Analysis of genetic variabilities in root shape of sugar beet

II.[*] Taperness, relative growth and bilateral asymmetry

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Received May 1, 1973

Introduction

Root crops show naturally a variation of root shape, when lines within a species are compared, and in many cases a variety can be identified by the specific type of root shape. In sugar beet, ROEMER (1927) classified sugar beet varieties into three types of root shape, qualitatively. However, his three types of root shape are not sufficient for the consideration of root shape of sugar beet varieties made at present. Root shape is determined by the relative size of parts of root which vary continuously and quantitatively. Therefore, root shape may vary quantitatively and may not be independent of the root yield and root shape itself is one of the important economic characters, because it is a great convenience to harvest the wedge type of beet roots.

Thus an attempt to study the root shape of sugar beet as a quantitative character seems to be in order.

In a previous paper (SHIMAMOTO, 1972), the contributions of partial weight at each position to root weight were defined. Furthermore, root shape of sugar beet is characterized by taperness, relative growth of short-diameter with long-diameter and bilateral asymmetry between two corresponding radiuses. This paper deals with the variations of root diameters at each position of the root in an attempt to investigate the root shape in sugar beet as mentioned above.

Materials and Methods

Ten inbred lines were used for the present work, through the kindness of the National Institute of Sugar Beet, Japan. They were allowed to self-pollinate a few times and thereafter were propagated in closed population and were not selected for specific characters.

Ten inbred lines were seeded on May 9, 1968, at the Experimental

Farm, the Hokkaido University, with a few seeds per hill at a 60×30 cm spacing. After about six weeks from seeding, thinning was made to a single plant per hill. Fertilizers applied were the compound type of 12–16–13 N–P–K (kg./10 a) including other minor elements and an additional 25 kg./10 a of Chile saltpeter.

Records on plant basis were taken on October 9th, 1968, regarding weight of topping root and root diameter in five positions at two centimeter intervals from the topping face. Five positions were named as I, II, III, IV and V from the topping face, respectively (Figure 1). Root diameter was classified into two characteristics, short-diameter and long-diameter, from a standpoint of morphology of the sugar beet root. The measurements were made by half a diameter with the centercore as their starting points. Both the diameters were expressed by the sums of two halves of the diameter, respectively. The short-diameter was measured from one point to another, to which hair roots attached, through the centercore. The long-diameter was measured by the perpendicular diameter on the short-diameter through the centercore. Generally the short-dimeters were shorter than the long-diameters, though a few plants have longer short-diameters than long-diameters.

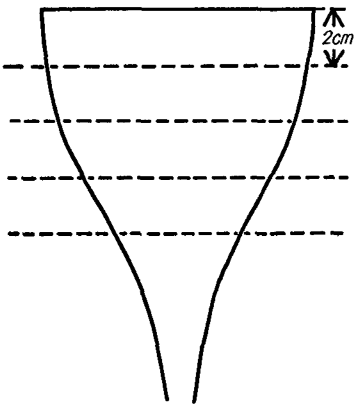

Figure 1. Schematic illustration showing how the measurements on each diameter of root were taken.

All ten measurements, five in short-diameter and five in long-diameter, and root yield showed higfily significant differences among the ten inbred lines used.

The calculations reported herein were made by FACOM 230–60 Computer at Hokkaido University Computing Center.

Results

1. Genetic variabilites in short-diameter, long-diameter and taperness.

Based on the data of ten inbred lines, mean values, genetic and error variances, heritabilities and genetic coefficients of variability for short-diameter and long-diameter are given in Table 1. Genetic and error (environmental) variances were estimated from the method of variance analysis. In short-diameter, dimension at I was largest and became gradually small towards the tail of root, and long-diameter showed the same tendency of short-diametr, except that long-diameter at II was larger than at I. Genetic variabilities of short-diameter and long-diameter which were expressed by genetic variance and heritability were pronounced at II and at IV, respectively.

