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# Graft-induced phenotypic changes in tomato mutants[1]

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**Summary**

Reciprocal grafts were made between normal tomato lines and 36 mutants characterized by different leaf shape and colour or by shortened internodes. Some yellow top mutants temporarily became darker green after grafting them on normal green stocks. Height of short-internode and of normal scions was only slightly affected by the genotype of the stock and the genotype of the scion was expressed almost independently from the genotype of the stock. No evidence was found for effects of movement of growth inhibiting or accelerating substances from stock to scion or from scion to stock. The same holds true for substances inducing 'virus like' symptoms.

In one graft combination normal scions on stocks of a 'wilty' short internode mutant were greatly reduced in total length, stem diameter and length of leaves. The mutant line grafted on normal rootstock did show increased vigour. Effects of the mutant as well as of the normal were expressed in one direction only, that is from stock to scion but not vice versa. The 'wilty' condition was induced in normal scion grafted on the mutant stock. Mutant scions grafted on normal stocks did still show signs of wilting. The findings are interpreted as a result of a deficient transport system in the wilty mutant.

## Introduction

It is well known that growth promoting substances as well as inhibitors may affect characters as leaf shape, height of plants and fruit set. Results have usually been obtained after exogenous application of the substances concerned.

Experiments aimed at a distinctive change in the phenotype of plants by graftings between different types have usually been unsuccessful (Brix, 1952; Denna, 1963; Rick, 1952; Roberts, 1949). In a few exceptional cases striking phenotypic changes were induced by a different graft partner (Pirschle, 1938; Rick, 1952; Stein, 1939; Wettstein and Pirschle, 1938). The present work was performed in order to investigate eventual changes induced in naturally occurring and in radiation mutants of the tomato after grafting on normal varieties and vice versa.

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## Materials and methods

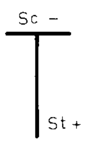
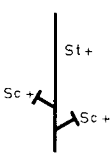
The material consisted of 6 colour or leaf shape mutants (C) characterized by variegated or yellowish leaves, green stem or by abnormal shape of leaves. A second group, 21 mutants was distinguished from the normals by short or medium internodes (S) and most of them even by leaf shape and colour (S + C). Three of the short internode mutants were of the sundwarf type; these had to be planted outdoors, as they do not express their specific character in the greenhouse. As graft partners served two normal varieties, *Moneymaker* and *Ailsa Craig,* and a long internode line, *Yellow Cherry.*

The seedlings were grown in pots in the greenhouse and were grafted approximately 5 weeks after germination. After grafting the plants were kept in humid chambers for 2 weeks and then were planted in the greenhouse. The grafting treatments are given in Table 1.

Treatments I to III were cleft grafted and treatment IV was bud grafted, all approximately 5–15 cm above soil level. Scions were pruned to a single stem. Grafting treatments I and II can show a possible upward transport, while treatments III and IV were added to demonstrate a downward movement. In treatment II the leaves of the scion were removed, because in many cases scion leaves can inactivate a possible transported substance.

All of the mutants in combination with one of the normal or long internode lines were — reciprocally — grafted and treated according to treatment I, most of them

*Table 1 Grafting treatments*

| *Symbol and No.* | *Description* |
|---|---|
|   I | Scion (Sc +): All the leaves on the single stem were allowed to develop.<br>Stock (St +): Side branches were removed, 3–6 leaves were kept. |
|   II | Scion (Sc —): All except the youngest leaves were removed once a week.<br>Stock (St +): As in No. I. |
|   III | Scion (Sc +): As in No. I.<br>Stock (St +): Two side branches were allowed to develop. |
|   IV | Scion (Sc +): Two buds were grafted into the lower part of the stock plant<br>Stock (St +): Side branches were removed, all leaves were allowed to develop. The top was pruned 4 weeks after grafting. |

even by treatment II, some by treatment I, II and III, and a few mutants received all four treatments. Two months after the grafting-date the length of scion or of stock side branches (III) was measured. Qualitative changes occurring were described once a week.

The respective graft combination in the following text and tables is indicated by the letters M (mutant) and N (normal). Thus M/N, for example, means a mutant scion grafted on a normal stock. In treatment IV the type of the top was identical with that of the stock and has been omitted. The statistical analysis was made according to Fisher's sign test.

## Results

The young yellow leaves of some yellow top mutants appeared to become darker and more green in grafts on normal green plants than in the yellow on yellow controls. This only temporary and not very distinct shift was the only *qualitative* effect found in the colour or leaf shape material. Normal scions on mutant stocks did not show any changes in qualitative characters as leaf shape or leaf or stem colour.

