location	2	1.096	.426	.655
Error	60	2.574		

Table A6.--Summary of analysis of variance of glucose raw data for carrots by replications, years, parental lines and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	1.605	.712	.402
Year	2	67.010	29.707	.001
Parental Line	4	54.435	24.132	.001
Location	2	.541	.240	.788
Error	60	2.256		

Table A7.--Summary of analysis of variance of sucrose raw data for carrots by replications, years, parental lines and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	120.127	2.960	.090
Year	2	827.316	20.389	.001
Parental Line	4	617.793	15.225	.001
Location	2	1.603	.040	.961
Error	60	40.577		

Table A8.--Summary of analysis of variance of total sugar raw data for carrots by replications, years, parental lines and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	170.352	3.224	.078
Year	2	1697.417	32.120	.001
Parental Line	4	604.570	11.440	.001
Location	2	8.612	.163	.850
Error	60	52.847		

Table A9.--Summary of raw data of fructose (mg/g root fresh weight) for growing location, carrot cultivar, year and replication.

Location	Cultivar	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	Danvers	5.5	5.7	-	-	7.4	7.4
	Gold Pak	4.8	4.8	-	-	5.0	5.6
	S. Bonus	5.5	5.5	-	-	7.7	7.7
	S. Delite	3.8	4.2	-	-	4.7	4.9
	S. Fancy	3.9	4.5	-	-	3.8	3.8
	S. Sweet	4.2	4.2	-	-	4.5	3.9
Imlay City	Danvers	6.7	6.3	10.8	11.0	7.2	7.0
	Gold Pak	5.7	5.5	5.9	6.3	7.1	7.1
	S. Bonus	4.3	4.1	9.1	9.3	7.4	8.0
	S. Delite	6.0	6.0	9.9	9.5	4.4	5.0
	S. Fancy	5.6	5.8	10.3	10.3	4.9	4.9
	S. Sweet	3.3	3.7	7.8	8.0	3.2	3.0
Grant	Danvers	7.7	7.7	11.2	11.4	8.7	8.9
	Gold Pak	6.6	6.6	5.7	5.7	5.5	5.1
	S. Bonus	4.5	4.7	9.0	9.0	6.7	6.7
	S. Delite	4.4	3.8	11.3	10.9	4.8	4.8
	S. Fancy	5.3	5.7	9.5	10.1	4.4	5.0
	S. Sweet	2.9	2.3	7.8	7.2	4.4	4.2

Table A10.--Summary of raw data of glucose (mg/g root fresh weight) for growing location, carrot cultivar, year and replication.

Location	Cultivar	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	Danvers	6.2	6.4	-	-	5.6	5.6
	Gold Pak	4.9	4.9	-	-	5.4	5.0
	S. Bonus	6.1	6.1	-	-	7.8	8.4
	S. Delite	4.3	4.1	-	-	4.4	3.8
	S. Fancy	4.3	4.5	-	-	5.2	5.8
	S. Sweet	4.2	4.2	-	-	5.7	6.1
Imlay City	Danvers	5.8	6.4	11.3	11.3	7.4	8.0
	Gold Pak	4.9	5.1	5.9	6.1	5.6	5.8
	S. Bonus	4.3	4.7	8.8	9.0	6.3	6.3
	S. Delite	4.1	4.1	10.1	10.7	4.5	4.5
	S. Fancy	5.3	5.3	11.8	12.2	6.4	6.4
	S. Sweet	3.6	3.8	6.1	6.3	5.4	5.6
Grant	Danvers	7.9	7.9	15.1	15.1	6.2	6.6
	Gold Pak	5.4	6.0	5.2	5.4	4.2	4.2
	S. Bonus	5.7	5.1	10.5	10.9	7.7	7.9
	S. Delite	3.0	3.2	12.0	12.0	4.9	4.9
	S. Fancy	5.1	5.1	11.0	11.6	5.8	5.8
	S. Sweet	3.4	4.0	6.4	6.6	5.6	6.0

Table All.--Summary of raw data of sucrose (mg/g root fresh weight) for growing location, carrot cultivar, year and replication.

Location	Cultivar	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	Danvers	18.0	20.0	-	-	26.0	38.0
	Gold Pak	38.0	42.0	-	-	36.1	38.3
	S. Bonus	38.3	43.3	-	-	53.1	57.5
	S. Delite	36.8	36.8	-	-	60.6	60.6
	S. Fancy	47.9	47.9	-	-	63.4	63.4
	S. Sweet	43.9	45.9	-	-	46.9	52.9
Imlay City	Danvers	26.6	26.6	48.3	48.3	38.0	40.0
	Gold Pak	29.0	33.6	48.3	50.5	26.8	28.8
	S. Bonus	41.8	41.8	49.4	49.4	55.9	57.9
	S. Delite	40.4	40.4	51.2	52.2	59.7	61.9
	S. Fancy	48.5	48.5	56.4	60.8	59.8	63.8
	S. Sweet	39.7	41.9	51.4	51.4	56.7	62.7
Grant	Danvers	20.5	24.9	46.6	48.6	35.8	38.8
	Gold Pak	29.0	35.6	43.7	49.7	38.3	38.3
	S. Bonus	38.5	44.0	57.7	57.7	50.2	56.2
	S. Delite	43.1	49.1	54.5	56.7	59.3	59.3
	S. Fancy	48.8	48.8	57.2	63.2	62.9	62.9
	S. Sweet	46.3	50.7	52.1	57.1	47.5	53.5

Table A12.--Summary of raw data of total sugar (mg/g root fresh weight) for growing location, carrot cultivar, year and replication.

Location	Cultivar	1976		1977		1978	
		Rep 1	Rep 2	Rep 1	Rep 2	Rep 1	Rep 2
Bath	Danvers	29.7	36.1	-	-	49.0	51.0
	Gold Pak	47.7	51.7	-	-	46.0	49.3
	S. Bonus	49.9	54.9	-	-	68.6	73.6
	S. Delite	44.7	45.3	-	-	69.6	69.6
	S. Fancy	56.1	56.6	-	-	72.4	73.0
	S. Sweet	52.8	54.3	-	-	56.5	63.5
Imlay City	Danvers	38.7	39.7	70.4	70.6	52.4	55.2
	Gold Pak	39.4	44.4	60.1	62.9	39.5	41.7
	S. Bonus	50.2	50.8	67.3	67.7	69.6	72.2
	S. Delite	50.5	50.5	70.8	72.8	68.6	71.4
	S. Fancy	59.4	59.6	76.0	83.3	71.1	75.1
	S. Sweet	56.6	49.4	65.3	65.7	65.1	71.5
Grant	Danvers	36.1	40.5	72.9	75.1	50.7	54.3
	Gold Pak	41.0	48.2	54.6	60.8	47.6	48.0
	S. Bonus	48.1	54.4	77.7	77.6	64.6	70.8
	S. Delite	49.9	56.7	77.4	80.0	69.0	69.0
	S. Fancy	59.2	59.6	77.7	84.9	73.1	73.7
	S. Sweet	52.0	57.6	65.7	71.5	57.3	63.9

Table A13.--Summary of analysis of variance of fructose raw data for carrots by replications, years, cultivars and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	1.378	1.034	.312
Year	2	104.336	78.280	.001
Cultivar	5	21.183	15.893	.001
Location	2	.957	.718	.491
Error	85	1.333		

Table A14.--Summary of analysis of variance of glucose raw data for carrots by replications, years, cultivars and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	1.170	.585	.446
Year	2	146.141	73.084	.001
Cultivar	5	24.162	12.083	.001
Location	2	1.666	.833	.438
Error	85	2.000		

Table A15.--Summary of analysis of variance of sucrose raw data for carrots by replications, years, cultivars and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	84.402	3.617	.180
Year	2	9079.981	389.109	.001
Cultivar	5	1132.651	48.538	.001
Location	2	11.071	.474	.624
Error	85	23.335		

Table A16.--Summary of analysis of variance of total sugar raw data for carrots by replications, years, cultivars and growing locations.

