Pakistan J. Sci. Ind. Res., Vol. 15, Nos. 4–5, August–October 1972

COMPARATIVE CYTOLOGY OF SELF-COMPATIBLE AND SELF-INCOMPATIBLE APRICOTS

FAROOQ LODHI*

Department of Pomology, University of California, California, U.S.A.

(Received November 29, 1971)

Abstract. Pollen-tube growth and fertilization were studies in two apricot clones and five representative F1 seedlings, to determine whether incompatibility is responsible for the higher degree of sterility in most members of the progeny. Hand-pollination in the laboratory of emasculated flowers included (a) self and cross-pollination of the parents, Perfection and University of California selection 3-10, (b) self-pollination involving two and three cross-pollinations involving four members, all representing a cross-section of the fruiting behaviour of the F1 progeny. Pistils were fixed at 6 hr intervals up to 96 hr after pollination and serial sections were studied for the extent of pollen-tube growth at each time of fixation and for pollen-tube features indicating incompatibility. Evidence of incompatibility appeared in all pollinations, in inhibition of growth of some tubes, in their coiling, and having swollen or bent ends. Evidence has been cited to suggest that incompatibility in apricot probably involves the gametophytic system of pollen control. The evidence also led to the hypothesis that most of the fertility in plants concerned here is pseudofertility.

The occurrence of incompatibility has been established in sweet cherry (*Prunus avium*) and European plums (*P. domestica*) by Crane and his coworkers.[1–8] Determination of the occurrence of incompatibility in *Prunus* through genetic investigation requires many years since seedlings do not flower for several years after planting of seeds. It is possible, however, to learn more rapidly whether incompatibility exists through studies of pollen-tube growth and fertilization in self and cross-pollinations. This method may furnish more accurate information than data concerning fruit and seed-set, since failure of fruit and seed-set may be unrelated to incompatibility. In cytological studies of various *Prunus* fruits, the incompatibility symptoms such as poor germination of the pollen, inhibition of pollen-tubes at various lengths of the style, coiling of the tubes and the tubes having swollen or bursting ends have been observed.[4,9–11] The subject of incompatibility has so far not been investigated in the apricot (*P. armeniaca*). Present paper deals with pollen-tube growth in two apricot clones and some of their F1 hybrids.

Materials and Methods

The material for cytological studies included two apricot clones, University of California selection 3-10 and Perfection and five of their hybrids representing a cross-section of the fruiting behaviour of the F1 progeny. The female parent, 3-10 was selected from an open-pollinated progeny of the Casaba cultivar. Perfection and Casaba originated as chance seedlings and their parentage is unknown. The plants of the hybrid progeny could not be classified clearly into cross-compatible and incompatible groups as expected on the basis of the oppositional factor hypothesis (S-allele system).

Branches with unopened buds were cut and held in water in an air-conditioned laboratory at 25°C for the experiments. Buds were emasculated and the following hand-pollinations were made:

Perfection × self	
3-10 × self	10-13P × 11 -29P
Perfection × 3-10	7 -40Q × self
3 -10 × perfection	7 -40Q × 10 -13P
11 -29P × 11 -27P	7 -39Q × self

Twenty-five pistils were removed 6, 12, 18, 24, 48, 72 and 96 hr after pollination and fixed in Newcomer's fixative[12] modified by including 4 instead of 3 parts propionic acid. They were embedded in paraffin and longitudinal serial sections were cut at 10–12 microns. The sections were stained with lacmoid by the procedure of Cheadle *et al.*[13] for phloem and contiguous tissues, but with the omission of the tannic acid-ferric chloride. Lacmoid is specific for callose and the cell walls of pollen-tubes contain callose.

The extent of pollen-tube growth at each time of fixation was determined in each of the nine pollinations. Some loss of material and consequent reduction in sample size was caused by the inclusion of some pistils with nonreceptive stigmas, and also by loss of some critical sections during microtoming. The length of the longest pollen-tubes seen either in the style or in the ovary after each interval of time was used as the measure of relative growth rates. Coiling of tubes, swelling and upturning of their ends, and restricted growth as reported by other workers[4,9,14] were considered as indications of incompatibility. Since many ungerminated pollen-grains were lost during processing, particularly when the stigmas were not receptive, germination was judged as 'poor', 'fair' and 'good' from the grains remaining on the stigma. Because of difficulty in determining in sections just where pollen-tubes ended when many tubes were in the style, counts of tubes in different length

* Now at College of Agriculture, University of Peshawar, Peshawar.

categories were not made. The embryo sacs of a number of pistils were checked for developmental stages and conditions of the structures contained.