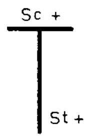
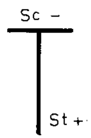
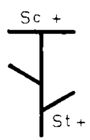
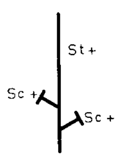
*Quantitative* changes observed in the present material were concerned mainly with height of plants, a character which is affected by vigour of the root system and/or by inhibiting or accelerating ('gibberellin-like') substances transported from stock to scion or vice versa. The results of the length measurements have been compiled in Table 2.

The comparison of the mutants on their own rootstock M/M with the controls N/N, given in column 5, shows that practically all the M/M are much smaller than their controls, the dwarfish character of most of them induces this effect. Column 6 shows that M/N is inferior in length of scion to N/M, indicating that the scion itself plays a more important role in the graft combination than the rootstock does. From the comparisons N/N : M/M and M/N : M/M, columns 7 and 8, it can be concluded that the normal rootstock in most cases allowed a somewhat stronger growth of the scion than the mutant rootstocks. This effect was only significant in some cases of removal of leaves of the mutant scion (treatment II). Comparisons N/N : M/N and N/M : M/M, columns 9 and 10, make clear that the mutant scion on the average reached only 50–70 % of the length of the normal scion even on the normal as well as on the mutant rootstock, again indicating that the genotype of the scion plays a decisive and in most cases significant role in grafts both with normal and with mutant stocks.

Thus, no evidence for major effects of upward movement of growth promoting or inhibiting substances could be found employing methods I and II. Essentially similar results were obtained with methods III and IV in which effects of downward movement could be expressed. On the contrary, the comparison N/M : M/M, column 10, in method III did show, that mutant stock side branches were slightly, but significantly longer when the mutants and not when normals served as scions.

Additional results can be added of an experiment in which nine virus-like mutants were grafted on normals and vice versa, to see whether abnormalities showing up in the mutants can be transmitted by grafting. The results were again totaly negative. Also, inoculation of sap from the graft partners on cucumber and tobacco leaves did not react positively.

*Table 2 Length of scion or stock branches as comparisons between different graft combinations; columns 5–10: the second graft combination in % of the first*

| 1 Treatment [1] | 2 Material [1] S = short C = colour | 3 Minimum number of comparisons | 4 Part of graft | 5 Comparisons [1] N/N : M/M | 6 N/M : M/N | 7 N/N : N/M | 8 M/N : M/M | 9 N/N : M/N | 10 N/M : M/M |
|---|---|---|---|---|---|---|---|---|---|
|   I | Sundwarf | 3 | scion | 42.6 | 49.8 | 89.3 | 95.9 | 44.4 | 47.7 |
| | S + (S + C) | 19 | scion | 51.1 [2] | 59.9 [2] | 93.0 | 91.8 | 55.7 [2] | 55.0 [2] |
| | C | 7 | scion | 92.4 | 96.2 | 92.6 | 103.7 | 89.2 | 99.7 |
|   II | S + (S + C) | 15 | scion | 55.9 [2] | 70.1 | 98.5 | 80.9 [2] | 69.1 [2] | 56.7 [2] |
| | C | 6 | scion | 67.5 | 87.4 | 92.5 | 83.4 | 80.9 | 72.9 |
|   III | S + (S + C) | 16 | scion | 52.7 [2] | 59.4 [2] | 91.3 | 97.3 | 54.2 [2] | 57.8 [2] |
| | S + (S + C) | 16 | stockbr. | 49.0 [2] | 204.1 [2] | 45.2 [2] | 53.1 [2] | 92.2 | 108.4 [3] |
| | C | 1 | scion | 101.8 | 86.2 | 105.5 | 112.0 | 90.9 | 96.6 |
| | C | 1 | stockbr. | 103.5 | 94.5 | 96.5 | 113.5 | 91.2 | 107.3 |
|   IV | (S + C) | 4 | scion | 42.1 [3] | 50.7 | 105.6 | 78.7 | 53.5 [3] | 39.9 |

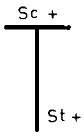
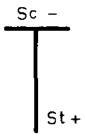
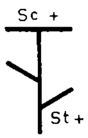
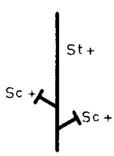
[1] Explanation in section 'Materials and methods'
[2] Significant at 1% level
[3] Significant at 5% level

