Theor Appl Genet (1998) 97: 705–713

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Graft-induced genetic changes and the inheritance of several characteristics in pepper (*Capsicum annuum* L.)

Received: 30 December 1997 / Accepted: 3 March 1998

Abstract The general characteristics of several graft-induced changes in pepper were investigated in a cross experiment. F_1, F_2, and BC_1 progenies derived from crosses of the original stock and scion cultivars 'Spanish Paprika' and 'Yatsubusa', respectively, as well as their graft-induced variant strain G_5S_{25} were analyzed for inheritance of the most conspicuous graft-induced variant traits. As part of a research program with the aim of revealing the mechanism of graft induction, the present study was carried out to examine the stability of the phenotypic changes and the characteristics of the graft-induced variants. For the fruit apex, a two-gene system was suggested, with other factors having a modifying influence. One of the two apex genes acted for pointed fruits and the other for inverted-blunt fruits. The inverted-blunt gene, the apex gene of the stock, was unambiguously present in the graft-induced variants, while the pointed gene that acted in the dominant mode in the original scion was inactive and expressed only under certain conditions in a mosaic state. The stable inverted-blunt cultivar used for the stock maintained certain factor(s) for pointed fruit, but the presence of that factor(s) could not be detected in graft-induced variants. The results of pungency analysis suggested a gene for non-pungency that appeared to be introduced in the graft-induced variants. The fruiting habit and fruiting direction that appeared in a mosaic state in graft-induced variants were found to combine factors of the stock with the appropriate characteristics of the scion asymmetrically. The bushy plant type appeared in a transgressive state in the variants, showing a definitely higher number of branches on the main stem and more frequent ramifications on the complete plant than on either the stock and scion cultivars or the progeny derived from sexual crosses. A change in mature fruit color from red to yellow occurred in an early generation of graft-induced variants. Our results demonstrate that some of the characteristics of the stock were introduced into the progeny obtained from selfed seeds of the scion and that novel characteristics appeared as a result of graft induction.

Key words Grafting · Transformation · *Capsicum annuum* · Red pepper · Genetic analysis

Introduction

Graft-induced changes have been reported in many cultivated plants, such as eggplant (Hirata 1979, 1980a; Hirata et al. 1986), red pepper (Yagishita 1961; Kasahara et al. 1971; Ohta and Choung 1975), petunia (Frankel 1961; Corbett and Edwardson 1964), soybean (Hirata and Yagishita 1986), tobacco (Hirata et al. 1989), and tomato (Hirata 1980b). Several grafting techniques have been used, and in pepper a higher rate of variants has been obtained by applying the mentor-grafting method. When selfed seeds of the scion are sown, individuals with variant characteristics can develop. In the present investigation new characteristics completely different from those of the stock or scion appeared in a mosaic state in both fruits as well as vegetative organs after the first grafting, and all repeated grafting with seedlings derived from the changed fruits of the previous scion increased the ratio of these characteristics. Analyses of changes in general characteristics (Yagishita 1961, 1964; Kasahara et al. 1971, Hirata and Yagishita 1993), fruit shape (Yagishita and Hirata 1987), pungency (Yagishita et al. 1990), plant

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Communicated by G. Wenzel

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type (Yagishita and Hirata 1986), and regeneration ability in tissue culture (Saito et al. 1992) have been reported, while changes observed in other traits, such as fruiting habit, fruiting direction, stomatal size, and leaf shape have been discussed by Hirata et al. (1995). Here we describe a detailed analysis of the inheritance of graft-induced variant traits.

Materials and methods

Plant material

Originally the bell-type pepper cultivar ‘Spanish Paprika’ (Sp) was used as a stock and the elongated and pointed-type cultivar ‘Yatsubusa’ (Y) as a scion. The different characteristics of these two cultivars that were changed as a result of grafting in the selfed progeny of the scion are given in Table 1. The graft-induced variant strain G_5S_{25}(G) that was obtained after five successive graftings and maintained by selfing for 25 generations was included in the analysis. F_1, F_2, and BC_1 progenies of Sp, Y, and G were produced by reciprocal crosses.

Grafting

Variant plants discussed here were obtained from Y scions after the young seedlings of the latter were grafted by the mentor-grafting method onto Sp stocks. Seedlings derived from selfed seeds of the scion were again grafted onto Sp. This preparation was successively repeated five times (Yagishita 1961).

Analysis of graft-induced variant characteristics

The inheritance of fruit shape, pungency, fruiting direction, fruiting habit, and plant type was investigated to determine the genetic nature of the changed characteristics.

Results

No substantial difference was found between the results of crosses and reciprocal crosses in each combination.

Fruit shape

‘Spanish Paprika’ is a typical bell pepper, having cubical shaped fruit with a fruit apex generally consisting of three to four lobes that create the inverted-blunt characteristic of this cultivar. In contrast, ‘Yatsubusa’, the cultivar that was grafted onto Sp, has elongated fruit and a pointed fruit apex. Graft-induced variants are rather more cylindrical than cubical or conically elongated. The fruit apex appeared non-pointed (all type of fruits which vary from the original Y fruits) or inverted-blunt as in Sp (Figs. 1, 2). Currently there are two lines; one of them, with two-lobed fruits, was selected immediately after inverted-blunt fruits had appeared in graft-induced variants. Eighty percent of its fruits are two-lobed and 90% are non-pointed. The other line for three-lobed fruits was selected from the 16th selfed generation of graft-induced variants (Fig. 3).