Source	d.f.	M.S.	F	P
Rep.	1	23.250	.945	.339
Year	2	10136.556	412.215	.001
Cultivar	5	999.750	40.656	.001
Location	2	24.206	.984	.378
Error	85	24.590		

SECTION 2

PHYSIOLOGICAL BASIS FOR DIFFERENTIAL SUGAR
ACCUMULATION IN CARROT (DAUCUS CAROTA L.)

PHYSIOLOGICAL BASIS FOR DIFFERENTIAL SUGAR
ACCUMULATION IN CARROT (DAUCUS CAROTA L.)

ABSTRACT

Cultivars and breeding lines of carrot (Daucus carota L.) with established differences in sugar accumulation capacity were studied by growth analyses to identify associations with high and low sugar content. Carrots were grown on both organic and sandy loam soils. At both locations the seasonal pattern for sugar content of high sugar accumulating lines (HSL) and low sugar accumulating lines (LSL) was similar. There was little or no association of growth indicators (dry weight accumulation, tap root dry weight and leaf area index) with high or low sugar accumulation. Differences in sugar yields were associated with mean net assimilation rate ($\overline{\text{NAR}}$), mean relative growth rate ($\overline{\text{RGR}}$) and leaf area ratio (LAR) late in the growing season. HSL had increasing $\overline{\text{NAR}}$, $\overline{\text{RGR}}$ and LAR, whereas LSL had decreasing $\overline{\text{NAR}}$ and LAR and a stabilizing $\overline{\text{RGR}}$.

In general, carrot cultivars and breeding lines producing high free sugar concentrations were distinguished from low sugar accumulating carrots by delayed physiological maturity resulting in prolonged photosynthetic activity late in the growing season.

The utilization of growth analysis with time has been a valuable aid in identifying the mechanisms contributing to diversity among genetically divergent lines and to exploit further the existing diversity (5). In common bean (Phaseolus vulgaris L.), mean leaf area was defined as an important component influencing economic yield differences among cultivars (16). Comparisons of common bean reduced-leaf mutants with nonmutants for total plant yield could be determined by leaf area index (cm^2 leaf surface area/ cm^2 land area covered) and leaf area duration [$(\text{cm}^2 \text{ leaf surface area}/\text{cm}^2 \text{ land area covered}) (\text{number of days of leaf duration})$] (7). Harvest index (seed weight/total plant dry weight) in common bean (17), and certain cultivars of dwarf wheat (13) have been positively correlated with biological yield and has aided in genetic improvement of these crops. However, in mungbean (Phaseolus aureus Roxb.) growth analysis revealed no direct associations with yield expression, but seemed to be a valuable supplementary criterion for detecting genetic diversity among parental lines in a breeding program (4). In cotton (Gossypium hirsutum L.), measuring for differences in net assimilation rate (increase in plant material per unit of assimilatory material per unit of time) and leaf area index aided in the selection of higher yielding cultivars (8). Improvement in kale (Brassica oleracea var. acephala) yields in existing cropping systems was brought about

mainly by selecting for high leaf area index (18). In sugar beet, cultivars with high root/shoot ratios maintained higher net assimilation rates during the later stages of plant growth and produced greater sugar yields than cultivars with a low ratio (6). Also in sugarbeet, selecting for large tap root to leaf weight ratio (TLWR) in the seedling stage resulted in increased sugar yields at harvest (14).

In carrot, breeding for high total sugar yield has been recommended (2, 3, 11, 12) as a valuable aid in genetically improving the culinary quality of this crop. The objective of this study is to identify what growth analysis factors may be influencing differential sugar accumulation, so that carrot breeding programs may consider the physiological mechanisms contributing to the diversity in sugar yield.

MATERIALS AND METHODS

Investigations of 24 carrot cultivars and breeding lines revealed three-fold differences in total water soluble sugars (Table 1). These differences were of a magnitude to call the genetic material used in this study diverse. From these, two high sugar lines (HSL) and two low sugar lines (LSL) were selected for detailed study. The high sugar selections were 'Farba,' a cultivar from the Netherlands and MSU-6000, a breeding line from Michigan State University (MSU). The low sugar selections were 'Gosinoostrovakaja 13' (Gosin), a cultivar from the U.S.S.R., and MSU-5986, a breeding line from MSU.

All four selections were planted May 16, 1979 in a randomized complete block design utilizing three replications with split plots for ten harvest dates. Plantings were in East Lansing, Michigan on a sandy loam soil and on organic soil near Imlay City, Michigan. Carrot seedlings were thinned to stand 2.5 cm between plants, rows 45 cm apart. Plots were fertilized with a preplant application of 400 kg/ha 19-19-19 ($\text{N-P}_2\text{O}_5\text{-K}_2\text{O}$). The plots on sandy loam were watered by sprinkler irrigation and hand-cultivated as needed and on the muck by using standard cultural practices for organic soil (1).

Table 1.--Total root sugars from foreign and domestic cultivars and MSU breeding lines of carrots grown near Bath, MI., 1978, on organic soil.

Name	Origin	Total Sugars (mg/g fresh weight)
Farba	Netherland	96.7a ^z
MSU-6000	USA	88.9a
Flamm	Netherland	87.3a
44C	Netherland	86.9a
Vitaminaya 6	USSR	85.8a
Kuronan	Brazil	85.1a
Kinko Chantenay 6	Japan	84.4a
Nacional	Brazil	69.2 b
King Emperor	USA	68.9 b
Imperial Long Scarlet	Japan	68.9 b
Kuroda ESALQ	Brazil	67.0 b
Shin Kuroda	Japan	65.3 bc
MSU-9541	USA	64.7 bcd
Imperial Long Scarlet	Japan	60.7 bcde
MSU-1410	USA	60.5 bcde
Criolla	Argentina	59.2 bcdef
MSU-1385	USA	58.8 bcdef
Kokubu	Japan	57.2 bcdef
Birinoekutskaja 415	USSR	55.4 bcdef
Waltham HiColor	USA	51.2 cdefg
MSU-5986	USA	50.1 defg
San Nai	Japan	49.5 efg
Mirzoi Krasanaja	USSR	45.2 fg
Gosinoostrovakaja 13	USSR	39.8 g

^zMean separation by Tukey's HSD test, 5% level.

Five representative plants from each line were selected at random from each replication at every harvest for growth analysis. Whole plants were sealed in plastic bags and placed on ice in a styrofoam chest for transport to the laboratory for same day analysis. The roots were washed free of soil and the plants were separated into leaf blades, petioles with hypocotyl attached and tap root; and weighed immediately. Fibrous roots were not harvested. Leaf areas were measured, after weighing using a Ll-3100 area meter.¹ Leaf blades and petioles with hypocotyl were placed in separate paper bags and dried for five days in a forced draft oven at 80 C for dry weight determinations. Roots were sliced longitudinally then radially in the center, then frozen at -10 C. For sample preparation, all root samples were lyophilized in an automatic Virtis unit at a plate temperature of 60 C, a condensor temperature of -60 C and vacuum of less than 5.0 μ m. The lyophilized samples were weighed, ground through a #40 mesh screen in a Wiley mill and collected in capped glass jars. Jars with carrot powder were stored in dry atmospheric conditions at -10 C.

