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(Citation)
神戸大学農学部研究報告,14(2):253-263

(Issue Date)
1981-01-30

(Resource Type)
departmental bulletin paper

(Version)
Version of Record

(JaLCDOI)
https://doi.org/10.24546/00227221

(URL)
https://hdl.handle.net/20.500.14094/00227221

KOBE UNIVERSITY

神大農研報 (Sci. Rept. Fac. Agr. Kobe Univ.) 14 : 253-263, 1981

EFFECTS OF CHROMOSOME DOUBLING AND A CHEMICAL IMMUNOSUPPRESSANT ON CROSSABILITY BETWEEN *SOLANUM TUBEROSUM* AND ITS RELATED DIPLOID SPECIES

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(Received for publication on August 11, 1980)

Abstract

A study has been made on the effects of chromosome doubling and a chemical immunosuppressant, ε-amino caproic acid (EACA), on crossability between *S. tuberosum* (*tbr*) and its related diploid species *S. chacoense* (*chc*) and *S. pinnatisectum* (*pnt*). The results obtained are summarized as follows:

1). Chromosome doubling was effective for overcoming cross-incompatibility of *tbr* with *chc* but not with *pnt*, indicating that in the former the cross-incompatibility is due to chromosomal sterility but in the latter it may result probably from an antigen-antibody reaction controlled by the S allele system.

2). For suppressing the above reaction, the *tbr* female parents were treated with EACA in the dosage of 1000 ppm by means of the hydroponic method, mainly in the crosses involving *pnt* as males. Histological observations showed, regardless of the chemical treatment, that pollen germination on the stigmas was good and pollen tube growth was nearly normal up to the middle site of the styles in all instances. Cross-incompatibility reaction, thus, appeared to occur at the middle site or lower of the styles, suggesting that EACA may be little effective for enhancing pollen tube growth in the styles as well as pollen tube penetration into the ovaries, although there is a clear need for further investigations of this point.

With respect to the methods for overcoming cross-incompatibility between tuberous *Solanum* species, various devices have so far been made by earlier workers; such as doubling the chromosomes of the parents at lower ploidy levels[10,14-16,23], *in vitro* culturing the abortive embryos[8], applying an artificial medium on the cut surface of the style[24], treating the ovaries with phytohormones after pollination[6], utilizing bridge species[7,9], using the pollen parents treated with X-ray at flowering[9], and others. All of these devices, however, appear available only in the cases where the pollen tubes are unartificially penetrable into the ovules but not in overcoming such a cross-incompatibility resulting from S allele systems as encountered between South American and Mexican diploid species.

The use of chemical immunosuppressants has been reported to give hopeful results for this respect. BATES and his coworkers[1-5] have suggested that crossability barriers, though of cross-incompatibility nature, may be controlled by animal-effective immunosuppressants or a similar class of reactants more specific for plants, i.e. ε-amino caproic acid, lysine, salicylic acid, acriflavin, gentisic acid and chloramphenicol, basing on the successful results obtained from intergeneric crosses between wheat and the other cereals. Successful results have also been reported elsewhere[25].

Such being the case, it seems to be expected that immunosuppressants may be availably ap-

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plied for breaking down crossability barriers in *Solanum* species. In *Solanum* crosses, however, any information about it does not yet appear in the literature concerned. The present study, thus, has been undertaken with the purposes to ascertain the effect of chromosome doubling on crossability of the diploid species involved to *S. tuberosum*, and then to analyse histologically the action of ε-amino caproic acid in breaking down the crossability barrier which was not affected by means of chromosome doubling.

Materials and Methods

The *Solanum* materials used in the present study comprise the species and their tetraploid derivatives listed in Table 1. Of these materials, the tetraploid forms of *chc* and *pnt* are ones which were induced by colchicine treatment at the Laboratory of Plant Breeding, Kobe University and at the Shimamatsu Potato Branch, Hokkaido National Agricultural Experiment Station, respectively.

Cross-pollinations using *tbr* as the female parent and *chc*, *pnt* and their chromosome-doubled forms as the male parents were attempted under galsshouse conditions at Kobe. Further attempts to pollinate *tbr* with *pnt* and its chromosome-doubled forms were made at the Hokkaido National Agricultural Experiment Station, Eniwa.

In order to make sure the effect of chemical immunosuppressants on the breakdown of cross-incompatibility, ε-amino caproic acid (EACA) was applied in pollinations for crossing *tbr* with *pnt* and its chromosome-doubled forms. In *Solanum* crosses, no reports on the dosage of EACA have come to the present authors' notice in the available literature to date. Bates[1] has used in certain cereal crosses several chemials with concentrations ranging 100 to 2000 ppm, though higher dosages have been reported for other genera[12].

Thus, in the present study the dosage of 1000 ppm was adopted as an initial attempt. The chemical was applied empolying the hydroponic method[17 20], its procedures being as described in the following. Stems 30-40cm long with an inflorescence and several leaves were cut off and transported into plastic bottles filled with the solution containing EACA and a nutritive component (Hyponex). These stems were left in the bottles until sampling of the pollinated flowers, renewing the solution every other day.

