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# MODIFICATIONS TRANSMITTED TO THE OFFSPRING, PROVOKED BY HETEROGRAFT IN *SOLANUM MELONGENA*

by

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During the past two decades different publications have reported results in which some characteristics of grafted plants seemed to be altered in the offspring (1, 4, 5, 6, 7, 8, 10, 11, 13, 14, 17, etc.). On the other hand some other attempts have proved to be failures (2, 9, 12, 15, etc.).

Following different authors (3, 4, 7, 8, 14, etc.), we are studying the problem of transmission of altered characteristics by means of grafts in *Solanum melongena*. This work has been in progress since 1957.

## MATERIAL AND METHOD

We have made intervarietal grafts in *Solanum melongena* and interspecific grafts between a variety of *Solanum melongena* and a strain of *Solanum nigrum*.

The following operating procedure has been used: mentor epibiota on pupil hypobiota. We pluck off almost all the leaves during the whole development of the pupil plant, the one we want to influence, and which is younger than the mentor plant. We leave only one or two young sap-pumping leaves. On the other hand, the mentor plant keeps its foliage, but its flower-buds are cut off as soon as they appear. Therefore the nutritive substances of the pupil plant are nearly all elaborated by the mentor plant.

Homografts of the pupil variety represent the *check-plants*. Their symbionts are of course treated like those of the heterografts.

We have ascertained the genetic stability of our plants over six generations; they form our *control* strains.

For the intervarietal heterografts, we have used three egg-plant varieties. The "Violette hâtive" (Early violet) variety served as mentor plant; it is distinguished

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by a long violet fruit, brown-edged stamens and a violet stem. The “Blanche longue” (White long) and the “Blanche ronde” (White round) are the pupil specimens which we try to influence; their fruits are respectively long or round, white coloured, their stems are green.

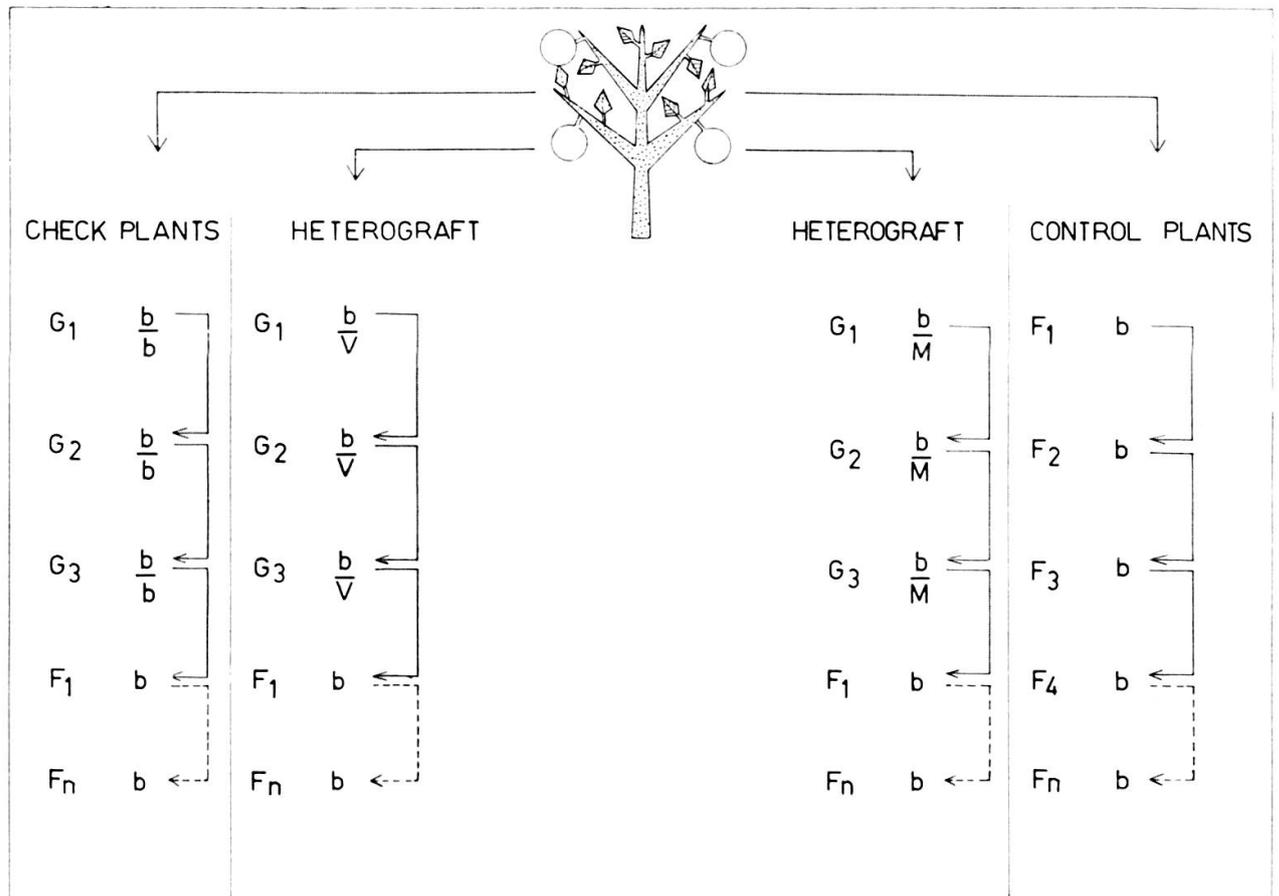


Figure I.

