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A Study on the Interspecific Variation of Panicle Structure in the Genus *Oryza**

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Abstract: This study was undertaken to (I) clarify the gross morphology of the panicle from the view point of growth and differentiation and (II) observe the variation in the panicle structure according to species, strains and genomes in the genus *Oryza*. In this study 41 strains representing 17 species of wild and cultivated rices were used. Among the characters investigated those concerned with growth were the length of panicle, rachis, internode of rachis, primary branch, and secondary branch, and the diameter of neck node of the panicle, and those concerned with differentiation were the number of primary branch, nodes in primary branch, secondary branches per primary branch and nodes in secondary branch, and percentage of development of secondary branches. There existed a wide range of an interspecific variation in the panicle structure. In Asian race of *O. rufipogon*, there had been a reduction in respect of growth and differentiation of panicle of the perennial type during the course of its evolution to annual type. In terms of growth and differentiation, the panicles of the species representing *Angustifoliae* were inferior to those of the species representing *Oryzae*. On cluster analysis the strains could be divided into 5 groups based on the degree of growth and differentiation of the secondary branch in the panicle.
Key words: Annual rice, Cluster analysis, Cultivated rice, Genus *Oryza*, Panicle structure, Perennial rice, Secondary branch, Wild rice.

イネ属植物における穂構造の種間変異に関する研究：廣井清貞・Abdullah Al MAMUN・和田富吉・武岡洋治（名古屋大学農学部）

要　旨：本研究は，イネ属植物における穂の構造の特徴を明らかにする目的で，(1)穂の形質を長さ・太さと数に関するものとに分けて，穂構成器官の生長と分化の面からこれらを解析し，(2)イネ属の種・系統・ゲノムごとの変異を調査し比較した．供試材料には本属の内17種41系統の野生稲および栽培稲を用いた．生長に関する形質として，穂長・穂軸長・穂軸節間長・一次枝梗長・二次枝梗長・穂首直径を選び，分化に関するものとして，一次枝梗数・一次枝梗節数・一次枝梗あたりの二次枝梗数・二次枝梗節数・二次枝梗発生率を選んでこれらを調査した．計測値をクラスター分析して穂構造の特徴にもとづく類別化を行った．その結果，(1)穂構造には広範な種間差異がみられた．(2)アジアの *O. rufipogon* には，多年生型から一年生型への変遷にともない，穂の生長と分化の両面においていわゆる"縮小効果"が働いていた．(3) *Angustifoliae* 節の種は *Oryzae* 節の種に比較して，分化と生長の面で劣っていた．(4)各系統はクラスター分析の結果，二次枝梗の生長と分化の程度により5つのグループに分類され，各グループにおける穂の形態構造的な特徴が明らかにされた．
キーワード：一年生イネ，イネ属，クラスター分析，栽培稲，多年生イネ，二次枝梗，穂構造，野生稲．

Panicle bears the spikelets or, in other words, the seeds, the production of which is the ultimate goal of a rice plant. It is in this sense, Togari and Amatatsu[20] rightly expressed 'Yield is expressed in the panicle first'. This importance of the panicle as an organ in the rice plant has attracted the crop scientists to take up it as a topic of investigation. And, so far, a good number of studies have been documented in the literature, for example, (I) classification of stage of development in the panicle[1], (II) the process of development of the tillers in relation to yield determination in rice[10], (III) the branching system and type, and the process of formation of panicle[5~9], and (IV) classification of panicle on the basis of the number of secondary branches in each node of the rachis, and variation in the panicle type as influenced by planting density and fertilizer level[17]. All of these studies are unique in their perspectives and provide information on the growth, differentiation, development, type and branching of the panicle of cultivated rice. But no study has yet been undertaken on the structure of panicle based on the growth and differentiation of the panicle components as a whole.

As for the wild species of rice, studies were mainly concerned with differentiation of species from the viewpoint of heredity, taking account of panicle length and some physiologi-

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cal characters only. Comparative panicle structure in reference to interspecific or genome variation and morphology of the panicle components has not yet been studied. But these aspects of panicle structure are extremely important in tracing the morphogenetic pathway of the formation of panicle and in identifying which part has changed, which part has not been relatively changed, and/or which part has been inherited in the cultivated rice during the course of its evolution from the wild ancestors.

This work has, therefore, been undertaken with a view to (I) studying the gross morphology of the panicle from the viewpoint of growth and differentiation, and (II) understanding the variation in panicle structure according to species, strains, and genomes in the genus *Oryza*.

Materials and Methods

Materials used for the experiment in this study, as shown in Table 1, were forty one strains representing seventeen species of wild (15 spp.) and clutivated (2 spp.) rice.

Seeds incubated at 50°C for 10 days to break dormancy were hulled, sterilized with 0.1% aqueous solution of Benlate, and soaked for 24 hours at room temperature. After soaking, the seeds were placed on moistened filter paper in petri dishes and kept for 2 days in an incubator controlled at 30°C. The germinated seeds were sown in trays with soil mixture and the trays were placed in a greenhouse on April 14, 1986. On May 14, seedlings were transplanted at the rate of 2 plants per 1/5000 a Wagner's pots filled with soil. For each strain, 8 plants were cultured. Mixed fertilizer (14 : 16 : 14 of N : P : K) was applied basally at the rate of 2 g per pot. Again the same mixed fertilizer was topdressed at 70 days after transplanting at the rate of 1 g per pot. The pots were kept in the greenhouse of School of Agriculture, Nagoya University, until the plant age of 60 days.

The 60-day-old plants were transferred to day-length treatment by the equipment NOSC-1A, Onishinetsugaku Kogyo Inc., and kept under short-day condition (11.5 hr of light/12.5 hr of dark) until July 19 (95 days old). After the treatment, the plants were raised under natural field condition. For investigation of panicles, the following seven characters concerning growth and five characters concerning differentiation were investigated.

