

SURVEY OF VARIATIONS IN PHOTOPERIODIC RESPONSE IN WILD *ORYZA* SPECIES⁽¹⁾

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The senior writer (Oka 1953, 58) has formerly shown that cultivated rice varieties can be divided into photoperiodically sensitive and insensitive types. Insensitive varieties were found in all the countries from which the materials were taken, while the distribution of sensitive ones was limited to the areas approximately between 10° and 40° northern latitude. The lack of sensitive varieties in the equatorial and northern temperate regions could be well explained as the results of adaptation. It was also found that among sensitive varieties, both "sensitivity" and "critical day-length" showed latitudinal clines. It was then concluded that photoperiodic response in rice might be a latitudinally adjusted character, subjected to a strong selection pressure.

In tropical Asian countries, besides the cultivated varieties which belong to *Oryza sativa*, various wild species of *Oryza* occur in swampy lands and forests. Among them, *O. perennis* Moench. and *O. sativa* f. *spontanea* Roschev. are known to be genetically closely related to *O. sativa*, in the sense that these three species are easily crossed with one another and produce fertile hybrids. *O. perennis* is usually found in deep water swamps, and in view of the presence of rhizomes, is of perennial habit. *O. sativa* f. *spontanea* grows in relatively shallow swamps which are flooded only in the rainy season, and may be propagated by seeds. However, according to recent investigations by the writers and their colleagues (Morishima and Oka, 1960, etc.), the variation between these two species is a continuous array of intergrades.

This study was planned with the view of investigating the pattern of variations in photoperiodic response of those wild *Oryza* species. For measuring photoperiodic responses, the method formerly adopted by the senior writer was used, and materials obtained from India and other tropical countries were observed. It was found that the wild species observed were mostly sensitive

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to photoperiod, while differences found between *O. perennis* and *O. sativa* f. *spontanea* in the response attracted our interest to the manner of adaptation of wild rice populations to outer conditions.

Materials and Methods

During investigation trips to India (in 1957) and Thailand (in 1958), seeds were collected from a number of populations of wild *Oryza* species by the senior writer. From each population, 40 to 100 panicles, each representing a plant, were taken at random. Seeds were also collected from the wild populations of *O. perennis* in Taoyuan Prefecture, Taiwan, in the same manner. In this experiment, however, we have mixed the seeds taken on a single plant basis from a population. In addition seeds of several *Oryza* species were sent from various research institutions (given in Table 5) to whom we are greatly obliged. Thus, 31 populations belonging to *O. perennis* or *O. sativa* f. *spontanea* (Table 2) and about 30 strains belonging to other species (Table 5) were used for this investigation. Plants from the seeds were grown in an experimental field in Taiwan Provincial College of Agriculture, Taichung (24°N), Taiwan, in 1958 and 1959, and were investigated regarding various characters by the junior writer.

Seed samples each representing a population or a strain were divided into two batches and were soaked in water for germination of one batch on May 23 and the other on June 22, in 1958 and 1959. Seedlings grown in pots, with four to five leaves, were transplanted to the experimental field, 25 cm between plants of a row and 37 cm between rows. A plot consisted of 10 to 100 plants when populations collected from the natural habitats were dealt with, and 5 plants for examining strains of various species. No fertilizer was applied, but the loamy paddy soil in the field supplied sufficient nutrient.

The plants thus raised reached heading from September to November. The average temperatures of the period from germination to heading were for most species between 26° to 28°C. It may then be assumed that the difference in number of days of growing period (water soaking of seeds to heading) between the May and the June seedlings is due to the difference in photoperiod. The use of the same test strain showed that the difference between 1958 and 1959 in heading date was so small that the data obtained in these two years needed no separate treatment.

The classification of the populations used into "*perennis*", "*intermediate*", and "*spontanea*" types in Table 2 was made as follows: A small number of plants belonging to the populations were grown in a greenhouse in Misima, Japan. From the data for various characters of the plants, correlation coefficients were calculated among length-width ratio of grains, ligule length, ratio

of anther length to grain length, panicle length and branch number per panicle. Having analysed the resultant correlation matrix by the technique of principal component analysis, the first component axis extracted seemed to represent the differentiation of *O. perennis* and *O. sativa* f. *spontanea*, but the scores given to respective populations by the first component axis (by weighting measurements for the above five characters according to the relative magnitudes of direction cosines), showed a continuous range of distribution. A conventional classification into the three types was then made by dividing the range of distribution into three parts. Details of this investigation will be published elsewhere (cf. Morishima, Chang and Oka, 1960).