Diagram of the experiments on intervarietal heterografting between the «Blanche ronde» egg-plant pupil (b) and the «Violette hâtive» egg-plant mentor (V) and on interspecific heterografting between the «Blanche ronde» egg-plant pupil (b) and the Black Nightshade mentor (M).

For the interspecific heterografts, we have used a strain of Black Nightshade (*Solanum nigrum*) as mentor plant and the “Blanche ronde” egg-plant variety as pupil plant.

The “Blanche ronde” pupils of the heterografts and of the homografts and the control plants all come from the same specimen (Figure I).

The flowers of the pupil plants are self-pollinated. At each generation, each fruit used to obtain the next generation is divided into two parts: the seeds of one part are used to give pupil-plantlets which will be grafted to mentor plants; the other half gives rise to plantlets that will develop without being grafted. We call G the graft generations (G<sub>1</sub>, G<sub>2</sub>, etc.) and GF the generations coming from symbionts but which

develop without being grafted ( $G_1F_1$ ,  $G_2F_1$ ,  $G_2F_2$ , etc.). 70% to 90% of the grafted plants bore fruits.

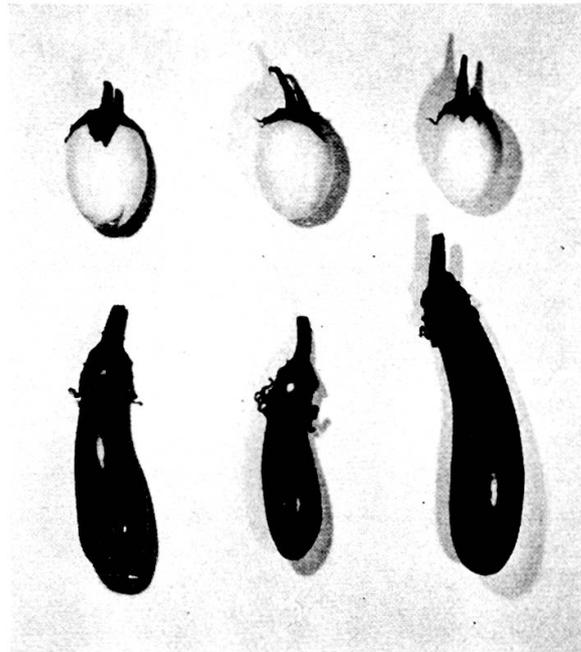
We have begun the study of the anthocyanins of the plants by paper chromatography\*. The pigments are extracted in methyl alcohol acidified by hydrochloric acid 1/100. We use Schleicher and Schuell 20-43 glatt paper. The migration takes place in a meta cresol-glacial acetic acid-distilled water medium.

## RESULTS

### *Intervarietal hererografts*

*First series: "Blanche longue" / "Violette hâtive".*

After two graft generations, we have not found any alteration of the "Blanche longue" variety and we have stopped the experiment.



Photograph I.

Above: white fruits of the « Blanche ronde » egg-plant variety (pupil).

Below: violet fruits of the « Violette hâtive » egg-plant variety (mentor).

(Photograph P. Schauenberg).

*Second series: "Blanche ronde" / "Violette hâtive".*

The 19 homograft check-plants "Blanche ronde" / "Blanche ronde" of the third generation of grafts (descended itself from 5  $G_2$  plants coming from 5  $G_1$  plants) have remained similar to the standard (Figure II).

\* This work is made in collaboration with Dr. L.A. DESHUSSES, Director of the "Laboratoire de Chimie agricole" of Geneva.

