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# A Study of Tropism of Pollen Tubes to the Pistils IV. Tropism in Different Species

## By

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It has been reported by several investigators that the germinating pollen tubes show the positive tropism to slices of the pistils when the pollen grains were spread around the slices on an agar medium (Molisch, 1893; Miyoshi, 1894; Lidforss, 1909; Brink, 1924; Tsao, 1949; Iwanami, 1953).

Results similar to above have been obtained in *Lilium longiflorum* and *Camellia sinensis* (MIKI, 1954, 1955). In these plants, it has also been confirmed that the pollen tubes showed different responses against different pistil parts, namely, the stigmas, the styles, the ovaries and the ovules (MIKI, 1954, 1955).

All investigations stated above have been carried out to see the tropism response of pollen tubes of a certain plant against the pistil slices of the same species. Then, it comes the question whether the pollen tubes of one species show positive tropism to the pistils of other species or not. It is the first aim of the present study to clear this question. The second aim is to see the response of the pollen tubes of one species against the different pistil parts of other species.

#### **Materials and Methods**

Plants used in the present study were shown in following tables. Pollen grains of these plants were obtained from anthers which were just at anthesis, and pistils were taken from castrated flowers when they just bloomed.

For culture media of pollen grains, 1.5% agar solution containing sucrose was employed. Concentrations of sucrose were determined after preliminary tests, because the optimum concentration for pollen germination was different according to species. Hydrogen ion concentration of these media was between pH 6.2 and pH 6.4.

Hot sugar-agar solution stated above was put on a slide glass to form a layer about 2 mm in thickness, and after cooling, slices of pistils were put on the agar plate. Preparation method of pistil slices was reported in the previous paper in detail (MIKI, 1954). Pollen grains were, then, spread around these

slices with a slender brush, leaving a clear zone about 0.2-0.5 mm width from the slices. Slide glasses, which carried the pistil slices and the pollen grains, were placed in a moist Petri-dish and incubated at  $30^{\circ}C^{1}$ . Response of the pollen tubes to the slices was confirmed after 3 hours under a microscope.

#### Results

In most cases, so far as the present study was concerned, the germination of the pollen grains was not always easy on artificial media. Results of a preliminary test showed that the pollen grains of the most plants, taken at random from fields, did not germinate on several different artificial media, but some successful results were obtained. Among the plants in which pollen grains were able to germinate on the agar media containing sucrose, only 45 species were used in the present study, because they had fairly large flowers and their flower season was not extremely limited.

Generally speaking, results of the preliminary study showed that pollen tubes far from a pistil slice, elongated at random directions, and those near to a pistil slice, showed positive tropism. The least distance within which pollen tubes showed positive tropism varied in different species. In most cases, the pollen tubes within 1 mm from a pistil slice showed positive tropism, therefore, those within this distance from a pistil slice were counted in following experiments.

Exp. 1. Tropism tests between two individual plants belonging to the same species.

A pistil of one species was separated into stigma slices, style slices and ovary slices. Ovules were tested in some cases. These pistil slices were put on agar culture media, and pollen grains of the same species were spread around these slices.

Results of this experiment are summarized in Table 1.

In this table, it is seen that the pollen tubes of one species always show positive tropism against the pistil slices of the same species in 68% of 41 species. In some cases, however, it is observed that pollen tubes of one species show different tropism responses against different pistil parts of the same species. The plants listed in Table 1 are classified into four types in respect to the behavior of pollen tubes against the stigma slices, the style slices and the ovary slices. In the first type, the pollen tubes show positive tropism against these three different parts of a pistil, as can be seen in *Narcissus tazetta*. In the second type, the pollen tubes show positive tropism to the stigma slices and the style slices, but show only at random tropism against the ovary slices. *Cucumis sativus, Camellia sinensis* and *Tradescantia reflexa* belong

<sup>1)</sup> Optimum temperature of germination determined in the preliminary experiment was  $30\,^\circ\text{C}.$ 

