POTATO GRAFTING EXPERIMENTS, II. SOME FURTHER RESULTS WITH THE SHORT-DAY SPECIES, *SOLANUM DEMISSUM*

By H. W. HOWARD
Plant Breeding Institute, Trumpington, Cambridge.

(Received April, 1962)

I. Introduction

In previous work (Howard, 1949) it was found that the short-day species, *Solanum demissum* Lindl., could be made to produce under long-day conditions a much larger yield of tubers if scions of a *S. tuberosum* variety, such as Epicure, which is tolerant of long days, were grafted on it. It was also found that plants grafted a second year with Epicure produced a higher yield of tubers than those grafted for one year only. There was in addition some carry-over of the effect of grafting to a second year in plants grown from grafted plants but not themselves grafted. These latter two results have been investigated further.

It was suggested in Howard (1949) that there were no long-term effects of grafting and that all the results could be explained as due to relatively immediate physiological effects. This is, of course, the answer that a geneticist educated in orthodox genetics would be expected to obtain, and there is also a tendency in designing experiments to make it impossible for any genetical modifications to be found. This tendency can be illustrated by considering the following example. Plants of *S. demissum* grafted with an early, cultivated variety, such as Epicure or Arran Pilot, produce larger tubers than ungrafted plants. If vegetative hybridization is expected, then the largest tubers from the grafted plants will be selected for growing on. If such effects are not expected, then tubers of comparable sizes from the grafted and ungrafted plants will probably be selected for the further experiments. In the second series of experiments reported in this paper, the grafted lines were carried on by selecting the plants with the largest yields each year and by using the largest tubers of these plants. This selection procedure should maximise the chances of obtaining vegetative hybrids with yields higher than the parent species, *S. demissum*.

Two separate sets of material have been investigated—further experiments with *S. demissum*, C.P.C. 19, which was the stock used by Howard (1949); and a series with C.P.C. 23, another clone of *S. demissum*. Experimental techniques were similar to those used by Howard (1949). The plants were grown as randomised blocks, each "plot" being a single pot.

II. Experiments with C.P.C. 19

A. *Results in 1949*

The experiment in 1949 (Table 1) was concerned mainly with investigations on the persistence of the effects of grafting. It had been found (Howard, 1949) that tubers formed by grafted plants produced plants which emerged earlier and flowered earlier than those from tubers from non-grafted plants. On the other hand plants grown from tubers of grafted and non-grafted plants matured at the same time and gave similar, small yields of tubers under long-day conditions.

Table 1. *Experiments with C.P.C. 19 in 1949*

(*a*) Not grafted experiment (randomised blocks; 5 replications).

Treatment number	Treatments[1] 1946	1947	1948	Mean days from planting to Emergence	Flowering	Maturity	Mean yield in gms
1A	G	G	G	7·2	44·8	159·2	8·8
1B	G	G	G	6·6	47·6	164·8	8·3
2	G	N	G	9·0	47·0	166·4	10·0
3	G	G	N	9·0	49·6	162·4	7·0
4	G	N	N	14·4	57·2	162·4	10·1

[1] Treatments—G, grafted with Epicure; N, not grafted.

Significant differences

(*i*) Days to emergence—treatment 4 later than the others, P=0·01 level.

(*ii*) Days to flowering—treatment 4 later than 1A, 1B and 2 at P=0·01 level and than 3 at P=0·05 level; treatment 3 later than 1A at P=0·05 level.

(*iii*) Days to maturity and yield—no significant differences.

(*b*) Grafted in 1949 experiment.

Treatment number	Treatments[1] 1946	1947	1948	Yield in gms per pot when grafted with Arran Pilot
1A	G	G	G	116·4; 151·5
1B	G	G	G	165·0; 175·9
2	G	N	G	247·2; 142·6
3	G	G	N	142·4
4	G	N	N	132·6; 130·8

[1] Treatments—G, grafted with Epicure; N, not grafted.