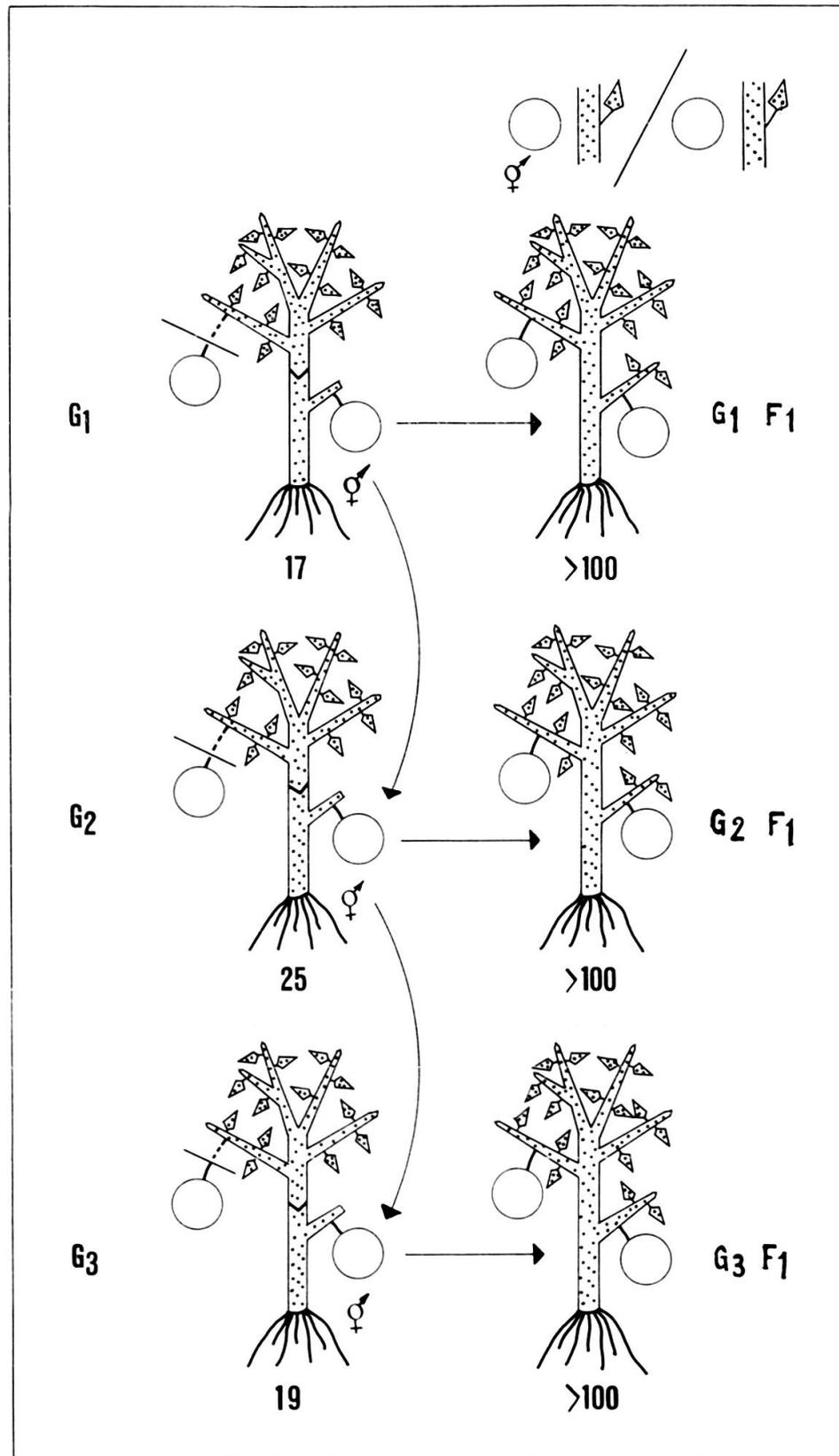


Figure II.

Homograft: The « Blanche ronde » mentor egg-plant (scion) and the « Blanche ronde » pupil egg-plant (stock) have their green stems dotted; their white fruits are represented by white circles.