TABLE 1. Means, genetic variances ($\sigma^2 g$) and error variances ($\sigma^2 e$) for ten lines

		mean (cm)	$\sigma^2 g$	$\sigma^2 e$	h^2 (%)	GCV (%)
Short-diameter	I	8.1	.333	.938	26.2	7.1
	II	6.7	.674	.992	40.5	12.2
	III	5.1	.484	.956	33.6	13.4
	IV	4.1	.365	.753	32.7	14.5
	V	3.2	.251	.585	30.0	15.5
Long-diameter	I	9.6	.220	.746	22.8	4.9
	II	9.9	.285	.722	28.3	5.4
	III	9.2	.386	.787	32.9	6.8
	IV	7.7	.549	.966	36.2	9.6
	V	6.1	.510	1.002	33.7	11.8

note: $h^2 = \frac{\sigma^2 g}{\sigma^2 g + \sigma^2 e}$, for line basis in % and $GCV = \frac{\sigma g}{\text{mean}}$, in %

TABLE 2. Analysis of linear and non-linear components of position source

Source	d.f.	Mean Squares: Short-diameter	Mean Squares: Long-diameter
Lines (L)	9	19.9974**	21.3145**
Positions (P)	4	381.7593**	253.8743**
Linear (LR)	1	1509.9494**	846.7680**
Quadratic (Q)	1	14.6473**	160.3475**
Cubic (C)	1	.4244	7.9924**
Quartic (QR)	1	2.0162	.3893
L×P	36	1.2006	.6281
L×LR	9	2.8648**	1.8828*
L×Q	9	1.0129	.2833
L×C	9	.7271	.2177
L×QR	9	.1974	.1286
Error	450	.8449	.8454

**, *: significant at 1% and 5% levels, respectively

Genetic coefficients of variability (GCV) were higher at the tail than at the topping face of root. Hence, genetic variations in root diameter were not always high at the largest part of the root.

In order to partition the gradient in diameter among positions into linear, quadratic, cubic and quartic parts, regression analysis on position for the diameter were made in accordance with FISHER and YATE's Orthogonal Polynomial Table (1963). As shown in Table 2, the position effects were affected significantly by the linear and quadratic parts in short-diameter. In long-diameter, the position effects were affected significantly by the linear, quadratic and cubic parts. In the interaction between the line effect and each regressional effect, only the linear effect on the position was statistically significant in both short- and long-diameters. Thus, in comparison with among-lines of position effects, the curvilinear effects without linear part were neglected.

The linear regression coefficients on five positions based on individual plants were calculated by the method of FISHER and YATE's Orthogonal Polynomial Table (1963). Average values for lines are given in Table 3. The linear regression coefficients (b_S in short-diameter and b_L in long-diameter in Table 3) explained the degree of taperness of root. The taperness was different significantly among lines and between b_S and b_L, but the interaction between the two sources were not significant (Table 4). It was shown that

TABLE 3. Linear regression coefficients on five positions in short-diameter (b_S) and long-diameter (b_L)

Line name	G65R	G37	P138	S12	G61W	G08	P55	S26	G91	G93	mean
b_S	1.06	1.50	1.15	1.40	1.34	.95	1.36	1.24	1.16	1.14	1.23
b_L	.86	1.10	.80	1.05	.92	.68	.83	1.04	1.07	.91	.93
mean	.96	1.30	.98	1.23	1.13	.81	1.10	1.14	1.12	1.02	1.08

TABLE 4. Analysis of variance for b_S and b_L

Source	d.f.	Mean Squares	Expectation M.S.
Lines	9	.389501**	.011728
b_S vs b_L	1	4.608648**	
Interaction	9	.082461	.001000
Error	180	.072476	
Intra-class correlation = .9214			

