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STUDIES ON THE DIMORPHISM AND TRANSITION OF BISEXUALITY OF HETEROSTYLOUS POLYGONACEAE

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韓昶烈 : 여귀科 異型莖植物의 *Dimorphism*과 *Bisexuality*의 變化
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ABSTRACT

HARN, Chang Yawl (Chonnam U, Kwangju Korea)— *Studies on the dimorphism and Transition of disexuality of heterostylous Polygonaceae*— Kor. jour. Bot 3(2): 6—18 1960 The present experiments were designed in order to clarify the differences between the long and short styled plants and the transgressive gradation in the degree of dimorphism among the three heterostylous species of the Polygonus, *P. japonica*, *F. esculentum*, and *P. senticosus*, based on investigations regarding the floral structure, ecological and physiological traits, the results of which are summarized as follows:

(1) *P. japonica*, although it exhibits typical dimorphism, has undergone so high a differentiation between long and short styled that its long styled individuals behave as if they were female; and short styled individuals as if male. In long-styled individuals, filament, anther, and pollen grains show signs of degeneration, most of the pollen being abortive. On the other hand, in short styled individuals, the filament, anther, and pollen grains have attained remarkable development; the pollen grains are large and fertile. In short-plant the fertilized flowers readily drop off in every stage of their embryo development. This species has completely lost the self-fertile property, which is characteristic of the non-dimorphic Polygonum genus. Although this species typically exhibits the physiological characteristics of dimorphism in controlled pollination, the short-styled individuals bear no seed in nature, thus misleading taxonomists to identify the short-styled plant as male.

2) The morphological feature of the flower organ of *P. senticosus* obviously indicates definite dimorphism. Physiologically, however, no differentiation towards dimorphism was observed, the species still retaining, both in long and short-individuals, the self-fertile property common to the Polygonum genus. Elaborate examinations revealed that regardless of the modes of pollination, both fertilization and seed setting flourish, no differentiation between legitimate and illegitimate unions being recognizable. This sort of physiological property has not been observed in the investigations of other heterostylous plants. It is assumed that this species is differentiated structurally into dimorphism, but not yet physiologically. In nature, however, this plant would have more opportunities to be cross-pollinated, i.e., legitimately combined, than self-pollinated because of the development of two forms of flowers.

3) In terms of heterostylism, the *F. esculentum* just occupies the intermediate position between *P. japonica* and *P. senticosus* structurally, ecologically, and physiologically. Description of some of the physiological behavior of the plant will suffice to demonstrate the above facts. While *P. japonica* has completely lost its self-fertile property, *P. senticosus* still retains it wholly. In *F. esculentum* 2—6% of self-fertility is the result in illegitimate combination. There occur occasionally hereditary self fertile individuals among some of the *F.*

esculentum. *P. japonica* have no such individuals. In *P. senticosa* since complete fertility is the result in illegitimate combination, it may be said that in this species the occurrence of self-fertile individual is 100%.

4) *P. japonica*, by the extreme structural differentiation of flower forms, not only gives the impression of its transition toward dioecious, but physiologically it also indicates the sign that the long-style plays the role of pistil, and the short-style, the stamen. Contrary to this, *P. senticosa* has developed two forms of flowers, thus exhibiting dimorphic features, but no differentiation has yet occurred physiologically, still retaining fully the original property of non-dimorphic Polygonum genus. *F. esculentum* takes the intermediate position morphologically, ecologically, and physiologically. If it is assumed that in these species the transition has taken place from hermaphrodite to dimorphism, *P. japonica* would be the most advanced type and the *P. senticosa*, the primitive type, and the *F. esculentum*, the transition type.

5) It is conceivable that Polygonum genus, originally homo-styled and self-fertile morphologically and functionally, developed a partial allogamous property through the formation of a nectary gland, and some of the species have attained the means of ensuring more cross-pollination through the development of dimorphism of flower form, and through alteration of the self-fertile property into a self-incompatible one. The degree of changes may vary in different species, with *P. japonica* attaining the most advanced type, and *P. senticosa*, the least. Moreover, the changes which *P. japonica* has undergone are so great that in appearance it exhibits some of the characteristics of a dioecious plant. These facts lead to the possibility that another course of differentiation of sex in the sporophytic generation of higher plants may exist from hermaphrodite through heterostylism leading to dioecious.

INTRODUCTION

Numerous studies have been made on the heterostylism of various Plants, since the classical works of DARWIN, by many workers such as SCOTT(1865), DELPTINO (1867), NAGELLI (1884), STRUSBURGER (1886), JOST(1907), GAIN(1908), SIRK(1919), TISCHLER(1918), COREENS(1924), ZOLLIKOFFER(1932), LEWIS(1943), present author (1957), and many others.

