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III. Geographical Distribution

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The geographical distribution of chlorosis in cultivated rice, *Oryza sativa* L., shows a wide variation in the region including India, Assam, Nepal, Bhutan, Burma and Southern China with the presence of all 5 types of chlorosis. The frequency of chlorosis tends to decrease from that region towards both the north and the tropical islands. This suggests that the Himalayan site and its neighborings can be considered as the origin center of cultivated rice and from there the divergent evolution was carried out towards the temperate region and the tropical islands. The course towards the north might lead to the selection of chlorosis by low temperature and to differentiate into a new ecotype well adapted to the climate condition of the temperate region resulting in the formation of the *japonica* subspecies. The course towards the tropical islands, Philippines and Indonesia, is very likely a result of the non-adaptive evolution or the parallel selection.

INTRODUCTION

Since Kato *et al.* (1930) classified *Oryza sativa* L. into two subspecies, *japonica* and *indica*, many other additional classifications were reported by many workers. Terao and Mizushima (1939) found out an intermediate group of cultivated rice distinguishable between *japonica* and *indica* subspecies. Based on the morphological, physiological and ecological features, Matsuo (1952) classified cultivated rice into 3 groups A, B and C. Oka (1953) proposed 2 different groups of cultivated rice: continental group and island group which was divided into tropical and temperate island sub-groups, after studying the distribution of the combination of many characters. It is known that depending on the cultivation season and harvesting time, there are 3 ecotypes of cultivated rice, Aus, Aman and Boro, in the subcontinent of India, and 2 ecotypes, Bulu and Tjereh, in Indonesia. Moreover, depending on the water system along the Mekong River area, 3 growing habits of cultivated rice were noted: single transplanting, double transplanting and floating rice. Again, upland and lowland rice were also classified according to the growing habit.

The classification of cultivated rice into so many ecotypes shows that on the course of divergent evolution, *O. sativa* had a high adaptability to the different environmental conditions ranging from the tropics to the temperate regions. This also suggests that the primary differentiation center existing

somewhere would reflect the common features of all the various ecotypes of the cultivated rice. Many workers almost agreed with the conclusion that the primary center of cultivated rice is situated in the Himalayan area and its neighborings (Morinaga, 1968; Kihara, 1968; Nakagahra *et al.*, 1975; Chang, 1976).

In the previous paper (Omura and Chuong, 1979), we reported the chlorosis expressed under low temperature condition in rice as a characteristic of *indica* subspecies. In this paper, we report the geographical distribution of chlorosis and discuss on the differentiation of the *O. sativa*.

MATERIALS

Materials used were 609 local varieties from three sources: the preservative stocks of the world rice of our laboratory and the National Institute of Agriculture Research, Ibaraki, and the collection from the survey trip in Indonesia, 1979. Table 1 shows the origin and the distribution of the materials. The culture condition was as same as that described previously (Omura and Chuong, 1979). Among 5 types classified at 17°C, types II, III and IV were grouped into chlorosis class of which the degree of chlorosis was $II < III < IV$ and types O and I into normal class because of their almost similarity and lack of sign of chlorosis. To distinguish type I from type O and type IV from type III, varieties without chlorosis appearance and those with albino-like leaf were grown again at 15°C and 20°C, the critical temperatures of type I and type IV, respectively, as reported in a previous paper (Chuong and Omura, 1980).

Table 1. Distribution of materials used

Location	No. of varieties	Source*
Japan	73	a
Korea	40	a
Russia	24	a
Northern China	28	a
Southern China	43	a
Sri Lanka-India-Bangladesh	77	a, b
Nepal-Bhutan-Assam-Burma	115	a, b
Thailand-Laos	17	b
Southern Vietnam	49	a
Philippines	15	a
Indonesia	128	a, b, c
Total	609	

* a: Rice stock of Plant Breeding Laboratory

b: Collection of the National Institute of Agriculture Research, Ibaraki

c: Collection from Indonesia survey trip

RESULTS

The chlorosis distribution is shown in Fig. 1. In the continent of Asia,

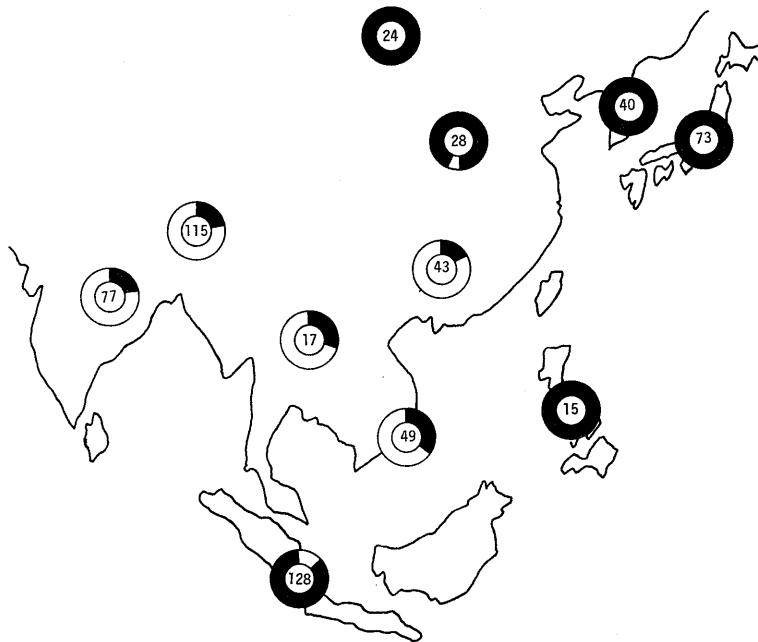


Fig. 1. Geographical distribution of chlorosis. Number inside the circle: Number of varieties, Black: Frequency of normal type, White: Frequency of chlorosis.