*Changes in graftings with a wilty mutant.* One of the short internode mutants (Verkerk 705–15 $\beta\beta$) was characterized by dark green leaves, smaller than normal but of normal shape. On bright days the plants showed serious signs of wiltiness, the top of the plants curving downwards and the leaves drooping. Results of reciprocal graftings between this mutant and *Moneymaker* are given in Table 3.
Comparing in column 3 the length of the normal scion on its own rootstock (N/N) and on the mutant rootstock (N/M) in treatments I, III and IV it is clear that the mutant rootstock reduces the length of the normal scion to approximately 50–60%. In treatment II, where there are no leaves on the scion, these differences are not clear, however.
The results can be understood assuming a certain factor being supplied by the mutant stock at a reduced rate. Only when the demand for this factor was greatly reduced by continuous removal of scion leaves, differences between N and M rootstocks were abolished.
Column 3 treatment III shows that the lengths of the normal stock side branches are the same irrespective of the genotype of the scion. From this the conclusion can be drawn that the diminishing effect of the mutant works in one direction only, i.e. from the stock to the scion but not vice versa. A comparison of columns 3 and 4 shows that the reduction in length of the scion was caused mainly by shortened internodes.
The above scion–stock interrelationship appeared to be true even for the 'diameter of stem' measurements, column 5. It was interesting to note that normal stock side branches were more vigorous when the scion was of type M than when it was of type N. This appears to be the result of less competition for substances supplied by the stock. Length of leaves of the normal scion was greatly reduced in grafts on mutant stock (Fig. 1). Mutant leaves on the other hand were always increased in length in grafts on normal stock. The results clearly indicate that both the genotype of the stock and that of the scion itself affect the length of scion leaves.
Wiltiness was the most interesting character observed in these grafts (Table 3, column 6). In grafts consisting of two components (treatments I and II) wiltiness of the scion occurred whenever one or both components of the graft were of the mutant type. Thus M/N scions were wilty — but less severe — as well as N/M or M/N scions. In treatment III the stock side branches of a normal rootstock show no wilting; those of the mutant, however, a severe one. In treatment IV the normal bud branch is wilting only, if it is bud grafted on the mutant, while the mutant bud branch is always wilting. No interrelationship between scion and side branch (III) or top and scion (bud branch IV) was observed, each reacting only to the genotype of the stock.

## Discussion

Tomato mutants, differing from normal lines in several qualitative characters, did show their great stability in grafts with normal plants. Even in grafts between short internode mutants and normal varieties no evidence was found for a pronounced effect of endogenous substances accelerating or inhibiting growth. The genotype of scion or of stock side branches was expressed essentially independent from their graft component. This expression was modified, to a certain extent, by differences in vigour of the root system and by competition between different parts of the grafts.
The changes observed in grafts with the wilty mutant can be understood if we con-

*Table 3 Results of graftings between a wilty mutant and Moneymaker*

| *1* Treatment [1] | *2* Scion/stock combination | *3* Length of scion or of stockbranch [2] (cm) | *4* Length of internodes [2] (mm) | *5* Stem-diameter [2] (mm) | *6* Wiltiness [3] |
|---|---|---|---|---|---|
| I  | M/N | 42 | 22 | 8.5 | wilting |
| | N/M | 80 | 56 | 8.2 | wilting |
| | M/M | 62 | 30 | 8.5 | wilting |
| | N/N | 137 | 66 | 13.1 | not wilting |
| II  | M/N | 56 | 32 | 7.9 | not or slightly wilting |
| | N/M | 89 | 41 | 7.1 | slightly wilting |
| | N/N | 102 | 48 | 9.0 | not wilting |
| | M/N [4] | 66 | 37 | 7.7 | not or slightly wilting |
| | N/M [4] | 105 | 68 | 8.0 | wilting |
| | M/M [4] | 44 | 28 | 6.7 | not or slightly wilting |
| | N/N [4] | 91 | 49 | 8.2 | not wilting |
| III  | M/N scion | 77 | 34 | 11.1 | slightly wilting |
| | stockbr. | 140 | 70 | 15.6 | not wilting |
| | N/M scion | 70 | 50 | 5.8 | wilting |
| | N/M scion | 53 | 26 | 7.5 | wilting |
| | N/N scion | 143 | 70 | 15.0 | not wilting |
| | stockbr. [5] | 148 | 71 | 13.8 | not wilting |
| | M/N [4] scion | 66 | 44 | 7.1 | not or slightly wilting |
| | stockbr. [5] | 154 | 72 | 15.9 | not wilting |
| | N/M [4] scion | 85 | 60 | 7.8 | wilting |
| | M/M [4] scion | 53 | 34 | 7.0 | wilting |
| | stockbr. | 40 | 32 | 6.7 | wilting |
| | N/N [4] scion | 158 | 76 | 14.6 | not wilting |
| | stockbr. [5] | 154 | 79 | 14.4 | not wilting |
| IV  | N/N — M mutant [6] bud | 46 | 43 | 7.9 | mutant bud wilting, top normal |
| | M/M — N normal [6] bud | 69 | 57 | 8.3 | normal bud wilting, top wilting |
| | M/M — M mutant [6] bud | 32 | 30 | 6.1 | mutant bud wilting, top wilting |
| | N/N — N normal [6] bud | 110 | 70 | 13.1 | normal bud not wilting, top not wilting |