Dimorphism, most prevalent and interesting among the heterostylism, of Polygonaceae has not been described yet except for the *F. esculentum* or buckwheat, extensive research of which has been made by STEVEN (1912), UBISCH(1923, 1925), GARBER and QUISENBERRY(1927), SCHOCH-BODNER(1930), EAST(1934), FROLOVA and co-workers (1946), MORRIS (1949), TATEBE (1949, 1953), SLOVJEV (1952), ESSER (1953), the present author (1957), and others. The reason why heterostylous Polygonaceae has not been reported yet is due exclusively to the fact that no heterostylous species have been known to exist in this family except for the *F. esculentum* just mentioned above.

During his studies on the fertility and other physiological properties of Polygonum genus of Polygonaceae, the present author happened to discover through the investigations of floral structures, fertility, pollen tube growth, and the fertility of pollen that the *Persicaria japonica*, known in taxonomy as dioecious plant whose male individual does not set seed (botanically seed) and whose female plant exclusively bears seed, is in reality not dioecious but typical dimorphic form morphologically and physiologically. That is, it was discovered that this species has two kinds of flower forms, one long-style short stamened, the other, short style-long stamened. Both styles set seed well regardless of the forms of flowers when legitimate combinations were made artificially. The peculiar behavior of this species, however, has led to the conclusion that this plant is assumed to be the most highly advanced type of dimorphism, the fact of which misled the taxonomists to recognize it as the dioecious plant.

* Polygonum = *Persicaria*
Persicaria japonica (Polygonum japonica)
Persicaria senticosa (Polygonum senticosa)

Fagopyrum esculentum (Polygonum esculentum)

Furthermore, in his investigations of *Persicaria senticososa*, described in taxonomy as a plant one form of flower, the author has found out that this plant has typical dimorphic floral structure, V i.e., two forms of flowers, long and short styled, and that the physiological behavior is rather different from those of conventional heterostylous species. In this respect this species, too, is considered to manifest a peculiar type of dimorphism; some properties of which appear to be just the converse of *P. japonica*.

Through the careful studies concerning the three heterostylous species, *P. japonica*, *F. esculentum*, and *P. senticososa*, it has been clarified that although these three species are typical dimorphic plants morphologically, ecologically, and physiologically, there exists gradual gradation in the extent of dimorphism among them. That is to say, *P. japonica* has lost completely the self-fertile property which is the universal characteristic of the non-heterostyle *Persicaria* (Polygonum) genus; the long-style pollen grain of this species is extremely sterile while those of short-style are fertile and viable. In general, some of the morphological traits and the functional behavior of *P. japonica* have so much altered as to give the impression that it has changed or is changing to dioecious.

P. senticososa, on the other hand, unlike the *P. japonica*, shows no sign of dimorphic character physiologically, still retaining the self-fertile property common to the non-heterostyle *Persicaria* species, although the floral organs show the typical dimorphic structures. Buckwheat takes the intermediate position of these two extremes in many respects.

In view of the facts that these three species of dimorphic Polygonum genus are different greatly in the extent of dimorphism, careful studies were designed to make comparison of further dimorphic differences morphologically, ecologically, and physiologically.

MATERIALS AND METHODS

Materials used in this experiment were those collected from various parts of the country and have been raised for several years. They were planted in pots and in the open field respectively.

Measurements of the floral parts were made with utmost care and precision.

Some of the ecological traits, the measurements of which are somewhat difficult, such as the nectary gland, were judged by rough estimation or observation.

Pollination, emasculation, microscopic works, and other experimental methods were carried out by the methods described in the present author's earlier papers.

RESULTS AND DISCUSSION

In the term, "heterostylism" are included various types of forms like those given below:

1) Two forms of flowers in which occur no difference in the style length, but marked difference between the filament length of the two flowers. This kind of heterostylism is termed as homostyle-heteroanther.

2) On the other hand, there are certain plants which have two kinds of individuals with different flower forms in which the conditions of the style and filament are exactly the reverse of the type described in (1), that is, heterostyle-homoanther.

3) The heterostylism which draws the botanists' attention most is the form in which one individual has a long style-short stamen; the other, a short style-long stamen. In this form of heterostylism the stigma of the long-styled flower stands at the same level as that of the short-style anther and the short style stigma stands at the same level as that of the long style anther. This form is termed as the hetero style-hetero anther. The term heterostylism in most cases refers to this type. Among the forms of heterostyle-heteroanther, however, there occurs two kinds of hetero style-heteroanthered flowers, one of the examples of which are noted in the *Primula*, *Fagopyrum esculentum* or common buckwheat, *Fortysia suspansa*, and the like; the other is observed

in the flowers of *Oxalis* in which here occurs three kinds of flowers each with different length of styles and filaments respectively. Notably in *Oxalis* two forms of filament of different length are present in single flower. The elaboration of this kind of heterostylism is really exquisite. In such a complicated heterostylism, the mechanism on the mode of pollination and fertility is accordingly complex.

As stated thus far, in the heterostylous plants are included various kinds of forms, of which the really interesting one is the heterostyle-heteroanther type which is rare. In this country less than 20 species appears to exist, of which three species belong to Polygonaceae.