The relationship of blunt and pointed fruit types upon crossing shows generally partial dominance for pointed varieties (Lippert et al. 1965). In contrast, McArdle and Bouwkamp (1983) have suggested a single dominant gene model for the blunt fruit apex, with modifying interaction of other genes that may act to produce a pointed fruit even if the apex gene dictates a blunt one.

The F_1 progeny of Y-Sp and Y-G crosses had pointed fruit, whereas those of Sp-G crosses F_1 had non-pointed fruit (Fig. 4, Table 2). When Y-Sp crosses were backcrossed to the pointed parent Y, the progeny showed incomplete dominance for pointed fruit, with a 15:1 segregation (177:13 = pointed:blunt). When the inverted-blunt type Sp was used in a backcross, a 1:1 (60:63) blunt to pointed segregation ratio was observed, although a 7:9 or 9:7 segregation could also be inferred. The F_2 progeny of the Y-Sp crosses (Fig. 5) showed a ratio closer to 13:3 with 71:10 pointed:blunt fruits than to a 3:1 ratio. Y-G crosses the F_2 (Fig. 5) showed a 7:9 (49:68) pointed:blunt segregation, while backcross progenies of Y-G crossed with Y yielded almost solely pointed fruits (150:7 = pointed:blunt). When Y-G crosses were backcrossed

Table 1 Characters of the stock (‘Spanish Paprika’) scion (‘Yatsubusa’), and graft-induced variants that were changed by the effect of grafting

Character	Spanish Paprika	Yatsubusa	Graft-induced variants
Fruit apex	Inverted-blunt	Pointed	Non-pointed (90%) Inverted-blunt (80%) (chimeric)
Pungency (Capsaicin content)	Non-pungent	Pungent (0.19%)	Moderately pungent (0.09%)
Fruiting direction	Pendent	Erect	Mainly erect (chimeric)
Fruiting habit	Non-fasciculated	Fasciculated	Mainly fasciculated (chimeric)
Plant type	Non-bushy	Weak bushy	Bushy
Stomatal size	Large	Small	Intermediate
Leaf size	Large	Large	Small
RAPD markers	+	−	+
Regeneration ability in tissue culture	Weak	Very weak	Relatively good

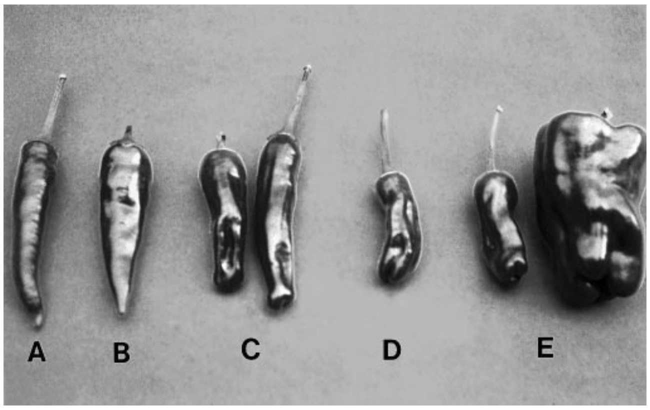

Fig. 1A–E Different types of fruit shape in graft-induced variants. **A** Fruit of the original pointed-type scion cultivar ‘Yatsubusa’, **B–D** pointed, non-pointed, and two-lobed inverted-blunt fruits of graft-induced variants, respectively, **E** three-lobed inverted-blunt fruit of a graft-induced variant and fruit of the original bell-type stock cultivar ‘Spanish Paprika’

Fig. 2 A cluster of typical graft-induced variant fruits

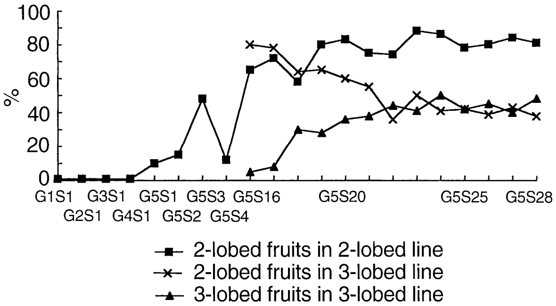

Fig. 3 Transition in frequency of two-lobed and three-lobed fruits in graft-induced variant strains. Selection for two-lobed fruits was done from the first generation (G_1S_1) and for three-lobed fruits from the G_5S_{16} generation using one line of the graft-induced variants. G_{1-5} Number of graftings from the first to the fifth, *S* number of selfed generations of the appropriate grafting