Sugars were determined by extracting one g carrot powder with 50 ml of 80% Ethanol (stirring 5 min at 98 C) filtering (#5 Whatman paper) and rewashing the residue with additive 25 ml hot (98 C) of 80% Ethanol, followed by filtration. A 2 ml sample of combined filtrate was purified

¹Ll-COR, Inc., Lincoln, NE.

by passing through a C₁₈ Sep-Pak filter (Waters Assoc.) prior to injection into a Waters high pressure liquid chromatograph (HPLC) equipped with a Waters R-401 differential refractometer. Twenty µl of Sep-Pak filtrate were injected onto a Waters C₁₈ carbohydrate analysis HPLC column with a solvent of 80:20 acetonitrile:water (v/v) at a flow rate of 3.5 ml/min. Solutions containing one mg/ml fructose, glucose and sucrose were used as standards for peak retention time associations. An internal standard containing one mg/ml xylose was injected with each sample. Peak area was measured by the technique of triangulation.

Growth analysis formulae were:

1. Increase in total plant dry weight = (g total plant dry weight₂ - g total plant dry weight₁ / sample time₂ - sample time₁) (subscript numerals (1 and 2) in growth analysis formulae indicate sampling at a given point in time = 1, followed by a sampling two weeks later = 2) ,
2. root/shoot ratio (R/S) = dry weight root / dry weight shoot ,
3. leaf area index (LAI) = (cm² leaf surface / cm² of land area) ,
4. leaf area ratio (LAR) = (cm² leaf surface area / g total plant dry weight) ,

5. mean relative growth rate ($\overline{\text{RGR}}$) = $(\log_e \text{total plant dry weight}_2 - \log_e \text{total plant dry weight}_1 / \text{sample time}_2 - \text{sample time}_1)$,
6. mean net assimilation rate ($\overline{\text{NAR}}$) = $[(\text{total plant dry weight}_2 - \text{total plant dry weight}_1 / \text{cm}^2 \text{ leaf surface}_2 - \text{cm}^2 \text{ leaf surface}_1) (\log_e \text{cm}^2 \text{ leaf surface}_2 - \log_e \text{cm}^2 \text{ leaf surface}_1 / \text{sampling time}_2 - \text{sampling time}_1)]$ (10).

RESULTS AND DISCUSSION

Sugars extracted from carrot root cochromatographed with standards (3.0, 3.5 and 5.8 min retention times respectively).

The final harvest at the Imlay City location was terminated earlier than at the sandy loam location in East Lansing because of frost damage.

The seasonal pattern for sugar content of all cultivars and breeding lines was similar for both locations. Fructose and glucose concentrations were relatively high in both HSL and LSL during the early part of the growing season, but there was a general decline in fructose and glucose and a corresponding increase in sucrose as the season progressed. 'Farba' was the only carrot that had a significant difference in fructose and glucose accumulation over the growing season (Tables 2 and 3). There were few significant differences in sucrose and total sugars among the lines early in the growing season (Tables 4 and 5). Later in the season (September 19 at East Lansing and September 26 at Imlay City), the HSL ('Farba' and 6000) accumulated significantly higher concentrations of sucrose and total sugars than LSL ('Gosin' and 5986).

Table 2.--Fructose concentrations (mg/g fresh weight) of high and low sugar accumulating carrot cultivars and breeding lines on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	9.4a ^z	7.4a	10.6a	12.3a	8.1a	7.4a	7.0a	6.8a	8.3a	5.4a
6000 (HSL)	6.9bc	4.4b	8.1b	6.7b	4.8b	3.8b	2.8b	2.6b	5.1ab	5.8a
Gosin (ISL)	8.3ab	6.6a	11.1a	8.5ab	6.1b	5.1b	4.1ab	4.5ab	3.4b	3.1b
5986 (ISL)	5.8c	4.8b	8.4b	8.4ab	4.9b	3.8b	6.9a	2.2b	2.7b	1.3b

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IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	9.5a	15.3a	11.6a	11.5a	10.8a	5.2a	5.9a	-
6000 (HSL)	-	-	6.9ab	9.4b	8.2b	3.3b	5.0b	2.1b	3.7ab	-
Gosin (ISL)	-	-	8.3a	10.2a	6.8b	7.9b	6.5b	3.9a	3.1b	-
5986 (ISL)	-	-	4.6b	8.1b	9.0ab	5.3b	7.1b	2.5b	2.0b	-

^zMean separation within columns by Tukey's HSD test, 5% level.

Table 3.--Glucose concentrations (mg/g fresh weight) of high and low sugar accumulating carrot cultivars and breeding lines on sandy loam soil at East Lansing, MI. and organic soil at Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	14.2a ^z	13.9a	11.9a	15.9a	8.9a	9.4a	10.0a	7.3a	7.1a	6.6a
6000 (HSL)	8.2b	7.6b	8.3b	6.8b	5.1b	4.3b	3.5b	3.8b	5.5ab	5.6a
Gosin (LSL)	12.1ab	11.5ab	14.3a	11.7a	6.5b	6.2ab	6.0ab	6.1ab	3.0b	3.1b
5986 (LSL)	13.3a	12.3ab	12.3ab	11.6a	6.1b	5.1b	4.3b	2.1b	4.2b	2.1b

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IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	12.2a	19.1a	14.0a	16.2a	12.1a	8.2a	8.0a	-
6000 (HSL)	-	-	6.1b	13.6ab	9.1b	4.6c	7.2c	3.0b	4.4b	-
Gosin (LSL)	-	-	9.1b	11.7b	8.6b	9.1b	8.1bc	4.4ab	4.6ab	-
5986 (LSL)	-	-	8.8ab	12.1ab	9.9ab	6.6bc	9.9ab	3.5b	2.9b	-

^zMean separation within columns by Tukey's HSD test, 5% level.

Table 4.--Sucrose concentrations (mg/g fresh weight) of high and low sugar accumulating carrot cultivars and breeding lines on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING										
Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	4.3b ^z	5.3b	11.3b	15.6a	20.3a	25.0b	29.5a	34.1a	43.6a	41.4a
6000 (HSL)	3.6c	4.6c	13.9a	28.2a	23.5ab	25.8b	28.3a	46.3a	48.8a	36.8a
Gosin (ISL)	5.2a	5.4b	14.3a	21.9b	24.1a	30.1a	36.1a	31.6b	23.7b	19.6b
5986 (ISL)	5.0a	6.0a	12.1b	21.3b	25.2a	27.1ab	28.6a	32.8b	29.1b	30.2a

IMLAY CITY										
Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	7.2a	9.8b	15.1b	17.9b	24.2b	31.5a	34.9a	-
6000 (HSL)	-	-	7.4a	12.9ab	24.7a	30.2a	32.4a	33.2a	38.3a	-
Gosin (ISL)	-	-	6.2b	15.9a	14.7b	25.0ab	22.3b	28.9b	27.7b	-
5986 (ISL)	-	-	5.5c	11.7ab	16.5b	16.3b	30.9a		26.0b	-

^zMean separation within columns by Tukey's HSD test, 5% level.

Table 5.--Total sugar concentrations (mg/g fresh weight) of high and low sugar accumulating carrot cultivars and breeding lines on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	27.9a ^z	26.6a	33.7b	43.8a	37.4a	41.8a	46.5a	48.2a	58.9a	53.5a
6000 OHSL)	18.7b	16.6b	30.4b	41.7b	33.1b	33.9b	34.7b	52.6a	59.4a	48.2a
Gosin (ISL)	25.7a	23.5a	39.8a	41.9b	36.6a	41.4a	46.2a	42.2b	30.1b	25.8b
5986 (ISL)	24.0a	23.1a	32.5b	41.3b	36.2a	36.0ab	39.8b	37.1b	36.0b	33.7b

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IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	28.9a	44.2a	40.7a	45.6a	47.1a	45.0a	48.9a	-
6000 (HSL)	-	-	20.4ab	35.9b	41.9a	38.1b	42.6b	38.3ab	46.4a	-
Gosin (ISL)	-	-	23.7a	37.9ab	30.1b	42.8ab	37.0b	36.6b	35.4b	-
5986 (ISL)	-	-	18.9b	31.9b	35.4b	28.3c	47.9a	34.9b	30.9c	-

^zMean separation within columns by Tukey's HSD test, 5% level.