Among the three species of heterostylous Polygonaceae, the *F. esculentum* (*Polygonum esculentum*) has been well-known and extensively investigated; the other two are *Persicaria japonica* (meissner) Gross et Nakai (*Polygonum japonica*) and *Persicaria senticosa* Nakai (*Polygonum senticosa* Fr & Sav.), the dimorphism of which has been recently discovered by the present author.

What are noteworthy discovered through the investigations of the above mentioned three heterostylous *Polygonum* genera are the facts that (1) although these three species are definitely dimorphic plants, the extent of dimorphic differentiation is remarkably varied, that is, certain species have undergone extreme alteration toward heterostylism, while in the other shows the signs of dimorphism exclusively in morphological traits; (2) there exist notably in Polygonaceae numbers of heterostyle-heteroanther type, the heterostylism which is of rare occurrence in nature.

When comparison is made among the above stated three dimorphic *Polygonum* species, there is observed clear-cut distinction in the degree of dimorphism among them. That is, in the *P. japonica* marked differences morphological and functional, and in the floral organs, exist between the long and short styled flowers. The stamens of long styled individual show the sign of deterioration which the pollens having been almost reduced to sterility. Furthermore, the dropping of the fertilized flowers or maturing seed is the outstanding physiological features in the short-styled plants of this species. The self-fertile property so characteristic of the non-heterostylous *Polygonum* genus has disappeared completely with the behavior of pollen tube corresponding to the mode of fertility. *P. japonica* in many respects displays the appearance of dioecious plant.

On the contrary, *P. senticosa* that exhibits typical dimorphism in the primary structural difference of long and short styles, shows nearly no dimorphic differentiation physiologically nor for the most part morphologically, still retaining most of the original properties of the non-heterostylous *Polygonum* species. The conspicuous common feature in connection with the fertility of heterostylous plants is that legitimate combinations yield good seed-setting, while illegitimate unions produce no or poor fertility. Contrary to this common property, *P. senticosa* sets seed well regardless of the modes of combinations, still preserving the self-fertile character. This physiological feature is apparently a deviation from the heterostylous plants' characteristic common property. Some of the behavior of this species in pollen tube growth and in fertility appears to be just the reverse of *P. japonica*.

In *F. esculentum*, differentiations between long and short styles in the floral structures, fertility, and pollen tube growth are observed to have proceeded considerably in many respects approaching those of *P. japonica*; but in certain ways remained undifferentiated, as a whole giving the impression that this species is just taking the intermediate position in the transgressive transition from home-styled, self-fertile non-heterostylous *Polygonum* to hetero-styled, self-sterile dimorphism.

As described so far, the above mentioned three species, although each typically dimorphic, show gradual gradation in their dimorphic structures and behaviors. This investigation was designed to further clarify in much greater detail the extent of difference supposed to exist among three dimorphic species.

Another interesting feature which draws one's attention is the fact that there occurs especially in this family considerably numerous heterostyle-heteroanther type heterostylism which is of rare occurrence in other families.

In the genus of *Polygonum* (*Persicaria*) there exist tens of species whose modes of pollination and fertilization have been investigated to be mostly of partially allogamous autogamy with homostyled floral structure. Furthermore, all these species equally have slightly developed nectary glands. The extent of the development of the nectary gland seems to be little as compared with that of three dimorphic species thus far mentioned.

In view of these facts the following speculation may be made: Originally the *Polygonum* genus had the self-fertilizing property with the homo-styled floral structure. Some of them, however, have undergone remarkable changes morphologically and physiologically, i.e., the floral structure has taken the structural transformation of dimorphism with the resultant alteration of mode of pollination toward cross-pollination; and certain species have made simultaneously the physiological changes, selfsterility or cross-fertilization. If these assumptions are to be correct, the *P. japonica* would be the most differentiated type. This type has not only changed to dimorphism structurally and physiologically, but some of the profoundly altered parts indicate the sign of dioecious features.

In order to clarify further these assumptions and to make clearer the degree of dimorphic difference existing among the above mentioned three species, the experiments on the structural, ecological, and physiological differences were attempted, the results of which are given below.

(1) MORPHOLOGICAL AND ECOLOGICAL DIFFERENTIATION

a. Differentiation of styles

Careful measurements of the style length and diameter of the three dimorphic species of *Persicaria* genus, *P. japonica*, *F. esculentum*, and *P. senticosa* were made; the differences between the long and short styles of respective species and the degree of differences among three species were compared.