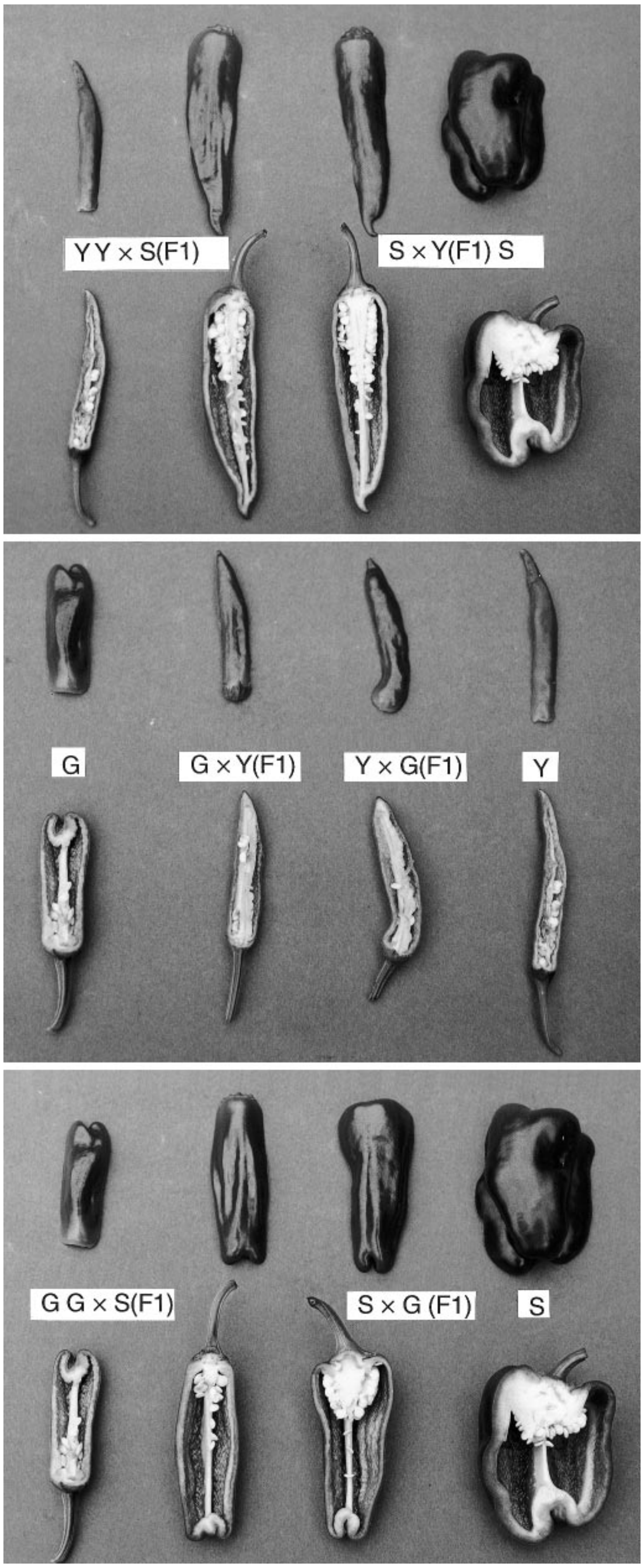

Fig. 4 Fruit shapes of F_1 fruits from reciprocal crosses of ‘Yatsubusa’ (*Y*), ‘Spanish Paprika’ (*S*) and the graft-induced variant line G_5S_{25} (*G*). Fruits are positioned according to their fruiting direction. No differences were evident in reciprocal crosses

Table 2 Segretation ratios of some graft-induced variant characteristics in parental, F_1, F_2, and BC_1 generations