1 Additional explanation in section "Materials and methods"
2 Mean of five internodes below third fully grown leaf from top
3 Three observations were made
4 Replication
5 Mean of upper and lower stock side branches
6 Mean of upper and lower bud branches

sider them as a result of a defect in the transport system of the mutant line. A normal root system then cannot entirely abolish the effect of the abnormal condition of mutant scions and a normal scion grafted on mutant stock will show the disorder because of insufficient supply of the substance in question. The relatively large leaf area of normal scion will accentuate the situation.

As the mutant plants were not wilty when temperatures were low or medium, and drooping symptoms became more serious with increasing temperatures, the deficiency may be concerned with water transport and related processes. The assumption that a different potential for water uptake by the normal and the mutant root system plays a role too is plausible but not necessary to explain the results. As shown earlier, mutant branches appeared wilty and their leaves did not reach normal size even in grafts on normal stock.

The above hypothesis conforms with the results of graftings made according to method II, i.e. removal of scion leaves. The grafts, irrespective of their combination, were not or only slightly wilting at times when grafts without removal of scion leaves did show serious signs of wilting. It is obvious that a limited supply of water or of other substances would have less serious effects in plants with a reduced leaf area. Nevertheless, plants with reduced leaf area still did show signs of water stress when temperatures in the greenhouse became very high — the most resistant combination involving the mutant being scion on normal stock.

The wilty condition of a dwarf tomato mutant investigated by Alldridge (1964) was caused by anomalous vessel elements, offering a barrier to conduction in all parts of the plants. Also Rick's (1952) grafting experiments with a wilty dwarf mutant

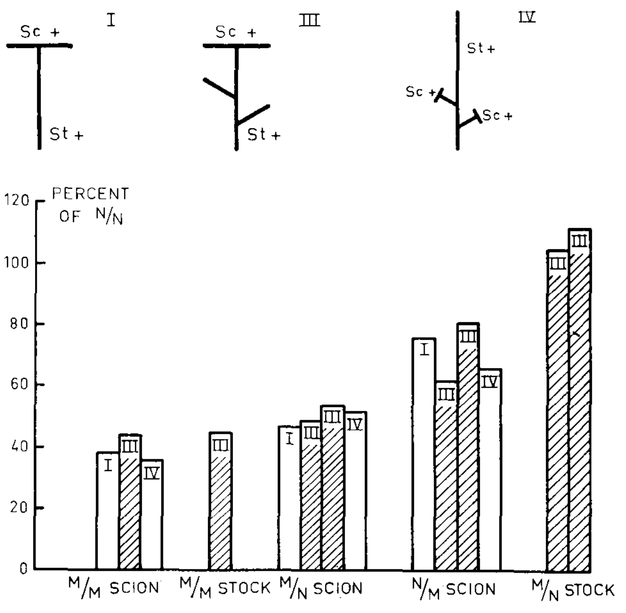



*Fig. 1 Length of leaves in grafts between a wilty mutant M and Moneymaker N. Mean of five leaves below the third fully grown leaf from top, in % of the normal control. Treatments I, III and IV see Table 1.*

gave experimental results similar to ours. His tentative conclusions, based on results with double grafts, were quite different. He concluded, that stocks modified the growth of scions in the combination M/N and N/M and that the influence of the stock was rested not in its stems or leaves, but in its root system. Both in Rick's and in our own experiments, mutant scions grafted on normal stocks were reduced in leaf area as compared to normal scions; they did show the wilty condition and other signs of abnormal growth. Therefore, the disorder appears to be based on abnormalities of both the stock and the scion part and it is expressed whenever one or both components belong to the mutant type.

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Wettstein, F. und Pirschle, K., 1938. Über die Wirkung heteroplastischer Pfropfungen und die Übertragung eines genbedingten Stoffes durch Pfropfung bei *Petunia*. *Biol. Zentralbl.*, 58 : 123–142.