At the end of the growing season, total sugar accumulation tended to decrease in all four lines; however, the decrease in total sugars was approximately one month earlier for the LSL than for the HSL (Figures 1 and 2). A change in the increase in total plant dry weight coincided with the decrease in total sugars for both HSL and LSL (Figures 1 and 2). The increase in total plant dry weight was more pronounced at the East Lansing location than at Imlay City. Possibly the growing season at Imlay City was insufficient to permit an increase in total plant dry weight and a decline in total sugars for the HSL.

Significant differences in dry weight accumulation were not exhibited between HSL and LSL during the growing season (Table 6). Also there were no significant regression coefficients for total plant dry weight regressed with total sugars for either HSL or LSL (Table 7). Thus, there was little or no association over the growing season of dry weight accumulation with sugar accumulation. However, during most of the growing season the cultivars were significantly higher for dry weight accumulation than were the breeding lines.

There were no consistent significant differences between HSL and LSL for root dry weight (Table 8), or any significant regression coefficients for root dry weight regressed with total sugars. This indicated that root dry weight had little association with sugar accumulation over

Figure 1.--Total endogenous sugars and the increase in total plant dry weight per harvest time of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. during the 1979 growing season.

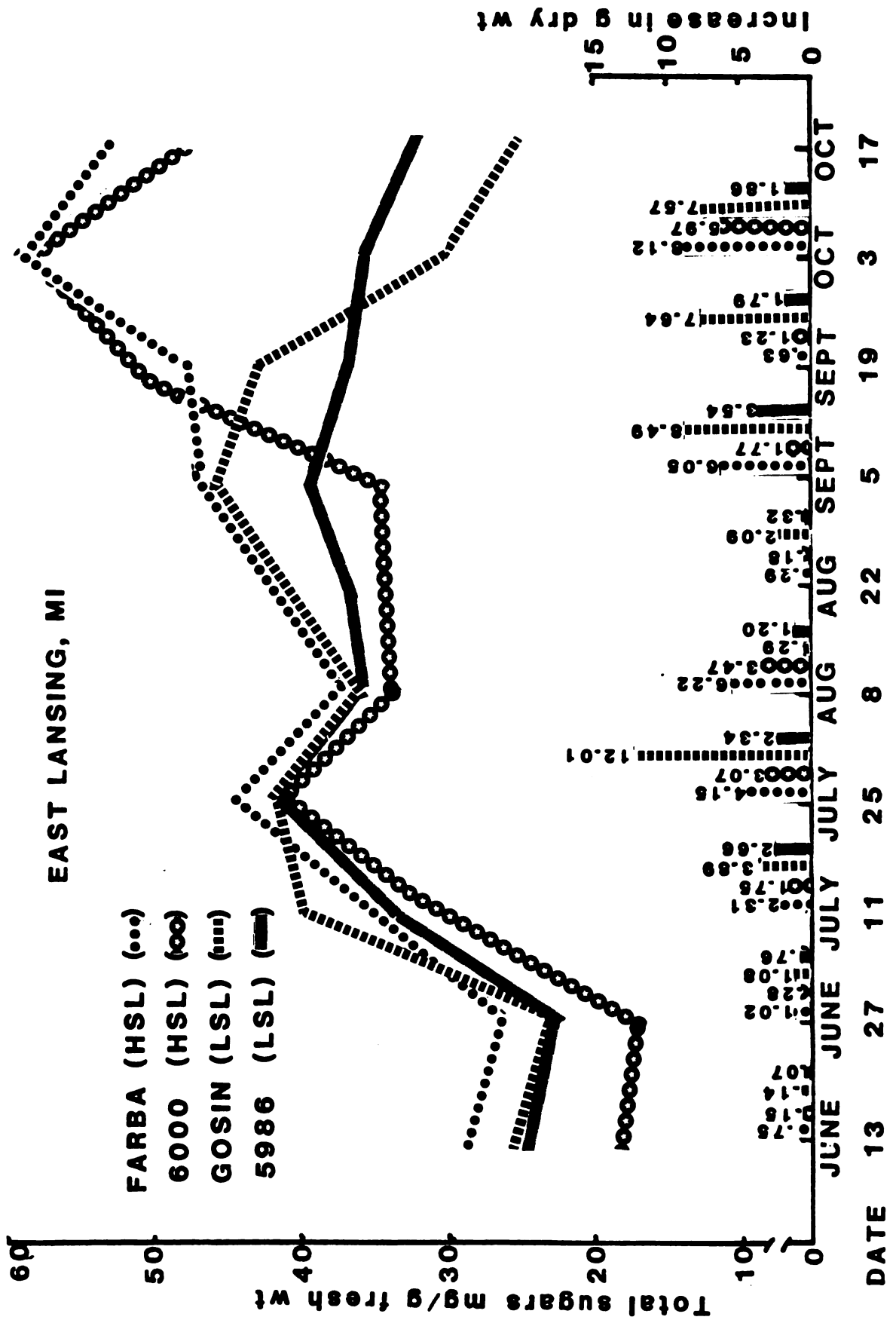


Figure 2.--Total endogenous sugars and the increase in total plant dry weight per harvest time of high and low sugar accumulating carrot cultivars and breeding lines grown on organic soil near Imlay City, MI. during the 1979 growing season.