	Tropism stigma	response style	to pistil ovary	slices ovule
Primula japonica P. sinensis	r r	r r	r r	r r
Cucumis sativus	р	р	r	
Campsis grandiflora	р	р	р	
Torenia fournieri	р	р	р	
Paulownia tomentosa Antirrhinum majus Salvia officinalis	p p r	p p r	p r	
Petunia violacea	р	р	r	
Rhododendron obtusum	r	r		
Camellia japonica C. sinensis C. sasanqua	p p p	p pp p	r r r	r
Eriobotrya japonica Rhaphiolepis umbellata Rosa multiflora	p r	p p r	р	
Ranunculus glaber	r	r		
Mirabilis jarapa	r	r		
Monochoria korsakowii	р	р		
Gladiolus gandavensis Gemmingia chinensis	p r	p r	p r	
Tradescantia reflexa	р	р	r	
Lycoris radiata L. sanquinea L. squamigera Crinum asiaticum C. latifolium Zephyranthes candia Hippeastrum hybridum Narcissus tazetta	r p p p r p	p p p p p p	r p p p p p	р
Lilium speciosum L. abeanum L. japonicum L. longiflorum L. philippinense L. auratum L. elegans Allium tuberosum Hosta sp. Hemerocallis disticha	pp pp pp pp pp p p r r r r	p p p p p r r r	p p p p r r r r	r r r r r
Agapanthus umbellatus	r	r	r	

Table 1. Tropism tests between two individual plants belonging to the same species.

p: Positive tropism (See Fig. a). pp: More intensive positive tropism than p.

r: At random tropism (Pollen tubes elongate quite at random in respect to direction. See Fig. b).

h: Germination inhibition of pollen grains.

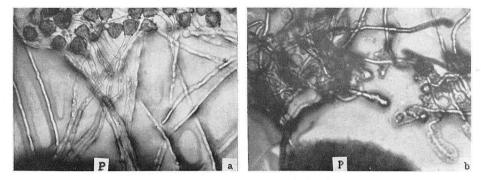


Fig. 1. Appearance of pollen grains spread around the pistil slice on agar culture medium.

- a. Positive tropism. Camellia sasanqua (style)×Camellia sinensis (pollen).
   b. At random tropism.
- Camellia sinensis (style)×Eriobotrya japonica (pollen). P: A pistil slice.

to this type, while *Lycoris radiata* belongs to the third type in which the pollen tubes show positive tropism against the style slices only, and show at random tropism against the stigma slices and the ovary slices. Contrary to the above types, the pollen tubes of the plants belonging to the fourth type show at random tropism against all pistil parts.

It must be added here that the difference in intensity of positive response of the pollen tubes against the three different parts of a pistil, was not confirmed in the present study, but it was confirmed in a previous experiment that, in *Camellia*, pollen tubes showed a stronger positive tropism against the style slices than against the other two pistil parts, while in *Lilium* the strongest response was found against the stigma slices (MIKI, 1954, 1955).

From the results obtained in Exp. 1, it is concluded that the pollen tubes of a certain plant show positive tropism against a pistil of the same species in most cases.

## Exp. 2. Tropism tests between two different species belonging to the same genus.

In Exp. 2, behavior of the pollen tubes of a plant against the pistils of other species which belong to the same genus was tested. As materials, several different species of *Camellia*, *Lilium* and *Primula* were used.

Results obtained in this experiment are shown in Table 2.

From Table 2 a, it is seen that the pollen tubes of *Camellia sinensis* show positive tropism against the stigma slices and the style slices, while they show at random tropism against the ovary slices of *C. japonica*. Similar results are obtained between the pollen tubes of *C. japonica* and the pistil slices of *C. sinensis*. In *Lilium*, however, pollen tubes show positive tropism in all cases, except pollen tubes of *L. auratum* which show at random tropism against the

Table 2. Tropism response within the same genus. a. In Camellia.

u. In Cument	<i></i>											
Pistil	С.	japo	nica	С.	sinen	sis	C. s	asang	ua			
Pollen	g	t	0 *	g	t	0	g	t	0			
C. japonica				p	р	r						
C. sinensis	р	р	r				р	р	р			
C. sasanqua				р	р	р						
b. In Primula	•											
Pistil	Ρ.	japo	nica	P. n	nalaco	oides	<i>P</i> .	obcom	ca	P. s	iner	isis
Pollen	g	t	0	g	t	0	g	t	0	g	t	0
P. japonica				r	r	r	r	r	r	r	r	r
P. malacoides	r	r	r				r	r	r	r	r	r
P. obconica	r	r	r	p	r	r				r	r	р
P. sinensis	r	r	r	r	r	r	r	r	r			
c. In Lilium.												
Pistil		n		m	un	iense			um	um		
		speciosum	abeanum	jaþonicum	longiflorum	philippinense	auratum	elegans	cordifolium	L. lancifolium		
Pollen		Γ.	Г.	Γ.	Γ.	Ľ.	Γ.	Γ.	Ľ.	L.		
		gto	gto	gto	gto	gto	gto	gto	gto	gto		
L. speciosum					ppp	ppp	ppp					
L. abeanum					ppp							
L. japonicum					ppp				,			
L. longiflorum		ppp	ppp	ppp		ppp	ppp	ppp	ppp	ppp		
L. philippinens	9	ppp			ppp					$_{\rm ppp}$		
L. auratum	and the second division of	ppp			ppp					$\mathbf{prr}$		
L. elegans					ppr							
* ~ . 2+:	am	. + .	Style	<u>.</u>	Overs	7						