Observations

General. The ovary of the apricot normally contains two ovules but one usually begins to degenerate before anthesis. The nuclei and cells of the embryo sacs were always typical in number, form and position aside from the antipodals which in some sacs were located on one side of the sac. The antipodals sometimes degenerated before the pollen-tube reached the sac. A prominent vacuole was present between the synergids and the egg and most of the cytoplasm and nucleus occupied the chalazal end of the cell (Fig. 1). One synergid was usually damaged by entrance of the pollen-tubes and the other persisted after fertilization. The polar neuclei in most cases fused before the pollen-tube contents were discharged into the sac.

Pollen-tube penetration was always porogamous (Figs. 9 and 10). Although in some cases a number of pollen-tubes entered the locule (Perfection × 3-10 and reciprocal combination) only one entered the micropyle. The length of time between pollination end fertilization varied depending on the entities selfed or crossed. In Perfection × 3-10 fertilization occurred in less than 18 hr after pollination (Table 1). In 3-10 selfed and 11-29P × 11-27P more than 72 hr were required. It was not possible to follow details of the fertilization process, although in several sacs the sperm and egg nucleus were seen in contact. Even in sacs containing many endosperm nuclei the zygote remained undivided. Only free nuclear endosperm was observed, therefore, the change from free nuclear to cellular endosperm did not begin until sometime after 96 hr.

In most pistils of most self and cross-pollination both germinated and ungerminated pollen-grains were present on the stigmas (Figs. 2 and 3). In no case was 100% germination found. Some stigmas in all pollination had only ungerminated pollen, and other stigmas had no pollen (Table 1). Both conditions were attributed to pistil immaturity and thus inadequate stigmatic fluid to hold the pollen on the stigma or stimulate germination. Since in most cases other stigmas of the same combination showed germinated pollen, the quality of the pollen in general was not at fault. 'Good' or 'poor' germination of pollen did not appear to be related to compatibility or incompatibility. Germination was sometimes better in incompatible than in supposedly compatible pollinations.

Results of Specific Pollinations

The data concerning pollen-tube growth for each self and cross-pollination (Table 1) show how far the most advanced tube or tubes had travelled within different pistils at each time after pollination. To facilitate comparison of different combinations, the positions of the most advanced tubes in any pistil for each combination are brought together in Table 2.

Perfection Selfed. In field experiments self-pollinated Perfection never set fruit. In pollen-tube growth studies the cause of sterility became apparent. Pollen germination was good in all fixations except 72 hr one, which included about 50% young pistils. No tubes appeared below the stigmas until 19 hr after pollination and some had grown three-fourths of the way down the style in 24 hr (Table 1a). In another 24 hr a few tubes were in the ovary wall, but none penetrated the locule. Evidences of incompatibility were (1) in all pistils of the later collections (where time for tube growth was ample), most tubes were confined to the stigmas. The relatively few that grew further stopped one-half to three-fourth of the way down the style. In two exceptional pistils one and five tubes, respectively, reached the ovary wall. The confinement of many tubes to the stigmas, while others grew part way down the style or into the ovary may indicate the incompatible classes of pollen and (2) incompatibility symptoms such as coiling, or swollen or bent ends were observed in all the inhibited tubes.

3-10 Selfed. In field tests 3-10 proved self-fruitful. It gave the same indications in laboratory experiments (Table 1b) despite the fact that conditions of the experiments were apparently unfavourable as pollen germination was poor. Only three pistils of the 6-hr collection had a few germinating pollen-grains and germination did not occur on any pistils in the 12–48 hr fixations. Most of them showed either no pollen-grains or a few germinating ones suggesting that stigmatic fluids were either lacking, or present in such small quantities that the grains could not germinate or even adhere in some cases. Pollen germination in the cross was 'fair' suggesting that stigma receptivity had improved during the 30-hr interval. Only three to six germinated grains were found on most pistils of the 72 and 90-hr fixations of 3-10 selfed.

Few pollen-tubes were found in the styles. That the initial growth of at least one class of pollen-tubes was rapid when conditions were most favourable was shown by the presence of some tubes in the upper one-fourth of one style of the 6-hr collection. A tube reached the micropyle in one pistil of the 72-hr collection, and tubes were in the embryo sacs in two from the 96-hr collections. Evidence of incompatibility was found in inhibition of most tubes in the stigma or upper one-half of the style in pistils of the last two fixations. A few grew further but were blocked in the ovary wall. The ends of inhibited tubes were swollen or bent. Fertilization occurred in less than 96 hr as shown by the presence of endosperm nuclei in 2 sacs of the 96-hr fixation. Normal zygotes were present in both.