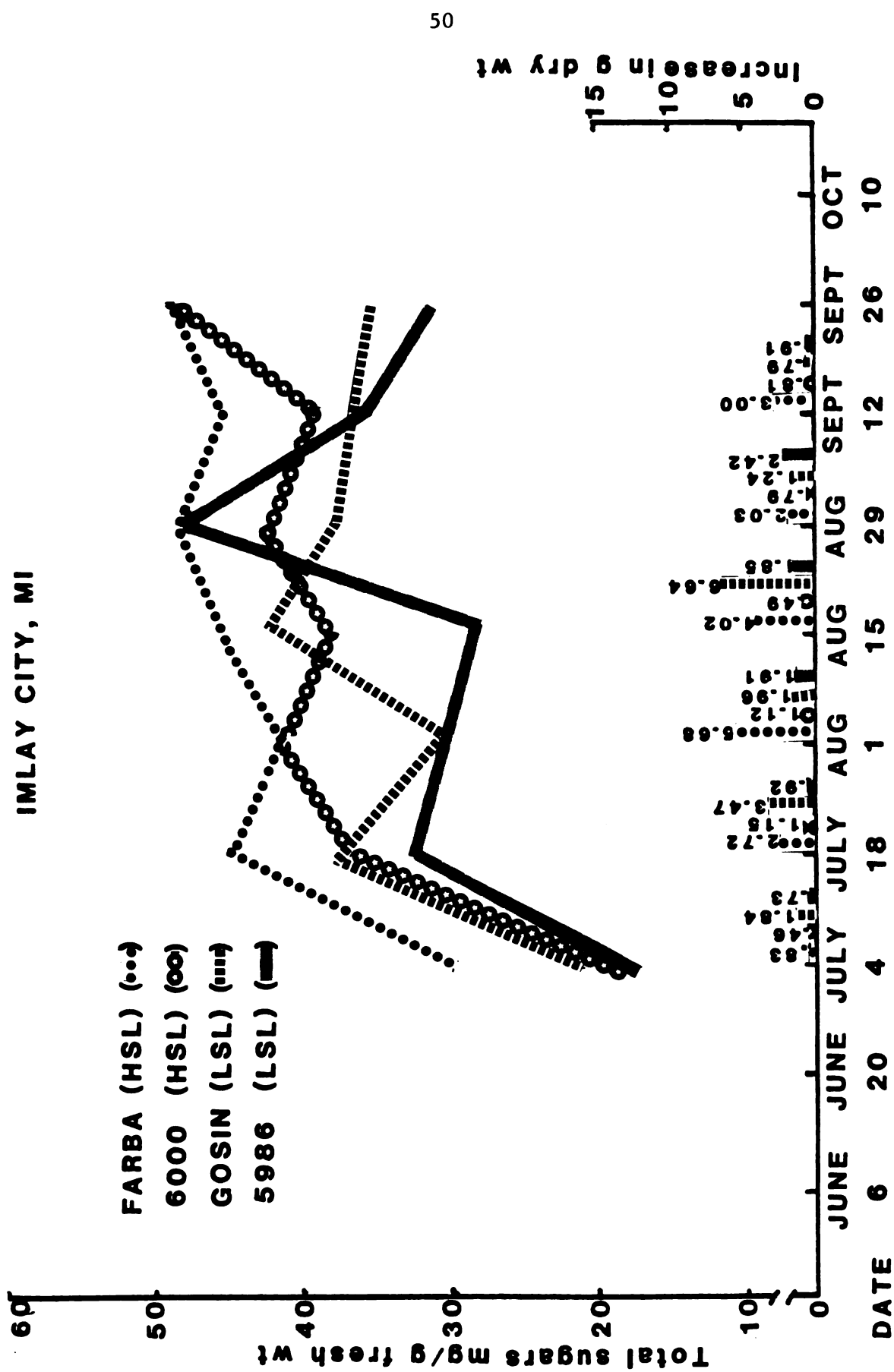


Table 6.--Dry weight accumulation (g total dry weight) of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	0.1a ^z	0.7ab	4.2a	11.9ab	23.2a	27.0a	25.6a	38.2a	27.6a	36.9b
6000 (HSL)	0.1a	0.4b	1.9b	6.5b	10.6b	14.9b	12.1b	15.9b	12.5b	18.9c
Gosin (ISL)	0.1a	1.0a	4.1a	15.5a	33.6a	29.8a	35.2a	43.1a	36.2a	58.2a
5986 (ISL)	0.1a	0.5b	2.4ab	8.3	10.9b	11.2b	17.7b	15.7b	16.3b	13.5c

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IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	0.8ab	3.9ab	10.7ab	18.8a	21.4a	18.3a	21.0a	-
6000 (HSL)	-	-	0.4b	1.7b	4.2b	4.9b	4.4b	3.3b	4.2b	-
Gosin (ISL)	-	-	1.1a	5.9a	14.0a	13.5ab	23.4a	24.1a	20.3a	-
5986 (ISL)	-	-	0.5b	2.0b	4.2b	7.0b	9.8b	10.1b	11.2b	-

^aMean separation within columns by Tukey's HSD test, 5% level.

Table 7.--Simple and multiple regression statistics between total sugars and growth analysis parameters of high and low sugar accumulating carrot cultivar and breed lines.

Cultivar/ Breeding Line	Simple Regression Coefficient							Multiple Regression Coefficient R^2
	TPDW ^y ^b	RDW ^x ^b	R/S ^b	LAI ^b	LAR ^b	$\overline{RGR}^b$	$\overline{NAR}^b$	
Farba (HSL)	.71	.03	1.36	1.02	1.03*	2.78*	-4.02**	
						X	X	.80**
			X				X	.91**
6000 (HSL)	.91	2.41						.69*
			X					
			X			X		
Gosin (LSL)	.57	.80	10.65*	.45	-6.27	2.35	-5.16	
						X	X	.80*
			X				X	.51
5986 (LSL)	.96	3.20						.24
			8.37*	2.13	-5.23	-5.22	-3.64	
			X			X	X	.83*
			X			X		.74*
								.68

^yTPDW = total plant dry weight

^xRDW = root dry weight

* P < 5% due to chance

** p < 1% due to chance

b = standard deviation change in total sugars/standard deviation change in regression variable

X = interaction of associated simple regression variable in multiple regression with total sugars

Table 8.--Dry weight of the tap root (g tap root dry weight) of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING										
Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	0.01a ²	.01a	1.0b	3.3b	7.5b	13.7ab	14.0ab	22.1ab	19.4a	27.6ab
6000 (HSL)	0.00b	0.1a	2.2a	5.3a	8.7ab	8.7ab	8.5b	10.3b	9.1b	15.0b
Gosin (ISL)	0.01a	0.1a	1.2ab	5.1a	17.2a	16.9a	25.5a	27.6a	25.8a	43.5a
5986 (ISL)	0.00b	0.1a	0.8b	3.5b	5.8b	7.0b	10.6b	10.9b	12.7b	10.8b

IMLAY CITY										
Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	0.2a	1.0ab	3.7ab	9.4a	13.4a	11.2a	14.1a	-
6000 (HSL)	-	-	0.05b	0.5b	1.7b	2.8b	3.3b	2.5b	1.6b	-
Gosin (ISL)	-	-	0.2a	2.0a	5.4a	7.4ab	14.1a	15.3a	14.5a	-
5986 (ISL)	-	-	0.1b	0.8b	1.7b	3.6ab	6.1ab	7.9ab	8.8ab	-

²Mean separation within columns by Tukey's HSD test, 5% level.

the growing season. In general, though, the cultivars exhibited higher root dry weights than did the breeding lines, especially in the second half of the growing season.

There were no significant differences between HSL and LSL for root/shoot ratio (R/S) (Table 9). However, regression coefficients between R/S and total sugars were significant ($P = .05$) for the LSL only. There was a significant interaction between R/S and $\overline{\text{NAR}}$ (mean net assimilation rate) with total sugars for the HSL ($P = .01$) and 5986 ($P = .05$) indicating that R/S may be influencing sugar accumulation. The R/S ratio for all four lines was less than 1.0 early in the growing season and greater than 1.0 later on. This indicated that over the growing season carrots partitioned more photosynthate to the roots than to the leaves. The breeding lines generally had a significantly higher R/S than did the cultivars throughout the growing season. Hence, the breeding lines were partitioning a greater proportion of assimilates to the root than the cultivars.

Significant differences were not detected between the HSL and LSL for leaf area index (LAI) (Table 10) and there were no significant regression coefficients for LAI regressed with total sugars. Significant differences for LAI occurred only between the cultivars and the breeding lines after June 27 at the East Lansing location. There were significant differences for LAI between HSL and LSL

Table 9.--Root/shoot ratio (g root dry weight/g shoot dry weight) of low and high sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	0.1ab ^z	0.1b	0.3b	0.4b	0.5b	1.0b	1.2b	1.4b	2.4b	3.0b
6000 (HSL)	0.2a	0.5a	0.3b	0.5ab	1.0a	1.4ab	2.4a	2.5a	2.6b	3.9a
Gosin (ISL)	0.03b	0.2b	0.4ab	0.5ab	1.0a	1.3ab	2.6a	1.8ab	2.5b	2.9b
5986 (ISL)	0.1ab	0.2b	0.6a	0.7a	1.2a	1.7a	1.5b	2.3ab	3.5a	4.0a

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IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	0.3a	0.4b	0.3b	1.0ab	1.7b	1.7b	1.9ab	-
6000 (HSL)	-	-	0.1b	0.4b	0.7a	0.6b	3.0a	3.1a	1.3b	-
Gosin (ISL)	-	-	0.2ab	0.5ab	0.6a	1.2a	1.5b	1.7b	2.5ab	-
5986 (ISL)	-	-	0.2ab	0.7a	0.7a	1.1ab	1.6b	3.6a	3.7a	-

^zMeans separation within columns by Tukey's HSD test, 5% level.

