

## Studies on Agronomic Traits of African Rice (*Oryza glaberrima* Steud.)

### III. Some grain morphological aspects of domestication and decrement\*

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**Abstract :** To identify some characteristics of *Oryza glaberrima* in grain morphology, length (L), width (W) and thickness (T) of unhusked grain were determined for two cultivated species, i.e. *O. sativa* and *O. glaberrima*, three African wild species, i.e. *O. breviligulata*, *O. longistaminata* and *O. punctata*, and three Asian wild species, i.e. *O. perennis*, *O. sativa* var. *spontanea* and *O. officinalis*. *O. glaberrima* and *O. breviligulata*, which belong to the *Series Glaberrima*, showed flatter grain shape than 4 species of *Series Sativa*, i.e. *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis* and *O. longistaminata*. The two species from *Series Glaberrima* were positioned within the following ranges in W/T, L/T and L/W:  $W/T > 1.45$ ,  $L/T > 3.75$ ,  $L/W > -4.88 \times W/T + 9.95$ . The two cultivated species had larger grain volume than six wild rice species. The ancestral species, such as *O. perennis* and *O. breviligulata* can be characterized among wild species by the large grain volume. Large grain cultivars were found in abundance in African *O. sativa* varieties as compared to Indian varieties. Although a large difference in grain volume could not be found between the two cultivated species, weedy strains of *O. glaberrima*, which have not been grown as cultivated species, had apparently smaller grain volume. These results suggest that the decrement of *O. glaberrima* had been done centering around strains of small grain, and that selection pressure for large grain was strong in Africa over that in Asia.

**Key words :** Decrement, Domestication, Grain shape, Grain volume, *Oryza glaberrima*, *Oryza sativa*, West Africa.

アフリカイネ (*Oryza glaberrima* Steud.) の農学的形質に関する研究 第3報 栽培化と漸減の過程からみた籾の形態的特徴: 片山忠夫・角 明夫 (鹿児島大学農学部)

**要 旨 :** アフリカイネ (*Oryza glaberrima*) の籾の形態的特徴を、アジアイネ (*O. sativa*)、並びにアフリカとアジアに生育するそれぞれ3種ずつの野生籾、*O. breviligulata*, *O. longistaminata*, *O. punctata* と *O. perennis*, *O. sativa* var. *spontanea*, *O. officinalis* と比較しながら検討した。両栽培種は、籾の形態的特徴において互いに重なりあったが、*Series Glaberrima* に属する *O. glaberrima* と *O. breviligulata* は *Series Sativa* に属する4種、すなわち *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis* および *O. longistaminata* よりも扁平な籾の形状を示し、さらに幅/厚比(W/T)、長/厚比(L/T)、長/幅比(L/W)において、 $W/T > 1.45$ ,  $L/T > 3.75$ ,  $L/W > -4.88 \times W/T + 9.95$  の3条件を満たす範囲内に分布した。栽培種は、野生種よりも著しく一籾容量が大きく、さらに両野生祖先種、すなわち *O. perennis* および *O. breviligulata* は、他の野生種と比較して大きな一籾容量をもっていることによって特徴づけられた。同じ *O. sativa* であってもアフリカ産品種群はインド産のものと比較して大きな一籾容量をもつものが多かった。両栽培種の間に平均一籾容量における種間差は認められなかったが、栽培種として栽培されていない weedy *glaberrima* の中には明らかに一籾容量の小さなものが多かった。これらの結果は、*O. glaberrima* の漸減が小粒系統を中心になされてきたこと、さらに大粒系統に向けての選択圧がアフリカにおいて特に著しかったことを示している。

**キーワード :** *Oryza glaberrima*, *Oryza sativa*, 栽培化, 漸減, 西アフリカ, 籾の形状, 籾容量。

*Oryza glaberrima* can fundamentally be distinguished from *O. sativa* in ligule shape<sup>23)</sup>, but, in all other characteristics, the two species overlap each other<sup>23)</sup>. The absence of apiculus hair, from which the name *glaberrima* was derived, did not always characterize *O. glaberrima*, because both hairy *glaberrima* and hairless *sativa* exist<sup>23)</sup>. So, it is impossible to draw

an exact line between the two cultivated species on just the absence or presence of apiculus hair alone. If other information on characteristics of *O. glaberrima* could be found from grain morphology, it seems useful to avoid, to some extent, the risk that hairy *glaberrima* varieties are buried in *O. sativa*, in case the shape of ligule could not be confirmed, for example, when the seed samples were collected from the farmer's store. One purpose of the present paper is to find some

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morphological grain characteristics of *O. glaberrima*.