Histological observations were made on the pollen germination on stigmas, pollen tube behavior in styles and pollen tube penetration into ovaries by employing Kho and Baër's fluorescence technique[11], i.e. the samples excised were fixed in a 5 : 5 : 90 solution of formalin, acetic acid and 70% ethanol for 48 hr. or more, and

Table 1 The materials used in the present study.

Species & cultivar[1]	Taxonomic series[2]	2n	Source
S. tuberosum ssp. *tuberosum* (*tbr*) cv. Merrimack cv. Eniwa cv. Toyoshiro	TUB	48	Hokkaido Nat. Agr. Expt. Sta.
S. chacoense (*chc*)	COM	24	Wisconsin Univ. (PI 217451)
,,		48	Lab. Plant Breed., Kobe Univ.
S. pinnatisectum (*pnt*)	PIN	24	Wisconsin Univ. (PI 186554)
,,		48	Hokkaido Nat. Agr. Expt. Sta.

1) The parenthesized letters are the abbreviations of species name proposed by Simmonds (1963).
2) TUB, COM and PIN indicate the taxonomic series, Tuberosa, Commersoniana and Pinnatisecta, respectively. (Simmonds, 1963)

softened in a 1N NaOH solution for 20–30 min. After washing, they were stained with a 0.1% solution of water-soluble anilin blue dissolved in 0.1N K_3PO_4 for 12–24 hrs., and then placed in a drop of glycerin on a slide for preventing rapid drying out of the preparations. Pollen germination was examined in the squashes made from 6–10 stigmas sampled at 12 hr. after pollination by counting 800–1000 grains for each case and its rate was expressed as:

$$\frac{\text{Number of pollen grains germinated}}{\text{Total no. of pollen grains observed} \times \text{pollen fertility}} \times 100$$

Pollen tube growth was observed in paraffin sections of the 3 styles sampled at 24, 36, 48 and 60 hrs. after pollination for each treatment. The styles were transversely sectioned at the four sites: i.e. the stigma base (I), 1/3 of the style length (II), 2/3 of the style length (III) and the style base (IV), as illustrated in Figure 1. The rate of pollen tube growth was expressed as the number of pollen tubes counted in each of these sites. Pollen tube penetration into the ovaries was observed in paraffin sections of the 5–7 ovaries sampled at 3 days after pollination by scoring the number of ovaries into which pollen tubes penetrated.

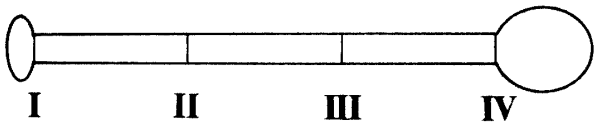


Fig. 1. Diagram illustrating the four sites observed in the style.

Results

A. Effects of Chromosome Doubling

1). *Cross-fertility*

Table 2 gives the results of crosses using *tbr* as the female parents and *chc*, *pnt* and their chromosome-doubled forms as the male parents. As seen from the table, *chc per se* did hardly cross with *tbr*, whereas its chromosome-doubled forms were readily crossable, showing 0.06 and 15.39 in the number of seeds per pollination, respectively. Similar results have also been reported by earlier workers [14,15 22,23]. In the crosses involving *pnt*, however, no success was obtained using it at the tetraploid as well as diploid levels.

2). *Pollen germination on the stigma*

The data on the pollen germination are presented in Table 3. Good pollen germination was found in all instances, its rates being as high as 40% or higher (Figs. 2, 3, 6 and 7). These values were even higher rather than in the *tbr* × *tbr* cross which was attempted as the controls. For both *chc* and *pnt*, neither diploid nor chromosome-doubled forms showed any significant differences in this respect, although there was present a little variation within the species at both ploidy levels.

3). *Pollen tube growth in the style*

Observations were done only in the instances where *tbr* was crossed with *pnt* and its chromosome-doubled forms, and the number of pollen tubes was counted at the four sites, I, II, III and IV, in each of the styles sampled at 24, 36, 48 and 60 hrs. after pollination. The results obtain-

Table 2. Crossability of *S. chacoense*, *S. pinnatisectum* and their chromosome-doubled forms with *S. tuberosum*[1)]

Cross combination	2n	No. of flowers pollinated	Berry setting		Seed setting	
			No.	%	No. of seeds /berry	/polli.
tbr × *chc*	48×24	78	2	2.6	2.5	0.06
tbr × *chc*	48×48	49	13	26.5	57.9	15.39
tbr × *pnt*	48×24	85	0	0	0	0
tbr × *pnt*	48×48	70	0	0	0	0

1) Used the cultivar Merrimack as the *tbr* females.

ed here are given in Tables 4, 5, 6 and 7 and also in Figures 10–13 and 18–21. As the results indicate obviously, nearly normal pollen tube growth was found up to the site II of the styles, but the tube number did progressively decrease with lowering sites in the styles, and there occurred a marked falling off between the sites III and IV of the styles. The location at which incompatibility reaction occurs, therefore, appeared to be between both sites. In all instances there were not encountered any features as definitely affected by the ploidy level of male parents.