In 1949, for plants not grafted in either 1948 or 1949, it was found that grafting in 1946 and again in 1947 (treatment 3) produced both earlier emergence and earlier flowering than grafting in 1946 only (treatment 4). In other experiments (see below) it is unusual for any effect of grafting to persist through one clonal generation of non-grafting.

Two plants of each treatment were grafted with Arran Pilot to produce material for experiments in 1950. The nine plants (one plant in treatment 3 died) all produced a much higher yield of tubers than the ungrafted plants. Tuber yields from all treatments are similar.

B. *Results in 1950*

The experiment in 1950 was again directed to investigate the persistence of any effects from grafting in previous years. The results (Table 2) show that for number of days to emergence and to flowering the only event of any significance in producing a difference is whether the line was grafted in 1949, or not. Grafting for three years and then not grafting for a single year (treatment 3) is just as late in emerging and flowering as grafting a single year and then not grafting for three years (treatment 5). Size of tuber planted has little or no effect.

Table 2. *Experiments with C.P.C. 19 in 1950 (randomised blocks; 6 replications).*

Treatment number	Treatments[1] 1946	1947	1948	1949	Size of tuber planted[2]	Mean days to Emergence	Flowering	Mean yield in gms.
1A	G	G	G	G	L (15·7)	13·3	63·0	8·3
1B	G	G	G	G	S (0·19)	16·2	67·7	6·5
2A	G	N	G	G	L (19·2)	15·9	62·7	5·9
2B	G	N	G	G	S (0·29)	17·2	65·0	7·8
3	G	G	G	N	M (2·51)	26·0	76·5	16·3
4	G	G	N	N	M (1·86)	27·5	79·0	6·8
5A	G	N	N	N	M (2·12)	26·4	75·0	6·2
5B	G	N	N	N	S (0·21)	27·2	75·5	12·2

[1] Treatments—G, grafted with Epicure in 1946-48 and with Arran Pilot in 1949; N, not grafted.
[2] Size of tuber planted—L, large; M, medium; S, small. (av. weight in gms. in brackets).

Significant differences

(*a*) Days to emergence. Treatments 1A, 1B, 2A and 2B earlier (P=0·01 level) than 3, 4, 5A and 5B. Treatment 1A earlier than 1B and 2B at P=0·05 level.

(*b*) Days to flowering. Treatments 1A, 1B, 2A and 2B earlier (P=0·01 level) than 3, 4, 5A and 5B.

(*c*) Yields—no significant differences.

III. Experiments with C.P.C. 23

Because there were not available any tubers of the C.P.C. 19 stock from plants which had never been grafted, a new series of experiments was started in 1951 with another stock of *S. demissum*, C.P.C. 23. Grown under glasshouse conditions in an English summer, C.P.C. 23 appears to be a more extreme short-day type for tubering than C.P.C. 19.

The C.P.C. 23 stock has been grown for ten years, the non-grafted line being maintained by late planting (beginning of June) so that it matures under relatively short-day conditions in October. Each year the two lines, grafted and non-grafted, have been planted from the largest tubers of the pots giving the highest yields in the previous year. Arran Pilot, not Epicure, has been the variety used as the source of scions for grafting.

Table 3. *C.P.C. 23, summary of yields of tubers from grafted and non-grafted lines*

1951, seedling year (not grafted), 19·8 gms.
1952, not grafted, 4·65 gms.; grafted, 62·6 gms.

Year	Average yield per pot in gms. from Non-grafted line			Grafted line		
	early plant	late plant	early+ grafted	early plant	late plant	early+ grafted
1953	0	14·2±3·1	42·1± 6·4	0	2·6±0·7	72·5± 6·4
1954	2·8±1·6	11·0±2·1	125·3±10·9	0	7·8±1·7	142·7±12·5
1955	0	6·3±1·8	79·0± 8·7	0	12·8±2·3	123·6±10·1
1956	0	3·1±0·9	26·0± 4·2	0	15·3±3·1	30·0± 4·5
1957	0	24·0±2·6	75·7±10·1	0	28·3±3·1	56·3± 9·7
1958	0	16·3±2·4	25·8± 2·8	0	12·2±1·8	79·2± 4·1
1959	1·2±0·6	2·2±0·9	32·7± 2·4	0	2·1±0·8	68·6± 6·0
1960	0	6·7±1·7	79·8± 5·9	0	5·4±1·9	137·0± 9·2
1961	0	2·6±0·7	..	0	1·5±0·3	..

