Japan. Jour. Crop Sci. 50(3) : 365-372 (1981)

Comparison of Root Systems among Hybrid Populations derived from Different Crosses in Potato (*Solanum tuberosum*)

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Received December 22, 1980

Cultivated potato (*Solanum tuberosum*) is heterozygous and autotetraploid. It is well known that for these reasons the genetic performances of their quantitative characters are very complicated. The classic studies of these aspects by MÖLLER[8] and TAGUCHI[12] indicated that the time of maturity and starch value of the segregating hybrid populations depended on the values of those parent clones used in the crosses. Though some workers (MULLIN *et al.*[9] and ROWE[10]) tried to discover the genetical basis of tuber yield, this has not yet been clarified.

In a previous report[7], we analyzed the relations between quantitative characters in a pooled hybrid population derived from crosses. This indicated that the clones with larger root dry weight tended to have a longer growing period and higher dry tuber yield. The purpose of this report is to clarify whether root dry weight and its relations with the other characters are different among hybrid populations derived from different crosses.

Materials and Methods

268 unselected clones used in this experiment were derived from six crosses with two cultivars as female parent and three selected breeding materials as male parent. The parents and the number of clones examined in each hybrid populations are listed in Table 1.

Danshakuimo (D) is the Japanese name of Irish Cobbler, and Toyoshiro (T) is a new variety coming from a population derived by several times backcrossing *S. tuberosum* to a wild race. Three WB materials (A, B, C) were selected from populations after two- to four-times backcrossing *S. tuberosum* to F_1 hybrid between *S. chacoense* and *S. phureja*.

On May 10 in 1979, 6 plants per individual clone were planted in a row with a space of 39 cm within the row and 75 cm between the rows. Only parental clones were replicated three times. A combination of fertilizer at the rate of 420 kg/ha of 12-18-12 (N, P_2O_5, K_2O) was banded just

Table 1. Parents and number of hybrid clones examined in each hybrid population.

Population				Number of clones
Female parent			Male parent	
Danshakuimo	(D)	×	WB 66109-34 (A)	44
Danshakuimo	(D)	×	WB 61037-94 (B)	44
Danshakuimo	(D)	×	WB 66201-10 (C)	55
Toyoshiro	(T)	×	WB 66109-34 (A)	49
Toyoshiro	(T)	×	WB 61037-94 (B)	32
Toyoshiro	(T)	×	WB 66201-10 (C)	44

before planting. Measurements were made in late July, at the stage when top dry weight approximately attained its maximum value (the top max. stage). One plant per individual clone was dug up to a 30 cm depth, and leaf, root and tuber dry weight (DW) were recorded after ovendrying at 80°C for 48 hrs. The method of root collecting was the same as that described in the previous paper[7]. At the harvesting stage, yield (dry tuber yield) was recorded from 3 plants per clone. All data obtained were analyzed by using a SPSS at Hokkaido University Computing Center.

Results

1. *Characteristics of the parents*

Of the male parents, A and B were the early maturity clones and C was the late one as shown in Table 2. Root DW and yield were largest in C, followed by B and smallest in A. On the other hand, tuber DW at the top max. stage was smallest in C, and leaf DW did not show significant differences between male parents. The female parents, D and T, were early maturity varieties. D tended to have a larger root DW and leaf DW than T, although yield did not show a significant difference between the female parents.

Therefore, the comparisons of the characters among the populations with different male parents will imply the influence of different maturity parents on the hybrid populations. On the other hand, the comparisons of the characters among the populations with different female parents will show the influences of the same maturity parents with different root DW and leaf DW on the hybrid populations.

2. *Comparisons of the characters among the populations with different male parents*

It is shown in Fig. 1 that the range of variation within the population in each characters was larger than the difference between the parents used in the cross. Especially, the populations with C male parent showed the wider range of variations in root DW, growing period and yield than those with A and B male parents.