4). *Pollen tube penetration into the ovary*

Pollen tubes were not at all observed inside the ovaries from the crosses involving *put* and its chromosome-doubled forms. On the contrary, in the cross *tbr*×*tbr*, pollen tubes appeared and were easily recognized in either transverse or longitudinal sections of the ovaries. Figures 30, 31 and 33 show some of the features observed in these sections.

B. Effects of Immunochemical Treatment

1). *Pollen germination on the stigma*

Pollen germination was good in all instances, and it was found to be not affected by treating the female parent *tbr* with EACA, since a noticeable difference was not recognized between the treated and untreated ones. Likewise, these instances did not significantly differ in pollen germination rate from the cross *tbr* × *tbr* in which the female parents were not treated with the same chemical (Tab. 3 and Figs. 4, 5, 8 and 9).

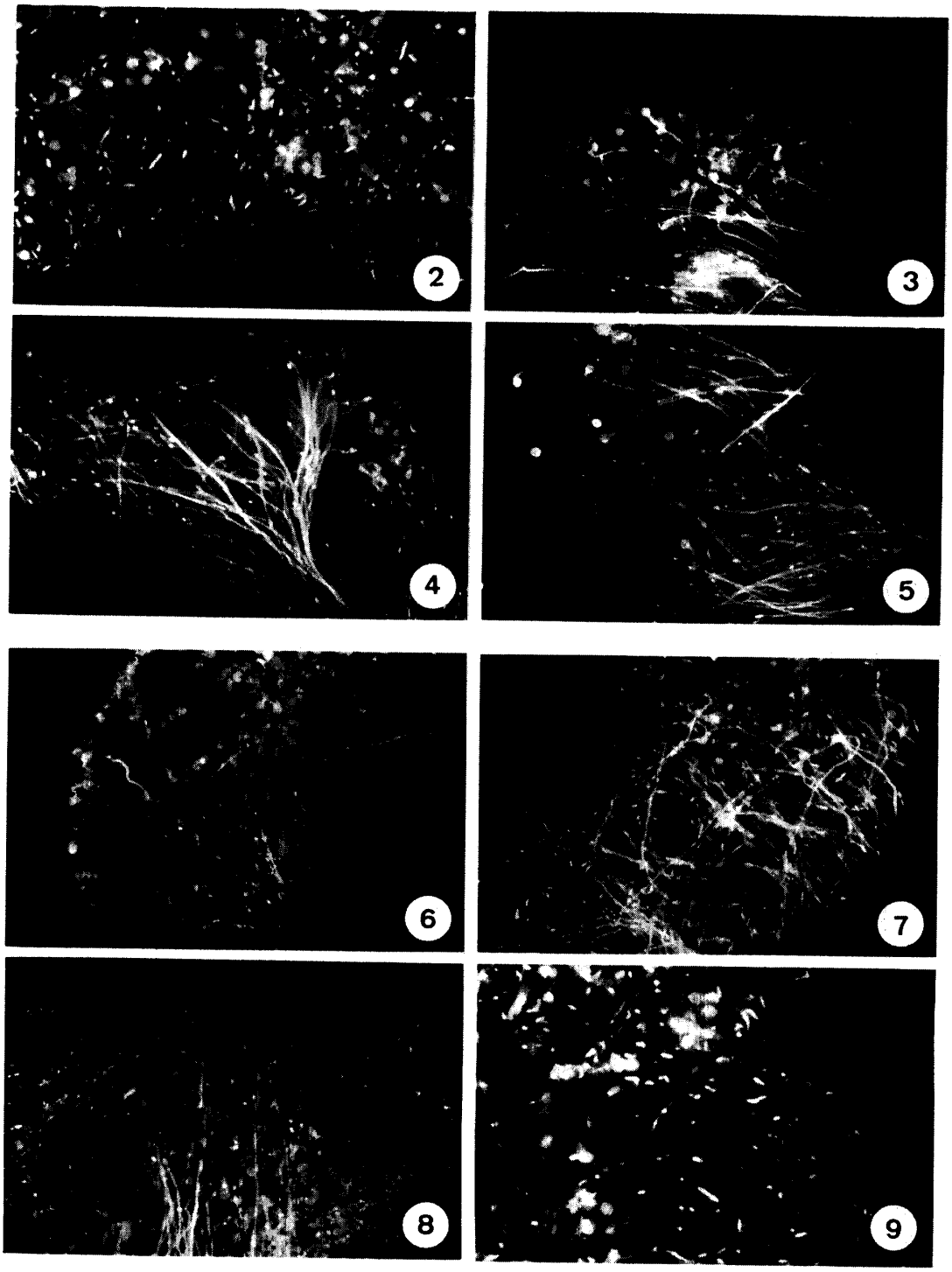
2). *Pollen tube growth in the style*

In the crosses involving *pnt* and its chromosome-doubled forms, the effects of EACA on the number of pollen tubes in the styles were examined for each site of the styles sampled at such different times after pollination as described already. At the site I, as seen from Table 4, pollen tubes were of frequent occurrence and there were present little differences between the instances where the *tbr* females were treated and their controls, irrespective of ploidy levels of the male parents (Figs. 14 and 22). At