Biometrical Breeding of Forage Turnip in Japan

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The forage turnip is a valuable crop which is used to increase milk production for industrious dairy farmers in Japan. Breeding of the forage turnip has been conducted since 1957 in the Hokuriku National Agricultural Experiment Station and 3 new varieties, Kenshin-kabu, Akane-kabu and Shirayuki-kabu, were bred.

"Kenshin-kabu" was bred by mass selection from a hybrid population synthesized from 2 cultivars and 4 bred-strains.[4] The effect of mass selection conducted for 4 generations in the breeding process was recognized in the leaf weight of this variety.

"Akane-kabu" was bred by the maternal line selection method from a hybrid population which was synthesized by polycrossing with 9 bred-strains.[5] The selection was effective for both root weight and total weight, due to the wide diversity of genotypes.

"Sirayuki-kabu" was bred by the maternal line selection method from a hybrid population obtained from the cross between the vegetable cultivar "Syougoin-kabu" and the forage cultivar "Shimofusa-kabu".[6] These 2 parental cultivars originally belonged to different groups.

Moreover, a strain "Takakei 38" was bred by a double cross using self-incompatibility. Using 2 cultivars, "Shimofusa-kabu" and "Murasaki-kabu", combining ability and self-incompatibility were tested throughout 4 generations, and 4 inbred lines were selected. Of the 4 inbred lines 2 lines were derived from "Shimofusa-kabu" and the other 2 from "Murasaki-kabu". Heterosis of the bred-strain was very large. However, it has not been registered as a cultivar, because mass production of a sufficient amount of the double cross seeds requires a large-scale seed multiplication system beyond the capacity of the present system available to forage crops.

With the advance of statistical genetics, various biometrical crop breeding methods have been studied. The biometrical method in the breeding of allogamous crops such as the forage turnip is more important than in autogamous crops, because in the former it is applied not only to selection process but also to crossing and isolation methods, to tests for heterosis and combining ability, to maintenance of hybrid populations and bred-strains and so on, while in the latter it is mainly applied to selection process.

In the process of breeding the above mentioned varieties and strain, genetic parameters of various kinds were estimated. Breeding methods and techniques were also studied from the viewpoint of biometrical breeding. The present paper gives a digest of the major parts of the work.[1]

Heritabilities of and correlations among agronomic characters

Heritabilities (h^2) of 10 agronomic quantitative characters, and the genetic (r_g), environmental (r_e) and phenotypic correlations (r_{ph}) among them were calculated using the following formulae for 20 cultivars (forage and edible turnips) and for 23 strains bred at the Hokuriku National Agricultural Experiment Station.

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Table 1. Heritability and correlation among agronomic characters