Tuber yields have varied considerably (Table 3). For yield of tubers when grafted, the grafted line exceeded the non-grafted in five years out of eight. For early planting and not grafting, it was usual for both lines to produce no tubers, the plants dying from becoming pot-bound rather than maturing. The occasional tubers formed by the non-grafted line after early planting without grafting resulted from the slow early growth of this line allowing an occasional plant not to die in the summer from becoming pot-bound and to mature under relatively short days in the autumn. For late planting and not grafting in a single year, there was no suggestion of any vegetative hybridization effects for tuber yield. Even after nine years grafting, the grafted line yielded similarly to the non-grafted when not grafted.

In addition to maintaining the two lines, grafted and non-grafted, observations were made, as with the C.P.C. 19 material, of dates of emergence of the shoot from the soil, of dates of flowering, and of yields both when grafted and not grafted. On the whole, as can be seen from the selected results discussed below, similar results to those obtained with C.P.C. 19 were found.

A. *Results in 1957*

Results for plants not grafted in 1957 are shown in Table 4. As in the 1950 results for the C.P.C. 19 experiments, but not as in the 1949 results, the only treatment with any significant effect on the time of emergence and the time of flowering is that of grafting in the previous year. Also, when tubers are planted late, the effect has more or less disappeared. This is evidently due to the longer storage period enabling the tubers from the non-grafted 1956 plants to sprout. Measurements made in other years have shown that tubers from plants not grafted in the previous year have at the end of March only very small sprouts compared with sprouts of an average length of 1·5 cms. on tubers from plants grafted in the previous year.

Table 4. *Results for C.P.C. 23 in 1957, plants not grafted in 1957 (randomised blocks, 6 replications)*

Treatment number	Treatments[1] 1952-55	1956	Early plant (April 7) Mean days to Emergence	Flowering	Late plant (June 13) Mean days to Emergence	Flowering	Mean yield in gms
1	G	G	5·1	42·0	4·8	35·2	28·3
2	N	G	4·1	42·8	4·8	34·0	25·0
3	G	N	12·9	52·0	5·5	34·8	35·0
4	N	N	9·3	51·8	6·5	36·8	24·0

[1] Treatments—G, grafted with Arran Pilot; N, not grafted.

Significant differences

(*a*) Early plant

(*i*) Days to emergence—treatments 1 and 2 earlier than 3 and 4 at P=0·01 level.

(*ii*) Days to flowering—treatments 1 and 2 earlier than 3 and 4 at P=0·01 level.

(*b*) Late plant—no significant differences.

B. *Results in 1958 and 1959*

In both 1958 and 1959 grafted plants of the grafted line produced a much bigger yield of tubers than grafted plants of the non-grafted line. This was not due to bigger tubers, but to the production of more tubers (Table 5). The 1959 results were exceptional in that for tuber yield grafting for two years has given a similar yield as grafting for one year only. This may be due to virus infection (see next section).

Table 5. *Results for C.P.C. 23 in 1958 and 1959, plants grafted with Arran Pilot (randomised blocks, ten replications in both years)*

Year of Experiment	Treatment number	Treatments[1] 1952-57	1958	Mean yield in gms. per pot	Mean tubers per pot	Mean tuber weight in gms.
1958	1	G	..	79·2	21·6	3·2
1958	2	N	..	25·8	6·0	4·3
1959	1	G	G	68·6	17·3	4·0
1959	2	N	G	35·8	8·3	4·3
1959	3	N	N	32·7	10·3	3·2

[1] Treatments—G, grafted with Arran Pilot; N, not grafted.