the site II, there was found a little effect of the chemical for enhancing pollen tube growth only in the styles sampled at 24 hr. after pollination in the crosses of *tbr* with the chromosome-doubled *pnt* males (Tab. 5 and Fig. 23). A similar effect was also found at the site III, although only in the styles sampled at 48 hr. after pollination in the cross *tbr*×*pnt* (Tab. 6 and Fig. 16). Of special notice is that there was encountered at this site a sharp decrease in the number of pollen tubes. At the site IV, the pollen tubes were of little or no occurrence in the instances concerned, while they occurred frequently in the cross *tbr*×*tbr* (Tab. 7 and Figs. 17, 25 and 33).

Table 3. Pollen germination rates on the *S. tuberosum* stigmas.

Cross combination [1]	Chemical treatment [2]	No. of stigmas observed	Pollen germination rate	
			Mean % observed	Arcsin $\sqrt{\%}$ Mean ±C.L.[3]
tbr × *chc* (2×)	Control	6	58.00	49.76±10.30
tbr × *chc* (4×)	,,	6	51.39	45.92±12.56
tbr × *chc* (2×)	Treated	7	49.17	44.47± 7.44
tbr × *chc* (4×)	,,	7	46.14	42.73± 5.76
tbr × *tbr*	Control	5	39.54	38.87± 6.46
tbr × *pnt* (2×)	,,	6	42.86	40.85± 5.11
tbr × *pnt* (4×)	,,	6	40.70	39.54± 6.39
tbr × *pnt* (2×)	Treated	6	44.00	41.55± 7.02
tbr × *pnt* (4×)	,,	7	35.40	36.51± 3.58
tbr × *tbr*	Control	10	33.10	35.14± 3.84

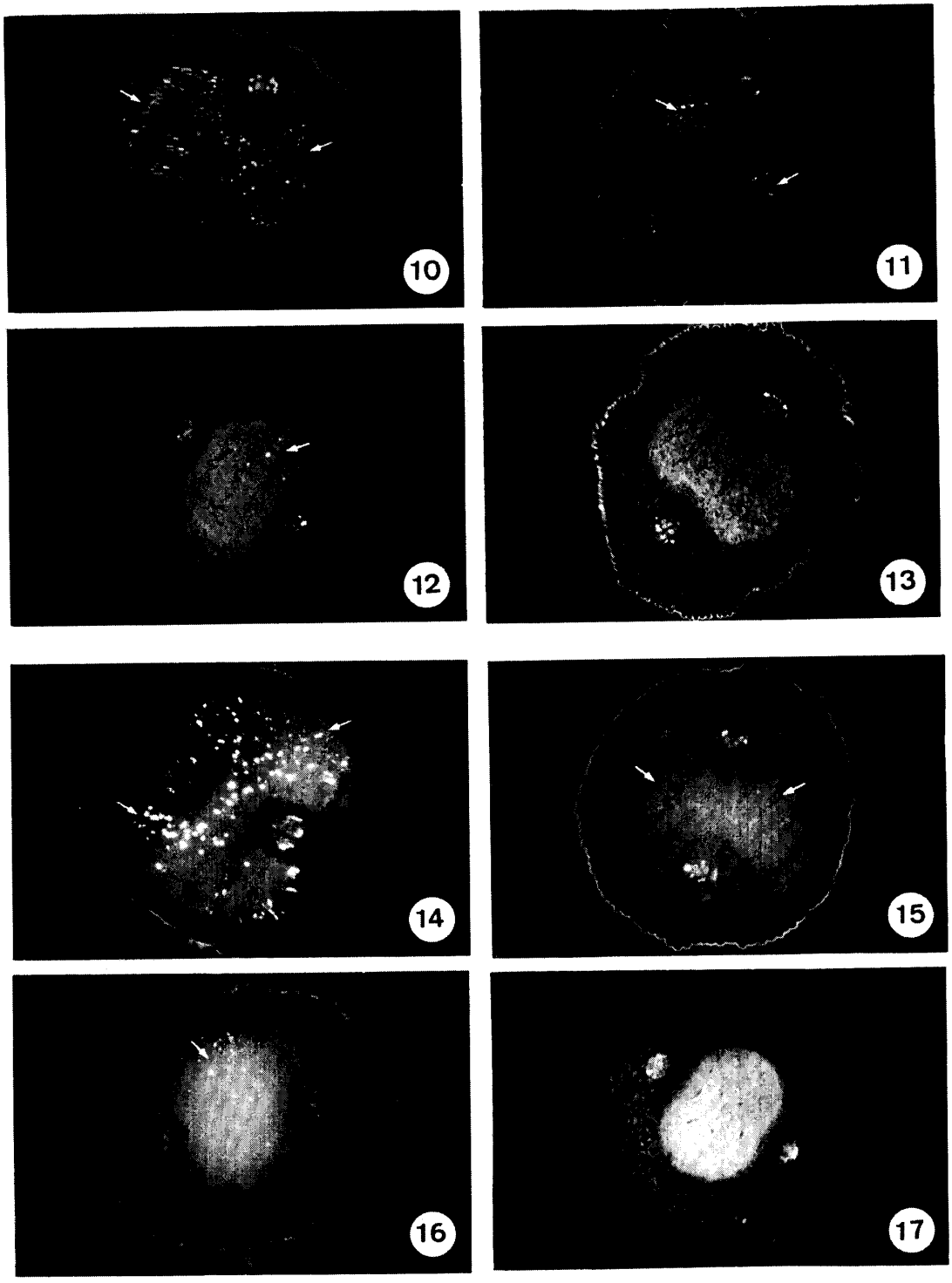
1) The parenthesized letters : ploidy levels of the male parents.
2) Treated with EACA at the concentration of 1000 ppm.
3) C.L. : confidence limit.