Generation	P^a p	C c	Up up	Fa fa	Number of nodes[b]	Number of branches[b]
S[c]	0:100	0:100	100:0	100:0	12.7 ± 1.53 (23)	0.2 ± 0.86 (23)
Y	100:0	100:0	0:100	0:100	15.0 ± 1.09 (36)	1.8 ± 1.63 (36)
G	0:200	200:0	0:200	0:200	22.6 ± 2.48 (20)	13.3 ± 3.88 (20)
S × T(F_1)	35:0	35:0	35:0	35:0	11.3 ± 2.05 (11)	1.4 ± 1.69 (8)
Y × S(F_1)	40:0	40:0	40:0	40:0	12.7 ± 2.24 (11)	1.2 ± 1.40 (11)
Y × G(F_1)	44:0	44:0	0:44	0:44	18.7 ± 2.56 (7)	6.7 ± 3.20 (7)
G × Y(F_1)	27:0	27:0	0:27	0:24	21.0 ± 2.65 (11)	4.2 ± 2.66 (11)
S × G(F_1)	0:20	20:0	20:0	20:0	14.8 ± 1.29 (64)	3.4 ± 2.34 (59)
G × S(F_1)	0:24	24:0	28:0	24:0	16.0 ± 1.63 (30)	1.4 ± 1.64 (27)
S × Y(F_2)	38:6	75:63	253:141	278:114	13.0 ± 3.07 (45)	1.5 ± 1.41 (44)
Y × S(F_2)	33:4	53:29	116:78	175:33	14.9 ± 2.79 (143)	1.5 ± 1.57 (77)
Y × G(F_2)	31:41	154:3	0:240	0:236	19.4 ± 3.80 (74)	6.3 ± 3.00 (61)
G × Y(F_2)	18:27	73:0	0:224	0:225	17.1 ± 2.92 (144)	4.7 ± 2.74 (68)
S × G(F_2)	3:55	39:32	359:184	425:121	17.8 ± 3.31 (92)	3.4 ± 2.12 (67)
G × S(F_2)	3:48	61:97	213:101	242:74	14.1 ± 2.87 (155)	1.9 ± 1.51 (71)
(Y × S) × Y	87:8	37:0	18:32	37:26	13.9 ± 1.86 (157)	0.8 ± 1.21 (122)
(Y × (Y × S)	13:0	14:0	8:5	8:6	15.7 ± 1.75 (157)	2.4 ± 2.10 (15)
(S × Y) × Y	59:0	71:1	47:42	52:28	16.2 ± 1.76 (119)	3.1 ± 2.41 (59)
Y × (S × Y)	18:5	6:0	3:3	7:2	14.2 ± 1.60 (37)	0.6 ± 0.96 (96)
(Y × S) × S	21:22	– : –	32:2	32:3	13.1 ± 1.86 (67)	0.7 ± 1.10 (64)
S × (Y × S)	1:12	– : –	9:0	8:0	11.9 ± 1.51 (22)	0.3 ± 0.55 (22)
(S × Y) × S	28:23	3:3	52:0	49:3	13.0 ± 1.32 (129)	1.4 ± 1.41 (77)
S × (S × Y)	10:6	– : –	27:0	28:0	11.9 ± 2.09 (49)	1.4 ± 1.17 (49)
(Y × G) × Y	24:3	29:0	0:29	0:29	15.0 ± 2.04 (29)	4.0 ± 2.24 (28)
Y × (Y × G)	25:0	33:0	0:68	0:33	15.5 ± 1.67 (32)	2.4 ± 1.95 (32)
(G × Y) × Y	51:2	48:0	0:67	0:67	17.3 ± 3.01 (87)	5.0 ± 2.33 (60)
Y × (G × Y)	50:2	39:0	0:68	0:68	16.3 ± 2.77 (100)	2.4 ± 1.55 (30)
(Y × G) × G	31:3	50:0	0:51	0:51	16.0 ± 2.65 (59)	3.7 ± 2.40 (37)
G × (Y × G)	2:74	89:0	1:117	1:117	18.7 ± 3.39 (139)	5.4 ± 2.84 (32)
(G × Y) × G	8:41	50:0	0:50	0:50	19.6 ± 3.61 (48)	6.9 ± 3.03 (48)
G × (G × Y)	0:26	35:0	0:35	0:35	18.4 ± 2.58 (32)	4.6 ± 2.84 (32)
(S × G) × S	2:29	0:2	39:0	41:0	13.4 ± 2.06 (77)	2.1 ± 1.54 (47)
S × (S × G)	0:14	– : –	8:0	8:0	11.7 ± 1.93 (38)	0.5 ± 0.89 (20)
(G × S) × S	1:19	0:2	43:0	43:0	12.6 ± 1.81 (84)	1.2 ± 1.31 (52)
S × (G × S)	1:19	– : –	14:0	14:0	14.1 ± 2.38 (25)	1.5 ± 1.48 (26)
(S × G) × G	2:26	3:1	41:23	52:12	17.5 ± 2.52 (132)	3.6 ± 2.49 (62)
G × (S × G)	0:23	– : –	5:6	7:4	18.0 ± 2.38 (13)	2.2 ± 1.69 (26)
(G × S) × G	0:34	11:10	32:22	46:15	17.3 ± 3.05 (113)	2.0 ± 1.53 (37)
G × (G × S)	0:21	8:3	15:15	21:8	16.6 ± 2.88 (64)	2.4 ± 2.00 (39)

[a] Gene symbols *P*, *p*, *C*, *c*, *Up*, *up*, *Fa* and *fa* indicate pointed, non-pointed, pungent, non-pungent fruits, pendent, erect fruiting direction and non-fasciculated, fasciculated fruiting habit, respectively

[b] Nodes and branches were counted between the cotyledonary node and the first main ramification, where the first flower is to be found. Data are shown as mean ± SD. For nodes and branches the number of analyzed plants are in parenthesis

[c] S = 'Spanish Paprika', Y = 'Yatsubusa', G = graft-induced variant line G_5S_{25}

to G, a 1:3 (41:144) pointed:blunt segregation was observed. However, each combination showed strong deviation. In three combinations, (G × (Y × G), (G × Y) × G, and G × (G × Y)), nearly all the fruits were of the blunt type (10:141 = pointed:blunt), but in one, ((Y × G) × G), exactly the opposite trend was observed (31:3 = pointed:blunt). In the cross between the two inverted-blunt parents Sp and G, pointed fruits also appeared in the F_2 progeny (6:103 = pointed:blunt) (Fig. 5) and in the BC_1 progency (4:81 = pointed:blunt) when Sp was the other parent. On the other hand, when Sp-G was backcrossed to G, none of the progency except for one combination bore pointed fruit (2:134 = pointed:blunt).