The size of a single harvested organ has been adopted consciously, or unconsciously, as an important criterion of varietal selection in the processes of domestication of some crops<sup>3,4,6,25,33</sup>). According to Evans and Dunstone<sup>4</sup>), the evolution in wheat has been accompanied by marked parallel increases in the size of grains and leaves. Inoue and Tanaka<sup>6</sup>) have found that *Solanum tuberosum* (cultivated species of potato) has large tuber size compared to wild species, i.e. *S. demissum* and *S. chacoense*. In the present paper, grain volume, expressed by the product of length, width and thickness, will be compared among two cultivated rice species, i.e. *O. sativa* and *O. glaberrima*, and six wild species, i.e. *O. breviligulata*, *O. longistaminata* and *O. punctata* (African wild species) and *O. perennis*, *O. sativa* var. *spontanea* and *O. officinalis* (Asian wild species). Where is *O. glaberrima* positioned in terms of the grain volume? The answer must be helpful in considering the domestication and decrement of *O. glaberrima*.

### Materials and Methods

110, 78, 49, 190 and 44 strains of *O. sativa*, *O. glaberrima*, *O. breviligulata*, *O. longistaminata* and *O. punctata* collected in 8 countries, i.e. Madagascar, Kenya, Tanzania, Nigeria, Ivory Coast, Liberia, Senegal and Gambia<sup>16-18,26-30</sup>), were used for morphological investigations of unhusked grain, respectively. In addition, the data of three Asian wild rice species, that is, 36 strains of *O. perennis*, 44 strains of *O. sativa* var. *spontanea* and 52 strains of *O. officinalis* collected in India, the Philippines, New Guinea, Borneo, and Java by the senior author<sup>8-13,15</sup>) were also referred.

Measurements were done on well ripened seeds collected at the respective locations. Length (L), width (W) and thickness (T) were measured, and the three ratios among them, i.e. length to width (L/W), length to thickness (L/T) and width to thickness (W/T) were also calculated. The product of L, W and T was calculated as an indicator of grain volume. The whole data referring to the respective characteristics were illustrated by the average values of 20 grains for each strain. In order to clarify the characteristic in grain volume of cultivated rice in Africa, as compar-

ed to that in Asia, the data of 100 strains of *O. sativa* collected in India<sup>14</sup>) were also taken into account.

To confirm the meaning of these grain volumes, the relationship between grain volume and single grain weight was examined. Single grain weight was determined for 10 strains of *O. glaberrima* and 9 strains of West African *O. sativa*, which were harvested at Kagoshima University in 1992 and sunk into salt water at specific gravity of 1.06. That is, the two results of grain volume and single grain weight differ entirely in the year and the subject investigated.

## Results

### 1. Grain shape

Fig. 1 shows the histograms of L (A), W (B), T (C), L/W (D), L/T (E) and W/T (F) in two cultivated species, respectively. In most characteristics, the variation ranges of *O. glaberrima* were within those of *O. sativa* but a remarkable difference could be found in the mode of W/T between the two species.

Fig. 2 shows the relationship between L/W and L/T, in *O. sativa*, *O. glaberrima* and *O. breviligulata*. Although L/W ratio was connected positively with L/T ratio in all species, strains of *O. sativa* tended to have smaller L/T than two species of *Series Glaberrima*, with the tendency was more conspicuous as L/W ratio increases. This also means that strains of *O. sativa* are characterized by lacking thickness in comparison with width, particularly when varietal difference in grain length was taken into consideration. In addition, *O. glaberrima* and *O. breviligulata* of the *Series Glaberrima* were 1.63 and 1.64 in specific means of W/T, whereas *O. sativa* and three wild species of *Series Sativa*, i.e., *O. sativa* var. *spontanea*, *O. perennis* and *O. longistaminata* had a W/T ratio from 1.46 to 1.54 (Table 1). This means that a basic balance between width and thickness has been kept constant as an important characteristics of each *Series*, in the process of evolution from *O. breviligulata* to *O. glaberrima*, or from *O. perennis* to *O. sativa*, even though there is a vast variation within each species, and that a high W/T ratio, that is a flatter grain shape, is regarded as an important characteristics of the *Series Glaberrima*.