Figs. 2–5. Pollen germination on the stigmas after pollinating *tbr* with *chc* and its chromosome-doubled forms (*ca.*×30). 2. *tbr*×*chc*. 3. *tbr*×*chc*(4×). 4. *tbr*×*chc*, treated with EACA. 5. *tbr*×*chc* (4×), treated with EACA.

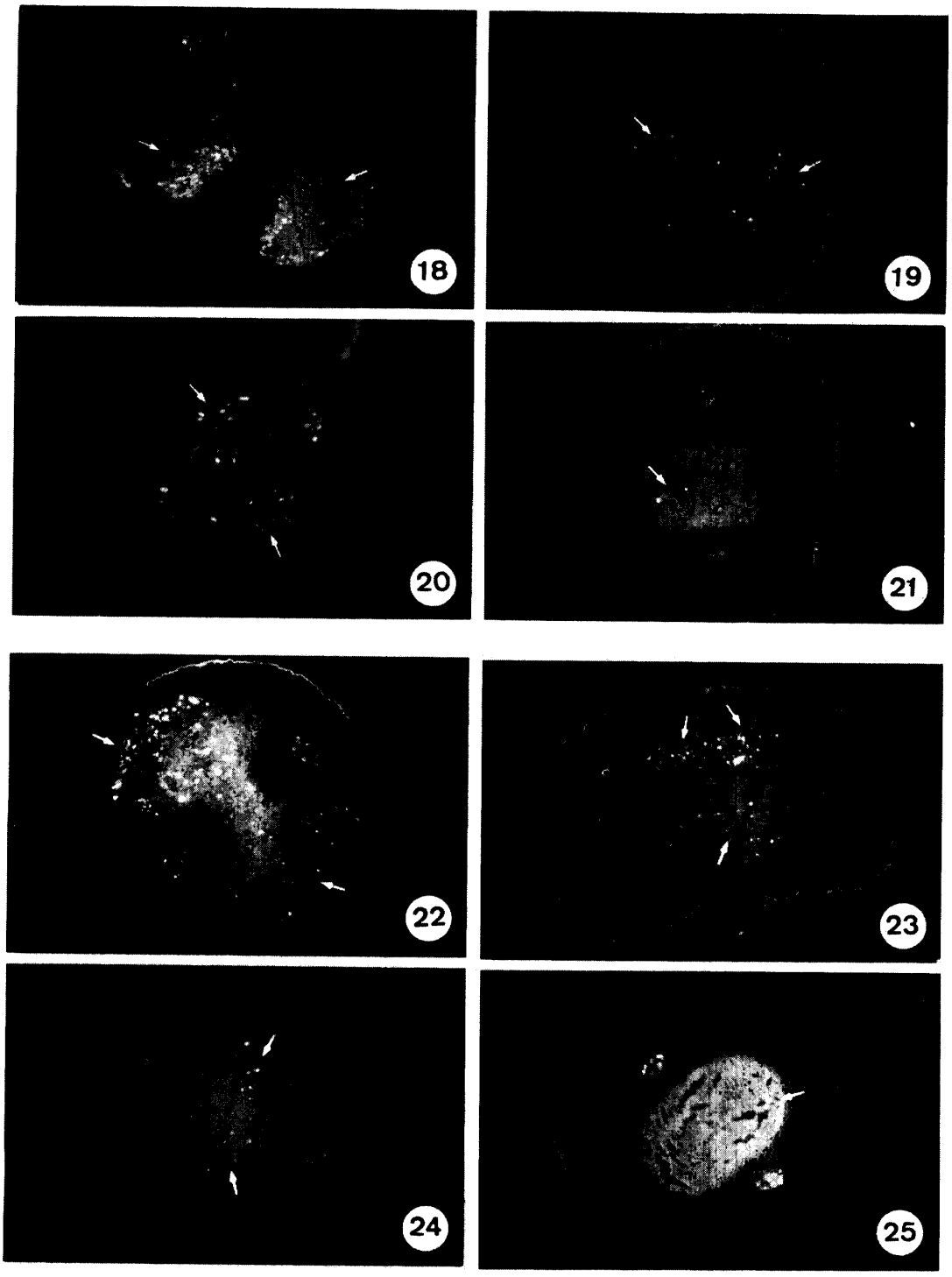
Figs. 6–9. Pollen germination on the stigmas after pollinating *tbr* with *pnt* and its chromosome-doubled forms (*ca.*×30). 6. *tbr*×*pnt*. 7. *tbr*×*pnt* (4×). 8. *tbr*×*pnt*, treated with EACA. 9. *tbr*×*pnt* (4×), treated with EACA.