Table 10.--Leaf area index (leaf surface cm²/soil surface area cm²) of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	0.1a ^z	0.7ab	3.7a	9.5a	11.0a	10.5a	6.7a	7.5a	3.0a	3.0a
6000 (HSL)	0.1a	0.4b	1.6b	4.2b	4.2b	4.1b	2.8b	2.2b	1.2b	1.6b
Gosin (LSL)	0.1a	1.0a	3.4a	9.6a	12.6a	8.5a	4.6ab	5.1a	3.2a	3.6a
5986 (LSL)	0.05b	0.5ab	1.8b	4.5b	4.1b	3.6b	4.3ab	1.7b	1.4b	0.9b

IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	0.9ab	3.2a	6.8a	9.2a	6.8a	4.3a	3.4a	-
6000 (HSL)	-	-	0.5b	1.4b	2.6b	1.7b	0.3c	0.2c	0.3c	-
Gosin (LSL)	-	-	1.3a	4.6a	8.5a	4.9ab	5.3a	4.4a	2.4ab	-
5986 (LSL)	-	-	0.6b	1.6b	2.9b	3.2b	2.0b	1.5b	1.3b	-

^zMeans separation within columns by Tukey's HSD test, 5% level.

at the Imlay City location but they were inconsistent over time. The lack of significant differences in LAI with HSL and LSL indicates the HSL may be more efficient in fixing CO_2 and/or more efficient in transporting assimilate to the roots than the LSL.

Significant differences between HSL and LSL for leaf area ratio (LAR) occurred after October 3 at East Lansing and after September 12 at Imlay City with the HSL having significantly higher LAR than LSL (Table 11). The time in the growing season at which significant differences occurred between HSL and LSL for LAR coincided with the time LSL were decreasing in total sugar accumulation. This indicates that LAR, which is a measure of photosynthetic assimilation might affect the accumulation of sugars at the end of the growing season in HSL and LSL carrots. However, significant ($P = .05$) for the regression coefficient for LAR regressed with total sugars occurred for 'Farba' only.

The mean relative growth rate ($\overline{\text{RGR}}$) was high for all lines at the beginning of the growing season (Figures 3 and 4). However, the $\overline{\text{RGR}}$ decreased steadily throughout the season for the LSL and eventually leveled off late in the growing season, while total sugars continued to decline. The HSL showed the same decline in $\overline{\text{RGR}}$ until September when the $\overline{\text{RGR}}$ began to increase. This increase in $\overline{\text{RGR}}$ was associated with an increase in sucrose and total sugars for the HSL, suggesting that $\overline{\text{RGR}}$ is associated with increased

Table 11.--Leaf area ratio (leaf cm²/g total dry weight) of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. and organic soil near Imlay City, MI. during the 1979 growing season.

EAST LANSING

Cultivar/ Line	June 13	June 27	July 11	July 25	August 8	August 22	September 5	September 19	October 3	October 17
Farba (HSL)	158.9ab ^z	119.4ab	98.2a	89.2a	53.4a	43.6a	29.4a	21.4a	12.4a	9.2a
6000 (HSL)	135.1b	95.9b	96.9ab	73.5ab	44.5ab	30.8b	16.3ab	15.8ab	10.7ab	9.3a
Gosin (ISL)	158.4ab	115.2ab	92.6ab	69.9ab	42.2b	32.0b	14.8b	13.8ab	9.9b	6.9b
5986 (ISL)	175.5a	126.1a	85.6b	61.7b	42.8b	36.0ab	27.1ab	12.4b	9.8b	7.9b

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IMLAY CITY

Cultivar/ Line	June 6	June 20	July 4	July 18	August 1	August 15	August 29	September 12	September 26	October 10
Farba (HSL)	-	-	133.2a	94.2ab	73.0ab	55.0a	35.9a	26.5a	18.1a	-
6000 (HSL)	-	-	122.7b	88.3ab	69.6b	40.4b	28.8ab	18.1b	17.9a	-
Gosin (ISL)	-	-	131.7a	86.9b	68.0b	40.9b	25.5b	20.5ab	13.1b	-
5986 (ISL)	-	-	127.1ab	87.7b	77.3a	51.8ab	23.4b	16.6b	12.8b	-

^zMean separation within columns by Tukey's HSD test, 5% level.

Figure 3.--Mean relative growth rate of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. during the 1979 growing season.

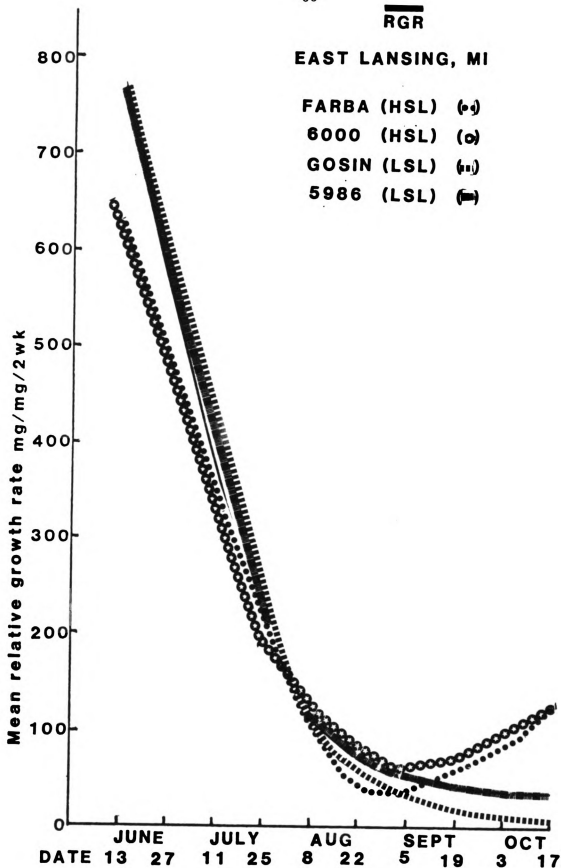
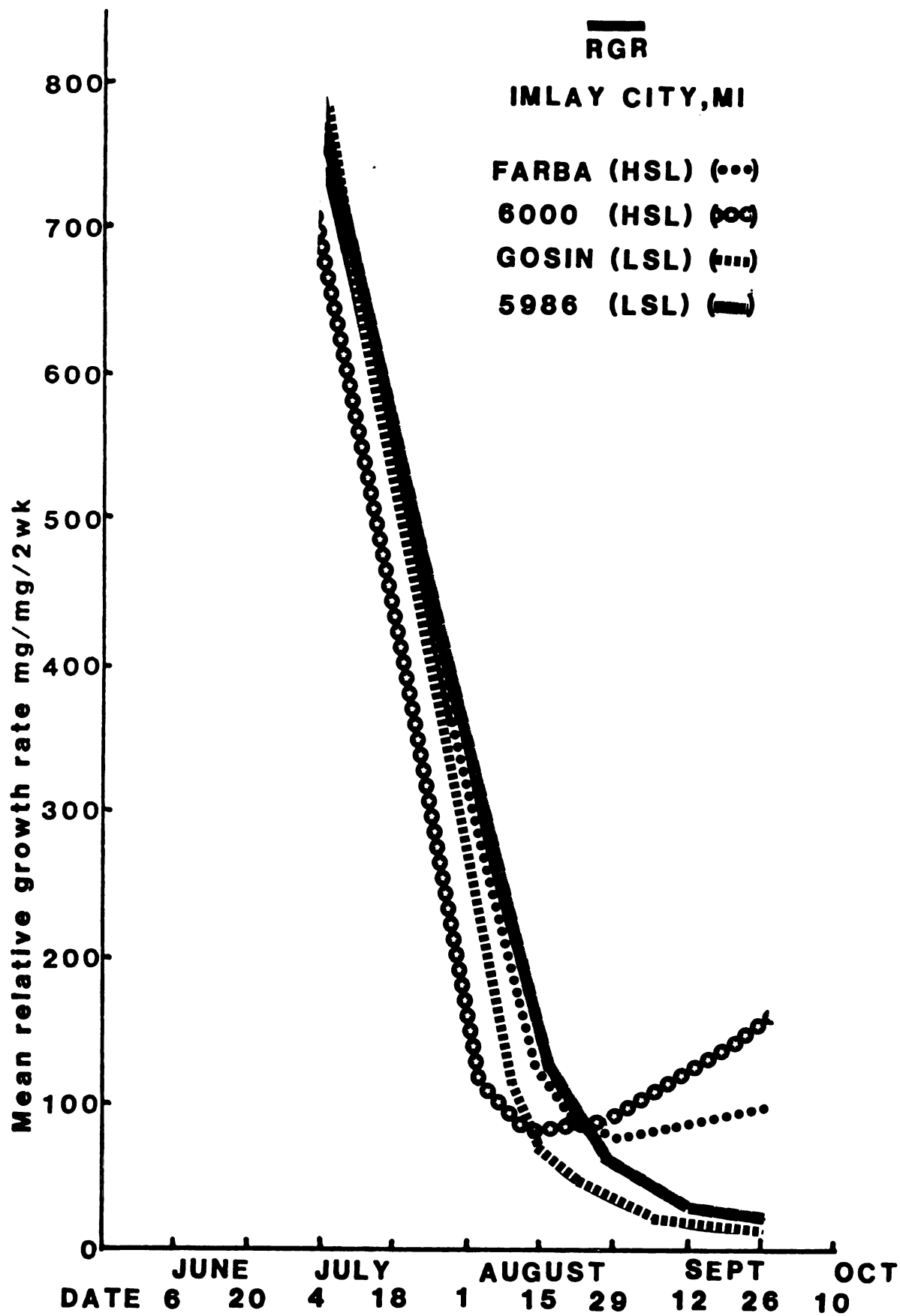
RGR**EAST LANSING, MI****FARBA (HSL) (••)****6000 (HSL) (○)****GOSIN (LSL) (•••)****5986 (LSL) (—)**