Prefection × 3-10. No fruit-set occurred in this cross in one year's experiments in the orchard. The results from pollination tests gave no indication why it should not be fertile (Table 1c). Pollen germination was judged as fair. The initial growth of pollen-tubes was exceptionally rapid and some of them reached the embryo sacs in less than 12 hr. The general pattern of distributions of tubes within individual pistils was inhibition of many in the stigma and others at various regions between the stigma and locule, while a few reached the embryo sacs. Perhaps

TABLE 1. POSITIONS OF THE MOST ADVANCED POLLEN-TUBES IN THE DIFFERENT PISTILS OF EACH COLLECTION AT EACH TIME OF FIXATION.

Pollination	Hr. after pollination	No. of stigmas without pollen grain	No. of stigmas with no pollen germination	Stigma	1/4 Style	1/2 Style	3/4 Style	4/4 Style	Ov. wall	Locule	Micropyle	Sac	Fertilized	Total pistils
(a) Perfection selfed	6	—	—	9										9
	12	—	—	9										9
	18	—	—	2	3	4								9
	24	—	—	—	2	2	5							9
	48	—	—	—	—	—	7	—	2					9
	72	4	4	2	—	1	1							12
	94			1	—	8	2							11
(b) 3-10 selfed	6	—	6	2	1									9
	12	2	6	—	—									8
	18	—	9	—	—									9
	24	4	5	—	—									9
	48	6	3	—	—									9
	72	—	2	—	1	2	—	1	5	—	1			12
	96	—	1	—	—	—	—	2	5	2	—	—	2	12
(c) Perfection ×3-10	6	—	5	2	2									9
	12	1	—	—	—	—	3	2	2	1				9
	18	4	—	—	1	1	—	1	—	—	—	—	1	8
	24	—	—	—	—	2	1	1	1	1	—	—	2	8
	48	—	—	—	—	—	—	4	1	1			1	7
	72						Not collected							
	96	3	—	—	—	—	—	—	1	3	—	—	1	8
(d) 3-10× Perfection	6	2	—	7										9
	12	1	—	8										9
	18	—	1	6	—	2								9
	24	—	—	2		7								9
	48	—	—	—	—	—		6	2	2	1	—	1	12
	72	—	—	—	—	—	—			2	1	—	9	12
	96	—	—	—	—	—	—	—	—	—	5	1	5	11
(e) 11-29P× 11-27P	6	—	3	4	2									9
	12	2	5	—	—	2								9
	18	2	1	1	—	—	5							9
	24	1	3	—	—	9	3	2	—	2				20
	48	3	1	—	—	—	2	6	—	—				12
	72	—	1	—	—	—	—	—	2	—	4	—	3	10
	96	1	—	—	1				3		1	1	4	11
(f) 01-13P× 11-29P	6	—	—	5	2	1								8
	12	—	3	1	4	1								9
	18	—		—	6	2	1							9
	24	—	2		1	3	2							8
	48	—	—	—	—	—	—	2	5	3	—	1		11
	72	—	1						3	4	1	1	2	12
	96								3		2	2	3	10
(g) 7-40Q selfed	6		1	7	1									9
	12			7	—	1	1							9
	18	2	—	6	—	—	—	1						9
	24	3	1	2	1	—	—	—	1	1				9
	48	4	—	—	1	2						2	—	9
	72	—	1	—	—				2	1	2	2	—	8
	96		—	3					4				1	8
(h) 7-40Q× 10-13P	6	3	—	5										8
	12	—	—	8	1									9
	18	—	—	—	8	—	1							9
	24	1	1	—	5	5								12
	48	2	—	—	—	—	3	4	1			1		11
	72	1	—	—	—	—	—	—	1	3			4	9
	96						Not collected							
(i) 7-39Q selfed	6	4	3	2										9
	12	—	3	2	2	1	1							8
	18	1	—	4	—	2	—	1						8
	24	3	2					1						6
	48	—	1	—	1	—	3	1	1					7
	72	2	—	—	—	—	5		1					8
	96	4		—	—	2	—	—	2					8

TABLE 2. POLLEN-TUBE GROWTH RATE AS INDICATED BY THE LOCALITIES WITHIN THE PISTILS OF THE MOST ADVANCED POLLEN TUBES AT DIFFERENT TIMES AFTER POLLINATION.