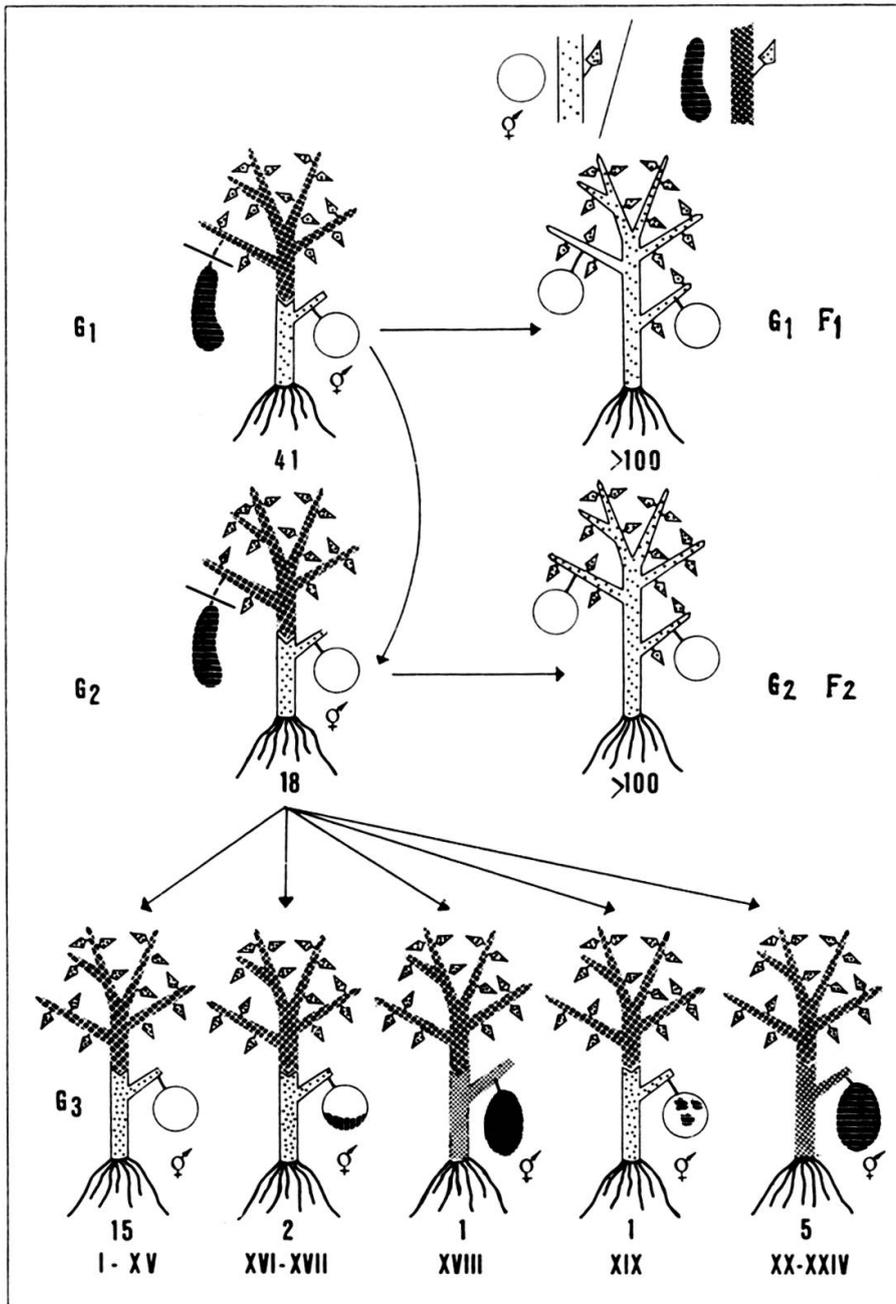


Figure III.

Heterograft: the mentor-epibiota is the « Violette hâtive » egg-plant; the pupil-hypobiota is the « Blanche ronde » egg-plant.

The influence of the "Violette hâtive" mentor on the pupil variety "Blanche ronde" (photograph I) appeared at the third generation of grafts (descended itself from 4  $G_2$  plants coming from 6  $G_1$  plants). Among the 24 symbionts that bore fruits, 9 showed various modifications (Figure III).

*Plant no. XVI:* the single fruit has a violet tinged aureole at its base.

*Plant no. XVII:* the first fruit which appeared has the same violet tinged aureole; the other fruits seem normal.

*Plant no. XVIII:* the first fruit which appeared is long and purplish violet, the other fruits are more or less long and of the same colour; the stem is pale violet.

*Plant no. XIX:* the first fruit is round and white, sprinkled with zones of violet dots; the other fruits are white, round and of extremely varied sizes.

*Plants no. XX to XXIV:* all the fruits are more or less oblong to long and violet coloured. The stamens have brown edges; the stems are violet tinged.

We have studied the sexual offspring  $G_3F_n$  of the different types of plants. Let us recall that the fruits are self-fertilized and that the plantlets descended from seeds gathered first in  $G_3$ , then during the successive  $G_3F_n$ , develop without themselves being grafted on the mentor variety. However we have not been able to study the offspring of plants XXII and XXIV since their fruits rotted before the seeds were ripe.

The sexual offspring  $G_3F_1$  of the 15 non modified pupil symbionts have remained similar to the standard "Blanche ronde". Such is not the case for the modified plants.

In the case of a sexual crossing between the mentor and the pupil varieties ("Blanche ronde" ♀ × "Violette hâtive" ♂) the segregation of characteristics occurs in  $F_2$ . In the offspring of the modified heterografts on the other hand, this can be observed already in  $G_3F_1$ . The new characteristics often present differences from those of the  $F_2$  sexual hybrid. The following tables show these results.

*Table I:* The  $G_3F_1$  specimens descended from plant no. XVI have a more or less violet tinged stem. The fruits do not seem to be altered.

Following the offspring up to  $G_3F_4$  we have observed the same modification of the stem pigmentation at each generation.

*Table II:* The  $G_3F_1$  specimens descended from the violet tinged aureole fruit of plant no. XVII have a more or less violet tinged stem. The fruits do not seem to be altered.

We can see the same modifications in specimens coming from normal  $G_3$  fruits. Following the offspring up to  $G_3F_3$  we have noticed at each generation the same modification of the pigmentation of the stems of the plants and this in both series.

TABLE I

Offspring  $F_1$  of the plant XVI ( $G_3$ )

Generations		Fruit shapes			Stem colours			Stamens' edges		
		round	oblong	long	green	violet tinged		yellow	brown	
<p><i>Sexual crossing</i> : Egg-plant « Blanche ronde » ♀ × Egg-plant « Violette hâtive » ♂</p>										
F <sub>1</sub>		47 plants. faded violet (47) X				+	++	+++		X
F <sub>2</sub>		147 plants. white (14): X X X X X green (56) X X X X X purplish-violet (47): X X X X X violet (30): X X X X X				X	X	X	X	X
<p><i>Heterograft</i> : Egg-plant « Blanche ronde » ♂/Egg-plant « Violette hâtive » plant XVI (<math>G_3</math>)</p>										
G <sub>3</sub> F <sub>1</sub>		7 plants. white (7) X								X











TABLE VII

Offspring  $F_1$  of the plant XXIII ( $G_2$ )