Method to Measure Photoperiodic Sensitivity

If a strain is insensitive to photoperiod, its plants seeded on May 23 will head one month earlier than those seeded on June 22. If highly sensitive, the May and June seedings will bring about the same heading date. This relation was used for measuring photoperiodic sensitivity. The procedures are briefly described below; details may be referred to Oka (1953 and 1958).

Taking a population of *O. sativa* f. *spontanea*, W106 (from Cuttack, India) as an example, distributions of heading dates found in the two plots seeded in May and in June are given in Table 1. In the table, the mean heading dates are September 14.3 and 29.3, and the mean number of days of growing period are 114.3 and 99.3 days, for the two plots respectively. It was assumed that flower initiation took place 30 days before heading. Then, the day-lengths to which the two groups of plants have responded are found, from the table of photoperiod at Taichung, to be 13 hours 60' (for August 15) and 13 hours 41' (for August 30), respectively (inclusive of twilights). It is then found, comparing the two groups of plants, that a 19-minute shortening of day-length has brought about a 15-day shortening of growing period. The arc-tangent of the ratio 15/19, 38°, was used as the sensitivity index (TDM degree), and the mean of day-lengths to which the plants responded, 13 hours 51', was regarded to be the "critical day-length". It may be said that the sensitivity measured by this method represents the degree of requirement of the given plants regarding a certain "critical day-length" necessary for flower initiation.

Further, within-population variations in sensitivity index and critical day-length were measured as follows: First, twice the standard deviation of heading date in each group was subtracted from, and added to, the mean heading date, to find the early and late marginal points of the distribution. Then, the early or late marginal dates for each of the two plant-groups were compared by the above-mentioned method to find the sensitivity index and

critical day-length of the earliest and latest plants. Those values found for W106 are given in Table 1. Then, one-fourth of the difference in sensitivity index (or critical day-length) between the earliest and latest plants was taken to be the standard deviation which represents the magnitude of within-population variation of sensitivity (or critical day-length).

In W106, the plants seeded in May varied on a wider range of heading dates than those seeded in June, as shown in Table 1. In such a case, a relatively large standard deviation of sensitivity index was found. When the two plant-groups had approximately the same range of heading date, the population showed a relatively large standard deviation of critical day-length.

Table 1. An example of computations for photoperiodic response
(in W106).

Seeded on	September																														October							
	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	1	2	3														
May 23	4	2	8	4	7	9	3	2	2	1	1	2																										
June 22																																						

Seeded on	Heading date Mean & S. D.	No. of days from seeding			Day-length at fl. initiation			Sensitivity index		
		E	M	L	E	M	L	E	M	L
May 23	9-14.3±2.80	108.7	114.3	119.9	14:06	14:00	13:52			
June 22	9-29.3±1.88	95.5	99.3	103.1	13:44	13:41	13:36	32	38	49
					(Critical day-lth.)					
					13:55	13:51	13:44			
					13:51±2.75			38±4.25		

E..Earliest plants, M..Population mean, L..Latest plants.

Presentation of Data

1) Variation among populations of *O. perennis* and *O. sativa* f. *spontanea*.

The results of the above-mentioned computations in various populations of *O. perennis* and *O. sativa* f. *spontanea* are given in Table 2. As the data in the table show, populations of the *spontanea* type generally had earlier heading dates than those of the *perennis* type, and those of the *intermediate* type varied in a wide range. The critical day-length may be regarded as another representation of heading date, since the later is the heading, the shorter becomes the critical day-length. Thus, the *spontanea* type had a long, the *perennis* type had a short, and the *intermediate* type had varying critical day-length.

In cultivated varieties, the lower the latitude of distribution area, the shorter was the critical day-length (Oka, 1953 and 1958). Whether wild populations also exhibit this kind of latitudinal variation or not was examined.