W/T and L/T of strains of *O. sativa*, *O. glaberrima* and *O. breviligulata* collected in

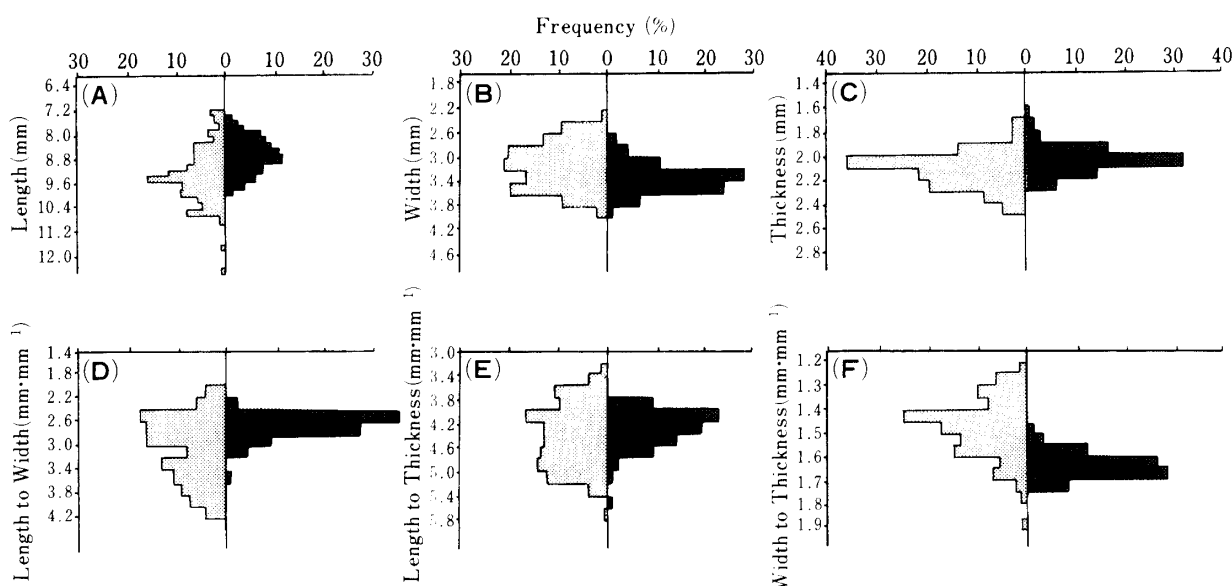


Fig. 1. Histograms of length (A), width (B), thickness (C), and ratios of length to width (D), length to thickness (E) and width to thickness (F) of unhusked grain in *O. sativa* and *O. glaberrima* collected in East and West Africa and Madagascar. Left: *O. sativa*, Right: *O. glaberrima*

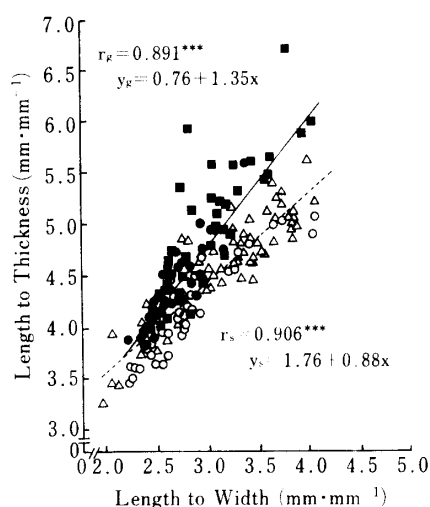


Fig. 2. Relationship between ratios of length to width and of length to thickness in *O. sativa*, *O. glaberrima* and *O. breviligulata*.  $\gamma_s$  and  $\gamma_K$  indicate correlation coefficients in *O. sativa* and *O. glaberrima*, respectively.  $\circ$  and  $\triangle$  indicate *O. sativa* collected in West Africa and in East Africa and Madagascar.  $\bullet$  and  $\blacksquare$  show *O. glaberrima* and *O. breviligulata* collected in West Africa. \*\*\*, 0.1% level of significance.