In all instances, there are seen a large number of the pollen tubes with callose plugs.



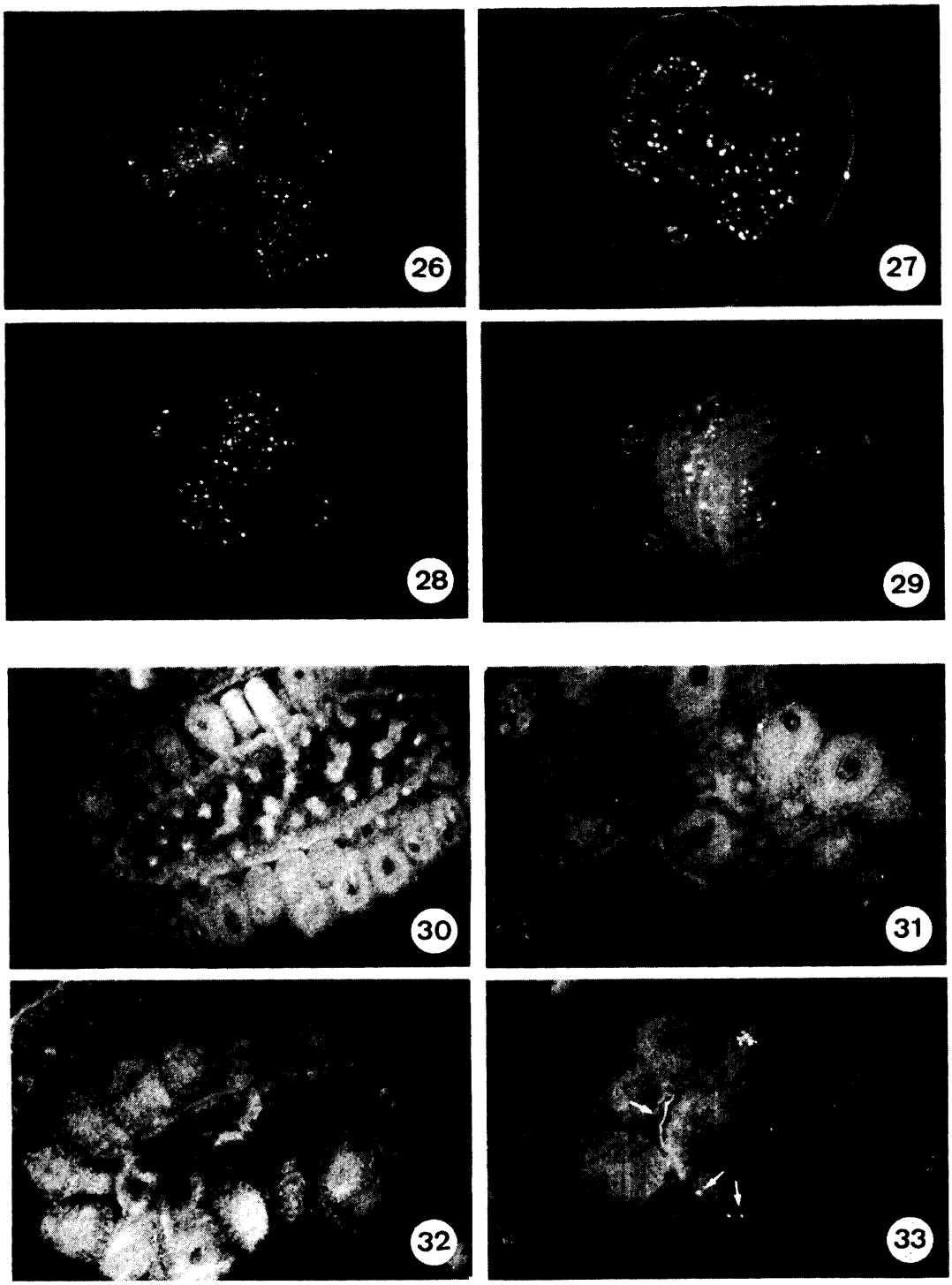
Figs. 10–13. Pollen tube number at the four sites of the styles after pollinating *tbr* with *pnt*, in the instances where the *tbr* females were not treated with EACA, pollen tubes being indicated by arrows (*ca.*×26). 10. At the stigma base (I). 11. At the 1/3 site of style (II). 12. At the 2/3 site of style (III). 13. At the style base (IV).