Tab. I Style size

	<i>P. japonica</i>		\bar{d}	<i>F. esculentum</i>		\bar{d}	<i>P. senticosa</i>		\bar{d}
	L	S	Sx	L	S	Sx	L	S	Sx
Length of style	100	53	47	100	31	64	100	51	17
Style diameter	100	93	7	100	105	4,3	100	100	-

As is shown in the Tab. 1, the style length is markedly longer in the long styled plants than in the short styled individuals in all three species. Style length is regarded in heterostylism as the most conspicuous feature along with that of filament length, and these differences are termed as primary differences. The style diameter is larger in the long style in the case of *P. japonica* with statistical significance. No difference, however, is measured in the *P. senticosa*. In the *F. esculentum* the style diameter is a little longer in the short style with no great significance. The amount of difference between the two styles in diameter is greatest in the *P. japonica*, least in the *F. senticosa*, the *F. esculentum* taking just the intermediate position.

b. Difference of stigma

Tab. II Stigma size

	<i>P. japonica</i>		\bar{d}	<i>F. esculentum</i>		\bar{d}	<i>P. senticosa</i>		\bar{d}
	L	S	Sx	L	S	Sx	L	S	Sx
Stigma, lengthwise	100	125	12	100	94	3,6	100	127	6
Stigma, crosswise	100	135	24	100	91	5,6	100	86	5,6
Size of stigma	-	-		-	-		±	±	
Stigmatic papillae	-	-		-	-		+	-	
Number of stigma	2	2-3		3	3		3	3	

The size of stigma of the *P. japonica* is strikingly larger in the short styled individuals than in the long styled individuals, while there is observed a slight difference in the *P. senticosa* in which the lengthwise stigma is larger in the short styled individuals and the crosswise length is conversely larger in the long styled plants. Both lengthwise and crosswise length of stigma is larger in the long styled plants in the case of *F. esculentum*, but the degree of difference is not so great as that of *P. japonica*.

In *P. japonica* there occurs outstanding stigmatic papillae or cellular outgrowth in the short styled individual exclusively. *F. esculentum* has no such outgrowth in either style whereas the long-style of *P. esculentum* has a slight sign of such outgrowth.

The stigma along with the style is parted definitely into two in the long styled individuals of *P. senticosa*, but in the short styled individuals occasionally three stigma occurs. No difference in the number or stigma is observed between the styles in the *F. esculentum* and *P. senticosa* respectively, both styles of the two species alike having equally three parted stigmas.

In general *P. japonica* has marked difference between the two styles in the size, outgrowth, and number of stigma. No particular difference between the long and short styles is observed in other two species.

c. Ovary

Tab. III

Ovary size

	P. japonica		\bar{d}	F. esculentum		\bar{d}	P. senticosa		\bar{d}
	L	S	Sx	L	S	Sx	L	S	Sx
Ovary, lengthwise	100	104	15	100	117	4, 4	100	103	0, 7
Ovary, crosswise	100	124	6, 8	100	110	2	100	92	1, 1

In *P. japonica* the difference between the long and short-styled plants of the length of the ovary is L: S=100:104, that is, the difference is slight, but the significance is great. No difference is noticed in *P. senticosa*, while the *F. esculentum* has the ratios of L: S=100:117 with not so great significance. On the other hand, the crosswise length of ovary of *P. japonica* is much larger in the short-styled individuals than in the long styled individuals. No such difference is observed in the other two species.

The differentiation of ovary size as a whole is great in the case of *P. japonica*, but no difference is observed in the *P. senticosa*. *F. esculentum* appears to occupy the intermediate position.

d. Filament length

Tab. IV

Filament size

	P. japonica		\bar{d}	F. esculentum		\bar{d}	P. senticosa		\bar{d}
	L	S	Sx	L	S	Sx	L	S	Sx
Filament, length	100	227	77	100	225	52	100	173	33
Filament, diameter	100	107	5	100	121	10	100	100	—

The difference of filament length between the two styles in the heterostylous plants is one of the conspicuous characters and is termed as a primary difference, along with the style length. In the measurements of the filament length it was observed that the filament length is far larger in the shortstyles in any of the three species in question, and the stigmas of long styles stand at the same level as the position of short style anthers, and the short style stigmas stand at the same level as the long style anthers, thus facilitating the preference of cross-pollination rather than the self or like-style pollinations. The extent of difference between the two styles of the filament, however, is greater in the *P. japonica* and *F. esculentum*, and in the remaining species the degree of difference is a little less as compared with the former two species.

e. Differentiation of anther

Tab. V

Anther size

	<i>P. japonica</i>			<i>F. esculentum</i>			<i>P. senticosa</i>		
	L	S	\bar{d} Sx	L	S	\bar{d} Sx	L	S	\bar{d} Sx
Anther, length	100	151	32	100	119	8	100	103	1,4
Anther, width	100	117	35	100	128	11,6	100	97	0,07
3+5 condition of stamen	not apparent	+++		+++	+++		+		+
Stamen number	5-6	8		8	8		8		8

The anther length of *P. japonica* is greater in the short styled individuals with the ratios of L:S=100:151. Although the anther length of *F. esculentum* is greater in the short-styled individuals, but the difference is far less-ascompared with that of the *P. japonica*. As for the *P. senticosa* no particular difference between the anthers of two styles is noticed. The difference of anther width between the styles and the extent of differentiation between the three species is almost identical to those of anther length, with the *P. japonica* being severe, none in the *P. senticosa*, and *F. esculentum* taking the intermediate position. In this way the anther appears to be well-developed in the short styles in the cases of *P. japonica* and *F. esculentum*, but no difference has taken place in *P. senticos*.