Character	Group	Root weight	Leaf weight	Total weight	Root length	Root diam-eter	Root-form index	Leaf length	Leaf number	Top-root ratio	Dry matter percentage
Root weight	Cultivar	**0.89**	0.58	0.89	0.03	0.30	−0.14	0.52	0.06	−0.31	0.16
	Strain	**0.29**	−0.74	−0.38	0.01	0.91	−0.60	−0.71	−0.59	0.90	−0.38
Leaf weight	Cultivar	0.50	**0.96**	0.89	0.01	0.12	−0.15	0.91	0.28	−0.94	0.64
	Strain	0.08	**0.84**	0.09	0.48	−0.77	0.67	0.07	0.79	−0.97	0.63
Total weight	Cultivar	0.88	0.85	**0.94**	0.02	0.23	−0.16	0.81	0.19	−0.71	0.47
	Strain	0.77	0.69	**0.35**	0.67	−0.47	0.56	0.55	0.71	−0.77	0.63
Root length	Cultivar	0.05	−0.00	0.03	**0.98**	−0.28	0.30	−0.54	0.13	0.01	−0.03
	Strain	0.37	0.29	0.45	**0.67**	−0.56	0.91	0.31	0.55	−0.09	−0.08
Root diameter	Cultivar	0.40	0.14	0.32	−0.26	**0.96**	−0.94	0.32	−0.44	−0.04	0.08
	Strain	0.82	−0.18	0.48	−0.09	**0.75**	−0.92	−0.71	−0.59	0.84	−0.23
Root-form index	Cultivar	−0.10	−0.16	−0.15	0.31	−0.87	**0.99**	−0.33	0.38	0.14	−0.12
	Strain	−0.21	0.37	0.07	0.78	−0.65	**0.85**	0.58	0.61	−0.66	0.14
Leaf length	Cultivar	0.43	0.86	0.73	−0.48	0.29	−0.28	**0.96**	0.04	−0.90	0.74
	Strain	−0.07	0.31	0.36	0.22	−0.23	0.34	**0.73**	0.47	−0.78	0.34
Leaf number	Cultivar	0.07	0.28	0.19	0.13	−0.38	0.34	0.03	**0.99**	−0.32	−0.09
	Strain	0.23	0.60	0.55	0.27	−0.02	0.21	0.18	**0.78**	−0.77	0.29
Top-root ratio	Cultivar	−0.13	−0.90	−0.58	0.03	0.00	0.15	−0.83	−0.28	**0.95**	−0.79
	Strain	0.50	−0.81	−0.15	−0.04	0.64	−0.42	−0.61	−0.40	**0.88**	−0.60
Dry matter percentage	Cultivar	0.09	0.44	0.29	−0.02	0.06	−0.08	0.56	−0.05	−0.51	—
	Strain	−0.40	0.06	−0.25	−0.01	−0.38	−0.03	0.11	−0.10	−0.29	—

Values of heritability are indicated on the diagonal (boldface). Genetic and phenotypic correlation coefficients are shown on the right and the left side of the diagonal, respectively.

$$h^2 = \frac{4\sigma_g^2}{4\sigma_g^2 + \sigma_e^2}$$

$$r_g = \frac{Cov_{g1\cdot 2}}{\sqrt{\sigma_{g1}^2 \times \sigma_{g2}^2}}$$

$$r_e = \frac{Cov_{e1\cdot 2}}{\sqrt{\sigma_{e1}^2 \times \sigma_{e2}^2}}$$

$$r_{ph} = \frac{Cov_{g1\cdot 2} + Cov_{e1\cdot 2}}{\sqrt{(\sigma_{g1}^2 + \sigma_{e1}^2) \times (\sigma_{g2}^2 + \sigma_{e2}^2)}}$$

where, σ_g^2, σ_e^2, Cov_g and Cov_e are the genetic and environmetal components calculated from the analysis of the variance and covariance of measurements obtained in the 4-replication trial. The results are shown in Table 1. Heritability estimates for root weight and total weight were low in the bred-strain group, while those for other characters were fairly high in both the cultivar group and the bred-strain group. Genetic correlations in the bred-strain group were relatively higher than those in the cultivar group.

It was shown that different selection criteria are necessary depending on whether the breeding objective is concerned with total weight or root weight because a negative correlation was found between the total weight and root weight.

It was also shown that the heritability estimates of and genetic correlations among the above characters did not greatly vary over 4 years and in 5 different districts of Japan.

Coefficients of individual variation for the agronomic characters were calculated in each of 5 forage cultivars, 5 edible cultivars, and 5 forage bred-strains. No significant differences were noted among the groups. Generally, little variations were observed in leaf length and root diameter, while the greatest variation was noted in leaf weight.

Plate 1. Parental cultivars used for varietal cross
Shimofusa-kabu, Murasaki-kabu, Oonobeni-kabu, Tokyonaga-kabu, Owarioo-kabu and Tsuda-kabu from left.