Figs. 14–17. Pollen tube number at the four sites of the styles after pollinating *tbr* with *pnt*, in the instances where the *tbr* females were treated with EACA, pollen tubes being indicated by arrows (*ca.*×26). 14. At the site I. 15. At the site II. 16. At the site III. 17. At the site IV.



Figs. 18–21. Pollen tube number at the four sites of the styles after pollinating *tbr* with chromosome-doubled *pnt*, pollen tubes being indicated by arrows; untreated with EACA (*ca.*×26). 18. At the site I. 19. At the site II. 20. At the site III. 21. At the site IV.

Figs. 22–25. Pollen tube number at the four sites of the styles after pollinating *tbr* with chromosome-doubled *pnt*, pollen tubes being indicated by arrows; treated with EACA (*ca.*×26). 22. At the site I. 23. At the site II. 24. At the site III. 25. At the site IV.



Figs. 26-29. Pollen tube number at the four sites of the styles after intervarietal crossing of *tbr*; untreated with EACA (*ca.*×26). 26. At the site I. 27. At the site II. 28. At the site III. 29. At the site IV.

Figs. 30-33. Pollen tube penetration into the ovaries after cross-pollinating. 30. *tbr*×*pnt*, untreated with EACA (*ca.*×50). 31. *tbr*×*pnt*, treated with EACA (*ca.*×70). 32. *tbr*×*pnt* (4×), treated with EACA (*ca.*×70). 33. *tbr*×*tbr*, untreated with EACA (*ca.*×80). Note that while pollen tubes reaching the ovules are frequently seen in Fig. 33, being indicated by arrows, they are not recognizable in Figs. 30-32.

Table 4. Mean number of pollen tubes at the stigma base in the crosses *S. tuberosum*× *S. pinnatisectum*.

Cross combination	Time after pollination (hr.)	EACA treatment[1]	
		Untreated	Treated
tbr×*pnt* (2×)	24	194.0	167.2
	36	204.0	218.0
	48	238.3	210.0
	60	175.6	204.0
	Mean	202.95	199.80
tbr×*pnt* (4×)	24	151.3	120.6
	36	150.0	126.0
	48	188.0	191.0
	60	132.0	176.3
	Mean	155.32	153.47

1) On the t-test, the differences between the treated and untreated ones were not significant in all instances.

Table 5. Mean number of pollen tubes at the 1/3 site of the styles in the crosses *S. tuberosum* × *S. pinnatisectum*.

Cross combination	Time after pollination (hr.)	EACA treatment[1]	
		Untreated	Treated
tbr×*pnt* (2×)	24	53.0	46.7
	36	69.9	82.6
	48	59.3	86.0
	60	38.3	71.3
	Mean	55.12	71.65
tbr×*pnt* (4×)	24	23.4	46.7*
	36	41.5	32.3
	48	84.0	111.0
	60	95.0	99.0
	Mean	61.12	72.25

1) Significant differences were not found by t-test between the treated and untreated ones in all, except for the instance marked with * (significant at 5% level).

Table 6. Mean number of pollen tubes at the 2/3 site of the styles in the crosses *S. tuberosum*× *S. pinnatisectum*.

Cross combination	Time after pollination (hr.)	EACA treatment[1]	
		Untreated	Treated
tbr×*pnt* (2×)	24	2.0	4.0
	36	7.0	4.0
	48	0	9.3**
	60	2.0	2.6
	Mean	2.75	4.99
tbr×*pnt* (4×)	24	2.0	11.3
	36	12.0	9.0
	48	23.6	13.6
	60	11.0	5.6
	Mean	12.15	9.87

1) See Tab. 5. The instance marked with ** was rather exceptional, indicating to be significant at 1% level.

Table 7. Mean number of pollen tubes at the style base in the crosses *S. tuberosum*× *S. pinnatisectum*.

Cross combination	Time after pollination (hr.)	EACA treatment[1]	
		Untreated	Treated
tbr×*pnt* (2×)	24	0	0
	36	1.0	0
	48	0	1.0
	60	0	0
	Mean	0.25	0.25
tbr×*pnt* (4×)	24	0	0
	36	0	0
	48	2.0	0.7
	60	2.0	1.0
	Mean	1.00	0.41

1) See Tab. 4.