Figure 4.--Mean relative growth rate of high and low sugar
accumulating carrot cultivars and breeding
lines grown on organic soil near Imlay City, MI.
during the 1979 growing season.



sugar accumulation late in the growing season. This association may be partially explained by the fact the $\overline{RGR}$, for a given point in time may be calculated from net assimilation rate (NAR), where $RGR = (NAR) (LAR)$ (10). Thus, the significant differences in LAR between HSL and LSL late in the growing season and a possibly dramatic association of $\overline{NAR}$ with HSL and LSL might be the reason $\overline{RGR}$ was closely associated with the HSL. Also there was significant (P = .05) for the regression coefficient for $\overline{RGR}$ regressed with total sugars for the HSL only. However, the lack of association of $\overline{RGR}$ with LSL may be explained by the fact that $\overline{RGR}$ is basically a function of the change in dry weight over time. It is known that the different weight measurements (R/S, dry weight accumulation and tap root dry weight) did not show a significant difference between the HSL and LSL over the growing season. Therefore, the association of $\overline{RGR}$ with sugar accumulation may be only superficial.

The $\overline{NAR}$ decreased for both HSL and LSL from the beginning of the growing season until September (Figures 5 and 6). In September, the HSL exhibited an increasing $\overline{NAR}$ while the LSL continued to show decreasing $\overline{NAR}$. The $\overline{NAR}$ increase in the HSL was associated with an increase in total sugars and the $\overline{NAR}$ decrease in LSL was associated with a decrease in total sugars. However, significant (P = .01) between $\overline{NAR}$ and total sugar occurred for the HSL only,

Figure 5.--Mean net assimilation rate of high and low sugar accumulating carrot cultivars and breeding lines grown on sandy loam soil at East Lansing, MI. during the 1979 growing season.