Table 2. Variations in photoperiodic response in *O. perennis* and *O. sativa* f. *spontanea*.

Type	Popul. no.	No.* of plants	Heading date seeded in		Critical day- length		Sensitivity index		Original habitat (Latitude-N)
			May	June	Mean	S.D.	Mean	S.D.	
Spontanea	W101	32	10-07	10-08	13:28		86		Cuttack, Ind. (21°)
	W105	41	9-27	10-05	13:38	3.50	65	7.25	Cuttack, Ind. (21°)
	W106	133	9-14	9-29	13:51	2.75	38	4.25	Cuttack, Ind. (21°)
	W107	131	9-26	10-04	13:39	4.30			Cuttack, Ind. (21°)
	W139	70	10-01	10-03	13:37	4.63	85	1.50	Trichur, Ind. (10°)
	W152	12	9-13	9-20	13:57	6.15	70	6.00	Hooghly, Ind. (23°)
	W168	34	10-05	10-14	13:21	10.0	45	14.25	Phimai, Th. (15°)
	W170	57	9-26	10-06	13:13	9.25	37	9.50	Chumpae, Th. (16°)
	W173	13	10-02	10-14	13:27		45		Chumpae, Th. (16°)
	W179	53	10-26	11-01	12:57	9.00	61	5.50	Rajburi, Th. (13°)
	Average		9-27.9	10-04.5	13:31	7.03	59.7	7.85	
Intermediate	W133	98	10-09	10-14	13:24	3.81	74	4.25	Samalkot, Ind. (17°)
	W134-5	154	10-16	10-16	13:16	2.39	90	2.25	Samalkot, Ind. (17°)
	W136	116	10-10	10-15	13:22	6.44	74	3.00	Samalkot, Ind. (17°)
	W153	11	10-18	10-24	13:10	3.75	71	6.25	Canning, Ind. (22°)
	W145	143	11-25	11-28	12:22	9.60	82	0.50	Bangkok, Th. (14°)
	W163	13	11-10	11-09	12:43		90		Chiengmai, Th. (19°)
	W164	39	11-11	11-08	12:44		90		Chiengmai, Th. (19°)
	W167	38	11-15	11-13	12:38	9.50	90	3.50	Sukothai, Th. (17°)
	W171	56	11-12	11-13	12:40	7.00	86	4.25	Nongkai, Th. (18°)
	(Popul. of Taiwan)	A	53	9-13	9-21	13:56	8.35	66	1.25
	B	123	9-14	9-23	13:54	8.89	62	1.50	Taoyuan, Tw. (25°)
	C	121	9-06	9-17	14:03	10.6	57	0.25	Taoyuan, Tw. (25°)
	Average		10-19.5	10-22.2	13:11	7.53	77.6	3.24	
Perennis	W109	39	11-03	11-09	12:48	9.39	72	0.75	Cuttack, Ind. (21°)
	W113-9	280	10-21	10-23	13:08	7.76	83	2.90	Cuttack, Ind. (21°)
	W132	98	10-29	11-03	12:50	9.05	76	3.75	Samalkot, Ind. (17°)
	W169	13	11-19	11-18	12:32		90		Chumpae, Th. (16°)
	W172	21	11-20	11-18	12:30		90		Chumpae, Th. (16°)
	Average		11-06.0	11-08.0	12:46	8.75	82.2	2.76	
Cultivated varieties	108	27	8-20	9-18			3	2.75	Taiwan (Indica)
	414	43	8-31	9-15	14:04	1.25	46	2.00	India (Indica)
	504	37	8-15	9-11			11	4.00	Taiwan (Japonica)
	521	35	8-10	8-27	14:23	1.25	41	2.50	Japan (Japonica)
	647	50	8-29	9-23			15	4.25	Celebes (Japonica)

* Total number of plants investigated, about 1/3 were seeded in May and 2/3 in June.
Ind...India, Th...Thailand, Tw...Taiwan

The results proved, as shown in Fig. 1, that the populations observed could be divided into two latitudinal clines in both of which the lower the latitude, the shorter becomes the critical day-length; one of them consisted of the *spontanea* and the *intermediate* populations (Class 1), the other consisted of the *perennis* and the *intermediate* populations (Class 2), and the former had longer critical day-length than the latter if populations from the same latitude were compared. Compared with cultivated varieties, "Class 1" (*spontanea*) showed the same range of critical day-lengths as found in cultivated rice. However, a population from Kerala State, India (10°N) (W139) was outside the clines. This seems to suggest that there occurs a different type of photoperiodic adaptation in the equatorial region, possibly due to the different from the northern regions distribution of rainfall and the reduction in seasonal change of day-length.