3). *Pollen tube penetration into the ovary*

Neither the instances where the *tbr* females were treated with EACA nor the untreated ones revealed pollen tubes reaching the ovaries in both the crosses involving *pnt* and its chromsome-doubled forms (Figs. 31 and 32). In the *tbr*×*tbr* cross, however, there were frequently recognizable the ovules entered by pollen tubes, despite being not treated with EACA (Fig. 33).

Discussion

A. Effects of Chromosome Doubling on Crossability of the Diploid *Solanums* with *S. tuberosum*

Cross-incompatibility between *tbr* and its diploid relatives may be usually considered as

follows : if crossability with *tbr* is able to be raised by chromosome doubling of diploid parents, its cause is chromosomal, but if not, its cause is not chromosomal but genic, being due probably to such an antigen-antibody reaction controlled by the S allele system as suggested by LEWIS and CROWE[13] and NASRALLAH *et al*[18]. Basing on such a consideration, the difficulty of *chc per se* to cross with *tbr* may be apparently interpreted as due to chromosomal sterility. However, the cross-incompatibility with *tbr* revealed by *pnt* was not broken down by chromosome doubling of the latter species. The same results have also been obtained by IRIKURA [10]. The cross-incompatibility found in this instance, therefore, may be assumed to be ascribable to an immunochemical mechanism as mentioned above. On this assumption, further discussion will be made in the next paragraph.

B. Effects of the Immunosuppressant on Crossability of the Diploid *Solanums with S. tuberosum*

With respect to the pollen germination on stigmas, there were not found significant differences in germination rate between the instances in which the *tbr* females were treated with EA CA and the untreated ones, no matter what the pollen sources might be involved. This suggests that the EACA treatment is not useful for enhancing the pollen germinability on stigmas.

Likewise, in respect to the pollen tube behaviour in the style, the instances where the *tbr* females were treated with EACA were not appreciably different from the untreated ones, both showing similar pollen tube numbers at the four sites of the styles. Even if a little difference was found in certain instances, it will be probable to consider that they are due to any factors other than the action of the chemical. The effect of EACA was also not found on the pollen tube penetration into ovaries. While the pollen tubes were frequently present in the ovules from the cross *tbr*×*tbr*, they were not at all recognizable inside the ovaries from the crosses with *tbr* using the diploid species and their chromosome-doubled forms as the males. These facts suggest that the EACA, so far as the present study is concerned, is little effective for breaking down cross-incompatibility barriers between *tbr* and its diploid relatives.

The use of EACA, however, has been reported as fairly effective for wide hy bridization in some other genera[1-5], in which the injection or spray method has been employed in treating the female parents with the chemical. In the present study, the hydroponic method described in the previous section was adopted as an attempt. Therefore, it is considered that such a difference in method may be one of the causes for bringing about a discrepancy in effectiveness of the chemical, because it is suspected that penetration of the chemical into the pistils might be not sufficient to affect an antigen-antibody reaction in the styles by the method employed in the present study. In addition, it is also suspected that the dosage of EACA applied might be too low to suppress the reaction. For these reasons, further work should be carried out using a range of higher dosages of EACA and employing any other methods for applying the chemical.

Acknowledgements

The authors wish to thank Dr. T. NAKANISHI of the Faculty of Agriculture, Kobe University for her helpful advice during the histological observations. The thanks are also due to Dr. Y. IRIKURA of the Potato Branch, Hokkaido National Agricultural Experiment Station for his kind help in providing the plant materials.

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Solanum tuberosum とその近縁2倍種間の交雑能力に対する染色体倍加及び免疫抑制物質の効果

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要約

S. tuberosum (2n=48) に対する近縁2倍種の交雑能力には，一般に，2つの遺伝的要因が関与しているものと考えられている。1つは両親間における染色体数の不均衡であり，他は交雑不和合性遺伝子の作用である。本研究は，この観点から，*S. tuberosum* を母本とし，南米産2倍種 *S. chacoense* (2n=24) 及びメキシコ産2倍種 *S. pinnatisectum* (2n=24) を父本とした場合の交雑能力に対して，2倍種親の染色体倍加と母本の免疫抑制物質 ε-amino caproic acid (EACA) 水耕処理がいかなる効果を示すかを明らかにするために行ったものである。

染色体倍加による両親染色体数の均衡化は，*S. chacoense* では極めて有効であったが，*S. pinnatisectum* には全く効果が認められなかった。したがって，後者の場合は，他属植物で指摘されているような不和合性遺伝子による免疫反応がその主因であろうと推察され，その反応に抑制効果をもつEACA処理を試みた。しかし，その効果は，本研究で用いた1000ppm溶液の水耕処理では，柱頭上の花粉発芽，花柱内の花粉管伸長及び子房内への花粉管侵入のいずれにおいても認められなかった。濃度と処理法に今後検討すべき余地があるものと考えられる。

上記処理のいかんをとわず，花柱内の花粉管数は花柱の下半部で激減することが認められた。したがって，バレイショ近縁種における交雑不和合性反応はほぼその部位で起こるものと推定される。