Particularly noteworthy is the fact the long style anther of *P. japonica* shows the sign of degeneration; while the short-style anther gives the appearance of full development. In the *P. japonica* the reduction of number of pollen grain, too, is noticeable.

In the above three dimorphic species alike the stamens are attached to the petals, that is, the stamens and petals have formed the condition of adnation with 5 stamens in outer whorl and 3 inside, the conditions of which is supposed to aid in ensuring the cross-pollination by insect-visitors. This 3+5 condition of stamen is distinct in either style of *F. esculentum*, and in the short style in case of *P. japonica*. But in the stamens of the long styled individuals of *P. japonica* such a trait is rather indistinctive. This is due mainly to the fact that in *P. japonica* the stamen number has reduced to 5-6 in the long styled individuals. *P. senticosa*, also, has the stamens of 3+5 in either style, but it is not so obvious as in the former two species.

The number of stamens in the *P. japonica* is 5-6 in the long style and 8 in the short style, thus, existing clear-cut difference in the number of stamen between the two styles. The remaining two species have respectively 8 stamens in both styles alike.

As stated above, in *P. japonica* there is marked difference in the stamen and anther between the long and short style, but no difference is noticed in *P. senticosa*. *F. esculentum* appears to be transitional in this respect, too.

Tab. VI

Pollen

	<i>P. japonica</i>			<i>F. esculentum</i>			<i>P. senticosa</i>		
	L	S	\bar{d} Sx	L	S	\bar{d} Sx	L	S	\bar{d} Sx
Pollen size	-	+++	18	-	+++	30	-	+++	18
Abortive pollen	+++	-		+	-		-	-	
Amount of pollen	-	+		-	+		-	++	

The pollen grain size of short styled individuals is outstandingly larger in the three species alike. This tendency is true in any of the heterostylous plants including the dimorphic Polygonaceae so far investigated. It seems to be of primary importance in the consideration of heterostylism that the short style pollen grain is invariably larger in heterostylous plants.

In the *P. japonica* the abortion of the majority of long style pollen is the characteristic, whereas those of short styled individuals are fertile and appear to be well-developed. In *F. esculentum* eight out of 474 long-

style pollen grains examined were abnormal, while two short style pollen out of 450 were abortive, the statistical significance of the difference, however, being not apparent. In *P. senticosa* both kinds of pollen alike were completely fertile, giving no indication of abnormality in either of the pollens. As described, marked differentiation in the function of pollen grain is observed in *P. japonica*, but in the *P. senticosa*. *F. esculentum* shows slight sign of degeneration in the long-style pollen. It is supposed to be of major importance in consideration of the transgressive change of the heterostylous Polygonaceae that the long style pollen grain of *P. japonica* has changed to be abortive. In heterostylism if it is assumed that with the further alterations in the long styled individual of the female organ and in the short styled individual of the male, the long styled individual eventually may change into the female and the short styled into the male individual, the fact that in *P. japonica* the anther and pollen grain of short styles are developed well and conversely the pollen grain of long styled plants have reduced to be abortive, together with the primary difference, obviously indicates that this species has undergone or is undergoing changes toward dioecious plant. In fact, in *P. japonica* some of the functions of long and short styles has made changes into female and male respectively as is shown in the subsequent experiment. (Expt, 11)

This species is known in taxonomy as dioecious plant with the short styled individual being the male plant which is unable to bear seed. In hand pollination, however, when legitimate combination is made the so-called male individual is capable of setting a considerable number of seeds as well as possessing good fertility, thus displaying a marked difference in seed-setting between natural fertility and artificial pollination. This peculiar behavior is largely responsible for the numerous sterile pollens of long styled individual. When artificial pollinations are made, as the work of pollination is undertaken with utmost care almost every flower of the short styled individual of this species would have the opportunities to receive the fertile long style pollen although the number is very few. In nature, on the contrary, there would be few chances that the short styled flower would receive the fertile long style pollen though this is splendid entomophilous plant whose well developed nectary gland and numbers of visiting insects appear to be much greater than the well known entomophilous species of closely allied plant, *F. esculentum* or buckwheat. Furthermore, this plant has the property of its fertilized flower or maturing seed to drop readily in every stage of its development in the short styled plant as will be described later.

The fertility or viability of long style pollen of *P. japonica* is highly variable. When the long-style pollen was stained with iron-aceto carmin, approximately 70% of them are empty in contents. The remaining 30% of the stained pollens are variable in their stainability, that is, they are mostly stained in light red color with very few pollen which are stain in dark brown color, while nearly all the pollens of short styled plants are stained dark brown which is supposed to be fertile with sufficient cytoplasm and abundant cytoplasmic substances. In addition to it, toward the end-season or approaching the end of the plant's life span there occur abundant giant or micro pollen grains supposed to be due to the meiotic irregularity. This kind of abnormality was found to be much greater in the long styled individual.