Pollination	Hr after pollination						
	6	12	18	24	48	72	96
Perfection selfed	ST	ST	½	¾	OV	¾	¾
3 - 10 selfed	¼	NG	NG	NG	NG	M	F
Perfection × 3 - 10	¼	L	F	F	F	–	F
3 - 10 × perfection	ST	ST	½	½	F	F	F
11 - 29P × 11 - 27 P	¼	½	¾	L	4/4	F	F
10 - 13P × 11 - 29P	½	½	¾	L	S	S	F
7 - 40Q selfed	¼	¾	4/4	L	S	S	F
7 - 40Q × 10 - 13P	ST	½	¾	½	S	F	—
7 - 39Q selfed	ST	¾	4/4	4/4	OV	OV	OV

The symbols stand for different regions of the pistil with most advanced pollen-tubes. ST, stigma; OV, ovary wall; L, locule; M, micropyle; S, embryosac; F, fertilization; NG, no germination. A fraction represents the portion of the style length traversed by the longest tube.

these represent three classes of pollen. Inhibited tubes were coiled and had swollen or bent ends as shown in Fig. 4. Fertilization occurred in one pistil in less than 18 hr after pollination of 31 pistils collected from 18 to 96 hr 5 were definitely fertilized as shown by the presence of several endosperm nuclei. All had normal zygotes.

3-10 × Perfection. In one year when this cross was made in the orchard, 10% fruit set was obtained. Laboratory results indicated potentially higher fertility (Table 1d). Germination of pollen was fair. The growth rate of tubes after passing through the stigma was fairly rapid but not as much as in the reciprocal cross, requiring almost 48 hr to reach embryo sacs and effect fertilization (Figs. 5 and 6). Many tubes were restricted to the stigmas of pistils collected 48–72 hr after pollination. Growth of most of the other tubes was checked in the styles or ovary walls. Thus, there was no indication of pollen-tube classes other than tubes confined and other not confined to stigmas. The ends of the tubes were swollen or bent. Each of the 16 fertilized pistils contained several endosperm nuclei and apparently normal zygotes (Figs. 5 and 7).

11-29P × 11-27P. This cross was relatively fruitful under field conditions. Pollen-tube studies confirmed that this should be the case (Table 1e). Pollen germination was fair. Some tube penetrated the upperone-fourth of the style by 6 hr, some appeared in the locule in 24 hr, and some reached embryo sacs before 72 hr. Fewer tubes were inhibited in thestigmas than in any other cross. Most tubes were blocked in the upper one-half to three-fourths of the styles. Their ends were bent or swollen. All seven sacs in which fertilization had occurred contained apparently normal zygotes and several to many endosperm nulei.

10-13P × 11-29P. Six per cent fruit-set was obtained in one year's field trials, but in another no fruit set. Laboratory experiments indicated that this cross should be somewhat fertile (Table 1f). Pollen germination was good. Some tubes were in the upper half of the style 6 hr after pollination in one pistil. Later tube growth through the style and ovary wall was slower. Evidence of incompatibility included inhibition of some tubes in the stigma and others in the upper three-fourths of the style. Inhibited tubes had swollen or bend ends. 9 Pistils of the 48–96 hr fixations had pollen-tubes in the embryo sacs and 5 of them were definitely fertilized, having several endosperm nuclei and apparently healthy zygotes as illustrated in Fig. 8.

7-40Q Selfed. Branches were bagged in 5 different years and 0–38 fruits were obtained in different years. Germination was fair. Rate of tube growth was relatively rapid in all regions of the pistils (Table 1g) and some tubes reached sacs in 48 hr. Many tubes were inhibited in the stigmas, others in different regions of the style and a few in the ovary walls. Five pistils of the last three fixations showed pollen-tubes in the sacs, but the only evidence of fertilization was in one sac which contained several endosperm nuclei but no zygote (Fig. 11). In 76% of the 25 pistils of the 24-hr and later fixations (24 hr were required for tubes to reach the micropyle) the eggs were abnormal, which accounted for low fruit set.

7-40Q × 10-13P. In two year's crosses in the field no fruits were set. Laboratory results confirmed that this cross should be highly unfruitful, at least in some years. Pollen germination was good and pollen-tube growth fairly rapid. The stigmas were the sites of inhibition of many tubes. Those able to penetrate the stigma were stopped mainly in the upper one-half of the style, although some were arrested beyond this region in the style and in the ovary wall. Most of the inhibited tubes had swollen or bent ends. Pollen-tubes were found in embryo sacs of 5 pistils of the 48–72 hr fixations. One of these showed no evidence of fertilization, while in each of the others several endosperm nuclei were present (Fig. 10). Double fertilization, however, did not occur. As in 7-40Q selfed, the extent of egg degeneration was so advanced in many cases at the time of fixation that degeneration probably began before the pollen-tube entered the embryo sacs. Moreover, signs of degeneration appeared in two sacs of 0 hs. Only the 20 pistils of the 24-hr and later fixationr were consistently checked for the condition of the

egg, 80% gave indications of degeneration; seemingly healthy eggs were found in the remainder.