Generations		Sexual crossing : Egg-plant « Blanche ronde » ♀ × Egg-plant « Violette hâtive » ♂			Heterograft : egg-plant: « Blanche ronde » ♀ / Egg-plant « Violette hâtive » plant XXIII ( $G_3$ )				
		Fruit shapes			Stem colours			Stamens' edges	
Generations		round	oblong	long	green	violet tinged		yellow	brown
					+	++	+++		
$F_1$	47 plants. faded-violet: X					X			X
$F_3$	147 plants. white (14): X   X   X   X					X			
	green (56): X   X   X   X				X	X			
	purplish-violet (47): X   X   X   X				X	X	X		
	violet (30): X   X   X   X							X	X
$G_3F_1$	126 plants. white (11): X   X   X   X			X	X			X	
	green (39): X   X   X   X			X	X			X	
	purplish-violet (15): X   X   X   X			X		X	X		X
	violet (61): X   X   X   X			X		X	X		X

*Table III:* The  $G_3F_1$  offspring coming from plant no. XVIII present a marked segregation not only in the colour of various organs of the plant but also in their shape. The differences between this segregation and the one of the sexual  $F_2$  are: *a)* the absence of brown edged stamens which are always found in sexual hybrid plants with violet and purplish-violet fruits and *b)* the presence of black-violet fruits and stems.

The offspring of the white and green fruits in  $G_3F_2$  look like the  $F_3$  descent of the  $F_2$  white and green fruits after sexual crossing. The specimens descended from violet and purplish violet fruits show in  $G_3F_2$  and in  $G_3F_3$  a segregation similar to the one noticed in  $G_3F_1$ . As for the strain coming from the black-violet fruits, it seems homozygous with reference to this characteristic which we have watched up to  $G_3F_4$ .

*Table IV:* The specimens  $G_3F_1$  descended from plant no. XIX also show a segregation of characteristics that alter the shape of the fruits but not their colour which remains white (Photograph II). The stems are green or violet tinged. The descent of a long fruit gives in  $G_3F_2$  a greater proportion of plants bearing long fruits than round fruits. This relation is reversed in the round fruited strain. The stems remain green or violet tinged.



Photograph II.

Offspring  $F_1$  of plant no. XIX ( $G_3$ ): the white fruits are of round, oblong and long shapes  
(Photograph P. Schauennberg).

*Table V, VI, VII:* The segregation noticed in  $G_3F_1$  offspring descended from plants no. XX, XXI, and XXIII resembles that observed in the sexual hybrids of the mentor and pupil varieties in  $F_2$ . We have not yet finished the study of  $G_3F_2$ .

These modifications can be transmitted by the male plant.

The anthocyanins which appeared in the descent of  $G_3$  modified pupil plants, have been studied by paper chromatography; the Rf values of the pigments are very close to those of the "Violette hâtive" variety. Moreover, in the descent of plant XVIII, new anthocyanins appear.

*Interspecific heterografts*

"Blanche ronde"/Black Nightshade.

The influence of the Black Nightshade mentor on the "Blanche ronde" egg-plant pupil appeared in the descent of the third graft generation, that is in  $G_3F_1$ , since the  $G_3$  plants themselves were not altered (Figure IV). From two  $G_2$  plants descended from 4  $G_1$  plants, we have obtained 7 "Blanche ronde" fruit bearing symbionts in  $G_3$ . The descent of two of them (plants VI and VII) showed alteration of the colour of the stems becomes slightly violet tinged. The pigmentation however is very thermolabile; it disappears when the temperature rises (Table VIII).

This characteristic remains for the moment up to  $G_3F_3$ . By paper chromatography we have found the same two anthocyanins in the descent of the two modified  $G_3$  pupils specimens; their Rf values are different from those of the Black Nightshade pigments. No pupil characteristic seems related to the Black Nightshade mentor in this interspecific heterograft.

TABLE VIII

Offsprings  $F_1$  &  $F_2$  of the heterograft *S. melongena* « Blanche ronde » ♀/*S. nigrum* ♂  
plant VI

Sexual crossing : <i>S. melongena</i> « Blanche ronde » ♀ × <i>S. nigrum</i> ♂			Heterograft : <i>S. melongena</i> « Blanche ronde » ♀/ <i>S. nigrum</i> ♂		
Generations	Fruits	Stem	Generations	round fruits white	green ← stem colours slightly violet tinged
$F_1$	/	/	$G_3F_1$	49 plants X	X $\xrightleftharpoons{t^0}$ X
$F_2$	/	/	$GF_2$	73 plants X	X $\xrightleftharpoons{t^0}$ X