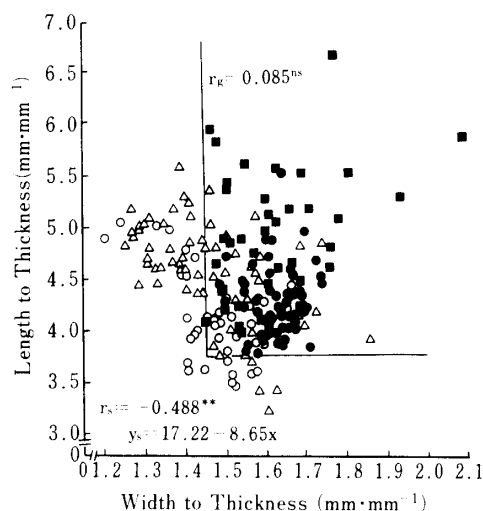


Fig. 3. Relationship between ratios of width to thickness and of length to thickness in *O. sativa*, *O. glaberrima* and *O. breviligulata*. \*\*, Significant at 1% level; ns, Not significant. The other symbols are the same as those shown in Fig. 2.

Africa are plotted in W/T~L/T diagram (Fig. 3). All strains of *O. glaberrima* and *O. breviligulata* were positioned within the following ranges:

$$W/T > 1.45, L/T > 3.75 \quad (1)$$

On the other hand, *O. sativa* contains many

strains of less than 1.45 in W/T, and 3.75 in L/T. In the same manner, W/T and L/W are plotted in Fig. 4. A negative correlation between L/W and W/T was found in both *O. sativa* and *O. glaberrima*, but such a relationship was still more conspicuous in *O. sativa*. The W/T and L/W of strains of *O. glaberrima* and *O. breviligulata* were positioned within the

Table 1. Six morphological characteristics of unhusked grains in *O. sativa*, *O. sativa* var. *spontanea*, *O. perennis*, *O. longistaminata*, *O. glaberrima*, *O. breviligulata*, *O. punctata* and *O. officinalis*.

		L (mm)	W (mm)	T (mm)	L/W (mm·mm <sup>-1</sup> )	L/T (mm·mm <sup>-1</sup> )	W/T (mm·mm <sup>-1</sup> )
<i>Series Sativa</i>							
<i>O. sativa</i>	(n=110)	9.28±0.95	3.12±0.37	2.11±0.14	3.02±0.53	4.42±0.51	1.48±0.12
<i>O. sativa</i> var. <i>spontanea</i>	(n=44)	8.44±0.86	2.75±0.35	1.80±0.24	3.09±0.38	4.77±0.81	1.54±0.13
<i>O. perennis</i>	(n=36)	7.09±1.42	2.19±0.40	1.51±0.23	3.24±0.32	4.77±1.22	1.46±0.27
<i>O. longistaminata</i>	(n=190)	8.47±0.64	2.36±0.22	1.60±0.11	3.61±0.26	5.31±0.31	1.48±0.08
<i>Series Glaberrima</i>							
<i>O. glaberrima</i>	(n=78)	8.76±0.54	3.33±0.22	2.04±0.12	2.65±0.20	4.31±0.30	1.63±0.05
<i>O. breviligulata</i>	(n=49)	9.22±0.80	3.04±0.25	1.86±0.16	3.06±0.41	5.01±0.65	1.64±0.09
<i>Series Latifolia</i>							
<i>O. punctata</i>	(n=44)	6.10±0.42	2.35±0.12	1.52±0.05	2.61±0.18	4.04±0.26	1.56±0.08
<i>O. officinalis</i>	(n=52)	5.22±0.53	2.33±0.10	1.20±0.13	2.24±0.21	4.44±0.80	1.98±0.26

L, W and T indicate length, width and thickness of unhusked grains, respectively. n shows the number of strains.

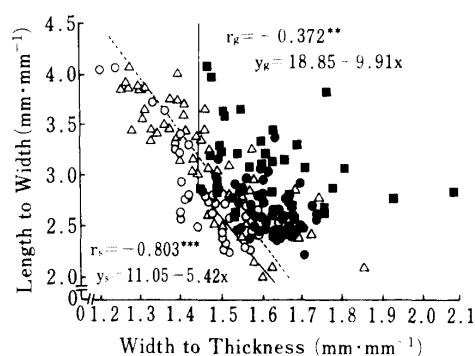


Fig. 4. Relationship between ratios of width to thickness and of length to width in *O. sativa*, *O. glaberrima* and *O. breviligulata*. Symbols are the same as those shown in Figs. 2 and 3.

following ranges:

$$W/T > 1.45, L/W > -4.88 \times W/T + 9.95 \quad (2)$$

In this relationship, the latter expression indicates a straight line joining the lowest limits of a 10% error of a regression line obtained in *O. sativa*.