7-39Q Selfed. In each of the four year's experiments in the field no fruit set when branches were bagged. In some pistils of the different fixations no pollen or only ungerminated pollen was found on the stigmas. Immaturity of the pistils was apparently the cause. Presumably because of poor germination relatively few pollen-tubes were seen in the styles. Growth of the tubes was rapid in the style but slower into the ovary wall. No tubes were found below the ovary wall (Table 1). Inhibition of most pollen-tubes occured in the stigma and those penetrating through the stigma were blocked at different regions of the style or ovary wall. Two pollen classes are suggested, tubes of one being confined to stigmas, those of the other distributed through the style and ovary wall. As in 7-40Q, egg degeneration was prevalent in 7-39Q. It occurred in 70% of the 20 pistils of the 24–96 hr fixations. Failure of fruit-set in 7-39Q selfed would, therefore, be expected on two counts (1) early degeneration of eggs, and (2) failure of pollen-tubes to reach the embryo sac.

Discussion

Pollen-tube behaviour as noted in these studies and field evidence show that incompatibility exists in the apricot. The system of incompatibillity involved has not been detrmined, but available indirect evidence suggests the homomorphic, gametophytic system according to Lewis'[15] classification of self-incompatible plants.

Brewbaker[16] has listed some characteristics of the sporophytic and the gametophytic systems; the pollen-grains of sporophytic species are trinucleate in contrast to the binucleate grains of gametophytic species. The apricot has binucleate pollen-grains. In gametophytic species inhibition usually occurs at the pollen-tube stage, while in sporophytic species inhibition occurs at the pollen germination stage. In the apricot, incompatible pollen apparently germinated as readily as compatible. According to Pandey[17] no family in the plant kingdom is known to contain both gametophytic and sporophytic genetic systems in different species. Since the gametophytic system has been established in sweet cherries,[6] and in view of the other