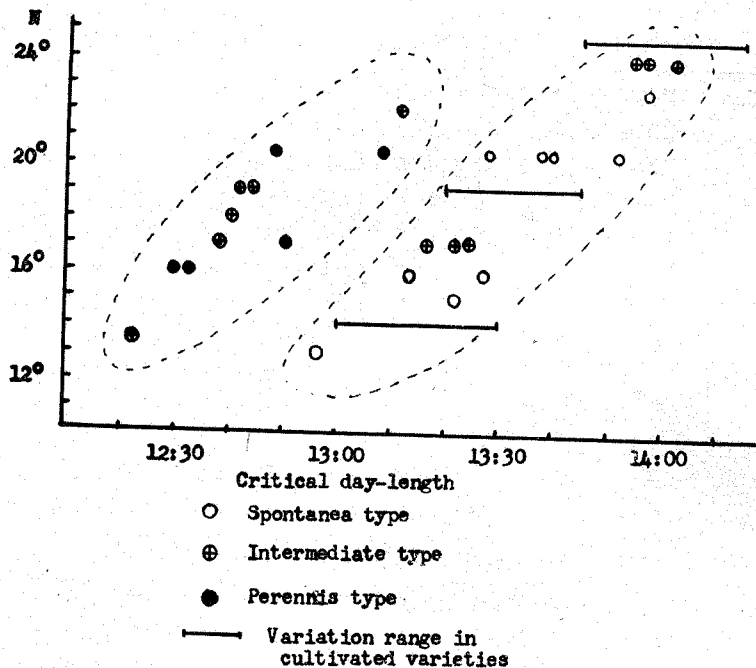


Fig. 1. Distribution of critical day-length in relation to latitude.

Besides the critical day-length, the photoperiodic sensitivity is a factor determining the mode of response to photoperiod. It is found in Table 2 that the *perennis* as well as the *intermediate* types are generally highly sensitive to photoperiod, while the *spontanea* type has relatively low sensitivities varying in a wide range. Comparing with the variation among cultivated varieties of various Asian countries (from Oka 1953 and 1958), it was found, however, that in contrast to the wild populations which were sensitive to varying degrees, a

characteristic feature of the cultivated rice was the occurrence of insensitive varieties in it (Table 3).

Table 3. Distributions of sensitivity index among wild populations and cultivated varieties of rice.

Class	Sensitivity index (TDM degree)									
	0	10	20	30	40	50	60	70	80	90
Wild populations:										
<i>Spontanea</i> (Class 1)					2	2	4	5	1	2
<i>Perennis</i> (Class 2)								2	3	6
Cultivated varieties*	30	44	11	5	1	7	11	12	16	26

* From Oka (1953,58)

It was formerly pointed out in photo-sensitive cultivated varieties that the lower the latitude of distributing area, the higher was the sensitivity (Oka, 1953 and 1958). This may be due to that the lower the latitude, the smaller becomes the range of seasonal change of day-length. The wild populations observed also showed such a latitudinal variation of sensitivity index among them, though some *spontanea* populations with relatively low sensitivities were not included in the latitudinal cline, as shown in Fig. 2.