**: significatn at 1% level

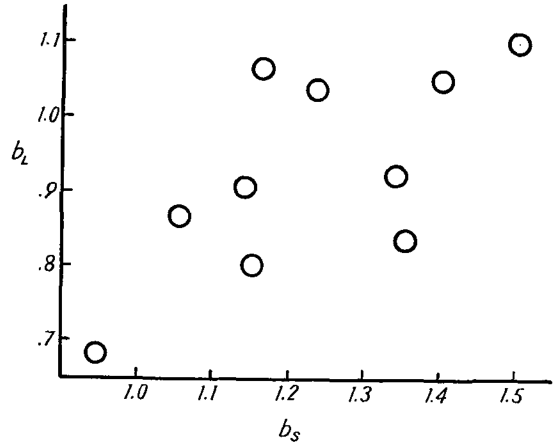

Figure 2. The ralation between short-diameter (b_S) and long-diameter (b_L).

taperness in short-diameter was strongly and genetically correlated with that in long-diameter. Figure 2 shows the relationship between the taperness in both diameters on a line basis.

2. Relationship between short-diameter and long-diameter.

Genotypic and environmental correlations between short-diameter and long-diameter at each position are given in Table 5. It shows that the short-diameter and long-diameter tend to be strongly correlated at I or V and weakly at the middle parts. Regression analysis of short (or long)-diameter on long (or short)-diameter in each source of variation is shown in Table 6. In the variation among lines, the short-diameter contributed linearly to long-diameter and *vice versa,* and independent variance (deviation from regeession line) was highly significant. In variation among positions, variances affected linearly by short (or long)-diameter on long (or short)-diameter were not significant, but its deviation variances were highly significant, and consequently the short-diameter and long-diameter became smaller independently towards the tail. In source of variatiion of line × position interaction and

TABLE 5. Genetic and environmental correlations between short and long diameters

	I	II	III	IV	V	pool
genetic	.859	.735	.446	.546	.804	.659
environmental	.455	.281	.352	.495	.624	.431

TABLE 6. Analysis of variances and covariances for short and long diameters

Source	d.f.	mean squares SHORT	LONG
Lines (L)	9	19.9947**	21.3145**
Linear	1	75.0478*	79.5846*
Deviation	8	13.1131**	13.9058**
Positions (P)	4	381.7593**	253.8743**
Linear	1	1155.4914	768.4148
Deviation	3	123.8486**	82.3608**
L×P	36	1.2006	.6281
Linear	1	5.3071*	2.7671*
Deviation	35	1.0874	.5670
Error	450	.8449	.8454
Linear	1	70.7268**	70.7805**
Deviation	449	.6888	.6897

***, *: significant at 1% and 5% levels, respectively

error, linear variances of short (or long)-diameter regressing on long (or shoot)-diameter were significant statistically. This indicates that the association of short-diameter with long-diameter are an apparent difference among inbred lines.

In order to know the relative size of long-diameter to short-diameter, long-diameter/short-diameter ratios were calculated at each position of the root. Mean values and genetic and environmental variances of the ten lines for long/short ratios in diameter are given in Table 7. Mean values of long/short ratios became larger towards the tail of the root. Both genetic

TABLE 7. Means, genetic variances (σ_g^2), evironmental variances (σ_e^2), heritability values (h) and genetic coefficients of variation for long/short ratio in diameter.

		mean	σ_g^2	σ_e^2	h^2	GCV
L/S	I	1.19	0.247	2.10	10.5	4.2
	II	1.51	2.129	6.07	25.9	12.6
	III	1.85	4.890	11.72	29.4	12.0
	IV	1.92	7.018	12.87	35.3	13.6
	V	1.95	4.329	12.71	25.4	10.7

note; $h=\frac{\sigma_g^2}{\sigma_g^2+\sigma_e^2}$, in % $GCV=\sigma_g/\text{m}$, in %

TABLE 8. Analysis of variance for Long/Short ratio in diameter

Source	d.f.	mean squares	Source	d.f.	mean squares
Lines (L)	9	1.63322**	L×P	36	.17068**
Positions (p)	4	10.57572**	L×LR	9	.40085**
Linear (LR)	1	36.71056**	L×Q	9	.15689
Quadratic (Q)	1	5.18503**	L×C	9	.01096
Cubic (C)	1	.02209	L×QR	9	.01539
Quartic (QR)	1	.38480*	Error	450	.09093