chlorosis appeared with higher frequency in the southern regions than in the northern regions. Chlorosis had the tendency to appear in great majority in the Indian subcontinent, Sri Lanka-India-Bangladesh (76.7 %), Himalayan site, Assam-Bhutan-Nepal-Burma (76.6 %), Southern China (81.4 %), Thailand-Laos (70.6 %) and Southern Vietnam (61.2 %). Chlorosis almost disappeared in Northern China with the frequency of only 3.6 % and was totally extinct in the temperate regions as Russia, Korea and Japan. On the other hand, in the tropical islands as Indonesia and Philippines chlorosis appeared with low frequency in Indonesia (14.8 %) and disappeared in Philippines.

The distribution of the chlorosis types is shown in Fig. 2. The area including the Indian subcontinent, Himalayan site, Thailand-Laos and Southern China showed a wide variation of chlorosis with the presence of all 5 types whereas the temperate regions comprising Russia, Korea and Japan, and the tropical islands a smaller and simpler variation of chlorosis types. The 4 regions, the Indian subcontinent, Himalayan site, Thailand-Laos and Southern China, showed almost the same frequency in chlorosis class, but type III occurred more frequently than types II and IV. The distribution pattern of chlorosis type in Southern Vietnam showed large difference from the other tropical regions, characterized by the presence of only 3 types: types O, I and II. Types III and IV were the characteristics of the Himalayan site and its neighborings but their inclination of distribution showed different from each

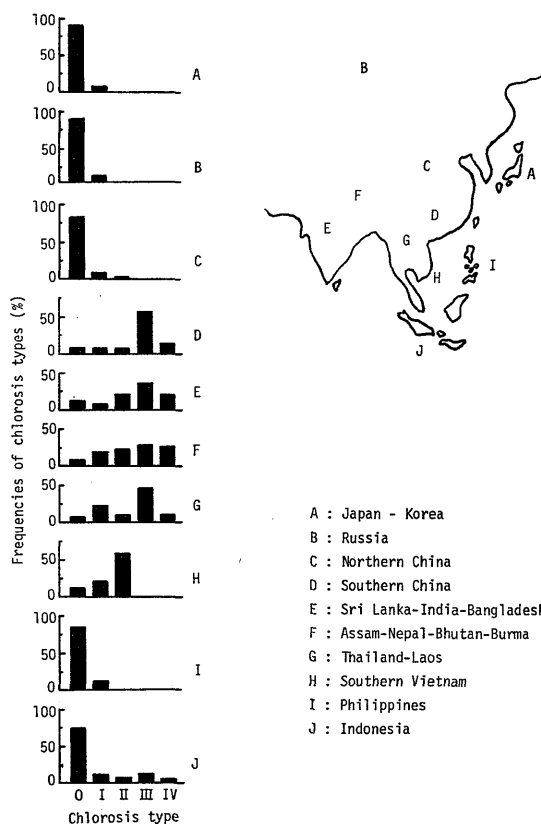


Fig. 2. Geographical distribution of chlorosis types.

other. Type III occurred with higher frequency in Southern China and Thailand-Laos than in Indian subcontinent and Himalayan site, and type IV in contrast, appeared more frequently in Indian subcontinent and Himalayan site than in Southern China and Thailand-Laos. Type II geographically occurred more widely than types III and IV. The occurrence of type II was highest in frequency in Southern Vietnam. Types O and I commonly distributed in all regions but their inclination was in contrast with types III and IV, that means they occurred in high frequency in northern regions but in small frequency in the Indian subcontinent and the Himalayan site. Again, although types O and I were classified as normal class under 17°C condition and appeared in all areas, their inclination differed from each other. Type I occurred with a relatively high frequency in the Himalayan site, Thailand-Laos and Southern Vietnam in contrast with type O which appeared in small frequency in the tropical regions of the continent and dominated over other types in the temperate regions and in the tropical islands.

As shown in Fig. 2, the tropical islands including Philippines and Indonesia showed a particular feature of chlorosis distribution, different from that

of the tropical regions of the continent. There was a total disappearance of chlorosis in Philippines and only a small frequency of chlorosis was found in Indonesia (14.8 %).