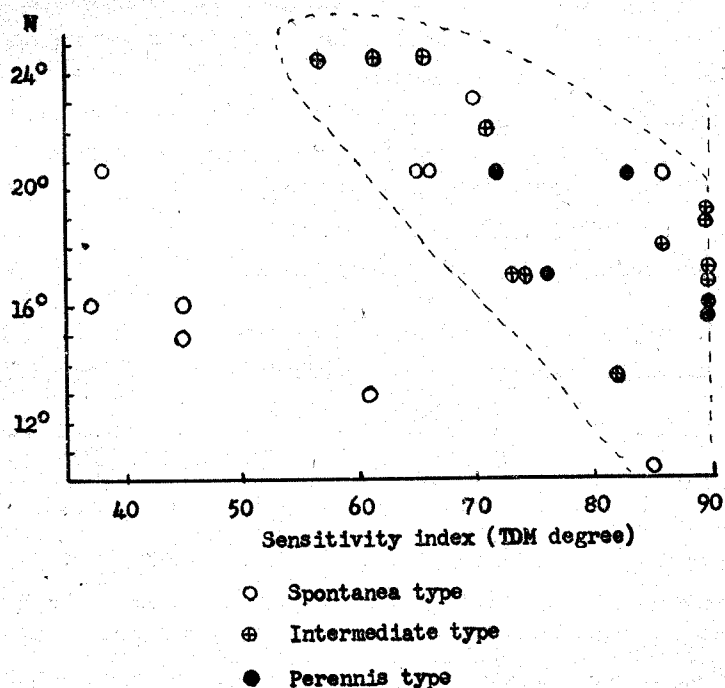


Fig. 2. Distribution of sensitivity index in relation to latitude.

2) Within-populational variations in *O. perennis* and *O. sativa* f. *spontanea*.

The populations under observation were divided, according to their distribution in Fig. 1, into two classes as mentioned in the previous section, and in each class, the genetic components of between- and within-populational variances were estimated for heading date, critical day-length and sensitivity index. For the estimation for heading date, the environmental component was assumed to be 4.0 in "Class 1" (*spontanea*) and 8.0 in "Class 2" (*perennis*) on the basis of the values usually found in cultivated varieties, and was subtracted from the mean of within-populational variances found in the two plant groups seeded in May and in June. The genetic component of between-populational variance of heading date was obtained by subtracting the component due to within-populational variation from the mean of variances of population means in each of the two groups. For the critical day-length and sensitivity index, the difference between the earliest and latest plants found in cultivated varieties may be the only information available for estimating the amount of environmental fluctuation or sampling error. Squares of the standard deviations of critical day-length and of sensitivity index found in an Indian variety 414 were taken to be representative values of environmental variances, and were subtracted from the squares of standard deviations of critical day-length and of sensitivity index found in wild populations, respectively, in order to estimate the genetic components of within-populational variations in these scores. Between-populational variances of these scores were not apportioned into components, since the component due to within-populational variation, though it seemed to be small, could not be estimated on a sound basis.

The results of these computations are given in Table 4. The data in the table show that in heading date and in critical day-length, "Class 2" (*perennis*) had larger within-populational genetic variances and smaller between-populational variances than "Class 1" (*spontanea*). But, in sensitivity index, "Class 1" (*spontanea*) showed larger values of between- as well as within-populational

Table 4. Between- and within-populational genetic variances of heading date, critical day-length and sensitivity index in *O. perennis* and *O. sativa* f. *spontanea*.

Class	Heading date		Critical day-lth.		Sensitivity index	
	σ_s^2	σ_p^2	σ_s^2	σ_p^2	σ_s^2	σ_p^2
1 (<i>spontanea</i>)	131.3	22.7	274.7	42.9	318.8	51.4
2 (<i>perennis</i>)	120.2	37.7	218.1	68.0	56.5	13.2

σ_s^2 ..Variance between populations

σ_p^2 ..Variance within populations

(Populations of Taiwan were not included in this computation.)

variances than "Class 2" (*perennis*). This might be due to the fact that in the *perennis* type, the variation of heading date within population is mainly due to differences in critical day-length, but in the *spontanea* type, the variation is caused not only by critical day-length but also by sensitivity to photoperiod.

3) Photoperiodic responses of *Oryza* species other than *O. perennis* and *O. sativa* f. *spontanea*.