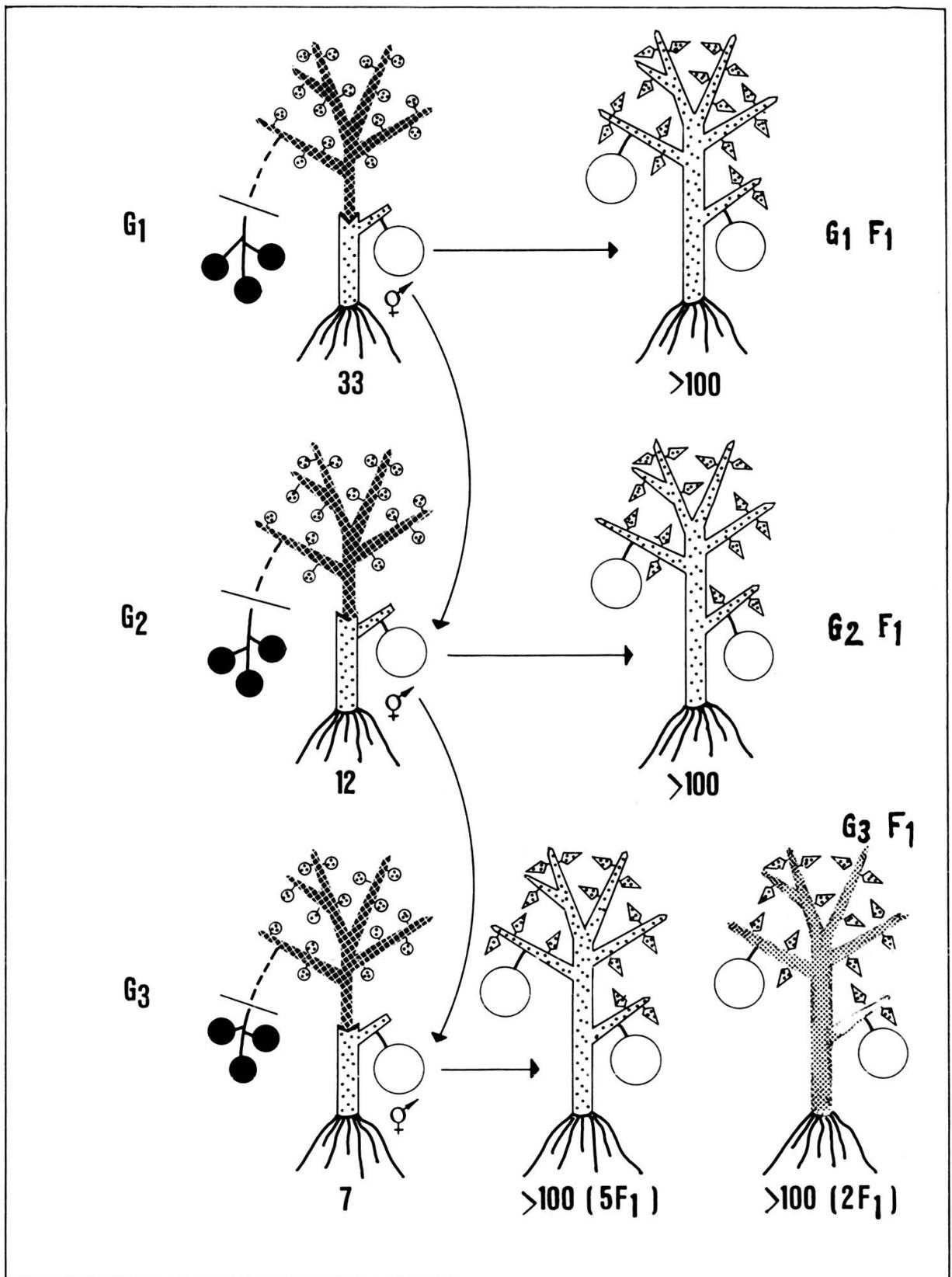


Figure IV.

Heterograft: The Black Nightshade mentor (scion): The violet tinged stem is black chequered; the violet-black fruits are represented by black circles.  
 The « Blanche ronde » egg-plant pupil (stock): the green stem is dotted; the white fruits are represented by white circles.  
 The slightly violet tinged stems of the plants descended from two G<sub>3</sub> specimens are grey chequered.

## DISCUSSION

Heterografting can provoke in genetically stable plants modifications capable of being transmitted to the non grafted descent of the pupil symbionts. We have noticed modifications affecting the shape and the pigmentation of the fruits, the appearance of the stamens and the colour of the plants.

We have observed a diversity of the alterations from one heterograft to the other. Moreover the sensitivity of the plants to the treatment varies; thus according to this experiment, the grafts have to be repeated during several generations to become effective. We have as yet no idea about possible sensitizing factors.

The descent of  $G_3$  grafts of the various influenced pupil symbionts show varying types of modifications, but we always notice in  $G_3F_1$  the segregation that does not appear till  $F_2$  after a sexual crossing between mentor and pupil. If we compare heterografts to sexual hybrids, we sometimes find (plants XX, XXI and XXIII) the same characteristics in  $G_3F_1$  as in  $F_2$ . In some other cases however, some of these characteristics appear: one characteristic, the violet tinged pigmentation of the stems in the offspring of plants XVI and XVII; two characteristics, the violet tinged pigmentation of the stems and the long shape of the fruits in the offspring of plant XIX; three characteristics, the violet tinged pigmentation of the stems, the violet pigmentation of the fruits and their long shape in the offspring of plant XVIII. Moreover, concerning the latter, the linkage between the violet colour of the fruit and the characteristic "brown edged" of the stamens, peculiar to the mentor plant, has been broken. An additional colour, black-violet, has appeared, unknown in the symbionts of the heterograft.

In some plants, the vegetative organs and the reproductive cells may show different modifications: the characteristics appearing in  $G_3$  are not encountered again in their descent which shows on the other hand new features invisible on the pupil specimen. This is the case in plants XVI, XVII and XIX. Moreover, modifications may affect the reproductive cells leaving the vegetative organs unaffected, such as in the interspecific heterograft "Blanche ronde"/Black Nightshade.