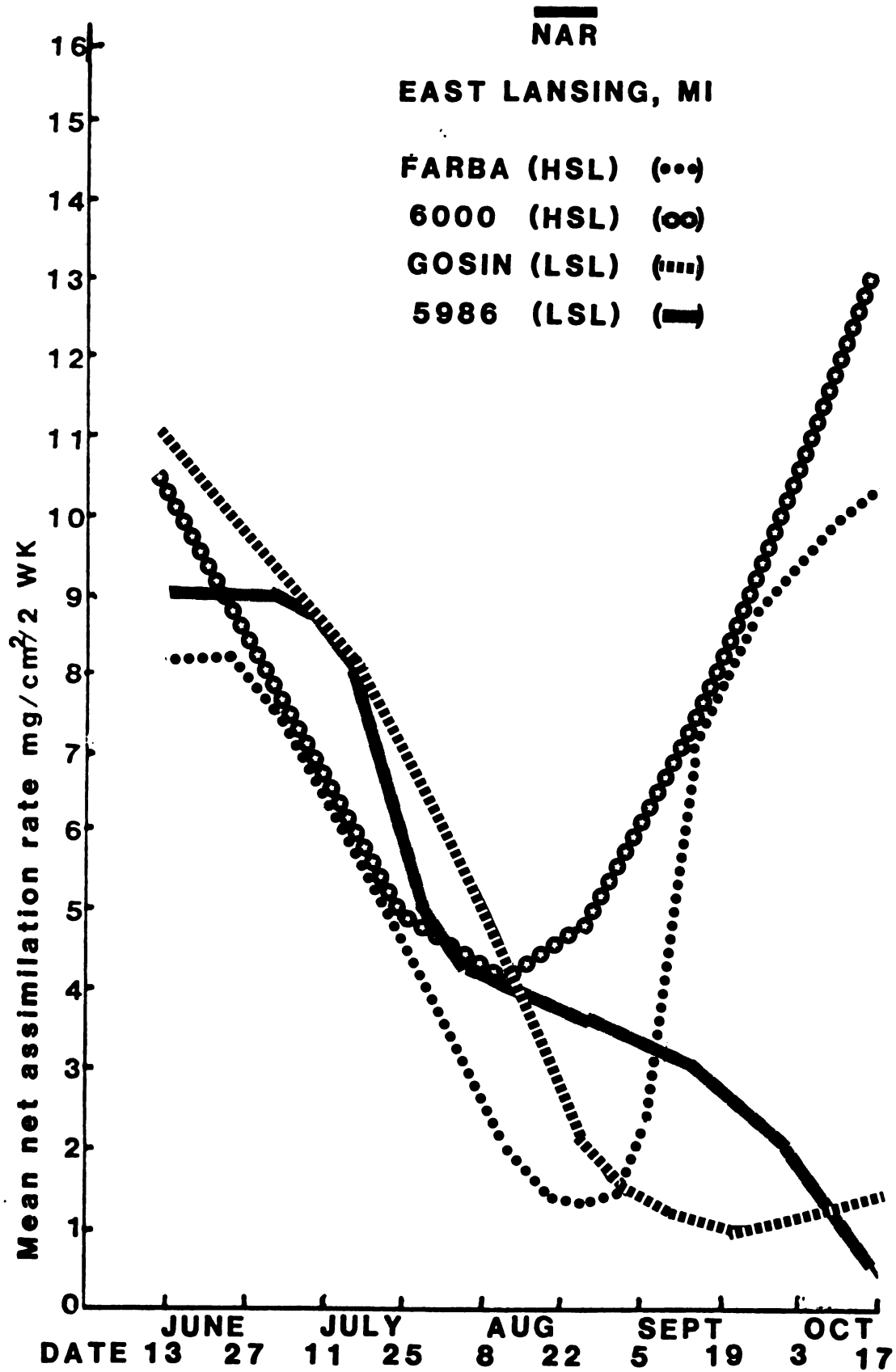
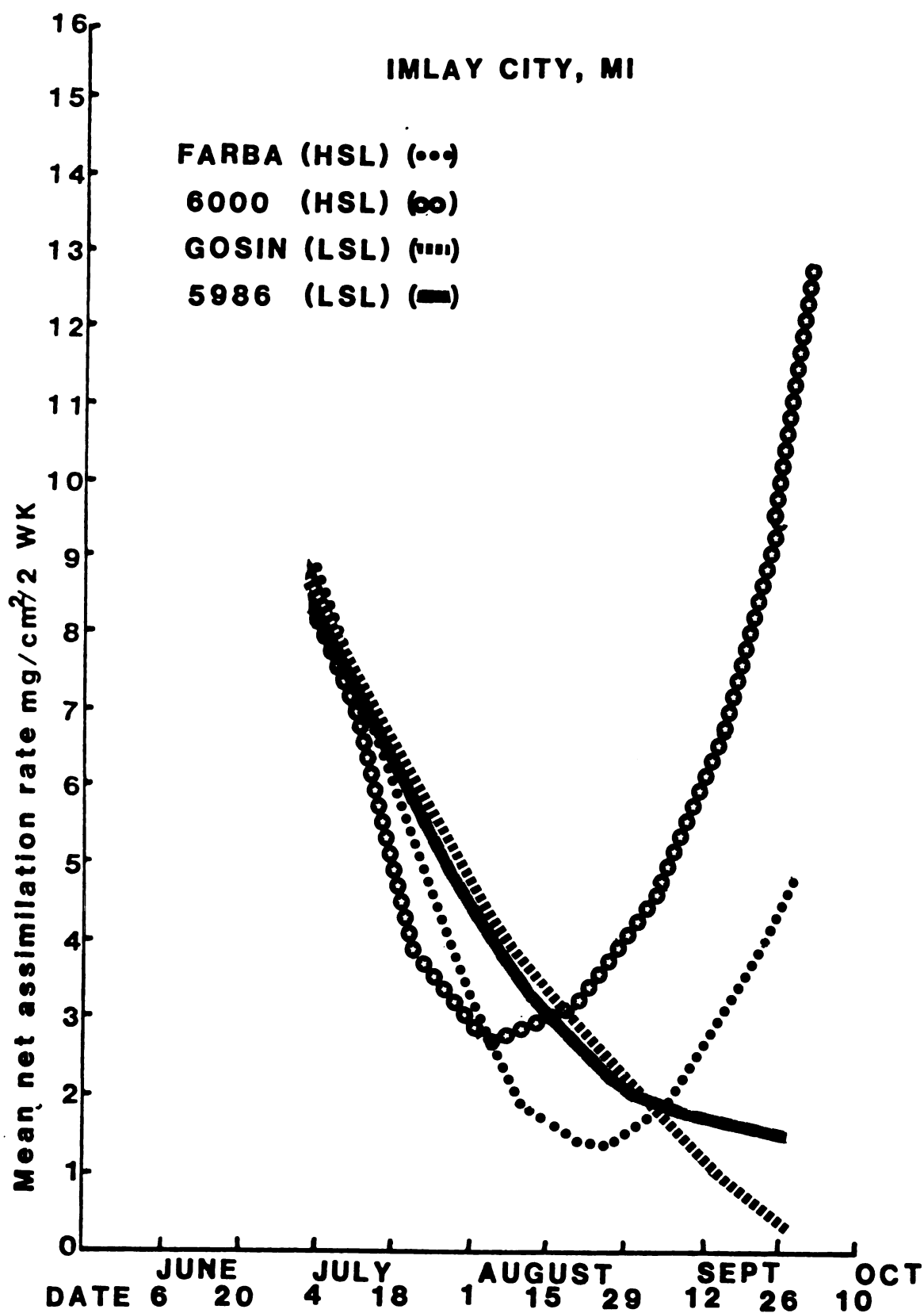


Figure 6.--Mean net assimilation rate of high and low sugar accumulating carrot cultivars and breeding lines grown on organic soil at Imlay City, MI. during the 1979 growing season.

NAR**IMLAY CITY, MI**

while multiple regression coefficients had $\overline{\text{NAR}}$ interacting at a significant level ($P = .01$) for HSL and ($P = .05$) LSL with $\overline{\text{RGR}}$ and total sugars. Loach (9) also found high $\overline{\text{NAR}}$ to be associated with high sugar yield late in the growing season in sugar beet.

$\overline{\text{NAR}}$ is primarily a function of photosynthesis (9). Therefore, the increasing $\overline{\text{NAR}}$ of the HSL indicates that photosynthesis remains active in the plants late in the growing season. In contrast, the decreasing $\overline{\text{NAR}}$ of the LSL was probably related to decreased photosynthesis. This observation of possible variability in photosynthetic activity is supported by the significant differences in LAR between HSL and LSL. The lack of significant differences in LAI indicated that the HSL and the LSL were not distinguished by their ability, or lack of ability, to accumulate sugar by producing new photosynthetic material. More likely, differences in sugar accumulation between HSL and LSL occurred because of the ability of HSL to remain photosynthetically active late in the growing season as represented by increasing $\overline{\text{NAR}}$. Subsequently, the photosynthate produced by HSL was translocated and stored in the roots as soluble carbohydrates.

$\overline{\text{NAR}}$ varies with leaf age (15). Thus, $\overline{\text{NAR}}$ may be affected by differing patterns of leaf production and leaf senescence within the canopies of the four varieties. Rate of leaf production and senescence were not directly

measured; thus it cannot be unequivocally determined if $\overline{\text{NAR}}$ in carrots is influenced by leaf age. However, LAI, a measure of photosynthate production area, was measured. Assuming that the change in LAI may be taken as an indication of the number of leaves produced, it can be inferred that late in the growing season carrots have little new leaf production because of the general decline in LAI. Therefore, it is hypothesized that $\overline{\text{NAR}}$ is more dependent upon the photosynthetic activity of mature carrot leaves than on the production of new photosynthetic area. $\overline{\text{NAR}}$ is controlled by two factors: (1) the ratio of immature to mature leaves and (2) the photosynthetic rate of mature leaves.

Multiple regression. Multiple regressions were calculated for the combinations of $\overline{\text{NAR}}$, $\overline{\text{RGR}}$ and R/S. The best multiple regressions used $\overline{\text{NAR}}$ and $\overline{\text{RGR}}$ although significant regressions were found with $\overline{\text{RGR}}$ and R/S, but only in the HSL. Thus, the generalization of $\overline{\text{NAR}}$ contribution to high sugar yield in carrot seems clear.

CONCLUSION

In general, HSL were distinguished from LSL in their ability to accumulate free sugars by time of physiological maturity. Physiological maturity in carrot occurs when total sugars decline late in the growing season and this decline coincides with the largest biweekly increase in total plant dry weight.

If carrot genotypes were selected for photosynthetic activity late in the growing season based on high $\overline{\text{NAR}}$, it would be expected that high sugar yield would result and the resultant high sugar content would possibly improve carrot culinary quality.

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