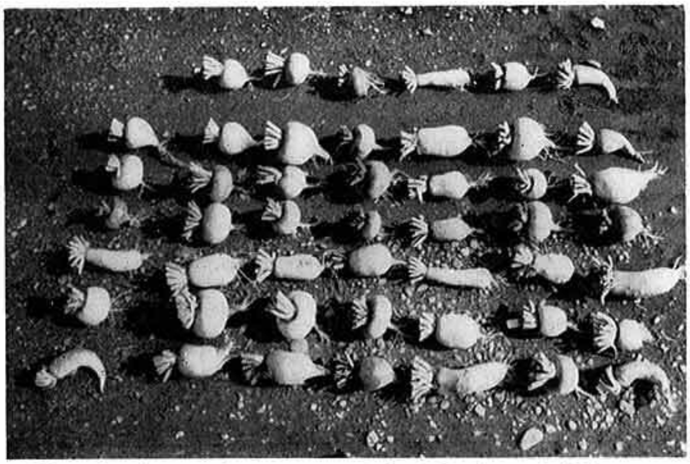

Plate 2. Roots of parents and their F_1 in a diallel cross among 6 cultivars
Parental cultivars are on the top and left rows (cultivar names are in the same order as Plate 1). Hybrids are placed on the corresponding intersections.

Variability and genetic effect in hybrid population derived from varietal polycross

In the hybrid populations derived from varietal polycross with 6 cultivars of forage and edible turnips (Plates 1 and 2), a high correlation was observed between the characteristics of parental cultivars and their general combining abilities. A specific combining ability was foremost in the root weight, and a general combining ability was foremost in the root length and root diameter.

The genetic effects in the 6 cultivars and their hybrid populations were divided into the additive (a_i), dominant (d_i) and heterotic effects (h_{ij}) by the following formulae.

$$P_i = a_i + d_i$$

$$S_i = a_i + \frac{1}{2} d_i$$

$$C_{ij} = \frac{1}{2}(a_i + a_j) + \frac{1}{2}(d_i + d_j) + h_{ij}$$

Table 2. The genetic effects of root weight

Cultivar and F_1	Additive a(g)	Dominant d(g)	Heterotic h(g)	Total (g)	d/a (%)	h/a+d (%)
1 Shimofusa-kabu	165	512		677	310	
2 Murasaki-kabu	161	400		561	248	
3 Oonobeni-kabu	245	90		335	37	
4 Tokyonaga-kabu	142	368		510	259	
5 Owarioo-kabu	353	162		515	46	
6 Tsuda-kabu	309	110		419	36	
Average	229	274		503	120	
1 × 2	163	456	28	647	280	5
1 × 3	205	301	111	617	147	22
1 × 4	153	440	97	690	288	16
1 × 5	259	337	167	763	130	28
1 × 6	237	311	106	654	131	19
2 × 3	203	245	74	522	121	17
2 × 4	151	384	186	721	254	35
2 × 5	257	281	185	723	109	34
2 × 6	235	255	88	578	109	18
3 × 4	193	229	79	501	119	19
3 × 5	299	126	149	574	42	35
3 × 6	277	100	113	490	36	30
4 × 5	248	265	67	580	107	13
4 × 6	225	239	142	606	106	31
5 × 6	331	136	215	682	41	46
Average	229	274	120	623	120	24

where P_i, S_i and C_{ij} are values of the isolate, selfing of and crossing between parents.

The effects of root weight are shown in Table 2. The proportion of additive and dominant effects was almost equal in the averaged root weight for the 6 cultivars, i.e., the total root weight of 503 g/plant was composed of 229 g of additive effect and 274 g of dominant effect in the average of 6 cultivars. However, the proportion (d/a) was quite different with different cultivars. Three cultivars (Shimofusa-kabu, Murasaki-kabu, and Tokyonaga-kabu) showed very high proportion of dominant effect, whereas other 3 cultivars (Oonobeni-kabu, Owarioo-kabu, and Tsuda-kabu) showed higher proportion of additive effect. The former group of cultivars belongs to the forage turnips, and their seed multiplication has been made on a large scale, whereas the latter group is edible turnips, which have been used to multiply on a small scale.