The rare chance of fertile long style pollen alighting onto the stigma of short styled individual in nature and the tendency of seed dropping particularly in the short styled plants appear to be the causes that the short styled plants behave like the male individuals.

g. Flower size

Tab. VII

Flower size

	<i>P. japonica</i>		<i>F. esculentum</i>		<i>P. senticosa</i>	
	L	S	L	S	L	S
Petal size	-	++	-	-	-	-
Sepal size	-	+++	-	-	-	-

There exists great difference in the size of flower between the two styles of *P. japonica* with the long style's sepal and petal being much smaller. No difference is noticed between the two styles in the other two species.

H. Nectary gland

Tab. VIII

Nectary gland

	<i>P. japonica</i>		<i>F. esculentum</i>		<i>P. senticosa</i>	
	L	S	L	S	L	S
Amount of nectary	+++	+++	+++	+++	+	+
Number of insect visiting	+++	+++	+++	+++	+	+

The extent of development of nectary gland and the number of visiting insects failed to be measured precisely, but they were made through crude observation. As a general rule, in *P. japonica* and *F. esculentum* alike, irrespective of the forms of styles, the nectary glands are well developed and the insect-visitors were abundant, while in *P. senticosa* the reverse was the case. The former two species appear to be more entomophilous than the latter. It is interesting to observe the fact that the degree of the ecological traits of these species more or less parallels to the amount of differentiation in the floral structures.

i. Habit of flower blooming

Tab. IX

Blooming habit

	<i>P. japonica</i>		<i>F. esculentum</i>		<i>P. senticosa</i>	
	L	S	L	S	L	S
Time, blooming	* -	++	-	++	-	+
Time, anther dehiscence	-	++	-	++	-	-

* - late + early

In the three species alike the times of flower blooming and the dehiscence of anthers are earlier in the long styled individuals. Mostly in the long styled individuals of both *P. japonica* and *F. esculentum* the flower opening and anther splitting were found to be 30-40 minutes earlier than in the short styled individuals whereas really slight difference was the case between the two styled individuals of *P. senticosa*.

Through the experiments concerning the floral structures and ecological traits, it was found that the *P. senticosa*, though distinctive and outstanding between long and short style in its primary difference, has undergone little alteration in other morphological and ecological features not only between the two styled individuals but also as heterostylous plant, still retaining much the original characteristics common to the *Polygonum* genus. In *P. japonica*, however, the high degree of difference between the two forms of flowers regarding primary and secondary morphological features together with the ecological and functional differentiations are conspicuous, some of the structural and functional traits apparently showing the dioecious features.

Although the change of *F. esculentum* as a dimorphic plant is far advanced it is nonetheless inaccessible to that of *P. japonica*. It may be fair to take *F. esculentum* as occupying the intermediate position between the other two extreme species in its course of heterostylic alteration if such assumptions are to be correct.

(II) PHYSIOLOGICAL DIFFERENTIATION

As mentioned above, it has been found that there exists not only differences in the structural, ecological, and some functional traits between the long and short-styled individuals, but also there exists clear-cut transgressive gradation in the degrees of difference among the three dimorphic *Polygonum* species, *P. japonica*, *F. esculentum*, and *P. senticosa*.

In order to compare in connection with the above results the physiological feature of the three species, their

fertility behavior was investigated.

a. Difference in the fertility

Tab. X

Differentiation in fertility

	<i>P. japonica</i>		<i>F. esculentum</i>		<i>P. senticosa</i>	
	L	S	L	S	L	S
Self-fertility	— 0%	— 0%	+ 2-6%	+ 2-6%	+++ 100%	+++ 100%
Difference of fertility between LxS & SxL	(LxS) +++	(SxL) —	—	—	—	—
Occurrence of self-fertile individual	—	—	+	+	+++	+++

In the series of the author's experiments on the dimorphic Polygonaceae, no instances occurred where self-fertilization succeeded in the *P. japonica* regardless of the forms of flowers. It has been clarified further that most of the non-dimorphic *Polygonum* (*Peršicaria*) species are homo-styled in their floral structure and self-fertile with occasional cross-fertility. *P. japonica* appears on the one hand to have completely lost the self-fertile property common to the genus, and on the other, to have undergone the highest structural deviation of dimorphism from the original homo-styled floral structure. In other words, this species has undergone the furthest changes from the original forms of its Polygonum genus. On the other hand, *F. esculentum*, well-known as self-sterile crop plant, still retains its somewhat self-fertile property in both styled individuals although it is very slight (2-6%). *P. senticosa*, morphologically typical dimorphic plant, does not exhibit the slightest indication of self-incompatible property in either styles, and it still wholly retains the self-fertile character so common to the non-dimorphic Polygonum genus. In the property of self-fertile ability, too, there exists distinctive order among these three dimorphic species, arranging in order *P. japonica* (not self-fertile), *F. esculentum* (slightly self-fertile), and *P. senticosa* (fully self-fertile).