## 2. Grain volume

Fig. 5 shows the histograms of grain volume in two cultivated and six wild rice species. *O. officinalis* and *O. punctata* of *Series Latifolia*, which are distantly related to two cultivated species, had definitively small grain volume as compared to two cultivated species and their wild ancestors. On the other hand, *O. perennis* and *O. breviligulata*, which are progenitors of *O. sativa* and *O. glaberrima*, were characterized

among wild species by their large grain volume. Both cultivated species possessed still larger grain volume than their ancestors. No difference was observed in grain volume between the two cultivated species.

Fig. 6 shows the histograms of grain volume in *O. sativa* collected in West Bengal of India (A), and in Madagascar and East and West African countries (B), and in *O. glaberrima* collected in four West African countries (C). Large grain type are found in abundance in strains of African *O. sativa* compared to Indian *O. sativa*. Of *O. glaberrima*, weedy strains, which were growing as weed in paddy field, tended to have small grain, while cultivated strains were demonstrated to possess large grain. The average grain volume of weedy types and cultivated types came near to *O. breviligulata* and African *O. sativa*, respectively.

## Discussion

Firstly, we must re-examine the meaning of length, width and thickness of unhusked grain measured on the respective spots. Although length and width of grain have been adopted as important morphological characteristics of each species<sup>23,24,32</sup>, or each strain<sup>22,26-31</sup>, in many cases, the thickness has been regarded as an insignificant characteristic, perhaps because it is easily affected by degree of ripening. However, we could obtain a close correlation between width and thickness (unshown). If someone assumes that thickness is a reflex of

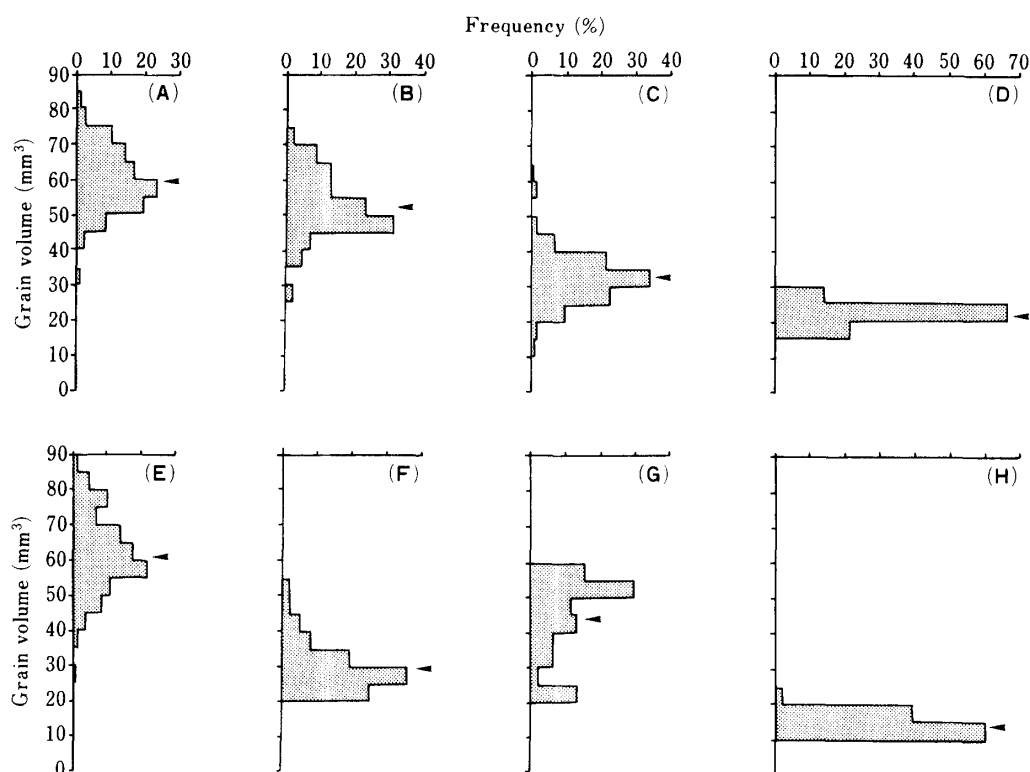


Fig. 5. Histograms of grain volume in *O. glaberrima* (A), *O. breviligulata* (B), *O. longistaminata* (C), *O. punctata* (D), *O. sativa* (E), *O. perennis* (F), *O. sativa* var. *spontanea* (G) and *O. officinalis* (H). Upper, African species: Lower, Asian species: ◄, Mean value