Significant differences for both yields and numbers of tubers

(*a*) 1958. Treatment 1 higher than 2 (P=0·01 level).

(*b*) 1959. Treatment 1 higher than 2 and 3 (P=0·01 level).

C. *Results in 1960*

The 1960 results (Table 6) for the early plant show that, for days to emergence and to flowering, grafting for one year is as effective as grafting for eight years. For yield after grafting in 1960, treatment 1 (the continuously grafted line) and treatment 3 (grafted in 1959) have significantly higher values than treatment 4 (the non-grafted line). Treatment 2 (grafted in 1958 and 1959), however, gave yields similar to treatment 4. It may be that this line had become infected with a virus in 1958. This would also explain its relatively low yield in 1959.

Table 6. *Results for C.P.C. 23 in 1960 (randomised blocks; 15 replications for early plant, 10 grafted and 5 left to flower; 5 replications for late plant)*

Treatment number	Treatments[1] 1952-57	1958	1959	Early plant (March 30) Mean days to Emergence	Flowering	Yield when grafted	Late plant (June 15) Mean days to Emergence	Flowering	Tuber Yield
1	G	G	G	5·6	43·6	137·0	2·5	35·6	6·7
2	N	G	G	7·2	42·6	68·8	3·2	35·6	6·9
3	N	N	G	6·0	43·4	118·9	3·0	42·0	14·9
4	N	N	N	22·8	71·6	79·8	4·2	44·2	5·4

[1] Treatments—G, grafted with Arran Pilot; N, not grafted.

Significant differences

(*a*) Early plant

(*i*) Days to emergence and to flowering. Treatment 4 later than 1, 2 and 3 (P=0·01 level).

(*ii*) Yield when grafted. Treatments 1 and 3 higher than 2 and 4 at P=0·01 level.

(*b*) Late plant

(*i*) Days to emergence. Treatment 1 earlier than 4 (P=0·05 level).

(*ii*) Days to flowering. Treatments 1 and 2 earlier than 3 and 4 (P=0·05 level).

(*iii*) Yields without grafting. Treatment 3 higher than others at P=0·05 level.

The results for the late plants show that, for days to emergence and to flowering, the effect of grafting in previous years is much smaller than in the early plant (see also section III A). For days to flowering there is a difference between treatments 2 and 3 but not between 3 and 4 (this was not found in the early plant where only treatment 4 was different from the rest). Treatment 3 (grafted in 1959 only) yielded more than all the other three treatments. No explanation is offered for this latter result.

D. *Results in 1961*

As 1961 was the last year of the experiments a large number of plants was grown to see whether there were any residual effects of grafting on time of emergence and of flowering when planted early. The results (Table 7) show that grafting in the previous

Table 7. *Results for C.P.C. 23 in 1961 (randomised blocks, 6 replications)*

Treatment number	Treatments[1] 1952-57	1958	1959	1960	Early plant Days to Emergence	Early plant Days to Flowering	Late plant Days to Emergence	Late plant Days to Flowering	Yield in gms
1	G	G	G	G	6·6	43·4	4·0	33·6	1·44
2	N	G	G	G	7·6	47·6	..	..	..
3	N	N	G	G	6·6	42·6	..	..	..
4	N	N	N	G	6·8	45·0	..	..	..
5	G	G	G	N	32·4	76·2	..	..	..
6	G	G	N	N	34·8	75·2	..	..	..
7	G	N	N	N	28·0	69·4	..	..	..
8	N	N	N	N	36·0	77·2	5·1	37·8	2·65

[1] Treatments—G, grafted with Arran Pilot; N, not grafted.