As mentioned already, a number of strains belonging to species other than *O. perennis* and *O. sativa* f. *spontanea* were also tested for photoperiodic response in parallel with the above-mentioned experiments. Except for two seed samples collected from Thailand, belonging to *O. officinalis* Wall. and *O. ridleyi* Hook., respectively, the seeds used did not represent the wild populations of the species in natural habitats, so that within-population variations were not taken into account. The results are given in Table 5. As the data in the table show, the species examined were mostly sensitive to photoperiod. The population of *O. officinalis* collected from Thailand, and a strain of *O. australiensis* Domin., were insensitive, however. In *O. glaberrima* Steud., which are cultivated in West Africa, a few insensitive strains were found in the same manner as in *O. sativa*.

Table 5. Photoperiodic responses of various *Oryza* species.

Species	No. of strains or popul.s	Critical day-length	Sensitivity index	Remarks
<i>Sativa Group:</i>				
<i>O. sativa</i> (Culti.)	163	12:45-14:30	0-90	From Oka (1953)
<i>O. sativa</i> f. <i>spontanea</i>	15	12:57-14:03	37-90	Class 1 in this study
<i>O. perennis</i> Moench.	11	12:22-13:10	71-90	Class 2
<i>O. perennis</i> (<i>barthii</i>)	1	13:20	90	From (1)
<i>O. perennis</i> (<i>cubensis</i>)	2	12:59-13:05	67-90	From (2)
<i>O. glaberrima</i> Steud. (Culti.)	15	12:40-13:23	0-90	From (3)
<i>O. breviligulata</i> A. Chev.	2	14:02-14:07	83-90	From (3)
<i>Officinalis Group:</i>				
<i>O. officinalis</i> Wall.	1	—	12±1.50	Bangkok, Thailand
<i>O. officinalis</i> Wall.	2	13:45-13:58	40-69	From (1)
<i>O. minuta</i> Presl.	2	13:27-13:30	78-90	From (2)
<i>O. latifolia</i> Desv.	4	13:19-14:08	52-70	From (1) & (2)
<i>O. eichingeri</i> Peter.	1	13:23	90	From (1)
Other groups:				
<i>O. australiensis</i> Domin.	1	—	10	From (1)
<i>O. ridleyi</i> Hook.	1	13:16±4.00	55±0.75	Bangkok, Thailand

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Discussion

The present study proved that wild *Oryza* species were mostly sensitive to photoperiod. In contrast to this, among cultivated varieties, some are insensitive to photoperiod. However, it is found that the varieties grown as the main crop are sensitive to photoperiod in most Asian countries. Excepting the equatorial regions such as Malaya and Ceylon, the summer monsoon whose rainfall is utilized for rice culture begins in June and ends in September to October. Insofar as the plants depend on natural rainfall, the vegetative growth in the rainy season and maturity in the dry season would be the most adaptive behavior. Photoperiodically sensitive plants may be adapted to it, because the photoperiod controls their heading to occur when the land tends to be dried, while other conditions than photoperiod would have a relatively minor effect on them.

In those Asian countries, photoperiodically insensitive varieties are grown in additional crops which are raised under long day. In most countries, the additional crop is limited to a small area where water is available in the dry season, and is generally poor in yield. In Taiwan, however, after the development of artificial irrigation and an intensive agricultural system, the first crop, which corresponds to the additional crop in tropical countries, has become vigorous and produces higher yield than the second crop which was the main crop several decades ago. Presumably, photoperiodically insensitive varieties have a large potentiality for improvement; they are generally sensitive to fertilizers and their planting becomes an advantage with the intensification of cultivation (Oka 1956). Thus, it is interesting to note that wild rice plants are generally sensitive to photoperiod, and the occurrence of insensitive plants is a characteristic feature of the cultivated rice, while the development of insensitive varieties becomes a basis for intensive cultivation of rice.

We may then look into the variations in photoperiodic response among wild rice populations. It may be taken for granted that the most important ecological agent regulating the habitat of wild rice is the seasonal change of water level, which is determined by rainfall and topography. If no water is available in the dry season, populations may be maintained only by seeds. If the habitat is constantly submerged in water, the plants already established may propagate asexually, but propagation by seeds may be hindered.