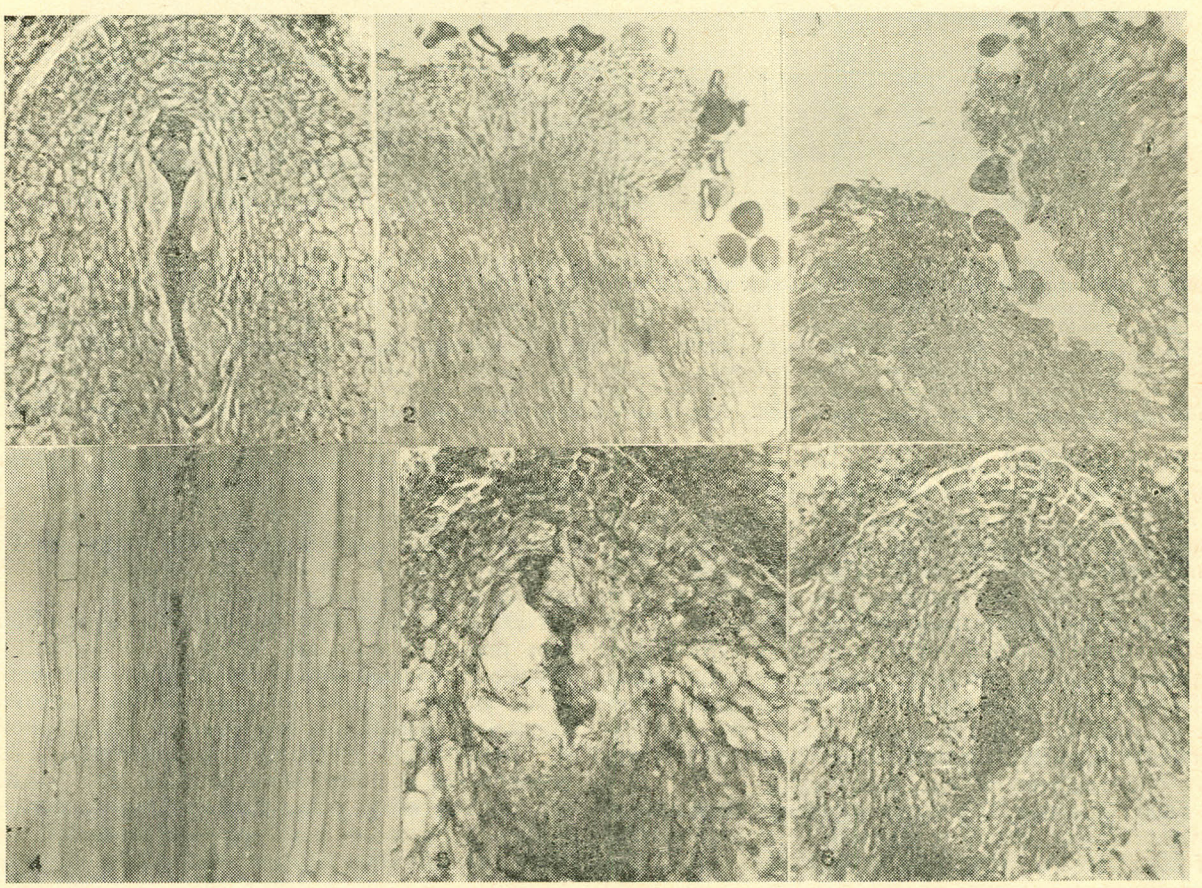

Fig. 1. An unfertilized embryo sac of 3-10, 72 hr after pollination, showing the typical structure for the apricot. Antipodals degenerated (phase, × 430). Figs. 2 and 3. The stigmas in Perfection selfed and 11-29P × 11-27P, respectively, 42 and 72 hr after pollination. showing both germinated and ungerminated pollen-grains on each. The collapsed grains are those which germinated and have lost all cytoplasmic content (×200). Fig. 4. Incompatibility symptoms shown by the pollen-tubes in the upper-one-half of the style in the cross Perfection × 3-10. Note the coiling, swollen and bent-ends (×200). Fig. 5. Early stage of fusion of egg and sperm in 3-10 × Perfection, 48 hr after pollination. Also seen are the remains of the pollen-tube (upper left) and part of endosperm (below the egg and sperm) (×450). Fig. 6. Section adjacent to the one in Fig. 5, showing two endosperm nuclei and their cytoplasm (lower part of sac). The darkness above is pollen-tube cytoplasm.