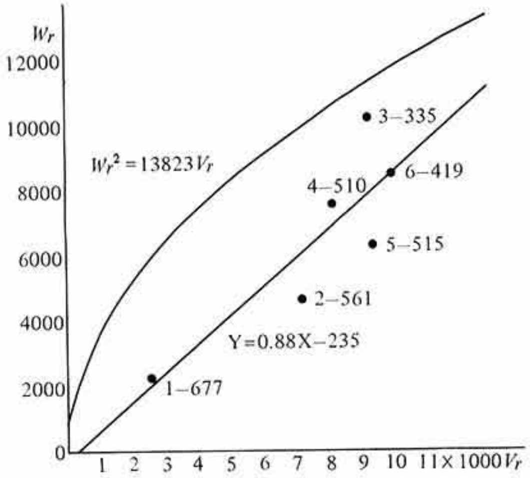

Fig. 1. V_r-W_r graph for the root weight

Numerals affixed to solid circles in the figure indicate parental number in Table 2 followed by root weight (g).

Diallel analysis proposed by Jinks[3] and Hayman[2] was applied to 15 F_1 crosses among the 6 cultivars. V_r, W_r and V_p values among these F_1 and parental cultivars were calculated by the following formulae, and a V_r-W_r graph of the root weight is shown in Fig. 1.

$$V_r=\{\sum_{s=1}^{n} {y_{rs}}^2-\frac{1}{n}\Big(\sum_{s=1}^{n} y_{rs}\Big)^2\Big/(n-1)$$

$$W_r=\Big\{\sum_{s=1}^{n} y_{rs}y_{ss}-\frac{1}{n}\Big(\sum_{s=1}^{n} y_{rs}\Big)\Big(\sum_{s=1}^{n} y_{ss}\Big)\Big\}\Big/(n-1)$$

$$V_p=\Big\{\sum_{r=1}^{n} {y_{rr}}^2-\frac{1}{n}\Big(\sum_{r=1}^{n} y_{rr}\Big)^2\Big\}\Big/(n-1)$$

where y_{rr}, y_{ss} and y_{rs} are values of rth and sth parents and the value of F_1 between them respectively, and n is the number of the parents.

Fig. 1 revealed that large root-weight was almost completely dominant, while small root-weight was recessive.

The crossing rate in polycross with the 6 cultivars was examined for each cultivar through the phenotypes of its progeny plants. The results obtained showed that the rate varied extremely, from 5 to 45%. Such bias of the crossing rate indicates that the calculation of the general combining ability using the average of the maternal lines may lead to a wrong estimation of their general combining ability.

Change of genetic composition of a population with the advance of generation and effects of selection and synthesis

Two different kinds of hybrid populations were synthesized by varietal polycrosses with 8 cultivars: 3 forage turnip and 5 edible turnip cultivars. Agronomic characteristics are distinctly different between the 2 groups of cultivars. A hybrid population was derived from the polycrossing of 8 plants, each representing each cultivar, while the other hybrid population was made of 400 plants composed of 50 plants for each cultivar. In both populations, the means and variations of 5 characters (root weight, total weight, root length, root-form index, and leaf length) were generally the largest in the first synthetic generation, while they gradually decreased in later generations.