Table 3 presents the mean value in the pooled population with the same male parent in each character. The CM population (D×C and T×C) had significantly larger root DW than the AM population (D×A and T×A) and the BM population (D×B and T×B). On the other hand, leaf DW did not differ significantly among these populations. As a result, the ratio of root DW to leaf DW was significantly higher in the CM population. In this population, although tuber DW at the top max. stage was smaller, the growing period was longer and the yield was higher than for those of other populations.

It is indicated by these results that the population from the cross with a late maturity parent has a wider range of variation and larger values in root DW, growing period and yield than those with early

Table 2. The characteristics of the parents.

Variable	Female parent[1]		Male parent[1]			LSD
	D	T	A	B	C	(p=0.05)
The top max. stage[2]						
Root DW (g/pl.)	2.41	1.65	0.99	1.64	2.14	0.63
Leaf DW (g/pl.)	25.92	17.45	19.63	27.67	21.12	NS
Tuber DW (g/pl.)	98.62	90.34	99.64	101.86	41.53	38.04
The harvesting stage						
Growing period[3]	81.0	81.3	83.7	84.7	137.3	5.8
Dry tuber yield (g/pl.)	230.2	196.5	166.2	246.6	342.4	68.7

Note. 1) Symbols are the same as those shown in Table 1.
2) The stage when top dry weight approximately attatined its maximum value.
3) Days from sprouting to leaf yellowing.

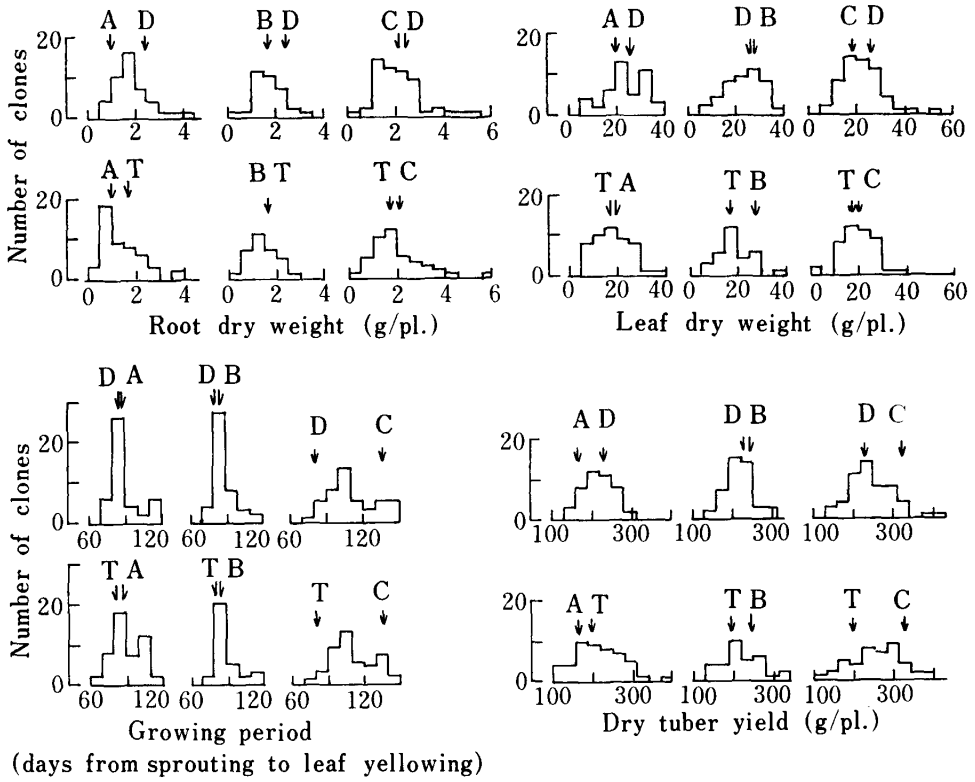

Fig. 1. Frequency distributions of hybrid clones of each cross for some characters measured.
Note. Symbols are the same as those shown in Table 1.