These results are not consistent with a single-gene model for the fruit apex. The dominance of the pointed type was complete in F_1 plants of pointed × inverted-blunt crosses. The segregation patterns in F_2 and BC_1 progenies of Y-G and Y-Sp crosses cast doubt on the monogenic dominance of the pointed fruit model and suggest the presence of another gene that is non-allelic for pointed and dominant for inverted-blunt fruit. Our results indicate that for the fruit apex both the pointed and inverted-blunt genes are dominant, and which of

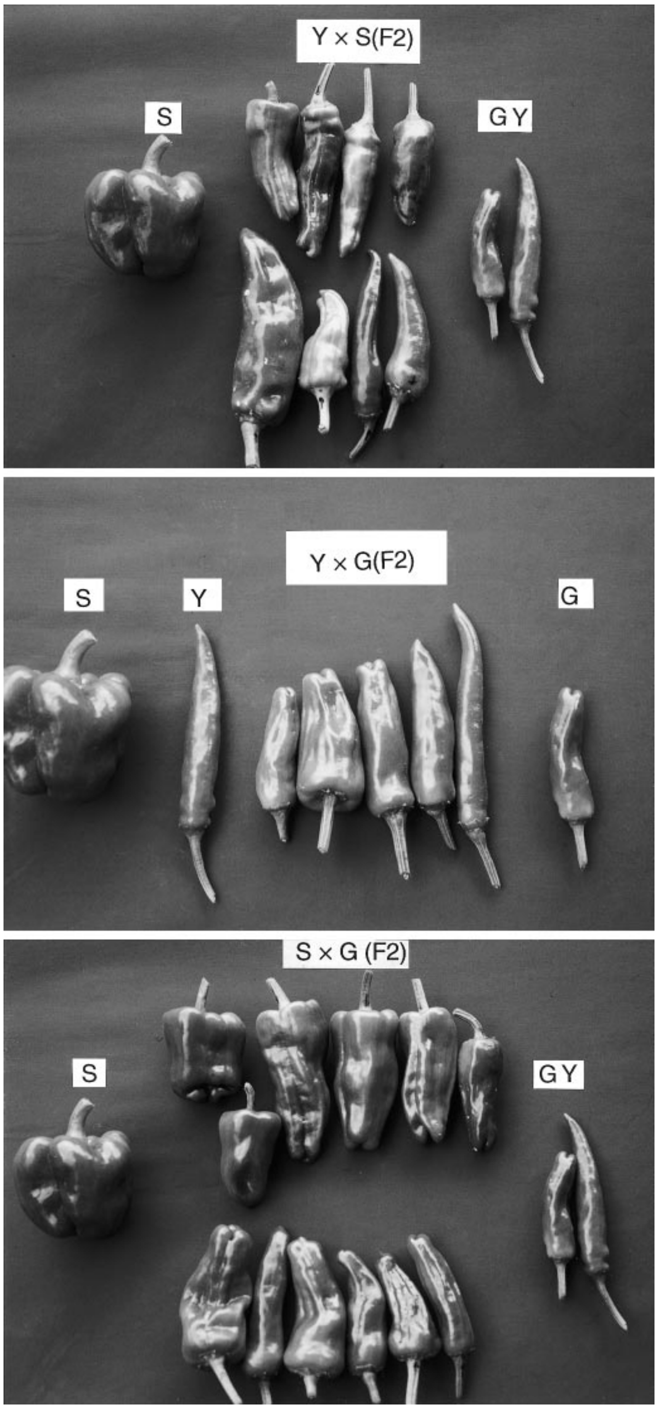

Fig. 5 F_2 fruits from crosses among 'Yatsubusa' (*Y*), 'Spanish Paprika' (*S*) and the graft-induced variant line G_5S_{25} (*G*). Pointed versus non-pointed, pendent versus erect fruits segregated out in the F_2 generations. Fruits are positioned according to their fruiting direction

them is expressed phenotypically if both are present depends on their genetic interaction as well as on the modifying influence of other factors. Because only inverted-blunt and pointed parents were used in this experiment and their relationship with other fruit shape formations was not examined, it would be hasty to propose a gene symbol for the above-described gene. However, we will refer to it here as the inverted-blunt gene. According to progeny analysis, this inverted-blunt gene is unequivocally introduced into the graft-induced variants.

In the (Y × G) × G and (S × G) × G backcrosses where G was the mother plant, the reason for the high segregation as well as the appearance for pointed fruits must be investigated.

Crosses with the Sp parent exhibited an even more complex system. Although Sp is a stable, inverted-blunt-type cultivar, pointed fruits were also produced from crosses with the other inverted-blunt parent G. Sp-Y crosses showed a 13 : 3 pointed to blunt segregation in F_2, while G-Y crosses segregated in a 7 : 9 pointed to blunt ratio in the F_2 generation. When Sp-G was backcrossed to Sp, several pointed fruits were detected, but upon backcrossing to G, none of the progenies except for one combination had pointed fruit. Considering the segregation patterns in F_2 and in the backcross progenies, we concluded that although Sp is an inverted-blunt cultivar, it maintains certain factors that are responsible for pointed fruit expression in several combinations.