These various phenomena show that the altering factors brought by the mentor can penetrate and maintain themselves in various ways in the different tissues of the pupil plant.

After intervarietal heterografts, the modifications obtained in the pupils resemble the characteristics of the mentor. On the contrary, after interspecific heterografts we have not noticed any alteration related to the mentor characteristics.

Such are the facts. The mechanism of these modifications is still to be explained. Only hypotheses can be expressed as to how these modifications come about. Let us review some of them.

In spite of the precautions taken to self-fertilize the flowers of the pupil specimens,

one could impute the modifications described above to a sexual crossing in  $G_2$  between mentor and pupil. This hypothesis seems hard to support. As a matter of fact we have always divided into two groups the seeds of the pupils  $G_1$  and  $G_2$ , one part giving rise to plantlets developing without being grafted again; these plants which became adult in  $G_2F_1$  (generation corresponding to  $G_3$ ), remained similar to the standard "Blanche ronde". Furthermore the characteristics studied are dominant in the mentor as compared with those of the pupil; a sexual crossing between the two varieties in  $G_2$  should have given then  $F_1$  hybrids showing the mentor characteristics. Besides, if we assume a sexual crossing in  $G_2$  with a segregation in  $G_3F_1$  offspring of the modified  $G_3$  pupils, we should notice the same segregation in each of the offspring and such is not the case. Moreover, sexual crossing is impossible between the two specimens of our interspecific heterograft, egg-plant and Black Nightshade.

Another hypothesis is that we have created a chimera between mentor and pupil. The method used to obtain a chimera is different from the one we use. In the first case, we cut the scion at the level of the graft pad in order to induce the formation of an adventitious bud made up of tissues coming from the two grafted species. In the second case, we let the scion develop and no adventitious bud appears at the level of the graft pad. The young offshoots appear at a distance from the pad. It is unlikely that a chimera should develop in our heterograft system, unless we assume the migration over a certain distance of some of the mentor cells in the pupil plant and that these cells should proliferate and organize themselves into tissues at the colonization points. Although such a phenomenon of cellular translation has not yet, as far as we know, been described, it could perhaps happen. However, even if we assume this possibility, we do not believe that our modified plants are chimeras, if we assume that the constituents of the chimeras do not interact (16). If the gametes only come from one of the partners of the chimera, the lineage is homozygous, if they are provided by both partners, the lineage is the same as a sexual hybrid. We have shown previously that the modifications noted in the offspring of our heterografts could not be explained by a sexual crossing between mentor and pupil. If one assumes that the constituents which are united to form a chimera can, under certain conditions, influence each other (7), we cannot completely exclude, as we saw above, the formation of a chimera. However in this case we must still account for the influence of a mentor on a pupil in a heterograft.

Solanaceae are quite sensitive to viruses. Could we explain our results by a viral invasion of various tissues of the pupils? At first sight the diversity of the modifications could lead one to think so. But we must then assume that these viruses are transmitted only by very close contact, as in the case in a graft; that they take effect in the same tissues and in the same way throughout the descent, during several generations. Besides, they would have to influence characteristics as different as the pigmentation of various organs and size of fruit; a single strain of virus would be unlikely to fulfill all these conditions. Several strains of viruses should then be

considered. In our opinion the accumulation of the necessary circumstances make this hypothesis seem very improbable.

We could consider that our results are due to the expression of some cryptic genes. In that case there would be two possibilities. 1) the cryptic genes have appeared by chance, by the simple fact of sexual crossing. We wonder why in that case the  $G_2F_1$  plants coming from the same fruits as the modified  $G_3$  symbiont pupils have remained identical to the "Blanche ronde" standard. Besides it would be strange that the 4 cryptic genes should appear at the same time in some of our plants. The probability is low. 2) The treatment, heterografting, promotes the expression of cryptic genes; perhaps by means of regulating mechanisms. This hypothesis is worthy of further investigations.

It is difficult to consider these modifications as spontaneous mutations since their rate is so high, since some of them are alike although they come from different heterografts and since their characteristics are similar to those of the mentor. We could imagine on the other hand the existence of "biologic" mutagenic substances provided by the mentor. Some of these substances could possibly provoke guided mutations.

Finally the idea of a transformation or a transduction such as can be found in microorganism could be considered. We must then assume that some nucleic acid molecules bearing genetic information can enter the somatic or reproductive cells at a propitious moment and remain active.

Other hypotheses can be put forward to explain the mechanism of the modifications observed. We must, in any case, begin to analyse the various factors involved in these phenomena.

(We thank for technical assistance Mr. A. Rossier and for the translation of this paper into English Mr. P. Anker).

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## RÉSUMÉ

Ces vingt dernières années, plusieurs publications ont fait état de résultats où certains caractères d'organismes greffés paraissaient modifiés dans la descendance (1, 4, 5, 6, 7, 8, 10, 11, 13, 14, 17, etc.). D'autres travaux par contre se sont soldés par des échecs (2, 9, 12, 15, etc.).

A la suite de différents auteurs (3, 4, 7, 8, 14, etc.), nous étudions le problème de la transmission de caractères modifiés par voie de greffe chez le *Solanum melongena*. Ce travail a été entrepris en 1957.