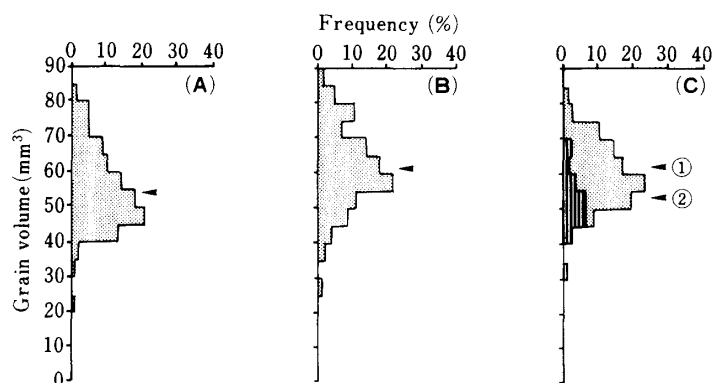


Fig. 6. Histograms of grain volume in *O. sativa* from West Bengal, India (A) and from East and West Africa and Madagascar (B), and *O. glaberrima* from West Africa (C). ———, Weedy types of *O. glaberrima*: ◄, Mean value. ① and ② show mean values of cultivated and weedy types, respectively.

degree of ripening, he will have to explain the reason why wide grain is connected with the high percentage of ripened grains. In addition, we could have a close connection between the single weight of ripened grain and grain volume expressed by the product of length, width and thickness, in spite of the fact that the two results differ entirely in the year and the

subject investigated (Fig. 7). These results also suggest that thickness as well as length and width can be regarded as important characteristics of grain morphology, under the condition that ripened grains are carefully picked up.

By using the data concerning length and width of grain, *O. sativa* had been classified

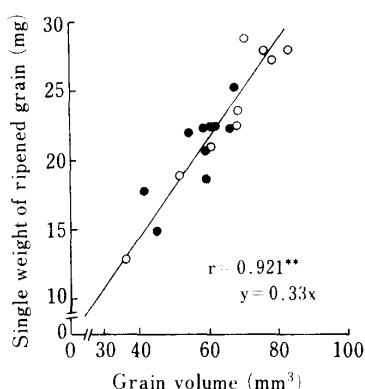


Fig. 7. Relationship between grain volume and single grain weight. Grain volume ( $\text{mm}^3$ ) = Length  $\times$  Width  $\times$  Thickness. Length, width and thickness were determined on the respective spots in 1984 and 1985. Measurements of single grain were done for grains harvested in Kagoshima University in 1992. \*\*, 1% level of significance;  $\circ$ , *O. sativa*;  $\bullet$ , *O. glaberrima*

into three grain types or ecotypes, namely, short type ( $\hat{=}$  Japonica type), large type ( $\hat{=}$  Javanica type) and slender type ( $\hat{=}$  Indica type)<sup>22</sup>. However, *O. glaberrima* could not be distinguished from *O. sativa* using these<sup>23,31</sup>. We found that the data concerning thickness can provide an important key in characterizing *O. glaberrima* or *Series Glaberrima*. That is, all strains of *O. glaberrima* were positioned on the following ranges in W/T, L/T and L/W, respectively.

$$W/T > 1.45$$

$$L/T > 3.75$$

$$L/W - 4.88 \times W/T + 9.95$$

Regretfully, these are necessary conditions but not sufficient conditions, because not only *O. glaberrima* but also some strains of *O. sativa* are scattered within the above ranges. Nevertheless, we think that these characteristics are useful in picking out strains of *O. glaberrima* for the following reasons. *O. glaberrima* has been generally believed to be distributed only in the West African region, but the senior author<sup>19</sup>, in Tanzania, collected 2 strains of *O. glaberrima* and listed a lot of information concerning *O. glaberrima*. This suggests a possibility that this species is widely distributed not only in West Africa but also in the adjacent regions. Strains of *O. glaberrima* from Tanzania are also listed in collections of IRAT<sup>20</sup>. In addition, it has been widely thought that *O. glaberrima* is distinguished from *O. sativa* by glabrous