As mentioned in the introduction, populations of the *spontanea* type are found in swampy patches which are flooded only in the rainy season, while those of the *perennis* type are found in deep water swamps such as water reservoirs. The fact that the *spontanea* type showed earlier heading or longer critical day-length than the *perennis* type may be due to the fact that water withdraws from the habitat of the former when the dry season comes, while

the habitat of the latter is always submerged in water. It may be advantageous for plants of the *perennis* type to continue the vegetative growth long, confining the reproductive phase to a certain period in the middle of dry season. The two parallel latitudinal clines of critical day-length found in this study, one representing the *spontanea* and the other the *perennis* type, suggest that heading at a certain proper time is essential for them, so that the critical day-length is subjected to a strong selection pressure, while the proper time differs between the two types.

Further, regarding the sensitivity to photoperiod, it was found that the *perennis* type was generally highly sensitive, while the *spontanea* type had relatively low sensitivities varying widely according to populations. The high sensitivity of the *perennis* type may be explained by their perennial habit, since if their sensitivity was lower than a certain limit, they would produce panicles throughout the year and would be exhausted. The relatively low sensitivities of the *spontanea* type may be explained as follows: The most favorable time for heading may vary year by year according to the duration of rainy season, since their habitat loses water in the succeeding dry season. However, the critical day-length is directly connected with the heading time and is subjected to a strong selection pressure. A population may acquire a certain critical day-length so as to adjust its heading to occur at the most favorable time on the average. The flexibility which enables the population to respond to annual fluctuation of the favorable time may then be brought about by a reduction in sensitivity, since if sensitivity is reduced to some extent, plants which have sprouted early will reach maturity early and a variation in heading date will result, but the offspring of the early plants are not necessary early.

Stebbins (1958) has demonstrated with many examples that plant species growing in "stable" habitats, such as constant swamps, are generally of long life, and through cross fertilization, store up a large amount of genetic variability within population, while those in "unstable" or easily disturbed habitats have an efficient method of propagation by seeds and a tendency to restriction of gene recombination, and are each adapted to a particular niche. It may be assumed that the habitats of the *perennis* populations are "stable", and those of the *spontanea* populations are relatively "unstable". Actually, populations of the *spontanea* type are found in swamps with varying water depths. Some of them grow adjacent to or in paddy fields, and the habitat is frequently disturbed by man (Oka 1959).

It was pointed out in this study that *perennis* populations had, regarding heading date and critical day-length, larger within-populational variances and smaller between-populational variances than *spontanea* populations. The same tendency was also found in many other characters (the writers' unpublished

data). In other words, *perennis* populations have a tendency to store up genetic variations, while *spontanea* populations tend to vary among them. This difference between the *perennis* and the *spontanea* types may be fairly accounted for by the theory of Stebbins. However, in photoperiodic sensitivity, *spontanea* populations showed larger within-population variances than *perennis* populations, or were more heterogeneous than the latter. For this fact, the same explanation as taken for their relatively low sensitivities may be adopted; owing to a variation in sensitivity, they show a flexibility in responding to different conditions.

These considerations lead us to the view that the photoperiodic response of wild rice populations is finely adjusted to outer conditions, and the system of adaptation may be in close relation with the breeding system. It seems that the knowledge of those adaptation systems may enable us to understand the significance of photoperiodic response in wild plants as well as in agricultural crops.

Summary

Seeds were collected from wild populations of *Oryza* species in India and Thailand, and the plants raised from the seeds were investigated in Taichung, Taiwan, together with other *Oryza* species sent from various research institutions. Seed samples were each divided into two batches, and were soaked in water for germination one on May 23 and the other on June 22, in 1958 and 1959. Photoperiodic responses of the plants were observed by the method formerly adopted by the senior writer, on the basis of the difference in heading date between the two plots seeded in May and in June. Thus, the "critical day-length" (to which a given population or strain responds) and sensitivity index (TDM degree; the degree to which given plants require a certain critical day-length) were measured in each population or strain. In *O. perennis* and *O. sativa* f. *spontanea*, which are known to be closely related to *O. sativa* and show a continuous array of intergrades between them, variations in photoperiodic response between as well as within populations were investigated. The results are summarized as follows:

- (1) The wild species investigated were mostly sensitive to photoperiod.
- (2) Populations of the *perennis* type, which grow in deep-water swamps, showed later heading dates and shorter critical day-lengths than those of the *spontanea* type, which are found in swampy patches flooded only in the rainy season.
- (3) Populations of the *perennis* type showed larger within-population variances of heading date and critical day-length than those of the *spontanea* type, consistently with the tendency found in many other characters.