Table 3. Comparisons of the characters among the hybrid populations with different male parents.

Variable	Population[1]						Significance[2]		
	AM		BM		CM				
	Mean	SD	Mean	SD	Mean	SD	AM:BM	AM:CM	BM:CM
The top max. stage									
Root DW (g/pl.)	1.65	0.80	1.76	0.73	2.05	0.98	NS	**	*
Leaf DW (g/pl.)	20.85	8.21	21.60	7.73	21.33	7.69	NS	NS	NS
Root/Leaf (×100)	8.1	3.0	8.3	2.8	10.3	6.8	NS	**	*
Tuber DW (g/pl.)	106.74	38.76	97.85	37.59	85.80	32.64	NS	***	*
The harvesting stage									
Growing period (days)	90.3	12.5	89.2	9.7	111.3	17.1	NS	***	***
Dry tuber yield (g/pl.)	216.3	49.5	218.5	39.1	249.1	59.9	NS	***	***

Note. 1) AM: D×A and T×A, BM: D×B and T×B, CM: D×C and T×C. Symbols are the same as those shown in Table 1.
2) *, ** and *** show significant differences at 5, 1 and 0.1% level, respectively.

maturity parents.

3. *Comparisons of the characters among the populations with different female parents*

The populations with D female parent and those with T female parent showed almost the same range of variation in each character (Fig. 1). Table 4 presented the mean value in the pooled population with the same female parent in each character. The DF population (D×A, D×B and

D×C) had a significantly larger root DW and leaf DW than TF population (T×A, T×B and T×C). Significant differences between the two populations in growing period and yield were not found. Hence, the ratios of yield to root DW and to leaf DW were significantly higher in the TF population. The TF population had larger tuber DW at the top max. stage, although this might be due to the difference in the sampling dates at the top max. stage, namely the TF population was sampled five days later than the DF population.

These results indicate that the hybrid population from T parent with smaller root DW and leaf DW had also smaller root DW and leaf DW than those from D parent with larger root DW and leaf DW. Growing period and yield did not show any differences among two populations with different female parents, there being no differences in these characters.

4. *Relationships between the characters in the population*

Root DW showed significantly positive correlations with leaf DW, growing period

Table 4. Comparisons of the characters among hybrid populations with different female parents.

Variable	Population[1]				Significance
	DF		TF		
	Mean	SD	Mean	SD	
The top max. stage					
Root DW (g/pl.)	1.99	0.81	1.64	0.89	***
Leaf DW (g/pl.)	23.21	7.99	18.98	7.09	***
Tuber DW (g/pl.)	87.14	31.52	107.18	40.35	***
The harvesting stage					
Growing period (days)	97.9	17.3	97.5	17.2	NS
Dry tuber yield (g/pl.)	227.3	46.8	231.1	59.8	NS
Dry tuber yield/Root DW	131.5	63.5	184.2	144.5	***
Dry tuber yield/Leaf DW	11.2	5.3	14.2	9.4	***

Note. 1) DF: D×A, D×B and D×C; TF: T×A, T×B and T×C. Symbols are the same as those shown in Table 1.

Table 5. Simple correlation coefficients between some characters in each population.

Variables	Population[1]					
	D×A	D×B	D×C	T×A	T×B	T×C
Root DW						
vs Leaf DW	0.73***	0.67***	0.72***	0.77***	0.70***	0.53***
vs Growing period	0.31*	0.36*	0.45***	0.47***	0.44*	0.73***
vs Dry tuber yield	0.42**	0.52***	0.48***	0.43**	0.37*	0.55***
Leaf DW						
vs Tuber DW	0.61***	0.52***	0.56***	0.59***	0.72***	0.26
vs Dry tuber yield	0.27	0.28	0.30*	0.51***	0.47**	0.58***
Tuber DW						
vs Dry tuber yield	−0.04	−0.01	0.07	0.23	0.23	−0.01
Growing period						
vs Dry tuber yield	0.51***	0.58***	0.37***	0.75***	0.39*	0.52***

Note. 1) Symbols are the same as those shown in Table 1.