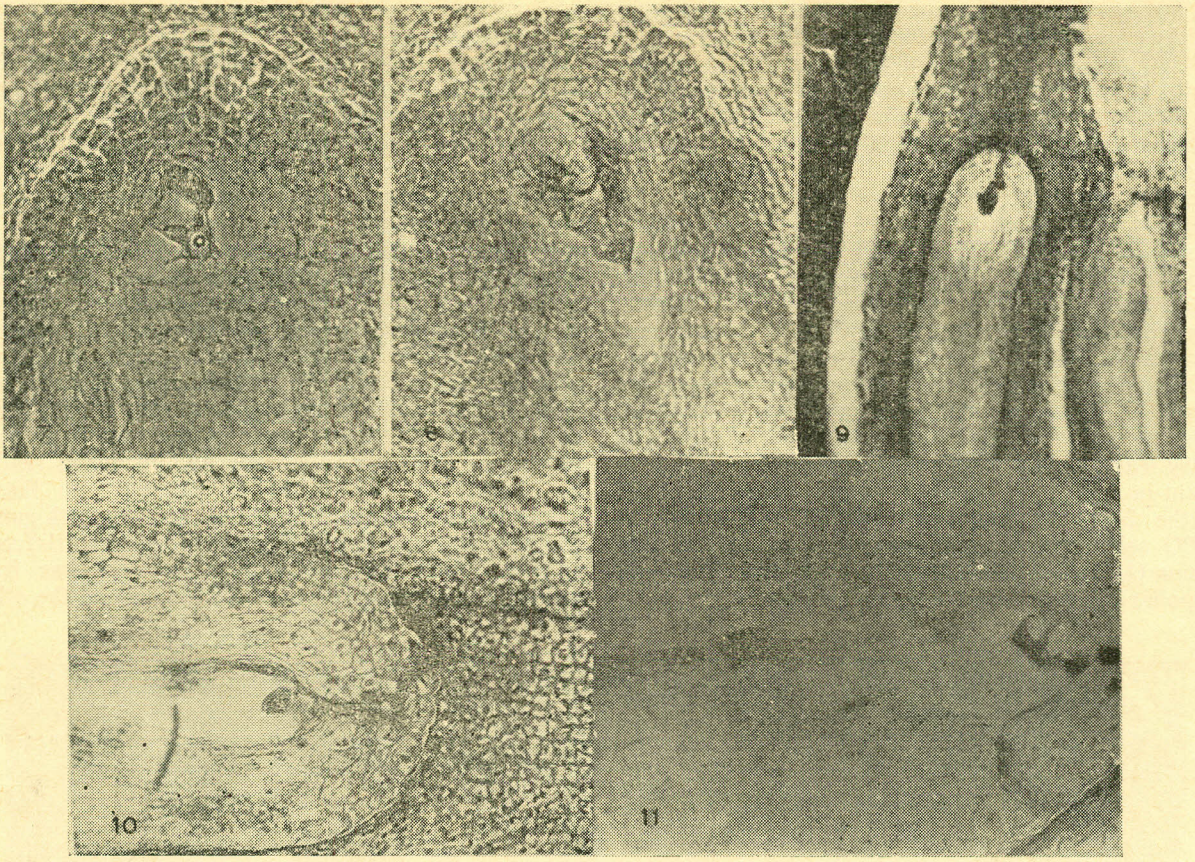

Fig. 7. The zygote and one endosperm nucleus (lower part of sac) in 3-10 × Perfection, 72 hr after pollination. A synergid nucleus is at the upper left, remnants of the other synergid and tube cytoplasm at the upper right. Several other endosperm nuclei were in other sections (phase, ×430). Fig. 8. A zygote (upper left) of 10-13 × 11-29P, 96 hr after. Fig. 9. Part of pollination, with free nuclear endosperm around it (phase, ×430) the endosperm in a sac of 7-40Q selfed, 48 hr after pollination (phase, ×200). Fig. 10. An ovule of 7-40Q × 10-13P, 72 hr after pollination, showing the pollen-tube in the micropyle, the degenerating egg, and to the left parts of two endosperm nuclei and their cytoplasm (×450). Fig. 11. Part of the endosperm in a sac of 7-40Q selfed, 96 hr after pollination. Two endosperm nuclei are seen below the egg cell and five other farther down. The egg nucleus (not shown) had degenerated. Remnants of the pollen-tube and degenerated synergids above (phase, ×200).

evidence presented, the apricot should have the gametophytic scheme of incompatibility.

According to the oppositional factor hypothesis of East and Mangelsdorf,[18] if two plants having a gametophytic system of pollen control are reciprocally compatible, only two situations are possible in their progenies, depending on the different genotypes of the pollen parent involved in the cross (a) two interfertile intrasterile groups, when the cross involves one allele difference (e.g., $S_1S_2 \times S_2S_3$); one of the groups will be compatible with the female parent, (b) four interfertile, intrasterile groups, when the cross involves two allele differences (e.g., $S_1S_2 \times S_3S_4$).

Field trials and the present cytological observations on the apricot clones is question show that neither of the above two situations in applicable here. The hereditary behaviour of incompatibility in these plants differs from that in the *Nicotiana* type in the following respects. (1) Both parent varieties, Perfection and 3-10, are reciprocally somewhat fruitful, but members of the progeny of their one way cross (3-10 × Perfection) appear to be cross-incompatible, certain ones being partially cross-fruitful in some years. They show similar behaviour when back-crossed to either of the parents. (2) No definite intrasterile, interfertile groups appeared in the progeny. (3) When selfed, the seedlings usually gave no fruit-set. But under certain conditions most conducive to setting, up to 5% set was obtained. In only one seedling about 20% set was obtained in one year in the field.

Neither the field data nor the cytological observation presented here are sufficient to warrant any definite conclusion about the S-alleles and possibly other genetic factors involved in this apparently anomalous hereditary behaviour of incompatibility. A hypothetical mechanism, pseudofertility, could account for it. According to East and Yarnell[19] the growth of a pollen-tube bearing a particular S-allele is dependent both upon environmental conditions and subsiding heritable factors. Temperature is an important external factor which may shift the rate of pollen-tube growth, as Lewis[20] has shown in a sweet cherry. Certain other conditions are also effective in breaking down self-incompatibility either completely or partialy. Bud pollinations or pollination at the end of the flowering season have resulted in seed-set in several species, e.g., *Nicotiana*[21] and *Petunia*[22]. Weakening of incompatibility also oc-

curred when plants of *Oenothera organesis* were kept in the dark for sometime before pollination.[23] In bud and end-season pollinations and after exposure to darkness, apparently the incompatibility reaction is weaker than normal either because of physiological immaturity or physiological debilitation.[24] In the apricot, bud pollination is apparently not effective. As concerns late pollination, a small amount of evidence has been obtained that pollen-tube growth is poorer when stigmas were pollinated 2 days after anthesis than at anthesis.