**, *: significant at 1% and 5% levels, respectively

TABLE 9. Mean values of relative growth and asymmetries

		G65R	G37	P138	S12	G61W	G08	P55	S26	G91	G93	mean
Relative growth		.37	.54	.53	.60	1.02	.47	.84	.51	.68	.45	.60
Asymmetry	S	5.5	7.1	8.0	7.8	9.6	7.4	8.7	7.5	9.5	6.6	7.8
$\|A-B\|/(A+B)$	L	4.4	4.9	5.5	3.4	4.7	4.4	4.2	4.4	4.2	5.2	4.5
$\sqrt{1-r^2}$	S	.33	.37	.48	.34	.35	.43	.34	.36	.40	.40	.38
	L	.48	.38	.62	.27	.47	.49	.43	.32	.34	.53	.43

and environmental variations of long/short ratios were highest at IV. Analysis of variances for long/short ratios were made, including analysis of regression on position, and the results are shown in Table 8. Source of lines, positions and their interaction were highly significant statistically. The position effect could be partitioned into significantly linear, quadratic and quartic components which were calculated by FISHER and YATE's Orthogonal Polynomial Table (1963). But the significant interaction of their components with lines was limited to the linear component of position effects. This shows that there are differences in relative growth of diameter, which was expressed by the linear regression coefficient of long/short ratios in five positions shown in Table 9 among lines.

3. Asymmetry in diameter.

Asymmetry in diameter can be measured generally by the difference between the radiuses of each side in root diameter. There are the three kinds of bilateral asymmetry (VAN VALEN, 1962), that is, directional asymmetry, antisymmetry and fluctuating asymmetry. In this experiment, the amount of asymmetry was measured in two ways: (1) $\sqrt{1-r^2}$, where r is the coefficient of correlation in five positions between radiuses of both sides

TABLE 10. Relationships between asymmetries

		$\|A-B\|/(A+B)$		$\sqrt{1-r^2}$	
		S	L	S	L
$\frac{\|A-B\|}{(A+B)}$	S	1.000	−.154	.123	−.204
	L		1.000	.605	.807**
$\sqrt{1-r^2}$	S			1.000	.592
	L				1.000

**: significant at 1% level
note: S is each asymmetry in short-diameter
L is each asymmetry in long-diameter

of the diameter, indicating fluctuating asymmetry (VAN VALEN, 1962), and (2) $|A-B|/(A+B)$, where A or B is a radius of both sides at each diameter. The absolute value expresses a degree of deviation of the centercore from the center point of topping face. If only the fluctuating asymmetry was included in the amount of asymmetry, the correlation between the two measurements of asymmetry would be stronger, and if the directional effects were considered without fluctuating asymmetry, the correlation would be lower. Table 10 shows the correlation coefficients on a line basis between the two ways for measuring the amount of asymmetry at each diameter. In the short-diameter, the value was not so high. Therefore, bilateral asymmetry in short-diameter measured by the absolute difference includes not only fluctuating but directional asymmetry. In the long-diameter, the value was strong and significant at a 1% level. This shows that the bilateral asymmetry in long-diameter measured by the absolute difference must also be fluctuating asymmetry, in addition to the consideration of the significant difference in two measurements among lines.

4. Relationships between root yield and shape characters.

The relationships between root yield expressed by root weight and the shape characters which were different significantly among the lines used were observed on the line basis. As shown in Figure 3, there were no relationship between root yield and the two measurements of taperness in the root. The relative growth of long-diameter to short-diameter and directional asymmetry were not correlated with the root yield. But the fluctuating asymmetry in long-diameter was correlated with the root yield, as shown Figure 4.