glume, from which the name *glaberrima* was derived. But, in fact, about 30% of *O. glaberrima* were hairy varieties<sup>23</sup>. Those two assumptions may lead to a mistaken conclusion that the hairy cultivars collected in the other regions are all *O. sativa* varieties, if the shape and length of ligule, the only characteristics by which *O. glaberrima* is clearly distinguished from *O. sativa*<sup>23</sup>, can not be confirmed, for example, when seed samples were derived from the farmer's store. But, even though a seed sample is hairy, it is obvious from the results that it is not always *O. sativa*. When it fulfills the necessary conditions mentioned above, the sample ought to be examined on ligule characteristics, for example, when it will be grown to renew the seed. On the other hand, hairless *sativa* varieties were only 4%<sup>23</sup>. Consequently, if a seed sample lacks apiculus hair and fulfills the necessary conditions above, we will be able to conclude with fair probability, that it belongs to *O. glaberrima*.

The necessary conditions of *O. glaberrima* in grain shape, proposed in the present paper can be also applied to *O. breviligulata*, which shows larger morphological variation than the former<sup>24</sup>. This seems to verify from grain morphology that the two species are nearly related to each other<sup>23,24</sup>. However, *O. glaberrima* tends to have glabrous glume, whereas *O. breviligulata* has apiculus hair. These results suggest that the morphological characteristics of flatter grain had been held in the process of evolution from *O. breviligulata* to *O. glaberrima*, as well as in distinguishing *O. glaberrima* from *O. sativa*, grain shape occupy priority as characteristics of *O. glaberrima* over the presence or absence of apiculus hair.

Nagato et al.<sup>25</sup> compared the yields between the current cultivar, its wild ancestor and the related wild species of four crop species, including rice, and concluded that the wild ancestor does not differ largely from current cultivars in yield performance. In addition, they pointed out that the ancestral species can be characterized among wild species by its large size of single harvested organ and that only the size of a single harvested organ had become considerably larger in the process of domestication. Our results showing that the wild ancestors of *O. sativa* and *O. glaberrima*, i.e. *O. perennis* and *O. breviligulata*, had larger grain volumes than *O.*

*officinalis* and *O. punctata* but smaller than cultivated forms agree strongly with their findings. The increase in grain volume would bring about not only a high harvesting efficiency<sup>25)</sup> but also an improvement of seedling growth<sup>3,7,21)</sup>. There is no doubt that those appealed strongly to the farmers in the process of varietal selection.

On the other hand, the difference in grain volume was larger between *O. perennis* and *O. sativa* than between *O. breviligulata* and *O. glaberrima*. The birth of *O. sativa* is said to date back to B.C. 6,000 or more, while *O. glaberrima* was originated in B.C. 1,500<sup>19,34)</sup>. Through the large difference between *O. perennis* and *O. sativa*, an intensive and persistent selection pressure for large grain could be exerted. As a result, the grain volume of *O. sativa* var. *spontanea* ranged between *O. perennis* and *O. sativa*. Besides, from this standpoint, this species may be positioned as an intermediate between *O. perennis* and *O. sativa*<sup>2,32)</sup>. On the contrary, it may be assumed that the small difference between *O. breviligulata* and *O. glaberrima* stresses the youth of domestication. But it should be also noted that *O. breviligulata* has distinctly larger grain volume than other wild species. Although there is no doubt that such a characteristic of *O. breviligulata* was profitable in the first step toward domestication, it can also be assumed that the selection pressure for large grain was attenuated all the more for its advantage.

As observed in transition of grain volume from wild to cultivated forms in Asia and Africa, the desire for large grain was common to both continents. As far as *O. sativa* was concerned, however, such a selection pressure was more conspicuous in African countries than in India (Fig. 6). This suggests that the introduction of *O. sativa* into Africa has been done centering around strains of the large grain type. There is a possibility that the decrement of *O. glaberrima*, which had been done centering around strains of small grain, may correspond to the pattern mentioned above. This selection must be applied to strains of *O. sativa*, too, but in many cases, the transposition is done by a strain of *O. sativa* as well. Therefore, in *O. sativa*, the dismissal of strains having small grain never corresponds to the decrement of the species in contrast to *O. glaberrima*. In this way, the fact that the

authors could collect or observe numerous strains of *O. glaberrima* around Ziguinchor, in Senegal, where the people eat broken rice by preference<sup>1)</sup>, is very interesting, for the selection pressure for large grain is thought to be difficult to develop in such a place.

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\* In Japanese with English abstract.

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