\* g: Stigma t: Style o: Ovary

style slices and the ovary slices of L. lancifolium. Contrary to the above types, in Primula, the pollen tubes show at random tropism in most cases.

Generally speaking, in the same genus, the pollen tubes of one species show positive tropism against the pistil slices of other species belonging to the same genus and in some cases pollen tubes show at random tropism.

Exp. 3. Tropism tests between two different genera belonging to the same family.

In experiment 3, tropism tests were carried out between two different genera within one family.

The results of this experiment are shown in Table 3.

From the results of the experiment shown in Table 3, it is seen that the pollen grains germinate in most cases and that the pollen tubes, which elongate normally, show positive tropism in some cases (about 44%), while they show at random tropism in the other (about 38%).

In Scrophularidaceae, the pollen tubes of a plant belonging to a certain genus show at random tropism against all three different pistil parts of a plant which belong to other genus, except the pollen tubes of *Paulownia tomentosa* which show positive tropism against the stigma slices of *Veronica caninotesticulata* (Table 3 a). Similar results are obtained in Rosaceae (Table 3 b).

In Liliaceae, similar to the above cases, the pollen tubes show at random tropism in most cases (Table 3 c). In some plants, however, pollen tubes of one species show positive tropism against the three different pistil parts of another plant belonging to other genera. For example, the pollen tubes of *Lilium longiflorum* show positive tropism against three parts of the pistil slices of *Tricyrtis affinis*. The behavior of the pollen tubes of *Lilium longiflorum* against the pistil slices of *Hemerocallis disticha* is different from the above

Table 3.	Tropism	response	between	two	different	genera	belonging
to the	e same fai	mily.					

Pistil	Ve conino	ronico testico			tirrhi maju			Salı officin	
Pollen	g	t	0	g	t	0	g	t	0
Paulownia tomentosa	p	r	r						
V. caninotesticulata				r	r	r			
A. majus	r	r	r				r	r	r
S. officinalis				r	r	r			
b. In Rosaceae.									
Pistil Pollen	a Prunus yedoensis	t P. japonica	of Pourthaca villosa	of Cratacqus cuneata	of Rubus palmatus	a Chaenomeles lagenaria	Anaphiolepis umbellata	od Rosa multiflora	of Exochorda racemosa
Kerria japonica	rrr	rpp				rrr	rrr		
Rhaphiolepis umbellata			rrr	rrp	prh			prr	prr
Rosa multiflora						rrr	rrr		rrr

a. In Scrophularidaceae.

- c. In Liliaceae. L. philippinense L. longiftorum Lilium cordifolium Pistil H. thunbergii L. speciosum Allium tuberosum Hemerocallis gapanthus umbellatus Hosta sp. **Tricyrtis** disticha affinis Pollen gto L. speciosum hhh L. longiflorum hhh hhh rpr hrp rrr pppL. philippinense ppp hhh L. auratum Allium tuberosum rrr Hemerocallis disticha rrr rrr H. thunbergii rrr Tricyrtis affinis ppp rrr rrr Agapanthus umbellatus hpr hrh rrr
  - d. In Iridaceae.