In the present consideration so far made, the self-fertile property has exclusively been dealt with. Exactly similar results were obtained in the fertility between like style crossings. That is, *P. japonica* is not fertilized nor sets seed in the illegitimate combinations whether it is selfing or like-style crossing. *F. esculentum* gives slight fertility (2-6%) in illegitimate unions while *P. senticosa* set seed as well in illegitimate pollinations as in legitimate ones.

In the legitimate combinations of *P. japonica*, L x S and S x L, when long-styled individuals were used as the mother plant both fertility and seed formation proceed normally regardless of whether the pollinations are artificial or in nature. On the contrary, when short styled individuals were used as the mother, almost no fertility was obtained in nature; but in the hand pollination in laboratory good fertility resulted although seed maturity is somewhat poorer compared with the case of L x S, due mainly to the nature of the seed dropping tendency in the short styled plants. No such difference in fertility or seed setting as is observed in *P. japonica* was noticed between the L x S and S x L combinations in the other two species, *F. esculentum* nor *P. senticosa*. In this respect too, *P. japonica* is greatly different in its behavior in fertility from the remaining two species, prompting the speculative suggestion that in *P. japonica* the differentiation between the two styles has so proceeded that the short styled individuals behave somewhat like male individuals, thus playing the role of pollen suppliers.

In the studies of *F. esculentum*, the author was able to find frequently the self-fertile individuals which are supposed to be hereditary. These phenomena were reported by other researchers not only in buckwheat but in other heterostylous species of various families. It is interesting to notice among these dimorphic species in question in which there exists marked difference in the occurrence of self-fertile individuals. That is, in the case of *P. senticosa*, as it is a self-fertile plant, it may be stated that the rate of the occurrence of self-fertile

individual is 100%. During the studies of *P. japonica* which is incompletely self-sterile, not a single self-fertile individual was found. Therefore, the ratio of the occurrence of self-fertile individual should be said to be 0%. Although in the present experiments as many individuals of this species as possible from various parts across the country were used, the numbers of individuals used were not so great as in the case of *F. esculentum*.

Throughout the fertility experiments it was apparent that in *P. japonica* the differentiation between the two forms of styles was in some respects so profound as to show the signs of dioecious traits, coupled with the entire loss of the original self-fertile property. On the contrary, *P. senticosa*, structurally dimorphic, has revealed no physiological alteration characteristic to heterostylism, and still has retained wholly the autogamous character of the non-dimorphic *Persicaria* species. *F. esculentum*, although in many respects it resembles more *P. japonica*, as a whole appears to be transitional between the two extremes.

b. Difference in pollen tube growth

Tab. XI Difference in pollen tube growth

	<i>P. japonica</i>		<i>F. esculentum</i>		<i>P. senticosa</i>	
	L	S	L	S	L	S
Selfed	- Checked	- Checked	+ Checked, occasionally to ovary	+ Checked, occasionally to ovary	+++ Ovary	+++ Ovary
Difference between Selfed & crossed	L selfed- L x S++	S Selfed- S x L++	*±	±	L selfed- L x S +	S selfed- S x L +
Difference between L x S & S x L	L x S ++	S x L -	*±	±	L x S +	S x L -

* Not sure.

In *P. senticosa* the selfed pollen tube in both styled individuals reached the ovary in about 30 minutes. This result exactly parallels that of fertility. In *F. esculentum* when illegitimate combinations were made the pollen tubes were checked in the definite regions of the pistils, allowing occasionally the incompatible pollen tubes to reach the ovary. In *P. japonica* not a single illegitimate pollen tube was allowed to reach the ovary, and the growth of the tubes was checked at definite regions in both individuals. The behavior of pollen tubes in the illegitimate combinations clearly shows the transgressive gradation among the three species.

Pollen tube growth was found to be faster in the legitimate combinations than in the illegitimate unions in any of the three species irrespective of the forms of style. This tendency seems to be more conspicuous in the *P. japonica* than in *P. senticosa*. In *F. esculentum* the tube growth is too rapid (15 minutes) to distinguish the difference.

The difference between the combinations of L x S and S x L of the rapidity of pollen tube growth was observed to be slightly faster in the unions of L x S than in the reciprocal unions in *P. japonica* and *P. senticosa* alike. The tube penetration to the ovary, however, is too rapid to present conclusive data. In general, the differentiation between the two styles in the pollen tube behaviors appears to be much greater in *P. japonica*.