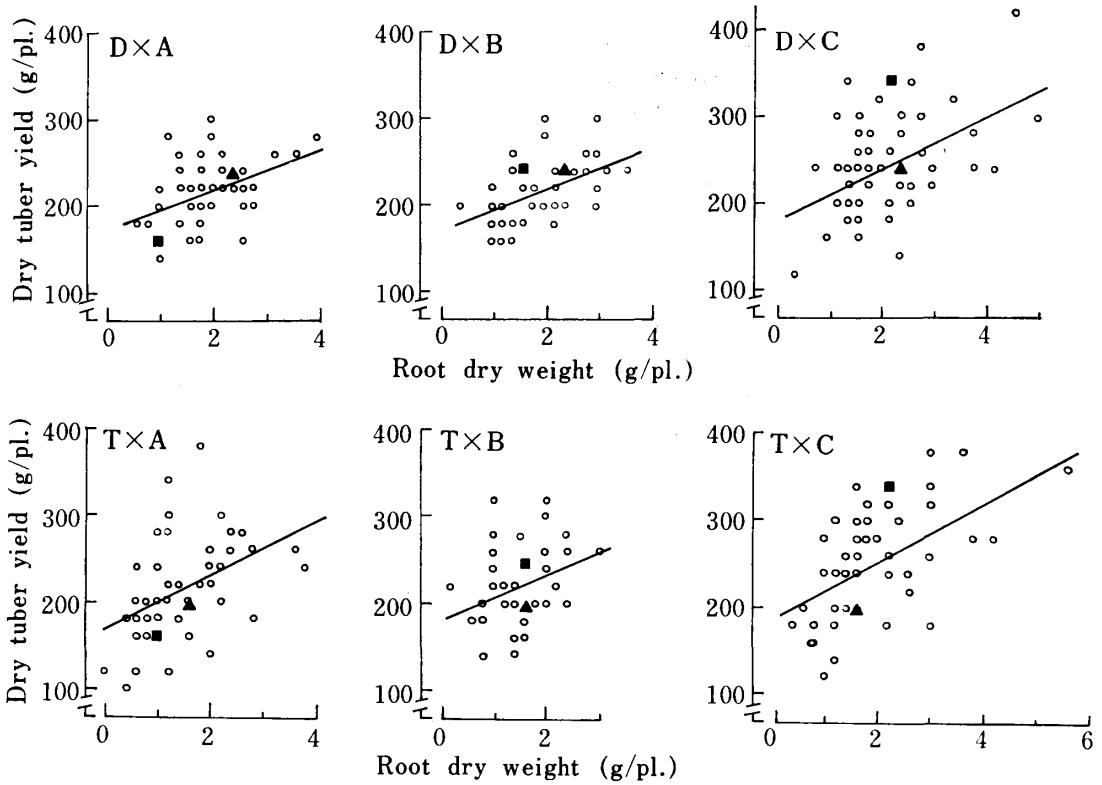

Fig. 2. Relationship between root dry weight and dry tuber yield in each population.
Note. D×A: y=21.5x+171.6, D×B: y=24.6x+168.4, D×C: y=29.4x+181.8,
T×A: y=30.8x+170.9, T×B: y=26.7x+181.3, T×C: y=33.5x+189.9.
■ : Male parent, ▲ : Female parent, ○ : Hybrid clone.

and yield in all populations, as shown in Table 5. Especially in the populations with C male parent, coefficients between root DW and growing period were higher than in the populations with A and B male parents. Leaf DW correlated positively with tuber DW at the top max. stage and yield. Coefficients between leaf DW and yield were higher in the populations with T female parent than in those with D female parent. Yield correlated significantly with the growing period in all populations, but not with tuber DW at the top max. stage.

Fig. 2 demonstrates the relationship between root DW at the top max. stage and yield in each population. The populations with C male parent showed larger root DW and higher yield, resulting from positive correlations of the growing period with two characters. The coefficients of the regression were higher in the populations with the T female parent.