	Pistil	Gladiol	us gano	lavensis	Gemmi	ngia ch	inensis
Pollen		g	t	o	g	t	0
Gladiolus gand	1				h	h	h
Gemmingia chir	iensis	r	r	r			

# e. In Amarillidaceae.

Pistil Pollen	the Lycoris radiata	the L. sanquinea	ta L. squamigera	b Crinum of asiaticum	of C. latifolium	o Zephyranthes candia	b Z. carinata	og Hippeastrum of hybridum	og Narcissus O tazetta	a Clivia nobilis
Lycoris radiata				rrr		rrr	rrr			
L. sanquinea							ppp			
L. squamigera				rrr						
Crinum asiaticum	ppp	ppp	ppp		ppp	ppp	ppp			
Zephyranthes candia	rrr			rp						
Z. carinata	ppp									
Hippeastrum hybridum									rrr	rrr
Narcissus tazetta								rrr		
Clivia nobilis								rpp	$^{\mathrm{rpp}}$	

cases, that is, the pollen tubes of the former plant show positive tropism against the ovary slices and at random tropism against the style slices of *Hemerocalis disticha*. In this case, the pollen grains do not germinate around the stigma slices.

Only two species which belong to Iridaceae were used in the present study, because germination of the pollen grains on the agar media was not easy in most cases. In Table 3 d, one would see that the pollen tubes of *Gemmingia* chinensis showed at random tropism against the pistil slices of *Gladiolus gandav*ensis, while the pollen grains of *G. gandavensis* did not germinate around the pistil slices of *Gemmingia chinensis*.

In Amarillidaceae a peculiar behavior of the pollen tubes is found, that is, the pollen tubes of *Crinum asiaticum* show positive tropism against all pistil parts of other species which belong to this family (Table 3 e). Moreover, it must be mentioned here that the pollen tubes of *Zephyranthes carinata* and *Lycoris sanquinea* show positive tropism against the all pistil parts of *Lycoris sanquinea* and *Zephyranthes carinata* respectively, and the pollen tubes of *Lycoris radiata* show at random tropism against all pistil slices of *Crinum asiaticum*, *Zephyranthes candia* and *Z. carinata*.

From the results of the study shown in Table 3, it is briefly stated here that the tropism response of the pollen tubes to the pistil slices between two species belonging to different genera within a family is at random or positive.

## Exp. 4. Tropism tests between two different families.

Results of tropism tests carried out between two plants belonging to different families are shown in Table 4.

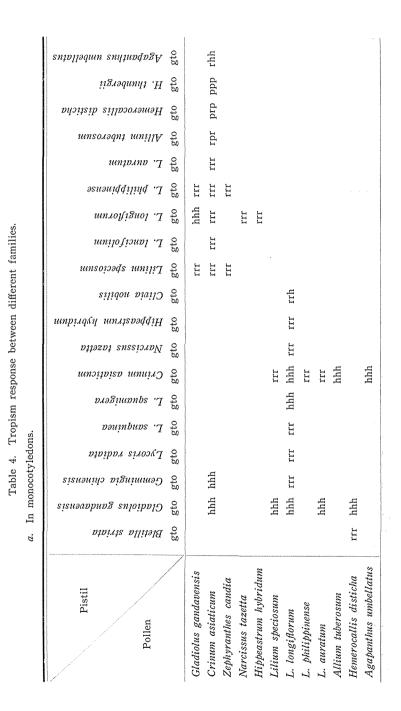
Table 4 *a* and *b* show tropism response between different families among monocotyledons and among dicotyledons respectively. In these tables, it is seen that the pollen tubes show at random tropism in most cases. For example, the pollen tubes of *Rosa multiflora* show at random tropism against all pistil parts of *Rhododendron obtusum*, *Camellia sinensis*, *Ranunculus glaber* and *Primula japonica*. In several cases, however, pollen tubes show positive tropism. The pollen tubes of *Crinum asiaticum*, for example, show positive tropism against the pistil slices of *Hemerocallis*.

It must be noted here that inhibition of pollen germination is observed in about 30% of the tested plants.

Moreover, between Archichlamydeae and Metachlamydeae, the pollen tubes elongate to random direction around the pistil slices except for some cases where the pollen tubes show positive tropism (Table 4 b).

In Table 4, it is also seen that the pollen tubes show, in most cases, a response similarly to the three different pistil parts, while the pollen tubes of *Crinum asiaticum* show different tropism response against three different pistil parts of *Hemerocallis disticha*. Several cases similar to the above are seen in this table.