### *Matériel et Méthode*

Nous avons pratiqué des greffes intervariétales chez le *Solanum melongena* et des greffes inter-spécifiques entre une variété de *Solanum melongena* et une souche de *Solanum nigrum*.

L'expérience fait appel au procédé suivant: mentor épibiote sur pupille hypobiote. La plante pupille à influencer, dont l'âge est moins avancé que celui de la plante mentor, est effeuillée presque complètement tout au long de son développement; on ne laisse subsister qu'une ou deux jeunes feuilles tire-sève. La plante mentor au contraire garde son feuillage, mais ses boutons floraux sont coupés dès leur apparition. Les substances nutritives de la plante pupille sont donc presque entièrement élaborées par la plante mentor.

Des homogreffes de la variété pupille représentent les témoins. Les symbiotes sont évidemment traités comme ceux des hétérogreffes.

Nous avons contrôlé dans notre Institut la stabilité génétique de nos plantes pendant six générations qui constituent nos *lignées* de contrôle.

Pour les *hétérogreffes intervariétales*, nous avons utilisé la variété « Violette hâtive » comme plante mentor; elle se caractérise par un fruit allongé de couleur violette, des étamines à côtes brunes et une tige violette (Photo I). La variété pupille est la « Blanche ronde » que nous cherchons à influencer; ses fruits sont ronds, de couleur blanche, les tiges sont vertes (Photo I).

Pour les *hétérogreffes interspécifiques*, nous avons utilisé comme plante mentor une souche de Morelle noire (*Solanum nigrum*) et comme plante pupille la variété d'aubergine « Blanche ronde ».

Notons que les sujets pupilles « Blanche ronde » des hétérogreffes, des homogreffes témoins et les plantes de contrôle sont tous issus d'une seule plante (Figure I).

Les fruits des sujets pupilles sont autofécondés. A chaque génération, chaque fruit utilisé pour obtenir la génération suivante est partagé en deux: une partie des graines fournira des plantules-pupilles greffées avec des plantes mentor, l'autre donnera naissance à des plantules qui se développeront sans être greffées (Figures II, III, IV). Nous appelons G les générations de greffe ( $G_1$ ,  $G_2$ , etc.) et GF les générations provenant des symbiotes mais se développant sans être elles-mêmes greffées ( $G_1F_1$ ,  $G_2^rF_1$ ,  $G_2F_2$ , etc.).

### Résultats

L'hétéogreffe peut provoquer chez des plantes génétiquement stables des modifications susceptibles de se transmettre à la descendance non greffée des symbiotes pupilles. Nous avons observé des modifications affectant la forme et la pigmentation des fruits, l'aspect des étamines et la couleur des tiges.

Nous avons constaté une diversité des modifications d'une hétéogreffe à l'autre (Figure III:  $G_3$ ). En outre, la susceptibilité des plantes au traitement varie, et, selon cette expérience, les greffes doivent être répétées sur plusieurs générations pour devenir efficaces.

Chez les hétérogreffes intervariétales la descendance de greffe  $G_3$  des divers symbiotes pupilles influencés manifeste des modifications de types variés, mais nous observons toujours en  $G_3F_1$  la disjonction qui ne survient qu'en  $F_2$  après hybridation sexuelle entre mentor et pupille. Si l'on compare les hétérogreffes aux hybrides sexuels, on retrouve dans certains cas (plantes XX, XXI, XXIII: Tableaux V, VI, VII) les mêmes caractères en  $G_3F_1$  qu'en  $F_2$ . Dans d'autres cas cependant, seule la partie de ces caractères apparaît: un caractère, la pigmentation violette des tiges, dans la descendance des plantes XVI et XVII (Tableaux I et II); deux caractères, la pigmentation violette des tiges et la forme allongée des fruits, dans la descendance de la plante XIX (Tableau IV et Photo II), et trois chez les sujets issus de la plante XVIII (Tableau III). En outre, chez ces derniers, le linkage entre la couleur violette du fruit et le caractère « côtes brunes » des étamines, propre à la plante mentor, a été brisé et une couleur supplémentaire violet noir s'est révélée, étrangère aux deux symbiotes de l'hétéogreffe.

Chez certaines plantes, les organes végétatifs et les cellules reproductrices peuvent présenter des modifications différentes: en effet, les caractères apparus en  $G_3$  ne se retrouvent plus dans la descendance qui révèle par contre des traits nouveaux, invisibles sur les sujets pupilles; tel est le cas chez les plantes XVI, XVII et XIX (Figure III et Tableaux I, II, IV). D'autre part, les modifications peuvent toucher les cellules reproductrices en laissant apparemment intacts les organes végétatifs: nous en avons un exemple avec l'hétéogreffe interspécifique « Blanche ronde »/Morelle noire (Figure IV).

Ces divers phénomènes attestent que les facteurs de modification apportés par le mentor peuvent pénétrer et se maintenir de façon variable dans les divers tissus de la plante pupille.

Après hétéogreffe intervariétale, les modifications obtenues chez les pupilles rappellent les caractères du mentor. En revanche nous n'observons rien de semblable après hétéogreffe interspécifique.

Tels sont les faits. Le mécanisme de ces modifications reste pour l'instant du domaine des hypothèses dont quelques-unes sont passées en revue.

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