These results indicate that, in each population, clones with larger root DW tend to have larger leaf DW, longer growing period and higher yield. More superior clones of root DW and yield were found in the populations with C male parent than in those with A and B male parents. In addition, the clones with the high ratio of yield to root DW were found in the populations with the T female parent more frequently than in those with the D female parent.

Discussion

The potato plant is genetically heterozygous in most of its characters. It is well noted that hybrid clones derived from crosses segregate widely in many characters, and that the superiority of the parents will not necessarily be inherited by the hybrid clones. In this experiment a very wide range of phenotypic variation in each population was also observed in the characters measured.

We report, however, that some parental

characteristics were transmitted relatively well to the hybrid clones. MÖLLER[8] and HOWARD[2] pointed out that the crosses with an early maturity clone as one parent presented the higher percentage of early hybrid clones than the crosses with a late maturity clone as one parent. TAGUCHI[12] reported that characteristics of the parents in the time of maturity, starch value and stem length were expressed clearly in the hybrid clones, suggesting that these characters might be controlled by rather few genes. In our experiment, the growing period was significantly longer in the populations derived from the crosses with the late maturity parent. A simple correlation coefficient between the mean growing period of the population and that of the parents used in the cross was very high, $r=0.99^{***}$. This result verifies earlier findings[2,8,12].

The most interesting finding in this experiment is that the characteristics of the parents in root DW were inherited by the hybrid clones. For instance, the characteristics of the hybrid populations in root DW and growing period coincided with and were linked in the same way as the parental pattern of these characteristics, i.e., the hybrid populations with the late maturity parent having larger root DW also showed a larger root DW and longer growing period. This result postulate that genes controlling the time of maturity have a pleiotropical influence on root DW.

In addition, tuber DW at the top max. stage was also different among the populations with different maturity parents. The populations with the late maturity parent showed a smaller value than those with the early maturity parents. In another experiment[4] we found that there were distinct differences among varieties in root and tuber growth rates during the period from the 4th leaf stage to the initial flowering stage. The growth rates in late varieties were higher in root DW, but lower in tuber DW, compared with early varieties. Our previous paper[7] also indicated that there was a highly negative correlation between root DW and tuber DW at the top max. stage among different maturity groups in the hybrid population. It is therefore presumed that the pleiotropy of the genes concerning the time of maturity is related to tuber growth during the relatively early stage of plant growth. The direction of the influence on tuber growth will be contrary to that on root growth. However, since larger root DW to maintain leaf and tuber bulking for a longer period is more important for higher yield than early tuber DW increase[5,7], clones with higher tuber yield should be obtained more effectively in the populations derived from the crosses with the late maturity parent than those with the early ones.

On the other hand, it was also found that two varieties of the same maturity produced the hybrid populations with different root DW. The populations with Toyoshiro as one parent had smaller root DW and leaf DW than those with Danshakuimo as one parent. Growing period and yield did not show any differences between two populations. Therefore, the populations with Toyoshiro as one parent had the higher ratios of yield to root DW and to leaf DW. The ratio of yield to root DW in the parents were 95.5 in Danshakuimo, 119.1 in Toyoshiro and 150.4 to 167.9 in male parents. The parents selected from the populations backcrossing *S. tuberosum* to wild races showed a higher ratio than Danshakuimo. In another experiment[6], Norin No. 1 derived from a hybridization with *S. tuberosum* had larger root DW than Hokkai No. 61 derived from the populations backcrossing *S. tuberosum* to wild races, although these varieties showed the same maturity and tuber yield. Thus, smaller root DW and the higher ratio of yield to root DW in the populations derived from the crosses with Toyoshiro may be due to the characteristics introduced from a wild race, being independent of the time of maturity.