Figure 5 gives the relation between the relative growth of long-diameter to short-diameter and directional asymmetry in short-diameter. The corre-

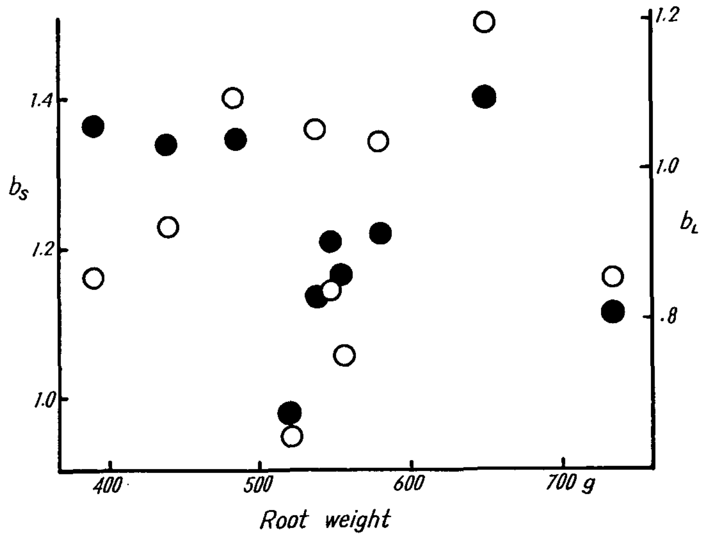

Figure 3. The relations of root weight with the taperness in short-diameter (b_S, in open circle) and long-diameter (b_L, in solid circle)

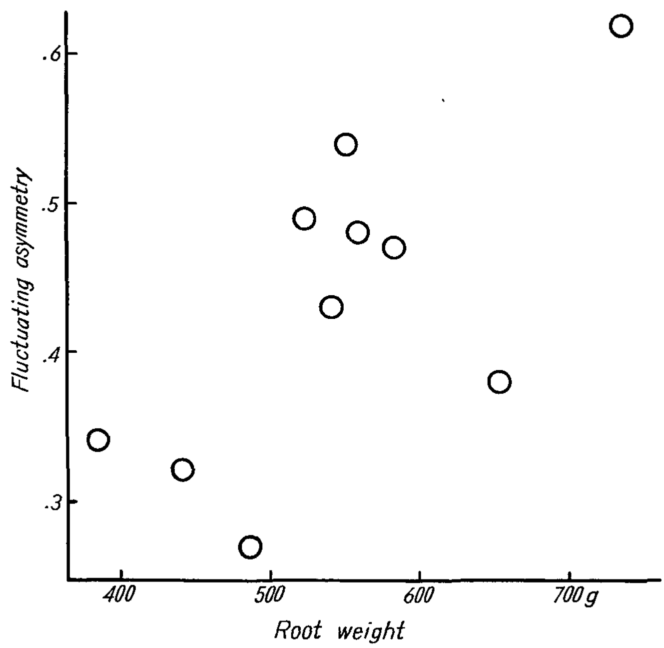

Figure 4. The relation between root weight and fluctuating asymmetry in long-diameter.

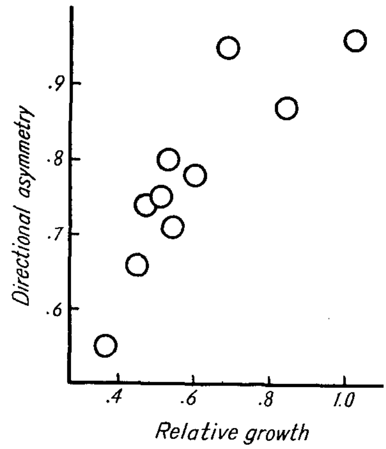

Figure 5. The relation between relative growth of long-diameter to short-diameter and directional asymmetry in short-diameter.

lation coefficient value was +0.8568, which was significant at the 1% level. This shows that the greater long-diameter growth is relative to the short-diameter with the increase in centercore deviation from the center point.

Discussion

It was found that root size measured by diameter at five positions was determined by control of genetic factors and also by the interaction between genetic source and linear component of position factors. The presence of the interaction confirmed that root shape expressed by taperness was determined by genetic control. Also, it was found that relative growth and bilateral asymmetry in diameter were different among the genotypes.