A Study of Tropism of Pollen Tubes to the Pistils, IV



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Hisako Miki
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Pistil Pollen	Paulownia tomentosa	Rhododendron obtusum	Camellia japonica	C. sinensis	Eriobotrya japonica	Rhaphiolepis umbellata	Rosa multiflora	Ranunculus glaber	Viola tricolor	Primula japonica	Weigela floribunda
	gto	gto	gto	gto	gto	gto	gto	gto	gto	gto	gto
Paulownia tomentosa						rrr	rrr	$_{\rm pp}$			
Rhododendron obtusum	hhh							hhr	r		
Camellia japonica					rrr						
C. sinensis					rrr		rr				
Eriobotrya japonica			rrh	rrh							
Rhaphiolepis umbellata	rpp	rrr						rr		rrr	rrr
Rosa multiflora		rrr		rr				rrr		rrr	

b. In dicotyledons.

## Exp. 5. Tropism tests between monocotyledons and dicotyledons.

Tropism tests of the pollen tubes of a plant, which belongs to monocotyledons, against the pistil slices of dicotyledons, and the pollen tubes of dicotyledons against the pistil slices of monocotyledons, were carried out in Exp. 5.

Results of the tropism tests are shown in Table 5.

Table 5 a shows response of the pollen tubes of monocotyledons against the pistil slices of dicotyledons. In this table, it is seen that the pollen tubes show at random tropism in most cases, while they show positive tropism in a few cases. For example, the pollen tubes of *Lilium longiflorum* show positive tropism against the all pistil parts of *Oenothera odorata*, and the pollen tubes of *Crinum asiaticum* show positive tropism against the all pistil parts of *Campsis grandiflora* and the stigma slices of *Oenothera odorata*. These facts show that positive tropism takes place between two species which are extremely remote in relationship. Results similar to the above cases are seen in Table 5 b, which shows response of the pollen tubes of dicotyledons against the pistil slices of monocotyledons. In this experiment, it is clearly confirmed that the pollen tubes of *Paulownia tomentosa* show positive tropism against the style slices of *Hemerocallis disticha*. This is another example, where positive tropism takes place between two species which are remote in relationship.

Summarizing the results of the Exp. 5, it is stated that at random tropism of pollen tubes is seen in 60% of tested cases between monocotyledons and dicotyledons. This value is nearly equal to that obtained in Exp. 4, and is higher than the value found between different genera within one family. It must be noted that, in Table 5, inhibition of the pollen germination is observed in about 30% of the tested cases.

Table 5. Tropism tests between monocotyledons and dicotyledons.a. Response of pollen tubes of monocotyledons against the pistil slices of dicotyledons.

Pistil Pollen	b Campsis grandiflora	🛱 Antirrhinum majus	ස් Salvia officinalis	a Ipomea pharabitis	ਲੈ Calystegia japonica	st Oenothera odorata	ष्ये Camellia japonica	ot C. sinensis	क of C. sasanqua	ta Eriobotrya japonica	ස් Rhaphiolepis umbellata	ರ್ಧಿ Rosa multiflora	a A Ranunculus glaber	A Mirabilis jalapa	a Torenia fournieri
Hemerocallis disticha											rrr	rrr	rr		
Lilium longiflorum	rrr	hhh	hhh	rrr	rrr	ppp	rrh	rhh	rrh	rrr		rr		hh	hhh
Crinum asiaticum	ppp	rrr		rrr	rhh	prr								rr	rrr
Gladiolus gandavensis		hhh													

b. Response of pollen tubes of dicotyledons against the pistil slices of monocotyledons.

Pistil	Hemerocallis disticha	Lilium longiflorum	Crinum asiaticum	Gladiolus gandavensis	Bletilla striata
Pollen	gto	/ gto	gto	gto	gto
Campsis grandiflora			rrr		
Paulownia tomentosa	rpr				rrr
Antirrhinum majus	hhh	hhh		hhh	
Rhododendron obtusum	rrr				
Camellia japonica	A CONTRACTOR OF	rrr			
C. sinensis		rrr			
C. sasanqua		rrr			
Eriobotrya japonica		hhh			
Rhaphiolepis umbellata	rrr				rr
Rosa multiflora	hhh	rr			

# **Conclusion and Discussion**

Several investigators have reported that the pollen tubes of a plant show positive tropism to the pistil slices of the same species (Molisch, 1893; MIYOSHI, 1894; LIDFORSS, 1899; EAST and PARK, 1918; BRINK, 1924; IWANAMI, 1953; MIKI 1954, 1955). It is found in the present study that the pollen tubes of most of the species studied in this experiment show positive tropism against the pistil slices of the same species, but the pollen tubes of some species show at random tropism against the pistil slices of the same species (Table 1).