Although there has been little information on the genetic aspects of the root system in the potato plants, in other crops many authors (HURD and SPRATT[3], BLUM *et al.*[1], STOFFELLA *et al.*[11], and TROUGHTON and WHITTINGTON[13]) suggested the possibility of the genetic manipulation of the root

system to get higher yield. We also conclude that characteristics of the parents in the root system will be inherited by the hybrid populations. Larger root DW resulting in higher yield will be obtained in the populations derived from the crosses with late maturity clones as one parent than in those with early maturity parents. A higher ratio of yield to root DW might be introduced, using the parents derived from the backcross populations of *S. tuberosum* to wild races.

Summary

Root dry weight (DW) and its relations with other characters were investigated among six hybrid populations derived from the crosses with two main early cultivars as female parent and three breeding materials, two early and one very late, as male parent (Table 1 & Table 2). Results obtained are summarized as follows:

The populations from the crosses with the late maturity male parent with larger root DW had a wider range of variation and significantly larger values in root DW, growing period and yield than those with the early maturity male parents, although tuber DW at the early stage was smaller in the populations with the late maturity parent (Fig. 1 & Table 3).

The populations from the crosses with Toyoshiro as female parent with smaller root DW and leaf DW also had a smaller root DW and leaf DW than those from Danshakuimo as female parent. The growing period and yield did not show any differences among these populations, so that the ratios of yield to root DW and leaf DW were significantly higher in the populations from the crosses with Toyoshiro as female parents (Table 4).

In each populations, root DW showed significantly positive correlations with leaf DW, growing period and yield (Table 5 & Fig. 2). Larger root DW resulting in higher yield should therefore be obtained more effectively from the populations derived from the crosses with the late maturity parent than from those with the early ones. A higher ratio of yield to root DW might also be effected, using Toyoshiro derived from the backcross population of *S. tuberosum* to a wild race.

Acknowledgement

The authors wish to thank Mr. K. HIOKI, Mr. K. YOSHIDA and members of Hokkaido National Agricultural Experiment Station for their generous assistance and valuable suggestion.

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* In Japanese with English Summary.

〔和 文 摘 要〕

異なるバレイショ交配分離集団間における根系の比較

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根系に関する交配親の特性と交配分離集団の特性との関係を明らかにするため，早生の男爵薯とトヨシロを母本，熟性の異なる3系統を花粉親とする交配より分離した6集団（第1表）を供試し，地上部最大期（7月下旬）の根，葉および塊茎乾物重ならびに収穫期の塊茎乾物収量を調査した．

1. 根乾物重（根重）の大きな晩生系統（第2表）を花粉親とする交配分離集団（CM 集団）では早生系統を花粉親とする分離集団（AM 集団および BM 集団）に比べ，根乾物重の集団内変異が大きく，また集団平均値が大であった（第1図，第3表）．さらに，生育日数ならびに塊茎収量も大きかった．しかし，葉重には集団間に有意な差異が認められず，また地上部最大期の塊茎重は逆に CM 集団で小さな値を示した．

2. 根重および葉重の大きな男爵薯（第2表）を母本とする交配分離集団（DF 集団）はトヨシロを母体とする分離集団（TF 集団）に比べ，根重および葉重が大きかった（第4表）．しかし，生育日数および塊茎収量には集団間に有意な差異が認められず，根重および葉重に対する塊茎収量の割合は TF 集団の方が DF 集団に比べ有意に高い値を示した．

3. 各々の集団内で，根重は葉重，生育日数および塊茎収量と有意な正の相関関係を示した（第2図，第5表）．

以上の結果より，根重の大きさは熟性に関係する遺伝子の多面発現による影響を受けるものと推察された．塊茎収量は生育日数と密接に関係しており，晩生系統を交配親に用いた分離集団では，根重が大きく晩性で高収の系統の頻度が高まるといえる．また，同一熟性の交配親間に認められる根重の差異も分離集団に遺伝することが明らかとなり，トヨシロのように野生種に由来する系統を交配親とする分離集団では，根重に対する塊茎収量の割合が高まることが示唆された．