Pungency

Graft-induced changes in the capsaicinoid content analyzed by HPLC have already been reported (Yagishita et al. 1990). However, the results of the present test crosses showed that complementary findings must be added to the previous ones. Cultivar Y and the graft-induced variant contained an average 0.19% and 0.09% capsaicinoid, respectively. HPLC analysis of Sp revealed the presence of capsaicinoids, although at extremely low levels; thus it is a stable non-pungent cultivar. In this experiment plants were classified by taste probes as being pungent or non-pungent. All of the F_1 and the backcross progeny of Y and G proved to be pungent (Table 2). Segregation into pungent versus non-pungent plants was detected when the F_1 progeny were backcrossed to Sp. The F_2s of the Sp-Y and G-Sp crosses segregated into 9 : 7 and 7 : 9 pungent : non-pungent ratios, respectively, suggesting that two genes may act in the expression of this characteristic. Moreover, the detection of non-pungent fruits in the F_2 of the Y-G cross and in the backcross progency of the Sp-G crosses indicated that factors establishing a non-pungent character do exist. The graft-induced variant contains this factor which is able to decrease the production of capsaicinoids. We speculate that this factor is non-allelic to the pungency gene and that a different locus acts for non-pungency.

When classification was based on taste probes, the segregation patterns of the F_2 and BC_1 generations

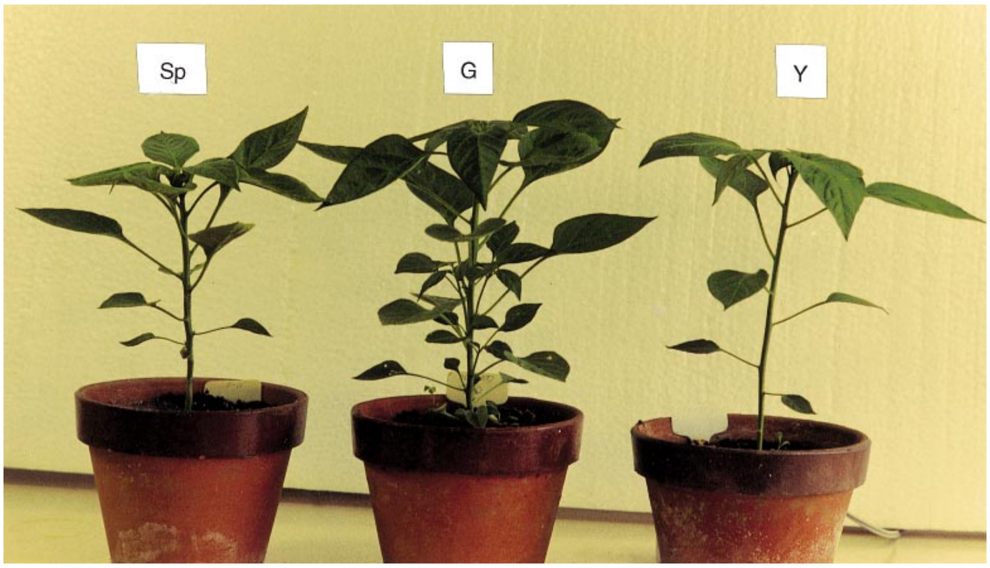

Fig. 6 The typical bushy plant type of graft-induced variant plants (*G*) compared to the stock cultivar 'Spanish Paprika' (*Sp*) and to the scion cultivar 'Yatsubusa' (*Y*)