Root in sugar beet begins to elongate as a taproot firstly and then continues to a fleshy growth in diameter from the top of the root. Thus each of the root diameters from the top to tail expressed the certain stage of development. The regression coefficient of long/short ratio on the stages might be an index of allometric pattern of the long-diameter to short-diameter. And if the index of the relative growth equals zero, the relative growth of long-diameter to short-diameter shows an isometric pattern and if it does not equals zero, an allometric pattern is seen. In the present case, as the index of relative growth was not zero, the relative growth of long-diameter to short-diameter in sugar beet was an allometric pattern. Furthermore, as the indices were significantly different among the genotypes, it was suggested that the differences in long/short ratio between top and tail parts of sugar beet roots varied among the genotypes.

Fluctuating asymmetry was observed as a measurement of root shape. Fluctuating asymmetry has been referred to by WADDINGTON (1957) to be the result of developmental noise. Root shape in fluctuating asymmetry could be considered to be the result of noise or instabitity in development of root diameter. SAKAI and SHIMAMOTO (1965) observed that fluctuating asymmetry of leaves in the tobacco plant as a measurement of developmental instability was correlated with productivity, and described that under certain circumstances, developmental instability in some characters could be an advantage in natural or artificial selection. In sugar beet, fluctuating asymmetry in long-diameter was correlated with root weight, in agreenment with SAKAI and SHIMAMOTO (1965)'s hypothesis.

It was found that bilateral asymmetry which was significantly different among the genotypes was directional in short-diameter and fluctuating asymmetry in long-diameter.

From the standpoint of allometric growth in short-diameter and long-diameter, it is of considerable interest that directional asymmetry in short-diameter is correlated with the relative growth of long-diameter to short-diameter.

The indices expressing the root shape in question had low heritability values. Probably artificial selection will have operated to eliminate the genotypes which were accompanied with both extreme deviants of rood shape. Therefore, the genetic variation of the measurement of root shape, though some limitation existed, could be produced by the mutation or indirect effect of the selections. It should therefore be interest to investigate what relation the shape characters have on the productivity. In sugar beet, root yield was not correlated with the measurements of root shape without fluctuating asymmetry. Furthermore, considerations must be given to the possibilities of the relations between the shape and productivity.

Summary

Inbred lines in sugar beet were investigated for genetic variabilities of root diameter and root shape. The results obtained were as follows :

(1) Genetic variability in short-diameter was high around the top of the root and in long-diameter it was high around the tail of the root.

(2) Taperness in root, expressed by the linear regression coefficient of each diameter from the tail to the top of the root, varied among lines.

(3) It was found that the relative growth of the long-diameter to short-diameter could be expressed by the linear regression coefficient of long-

diameter/short-diameter ratio from the top to the tail of the root, and it was discussed as to whether the value was one of the parameters expressing allometric growth of long-diameter to short-diameter.

(4) Bilateral asymmetries in root diameter were differentiated among inbred lines used, namely, directional asymmetry in short-diameter and fluctuating asymmetry in long-diameter were under genetic control.

(5) Root yield was correlated with the fluctuating asymmetry of long-diameter and was not with the taperness and the relative growth of long-diameter to short-diameter. It was suggested that developmental instability might be in contact with productivity in sugar beet.

Acknowledgements

The auther wishes to express his gratitude to Dr. S. HOSOKAWA, Professor of Faculty of Agriculture, Hokkaido University, for encouragement throughout the experiments.

Literatures cited

FISHER, R. A. and F. YATES. 1963. Statistical tables. 6th ed. Oliver and Boyd, Edinburgh and London.

ROEMER, TH. 1927. Handbuch des zuckerrüben Baues. Verlagsbuchhandlung Paul Parey, Berlin.

SAKAI, K. I. and Y. SHIMAMOTO. 1965. Developmental instability in leaves and flowers of *Nicotiana tabacum*. Genetics 51: 801–813.

SHIMAMOTO, Y. 1971. Analysis of genetic variabilities in root shape of sugar beet. I. Variation of root shape among lines. Memoirs of the Faculty of Agriculture 8: 118–124.

VAN VALEN, L. 1962. A study of fluctuating asymmetry. Evolution 16: 125–142.

WADDINGTON, C. H. 1957. The strategy of the genes. George Allen & Unwin Ltd.