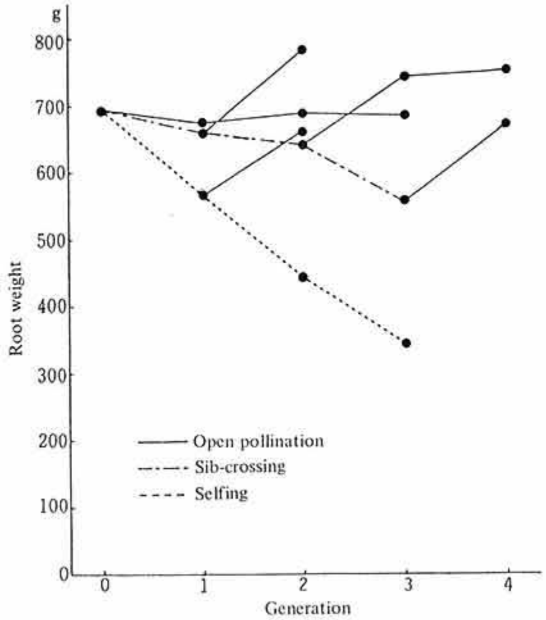

Fig. 2. Inbreeding depression of the root weight occurred with the advance of generation, and its recovery by open pollination

Inbreeding depression with an advance of generation was studied using open-pollinating, selfing, and sib-crossing populations. Inbreeding depression increased with repeated selfing or repeated sib-crossing, but the depressed individuals recovered their lost vigor immediately after they were crossed with an open-pollinating population, as shown in Fig. 2.

In a test, 4 different bred-strains, were grown for 7 generations, by taking about 50 plants from each strain to be used as the parents for polycrossing for the next generation. With these 4 bred-lines, characteristics of population were compared from generation to generation for 7 generations. Genetic shifts were not significant in 3 strains for almost all the characters measured, but were significant in one strain for such characters as root weight, leaf weight and root diameter. The values of these characters increased, as a whole, with each advancing generation.

As mass selection and maternal-line selection are considered most effective in breeding forage turnips, the effectiveness of selection of both methods was compared each other. For root-weight improvement, maternal-line selection was more effective than mass selection. In the former, the first cycle of selection gave the particularly remarkable effectiveness. Use of a fairly large number of maternal-lines was preferable for synthesizing and developing a new variety, though there was a case that only one progeny line, possessing a strong additive effect, was used for breeding a new variety.

Intra- and inter-specific competition and cooperation

Hill-seeding with later thinning is effective in preventing missing hills and is usually practised in forage turnip cultivation in Japan. However, the thinning operation has been a problem because it requires much labor and time.

Effects of competition and cooperation were investigated in relation to sowing methods, plant density and thinning.

1) Hill-seeding with thinning

Hill seeding was made in rows 67 cm apart at 4 different inter-hill distances, 50, 25, 12.5 and 6.3 cm, and the number of plants was reduced to one plant/hill by thinning. The maximum root yield was obtained at the density of 600 plants/are (25 cm of inter-hill distance, i.e. one plant per 67×25 cm area), while the leaf yield increased with the density up to 2,400 plants/are (6.3 cm of inter-hill distance).

2) Hill-seeding without thinning

Hill seeding with inter-hill distance of 25 cm and varying number of plants, 2, 4, and 8 plants/hill was made. The highest root yield was obtained at 2 plants/hill, while the leaf weight reached its maximum at 8 plants/hill.

In this experiment, the growth of individual plants in each hill was quite uniform, as a whole. Hills showing apparent difference in growth among individual plants of a hill were hardly observed. It suggests that severe competition did not occur within each hill.

The hill-seeding showed an advantage that the group of germinated seeds pushed up covering soil to help their emergence, but showed a tendency that the crowded seedlings were prone to be suffered from some diseases. However, the survival rate of plants at harvest time was consistently about 70% irrespective of the differences in sowing density or sowing methods, e.g., hill seeding or broadcast seeding. Thus, the conclusion is that a fairly high yield may be expected without thinning if about 1000 seeds are sown per are.

3) Mix-seeding

Mix-seeding of forage turnip with cabbage or radish in a hill gave higher yields of turnip without the removal of cabbage or radish. This was due to a cooperative effect followed by a specific competitive effect between the turnip and its partner crops. Sprouting and growth of the turnip in an early growth stage were promoted by the cooperative effect, and then the cabbage and radish were almost completely defeated by the turnip in the middle to late growth stage.

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