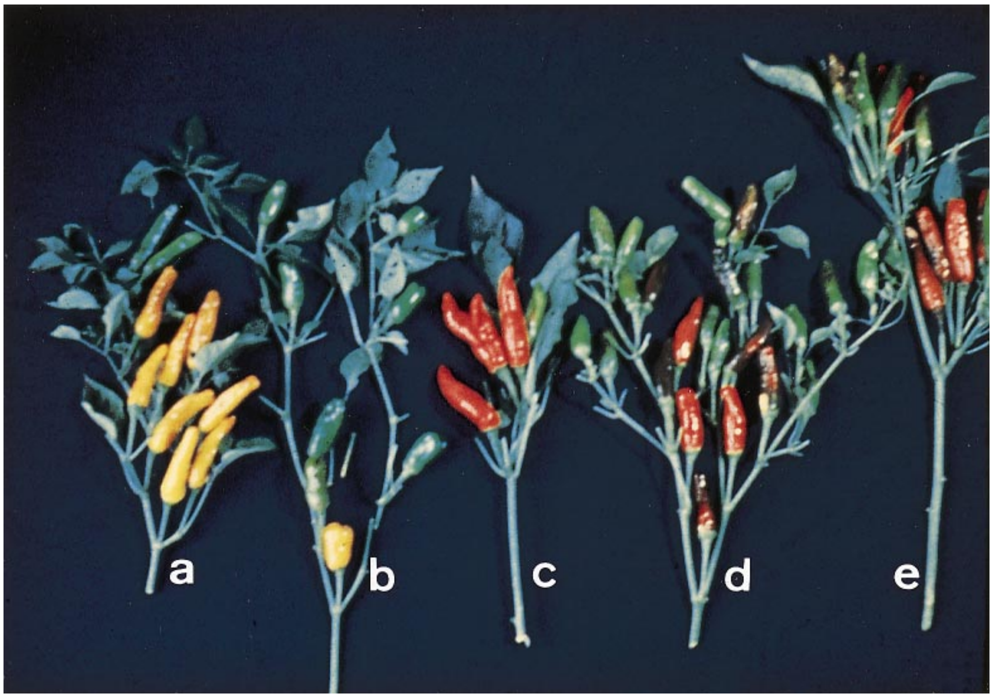

Fig. 7 Change in fruit color. The original stock (Sp) and scion (Y) cultivars as well as the graft-induced variants turn immediately from green to red during ripening. Yellow and yellow-orange fruits appeared in the G_5S_3 generation of selfed graft-induced variants (*a* and *b*). Others are variations in fruit shape and fruiting habit in this generation: *c* a branch similar to 'Yatsubusa', *d* non-fasciculated, pointed and inverted-blunt fruits, *e* fasciculated, pointed and inverted-blunt fruits

revealed that a two-gene system (pungency vs. non-pungency) regulates capsaicinoid synthesis, as suggested by Loaiza-Figueroa and Tanksley (1988). HPLC analysis revealed the presence of capsaicinoids in low amounts in the sweet stock cultivar as well as in some non-pungent individuals of the segregating progenies, indicating that the regulation of capsaicinoid production might be more complex than a two-dominant-gene model.

Fruiting habit and direction

Because of similarities in genetic behavior in this experiment, fruiting habit and fruiting direction are discussed together. Sp bears non-fasciculated pendent fruit, while Y and G have fasciculated erect fruits. In graft-induced variants, non-fasciculated as well as pendent fruits also appear in a mosaic state among the fasciculated as well as erect fruits. Both traits are considered to be single-gene-determined dominant characteristics for both non-fasciculated as well as pendent fruits. For fruiting direction, a two-gene system has also been suggested (Gopalakrishnan et al. 1989).

For fruiting direction, the F_1 showed no segregation (Fig. 4). F_2 of the Sp-Y crosses showed strong deviation from the expected 3 : 1 (369 : 219) ratio, but the segregation in backcrosses (76 : 82 when backcrossed to Y and 130 : 2 when backcrossed to Sp for pendent : erect, respectively) followed the prediction of a single-gene model (Table 2). The F_2 of Sp-G crosses bore pendent fruits at a higher rate than the Sp-Y crosses (572 : 285 pendent : erected), and BC_1 segregated for more pendent than erect individuals (93 : 66 when backcrossed to G and 106 : 0 when backcrossed to Sp). A pendent fruit-bearing plant appeared among 118 plants in the G × (Y × G) backcross, indicating that there is enough genetic materials in the graft-induced variants to express the pendent character of the stock in certain combinations.

Fruiting habit is also considered to be determined by a single gene. The F_1 progeny of Sp-Y and Sp-G crosses were all non-fasciculated, whereas in Y-G crosses both the F_1 and the F_2 were fasciculated (Table 2). The F_2 progeny of the Sp-Y and the Sp-G crosses (453 : 147 and 667 : 195 non-fasciculated : fasciculated, respectively) fitted the single-gene supposition, but the backcrosses showed deviation from the expected segregation ratios (104 : 62 when Y-Sp were backcrossed to Y and 126 : 39 when G-Sp were backcrossed to G, non-fasciculated : fasciculated, respectively). Non-fasciculated fruits appeared in a mosaic state on G, and the segregating progeny showed definitely higher segregation for non-fasciculated fruits, indicating that grafting changed the genetic basis of the fruiting habit.

Unexpected segregation and deviations from the expected segregation ratios revealed the complexity of both characteristics. Graft-induced variants show unusual behavior for the two traits, suggesting that they alloy parts of the stock with the original scion characters asymmetrically, that differing from the inheritance observed in sexual crosses.

Plant type

As a unique new characteristic, a high number of nodes and branches appeared on the main stem in the graft-induced variants (Fig. 6). This characteristic, called the bushy plant type, was analyzed by evaluating the number of nodes and offshoots between the cotyledonary node and the first main ramification of branches, the node where the first flower is to be found. The results showed the same strong fluctuation in the crosses as in the parents (Table 2). Although no conclusion can be drawn from these data, it is obvious that in the offspring the number of branches is closer to that of the lower-branch-number parent. However, this does not appear to be the case for nodes. It seems likely that environmental factors influence the genotypic expression. The cultivar Sp has the lowest number of nodes (11-14), and branches were found only in rare cases (0-1). For Y, a higher number of nodes (14–17) and branches (0-5) is characteristic, while the definitely bushy-type graft-induced variants have many nodes (20-25) and branches (7-17) on the main stem, and these are present at the same density on the other parts of the plant. The high number of nodes and branches may be one reason for the higher yielding ability of the graft-induced variants compared with Sp or Y. The bushy plant type of G was inherited stably in the progeny, whereas none of the several thousand individuals derived from crosses of Sp and Y analyzed up to now have expressed a similar characteristic. We consider that the occurrence of the bushy plant type is due to graft-induced transgression whereby genetic material of the stock combines in a different way with the scion genome.