The subsidiary heritable factors that weaken the incompatibility reaction are genes carried in other chromosomes than those carrying the S-gene.[25] A single gene causing this effect in *Nicotiana sanderae* has been established by Brieger.[26] Several reports of many undermined genes causing pseudofertility are present.[24,27-30] Thus some fertility can occur in normally incompatible pollinations, irrespective of the age of the flower and seasonal conditions.[28]

The observations on the two parents concerned here, one presumably self-compatible and the other self-incompatible, have shown them to be reciprocally cross-fruitful. The pollen-tube behaviour in Perfection selfed confirmed the field evidence that it is self-unfruitful. The available evidence concerning 3-10 was not enough to confirm the field evidence that it is relatively self-fruitful, but at least showed that its potential fruitfulness should be greater than that of Perfection. Therefore, if allelic modifiers that weaken incompatiblity occur in the grogeny, 3-10 would appear to be a more likely source than Perfection. However, the interaction of non-allelic genes from both would have to be considered. Differences in chilling requirements for normal development indicate origins of some ancestors of the two parents in widely separated localities. Geographical separation of ancestral forms would be expected to lead to other differences in the genetic constitution of their offspring as well as to those determining the chilling requirements. If nonallelic modifiers of incompatibility are present in Perfection, 3-10, or both, complexities would be expected in the progeny because of recombinations in each parent and interaction with those from the other.

The crosses 3-10 × Perfection and the reciprocal may be the only genetically compatible ones concerned here, with the possible exception of 3-10 selfed, for which the evidence was inconclusive. Some evidence for this is that they were the only pollinations in which several to many tubes appeared in the locules. This is to indicate that some degree of compatibility as concerns the S-alleles may exist between the parents.

Acknowledgement. The author wishes to thank Dr. Muriel V. Bradley, Department of Pomology, University of California, Davis, for valuable advice and assistance.

References

1. M.B. Crane, J. Pomol. Hort. Sci., **2,** 137 (1921).
2. M.B. Crane, J. Pomol. Hort. Sci., **3,** 67 (1923).
3. M.B. Crane, J. Genet., **15,** 301 (1925).
4. M.B. Crane, J. Pomol. Hort. Sci., **6,** 157 (1927).
5. M.B. Crane and W.J.C. Lawrence, J. Pomol. Hort. Sci., **7,** 276 (1929).
6. M.B. Crane and W.J.C. Lawrence, *The Genetics of Garden Plants* (Macmillan, London, 1952), fourth edition, p. 185.
7. M.B. Crane and A.G. Brown, J. Pomol. Hort. Sci., **15,** 86 (1937).
8. W.J.C. Lawrence, Genetica, **12,** 269 (1930).
9. A. Afify, J. Pomol. Hort. Sci., **11,** 113 (1933).
10. B. Roy, J. Pomol. Hort. Sci., **16,** 320 (1939).
11. T. Raptopoulous, J. Genet., **42,** 73 (1941).
12. E.H. Newcomer, Science, **118,** 161 (1953).
13. V.I. Cheadle, E.M. Gifford and K. Esau, Stain Technol., **8,** 49 (1953).
14. E.R. Sears, Genetics, **22,** 130 (1937).
15. D. Lewis, Advan. Genet., **6,** 235 (1954).
16. J.L. Brewbaker, Genetics, **42,** 361 (1957).
17. K.K. Pandey, Evolution, **14,** 98 (1960).
18. E.M. East and A.J. Mangelsdorf, Proc. Natl. Acad. Sci. (U.S.), **11,** 166 (1925).
19. E.M. East and S.H. Yarnell, Genetics, **14,** 455 (1929).
20. D. Lewis, Proc. Roy. Soc. (London), **131B,** 13 (1942).
21. E.M. East, Am. J. Botany, **1,** 46 (1923).
22. S. Yasuda, Botan. Mag. Tokyo, **44,** 678 (1930).
23. S. Emerson, Botan. Gaz., **101,** 890 (1940).
24. W. Williams, Heredity, **5,** 51 (1951).
25. E.M. East, Proc. Natl. Acad. Sci. (U.S.), **2,** 225 (1934).
26. F.G. Brieger, Biol. Zentr., **47,** 122 (1927).
27. E.M. East, Bibliog. Genet., **5,** 331 (1929).
28. A.B. Stout, Botan. Rev., **4,** 275 (1938).
29. K. Mather, J. Genet., **45,** 215 (1943).
30. M.V. Bradley and W.H. Griggs, Phytomorphology, **13,** 141 (1963).