DISCUSSION

Morinaga (1968) assumed that the primary center of *O. sativa* was in South-East Himalaya. As the primary center, it would be characterized by a complex of genotypes and no clear differentiation. These genotypes dispersed from the center to everywhere and on the way of evolution, the natural selection increased the frequency of the superior genotype which showed great fitness to the environment (Dobzhansky, 1950). Based on the existence of various ecotypes with the wide distribution range from the tropics to the temperate region, it is said that cultivated rice has a high adaptability to the environmental conditions they met with. Chang (1976) postulated that the subtropical region comprising Nepal, Sikkim, Assam and Upper Burma along with the high elevation area of Thailand-Laos and Southeast China showed the richest spectrum of varietal diversity and ecological specialization. Nakagahra *et al.* (1975) also suggested this region to be the center of genetic diversity of rice plants after studying the geographical cline of esterase isozyme pattern among native rice varieties. Besides, Nakagahra (1976) also stated that the region comprising Japan, Korea and Northern China was unique in a combination of 3 gametophyte genes *ga₁ga₂ga₃*, whereas the region including India, Assam, Southern China possessed a wide variation of their combination. The Northeast India comprising the eastern range of Himalaya and the valleys of Bramaputra and Surma river with many diversities in ecology, geography, and even in ethnics could be considered as a pivotal position for the differentiation of cultivated rice (Sharma *et al.*, 1971). Morinaga and Kuriyama (1955) and Kihara (1968) also assumed that the differentiation of *japonica* types took place in the Himalayan region and they were introduced into Japan.

Chlorosis distributed with high frequency in the area comprising the Indian subcontinent Himalayan site, Thailand-Laos, Southern Vietnam and Southern China, and showed the tendency to decrease its frequency in the northern region and in the tropical islands (Fig. 1). Moreover, the distribution of chlorosis types showed a wide diversity with 5 types in the Indian subcontinent, Himalayan site, Laos-Thailand and Southern China, whereas a simpler variation in the temperate region and in the tropical islands (Fig. 2). Among the regions with wide variation of chlorosis types, the Himalayan site and the Indian subcontinent showed the lowest peak of the histograms of chlorosis distribution. Thus, it is suggested that the primary center of cultivated rice, on the basis of chlorosis, could be situated in the Himalayan site and its neighborings. This is also not contradictory to the above mentioned suggestions on the origin center of the cultivated rice.

The distribution of chlorosis also showed that there were two courses of evolution: one towards the north and another towards the tropical islands.

Both courses led to the same result, that is the decrease in chlorosis frequency in the remote regions from the origin center.

From the fact that there was no linkage relationship between the germination ability under low temperature condition and chlorosis, Omura and Chuong (1979) suggested that the low temperature might not play the role of selection on chlorosis through the germination ability under low temperature condition but might do the direct selective agent on chlorosis in the temperate regions. Hitaka (1976) reported that the decrease of CO_2 assimilation in chlorotic rice seedlings with chlorosis degree more than 60 % resulted in the stopping of their growth and the remarkable decrease in root weight, plant height, leaf age, number of tillers, fresh weight and dry weight after 20 days of transplanting. The disappearance of chlorosis (Fig. 1), especially that of types III and IV, in the northern region and its highest frequency in the southern region of the continent (Fig. 2) support the conclusion that the low temperature is the selective agent of chlorosis.

Thus, on the way of evolution towards the north, chlorosis was very likely selected by low temperature in the temperate region and only the normal type well adapted with the low temperature could be survived.

On the other hand, the tropical islands, Indonesia and Philippines, though belonging to the tropics, showed a particular pattern of chlorosis distribution different from that in the continent. Chlorosis appeared with small frequency in Indonesia (14.8 %) and totally disappeared in Philippines.

The increase of normal type in the tropical islands can not be explained as the result of selection by low temperature on chlorosis. On the viewpoint of adaptation, type O, normal type with highest degree of chlorophyll content, is probably more preferable to the photosynthetic conditions in the temperate region such as low temperature and low light intensity in comparison with the tropics. It was found that the Bulu ecotype well distributed in these islands (Morinaga and Kuriyama, 1955; Takahashi, 1976) belonged to type O of chlorosis which was the major type existing in the northern region. Oka (1953) also postulated that the particular type, the tropical insular group, distributed in these regions. Takahashi (1976) also reported that the Bulu ecotype showed highly resistant to low temperature in comparison with the other ecotypes such as Aus, Aman, Boro and Tjereh which were easy to express chlorosis under low temperature condition. Thus, the increase of normal type of chlorosis, most in type O, can not be considered as the result of the adaptation to the temperature and light conditions of the tropics.

Shull (1951) described many cases of characters which appear to be no particular use in the case of non-adaptive evolution such as A and B blood cell antigens of human being, the white and blue pelages of arctic fox, and black color of leopards in Asia and Africa. He also stated that it seemed likely that races or even species might often be distinguished by characters which gave no advantage to their possessors. Mayer and Stresemann (1950) considered that geographical variation was not always adaptive and in particular most of the characters involved in polymorphism were completely neutral as far as survival value was concerned.

In the case of chlorosis distribution in the tropical islands, it is suggested that the inclination pattern of chlorosis would be caused by the non-adaptive evolution or the parallel selection due to the linkage of chlorosis locus or loci with the loci of other characters which are selected on the course of divergent evolution to these islands.

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