In the same genus, similarly to the above case, the pollen tubes of one species show positive tropism to the pistil slices of other species belonging to the same genus, but in some cases the pollen tubes show at random tropism (Table 2).

In the tropism tests between two different genera belonging to one family, the pollen tubes of one species which belongs to a genus do not show clear positive tropism against the pistil slices obtained from other genera. In these cases, the pollen tubes show at random tropism or positive tropism. In some cases, however, the pollen grains are inhibited of their germination (Table 3).

Between different families in monocotyledons or dicotyledons, the results of the tropism tests show that the pollen tubes of a plant elongate at random direction around the pistil slices of the plants which belong to other families in majority of cases, while the pollen tubes show positive tropism in some cases. It must be noted that the pollen grains are inhibited in their germination in many cases (Table 4). Between Archichlamydeae and Metachlamydeae (Table 4*b*) and between monocotyledons and dicotyledons (Table 5), the results similar to the above have been obtained.

Summarizing the results of experiments stated above, it is concluded briefly that positive tropism takes place between two plants which are near in relationship, while the pollen tubes showing at random tropism are found between two plants which are remote in relationship.

In the previous papers it has been reported that the pollen tubes of *Lilium* longiflorum and *Camellia sinensis* show positive tropism against some chemical substances contained in the pistil slices of the same species (MIKI, 1954, 1955). These substances have been assumed to be substances of low molecule, because they diffuse into the agar medium rapidly and pass a collodion membrane. Moreover, they have been assumed to be metastable to heat, because these substances have lost their activity by heating. There seem to be little doubt, therefore, in concluding that some active substance (or substances), which causes positive tropism of the pollen tubes against the pistil slices, is (or are) contained in the pistils of the plants which are listed in Table 1. Then, comes the question whether this active substance is specific for each species or not.

From the results shown in Table 1, it is highly suitable to conclude that this active substance is not specific for each species, at least in some species belonging to *Lilium* or *Camellia*.

Contrary to the above case, it may be stated generally that the substance contained in the pistil slices of a plant belonging to a genus or a family is not active to the pollen tubes of other genera or families. It must be emphasized here that, in some cases, the pollen tubes of a plant which belongs to a genus or a family show positive tropism against the pistil slices of other

genera or families (Tables 3, 4 and 5). To put it in other words, the active substance is non-specific for any species when the relationship of two plants is near, while it is assumed to be specific when the relationship of the two plants is remote.

It is also confirmed in the present study that, in some cases, the pollen tubes show different response to the stigma slices, the style slices and the ovary slices. It is not cleared in the present study whether this difference in response is due to different concentrations of the active substance contained in pistils, or not.

In Tables 3, 4 and 5, it is seen that the germination inhibition takes place frequently in the tropism reaction experiment, in which the pollen grains of one species are spread around the pistil slices of other species remote in relationship to the former plant. This phenomenon will be discussed in a paper to be published later.

#### Summary

1. Tropism response of the pollen tubes of one species to stigma slices, style slices, ovary slices and ovules of other species, which belong to the same or other species, is tested on agar culture medium.

2. In the tropism test within a species, it is seen that pollen tubes of most of the species studied in this experiment show positive tropism against the pistil slices belonging to the same species. In some species, however, pollen tubes of one species show at random tropism against the pistil slices belonging to the same species.

3. Between two different species belonging to the same genus, pollen tubes of one species show positive tropism against the pistil slices of other species, though pollen tubes show at random tropism in some cases.

4. It is found that, between two different genera belonging to one family, pollen tubes of a species of a genus show at random tropism or positive tropism against the pistil slices of plants belonging to other genera.

5. Between two species of different families among monocotyledons or among dicotyledons, pollen tubes of a plant belonging to one family show at random tropism against the pistil slices of plants belonging to other families in most cases. In some cases, however, pollen tubes of one family show positive tropism against the pistil slices of other families. Between pollen tubes of monocotyledons and the pistil slices of dicotyledons, and between pollen tubes of dicotyledons and the pistil slices of monocotyledons, results similar to the above cases (5) are obtained.

6. In the most plants studied in this experiments, it is observed that pollen tubes show the same response to stigma slices, style slices and ovary slices, but in several cases pollen tubes show different responses against the three different pistil parts. In these cases, it is not seen that pollen tubes respond only to a special part of the pistil.

#### Hisako Miki

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