(4) Having examined the relation between critical day-length and latitude of the original habitat, the populations observed were divided into two latitudinal clines, one representing the *perennis* and the other the *spontanea* type, and for each of them, it was found that the lower was the latitude, the shorter was the critical day-length. This indicates that the critical day-length is subjected to a strong selection pressure, while the most adaptive critical day-length differs between the two types.

(5) Populations of the *perennis* type generally showed a high sensitivity to photoperiod, while those of the *spontanea* type had relatively low sensitivities varying in a wide range. Also in within-population variation of the sensitivity index, the *spontanea* type showed a larger variance than the *perennis* type. It was inferred that a relatively low sensitivity to photoperiod might be advantageous for *spontanea* populations which are distributed in relatively "unstable" habitats and propagated by seeds. Based on these findings, discussions were made regarding the adaptation systems of wild rice populations.

野生稻種對日照感應性變異之研究

岡 彥 一 張 文 財

1957年及1958年自印度及泰國等地區採集之野生稻原種，連同其他研究機關贈送之野生稻，於1958及1959年栽培於臺中市省立農學院農藝系試驗田，供研究之用。於5月23日及6月22日兩次播種，調查出穗期，應用岡（1953，1958）之方法計算野生稻對日照時間之感應性，並比較 *Oryza perennis* 與 *O. sativa f. spontanea* 兩野生集團間及集團內對日照時間之感應性，其結果摘要列舉如下：

- 1) 野生稻大部分對日照具有感應性。
- 2) *Perennis* 型集團多係生長於深水沼澤地，*spontanea* 型集團則散生於許多低窪的小地區，且只在雨季被水淹浸。前者比後者出穗期較遲，臨界日照時間亦較短。
- 3) *Perennis* 型集團之出穗期及臨界日照時間之集團內變量較 *spontanea* 型為大，其他性狀亦發現有相同的傾向。
- 4) 調查野生稻的臨界日照時間及其與原產地緯度的相互關係，可將野生稻集團分為兩種「緯度型」，其一為 *perennis* 型，另一為 *spontanea* 型，且不論那一型，凡是緯度愈低，其臨界日照時間亦愈短。這表示野生稻的臨界日照時間受着強烈的淘汰壓，然而上述兩型的最適應臨界日照時間仍有差異。
- 5) *Perennis* 型集團一般具有高度的日照感應性，而 *spontanea* 型則日照感應性較低而變異較大。就感光性指數的集團內變量而言，*spontanea* 型亦較 *perennis* 型為大。據此推斷，可知較低的感光性似乎對於 *spontanea* 型集團較為有利，因為 *spontanea* 型集團大多分佈於比較不安定的地區，且以種子繁殖。根據上述的結論，本文曾就野生稻集團的適應體系加以檢討及論述。（摘要）

Literature Cited

- MORISHIMA, H. and H.I. OKA: Variation studies in wild rice species, *Oryza perennis* and *O. sativa* f. *spontanea*, by multivariate analysis. Annual Rep. Nat. Inst. Genetics, Japan, 10, 1960.
- OKA, H.I.: Varietal variation of the responses to day-length and temperature and the number of days of growing period. (Phylogenetic differentiation of the cultivated rice. III) Jap. Jour. Breed. 4: 92-100, 1953. (In Jap. with Eng. resume).
- : Variation in fertilizer response among rice varieties. Jour. Agr. Assoc. China, New Series 13: 35-42, 1956.
- : Photoperiodic adaptation to latitude in rice varieties. Phytion 11: 153-160, 1958.
- and W.T. CHANG: The impact of cultivation on populations of wild rice, *Oryza sativa* f. *spontanea*. Phytion 13: 105-117, 1959.
- STEBBINS, G. L.: Longevity, habitat and release of genetic variability in the higher plants. Cold Spring Harbor Symposia on Quantitative Biology, 23:365-378, 1958.