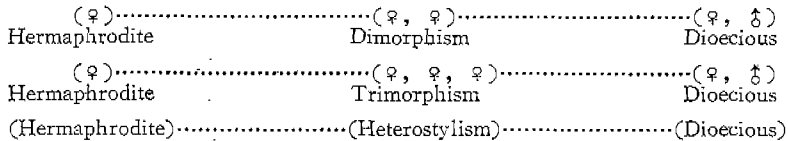
CONCLUSION

Through the results obtained in the investigations of floral structures, ecological and physiological features, and pollen tube behaviors of the three dimorphic *Polygonum* genera, the following facts have been made clearer:

In *P. senticosa*, although the primary structural difference as heterostylous plant is conspicuous, other dimorphic traits including secondary differences are not distinct. In *P. japonica*, on the other hand, not only the primary structural differences but also various physiological differentiations as heterostylous plant have proceeded

so highly that some of the morphological and functional characters disclose signs of a dioecious character, *F. esculentum*, that exhibits highly differentiated typical dimorphism morphologically and physiologically, has progressed still far less in the amount of alteration than that of *P. japonica*. That is, the amount of difference between the forms of styles varies with the different species. For instance, in *P. senticosa* there exists no differentiation of fertility among the modes of combinations, i.e., both self and cross-fertilization are carried on equally well. Under natural conditions however, it would be expected that cross-fertilization rather than the self-fertilization would be carried out more frequently due to the peculiarity of the floral structure. In *P. japonica*, the differentiation between the two style have proceeded so extremely in every respects, i.e., pollen grain size, abortion of long style pollen grain, degeneration of long style stamen, the tendency of seed-dropping in short styled individuals, and behavior of pollen tube growth that some traits of this species give the impression of transgressive changes from dimorphism to dioecious. *F. esculentum* appears to have in many respects the transitional features.

From the facts that (1) these three species are typical dimorphic, (2) there is gradual gradation in the extent of dimorphism, (3) among them, *P. japonica* has tended to dioecious, it may be assumed that in the course of sexual differentiation of the sporophytic generation of higher plants from hermaphrodite to dioecious, some kinds of plants have taken the course of heterostylism. This assumption may be illustrated as follows:



Furthermore, most of the prevalent characters of the non-dimorphic *Polygonum* genus is homo-styled, partially allogamous-autogamy. In view of the fact that in this genus particularly there occurs numerous dimorphic species, it may be assumed that some of the homo-styled, self-fertile plants have taken the course of allogamy with the development of the nectary gland and the structural and physiological alterations toward heterostylism.

These plants in their transition from autogamy to allogamy have taken dual courses, i.e., one, structural; and the other, physiological. Structurally the floral organ has changed to dimorphism and physiologically from self-fertility to self-incompatibility.

Upon the above speculations, the results obtained in the present experiments may be summarized like the following illustration:

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摘 要

本實驗은 여귀科의 Dimorphism 植物 3種, *P. japonica*, *F. esculentum*, *P. senticososa*에 대해서 L, S株間의 分化의 程度, 및 3種間의 分化의 差를 花器의 形態, 生態, 受精生理上으로 究明함으로써 여귀科 Polygonum屬에 特히 많은 Dimorphism 植物과 非異型蕊植物의 關係를 追究함과 아울러 植物造胞體世代的 性의 分化過程과 Heterostylism과의 關連性을 究明하기 爲하여 實施되었다. 成績의 要旨은 다음과 같다.

(1) 여귀科 Dimorphism 植物中 *P. japonica*에 있어서 L, S株間의 形態, 生態의 分化가 가장 甚하고 *P. senticososa*는 第一次差 以外에는 아직 거의 未分化狀態이고 *F. esculentum*은 大體로 前記 2種의 中間位置에 있다고 볼수 있다.

(2) 生理的 分化는 *P. japonica* 에서는 極도로 甚하여 雌雄異株와 같은 現象을 나타내고 있는點이 많다. *P. senticososa*는 生理的으로 거의 Dimorphism으로 分化가 發生거 있고 形態的으로는 아직 本屬 非異型蕊植物의 一般의 性質을 거의 保有하고 있다. *F. esculentum*은 受精生理上으로도 *P. japonica*와 *P. senticososa*와의 中間的 位置에 있다.

(3) *P. japonica*는 形態, 生態, 生理上으로 보아 L, S株間의 分化의 差뿐만 아니라 Dimorphism으로도 他 2種보다 그 分化의 程度가 가장 甚하고 *P. senticososa*는 가장 未分化狀態이다.

(4) 植物이 Hermaphrodite 에서 雌雄異株로 性의 分化가 생기는데 여러가지의 길이 있겠지만 Heterostylism 을 通해서 移行되는 수도 生覺할수 있다.

(5) 여귀科 Polygonum屬의 非異型蕊植物들은 大部分이 Homo-style이고 部分的 他家受精을 하는 自殖性植物인데 本屬에서는 自殖에서 他殖으로 移行하는데 있어서 一便으로는 蜜腺이 發達되고 他方으로는 形態上으로 花器의 異型化, 生理上으로 自家可稔에서 自家(또는 同型花時에) 不稔으로 變遷한것이나 아닐까, 또한 本實驗에 使用된 이 三種의 植物들은 그 變遷過程을 表示해 주는 善 證據가 아닌가 라고 生覺된다.

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