Significant differences

1. Early plant, days to emergence. Treatments 1-4 earlier than 5-8 (P=0·01 level); treatment 7 earlier than 8 (P=0·05 level).
2. Early plant, days to flowering. Treatments 1-4 earlier than 5-8 (P=0·01 level); treatment 7 earlier than 5 and 8 (P=0·05 level).
3. Late plant, no significant differences.

year only (treatment 4) is as effective as grafting for nine years (treatment 1), and that grafting for eight years but not grafting in 1960 (treatment 7) gives the same result as never grafting. Similar results were obtained for C.P.C. 19 (see section II B and Table 2). For late planting there is little difference between the grafted and the non-grafted lines, and the grafted line gives only a small yield when it is not grafted.

IV. Discussion

The results on the whole show that the effects of grafting can be explained on a physiological basis and that there are no reasons for suggesting that grafting changes the genetic constitution of the stock. Thus, as Howard (1949) pointed out, because day-length reactions for tuber formation must be determined by the tops, scions of a variety tolerant of long days must influence the tuber yield of a short-day stock. And it is also to be expected that the tubers formed relatively early in the growing season by the plants grafted with scions tolerant of long days will differ from those produced relatively late on non-grafted plants. Hence the effects such as shorter times to emergence and to flowering in the year following grafting occur. These effects should not last for more than one year, and this was usually found to be so. In addition, as was also observed, the effects should be less for late than for early planting.

Filippov (1940) reported that plants from grafts which were again grafted with similar scions showed effects more pronounced still after the second treatment. The results given in this paper show that this was found often for yield of tubers but not for earliness of emergence and of flowering. The effect on tuber yield (Table 5) is due to an increased number of tubers. It may be that the effect of the first year grafting is to give tubers which in the following year produce shoots with more tuber initials. The second year of grafting would then lead to these tuber initials producing tubers and not just growing as stolons as happens when the plants are not grafted.

For one set of grafts, treatment 2 of 1959 in Table 5 and treatment 2 in Table 6, it is suggested that the stocks became virus infected. This is always a possibility when working with potatoes and other plants in the family Solanaceae. It is difficult to guard against it, particularly as viruses, such as potato virus S, may produce few or no symptoms on the foliage.

In addition to the early work of Filippov (1938, 1940), more recent Russian work (references in Howard, 1960) has suggested that many other changes, including some for tuber colours, can be obtained by grafting, by eye-excision, or by the use of phasically juvenile shoots. It is possible that some of these changes also can be explained on a physiological basis of differences in maturity of tubers. This could be so, especially for tuber colours, because certain types of colour develop only late in the growth of a tuber (Howard, 1959) and because other types have variable phenotypes (Howard, 1962). Other changes may be due to some varieties being periclinal chimeras. But such explanations will not fit all the results obtained in Russia and not repeatable in other countries. This, of course, also applies to plants other than potatoes. Thus, for example, workers in England (Sachs, 1951; Bateman, 1955) and in Germany (Böhme,

1954; Stubbe, 1954) have found no graft hybridization effects in experiments with tomatoes. On the other hand it has been found that hereditable changes, all deleterious, can be induced in flax by growing the plants under conditions of low fertility (Durrant, 1958; Durrant and Tyson, 1960); negative results from similar experiments were, however, found for *Arabidopsis thaliana* (Hill, 1961). Changes in genotype from grafting and other treatments may, therefore, be possible occasionally under certain special conditions; they do not, however, usually occur.

SUMMARY

1. The wild Mexican potato, *Solanum demissum*, is a short-day type for tuber formation and under the long days of an English summer produces few tubers or none.

2. Top-grafted with scions of *S. tuberosum* varieties tolerant of long days for tuber formation, *S. demissum* produces a much higher yield of tubers than when not grafted.

3. The tubers from plants grafted in the previous year produce plants which emerge and flower earlier than those from plants not grafted.

4. Grafting for two years may produce a larger yield of tubers than grafting for one year only.

5. For both time of emergence and time of flowering, grafting in the previous year was just as effective in most experiments as grafting for two or more years previously. Also a single year without grafting led to the disappearance of any effects from grafting.

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