Fruit color

During maturation the fruit color of G, Sp, and Y turns immediately from green to red. However, after the fifth grafting in the third generation of selfed variants (G_5S_3), yellow and yellow-orange fruits also appeared (Fig. 7). While there is a possibility of mutation for this change in fruit color, we consider that extensive changes in the genome during the process of grafting and further rearrangements in the progeny could result in the new characteristics of yellow fruits. No further genetic analysis was performed for this character in the present study.

Changes in genomic DNA

Using random primers, several random amplified polymorphic DNA (RAPD) markers were detected. These

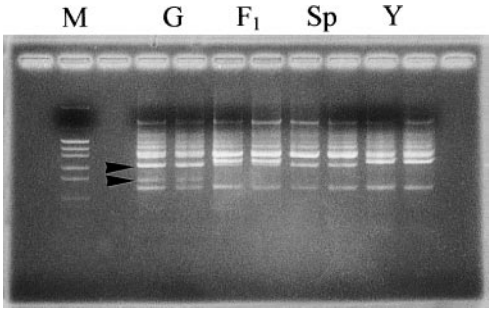

Fig. 8 A RAPD marker (*upper arrow*) is found in the stock cultivar (*Sp*) (*lanes 6*, *7*) and in graft-induced variants (*G*) (*lanes 2*, *3*), but is absent in the scion cultivar (*Y*) (*lanes 8*, *9*). A weaker band (*lower arrow*) was also detected by the same primer but only in *G*. *Lanes 4*, *5* are F_1s of Sp-Y; *M* (*lane 1*) is the DNA size marker

markers were found only in the stock cultivar Sp and the graft-induced variants but were absent in the scion cultivar Y (Fig. 8). New, graft-induced variant-specific markers were also detected, while the loss of Y markers was recognized. Details of molecular analysis will be published in the near future.

Discussion

We are interested in answering the question of how genetic changes can occur in grafts. The results of our cross experiments demonstrate that graft-induced variant traits are inheritable new characters. Changes were analyzed in traits whose genetic nature was not unequivocally established. These characters were expressed in a different way in the graft-induced variants than in either the stock or scion cultivars.

In the case of fruit shape, the segregating progeny showed that the graft-induced variants behave as stable inverted-blunt parents. Without the complicating factor(s) for pointed fruit, only the inverted-blunt gene of the stock seems to be introduced in G. The spares occurrence of pointed fruits in graft-induced variants may be due to environmental effects as well as the expression of the original pointed gene which, when completely expressed, is epistatic to the inverted-blunt gene. When the pointed gene is incompletely expressed, or when epistasis with the inverted-blunt gene is incomplete, neither the pointed nor the inverted-blunt type is clearly distinguishable, giving rise to a large spectrum of non-pointed fruit variations.

For pungency, the assumed non-pungency gene could have been partially introduced into the variants, causing a significant decrease in capsaicin production. A second locus determining pungency has already been suggested, but the inheritance of pungency versus non-pungency seems to be more complicated than a two-dominant-gene system.

In G fruiting habit and fruiting direction were found to express the dominant non-fasciculated as well as the pendent fruit characteristics of the stock in a mosaic state among the majority of fasciculated and erect fruits. Although no genetic basis could be established, graft-induced variants seem to contain some factors of the stock and express them along with the appropriate scion characteristics in the same individual. The effect of the stock is also detectable in segregating progeny derived from crosses of G with Sp and Y, showing deviation toward the stock characteristics.

The bushy plant type appeared as a unique and new trait in graft-induced variants. A high number of branches and nodes on the main stem as well as on the complete plant and a higher yielding ability than that of the stock or scion cultivars are characteristic for G. We can only suggest that certain introduced factors of the stock combined in an exceptional way with genes of the scion that control shoot differentiation or the hormonal balance, giving rise to this character.

This study was carried out to ascertain the genetic nature of several graft-induced variant traits. However, molecular analysis will be necessary in order to understand the mechanisms of the graft-induced changes. Several RAPD markers were detected using a limited number of primers. These markers were present in the stock cultivar and in G but absent in the scion cultivar. Graft-induced variant-specific markers could also be detected. Since no segregation in the selfed progeny of graft-induced variants was noticed after the first variants appeared, the possibility of accidental fertilization by unknown pollen can be rejected. All successive grafting increased the degree of variations (Yagishita 1964), indicating a gradual influence or a gradual genetic change that differs from the occurence of mutations. The detection of RAPD markers also reveals that mutation could not have been the reason for the changes, since it is difficult to imagine that mutations occurred in a way that produced thesame bands which are polymorphic in the stock when compared to the scion. Uptake of exogenous DNA via the vascular system and its expression in the plant has already been described (Hirata et al. 1995). Principally, graft-induced genetic changes can also be attributed to direct DNA uptake through the vascular system. A detailed molecular analysis of graft-induced genetic changes in pepper will be presented in the near future.

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