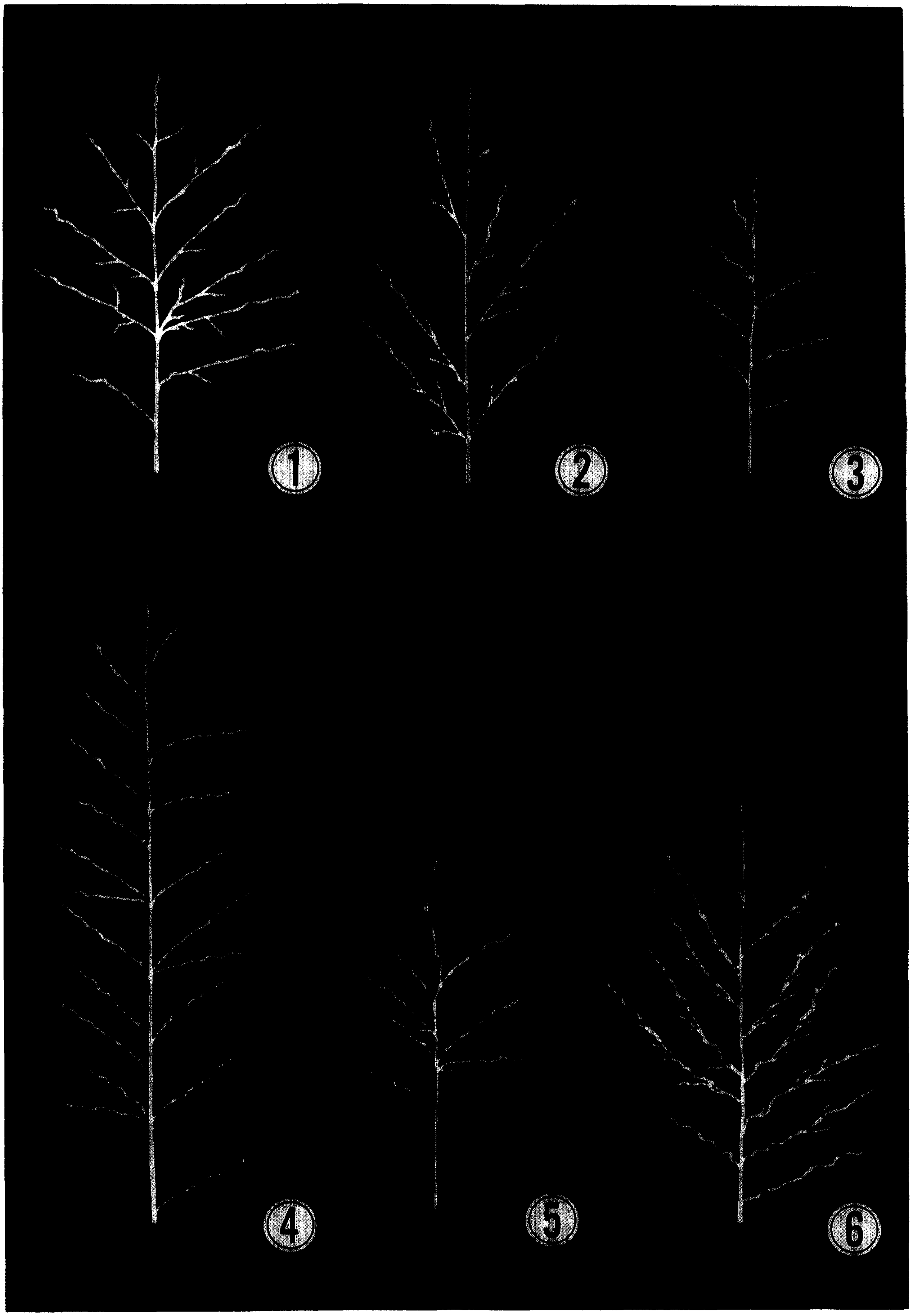
A. Characters concerning growth
1. Panicle length
2. Rachis length
3. Length of primary branch
4. Internode length of rachis
5. Length of secondary branch
6. Internode length in primary branch
7. Diameter of neck node of panicle

B. Characters concerning differentiation
1. Number of primary branches
2. Number of nodes in primary branch
3. Number of secondary branches per primary branch
4. Number of nodes in secondary branch
5. Percentage of development of secondary branches

The degenerated secondary branches were not taken into account and no data were collected regarding this. Standard size of five panicles obtained primarily from main culm were used in each strain respectively. Panicles were dried and the spikelets were removed very carefully. The panicles with the primary and secondary branches intact were affixed on the black Kent paper and photocopied. To measure curved line, image analyzer (IBAS-I, Zeiss) was used. Cluster analysis (mean average method)[19] was applied in the analysis of data.

Results

Typical panicles of *Oryza* plants are shown in Figs. 1 to 12; there is a wide range of interspecific variation in the panicle structure in this genus. Average data on the morphological characters concerning growth and differentiation of the panicle are presented in Table 2. Panicle was the shortest in *O. perrieri* (24.5 mm) and the longest in *O. australiensis* (372.8 mm). Correlation coefficient between panicle length and rachis length among the strains was highly significant ($r=0.947$, significant at 0.1% level). Among the species of known genome, length of primary branch was the greatest in *O. latifolia* and the smallest in *O. brachyantha*. Internode length of rachis was comparatively bigger in *O. punctata*, *O. officinalis*, and *O. eichingeri* than in the rest of the species studied; it was the biggest in *O. punctata*, and the smallest in *O. perrieri*. Internode in the primary branch was comparatively lon-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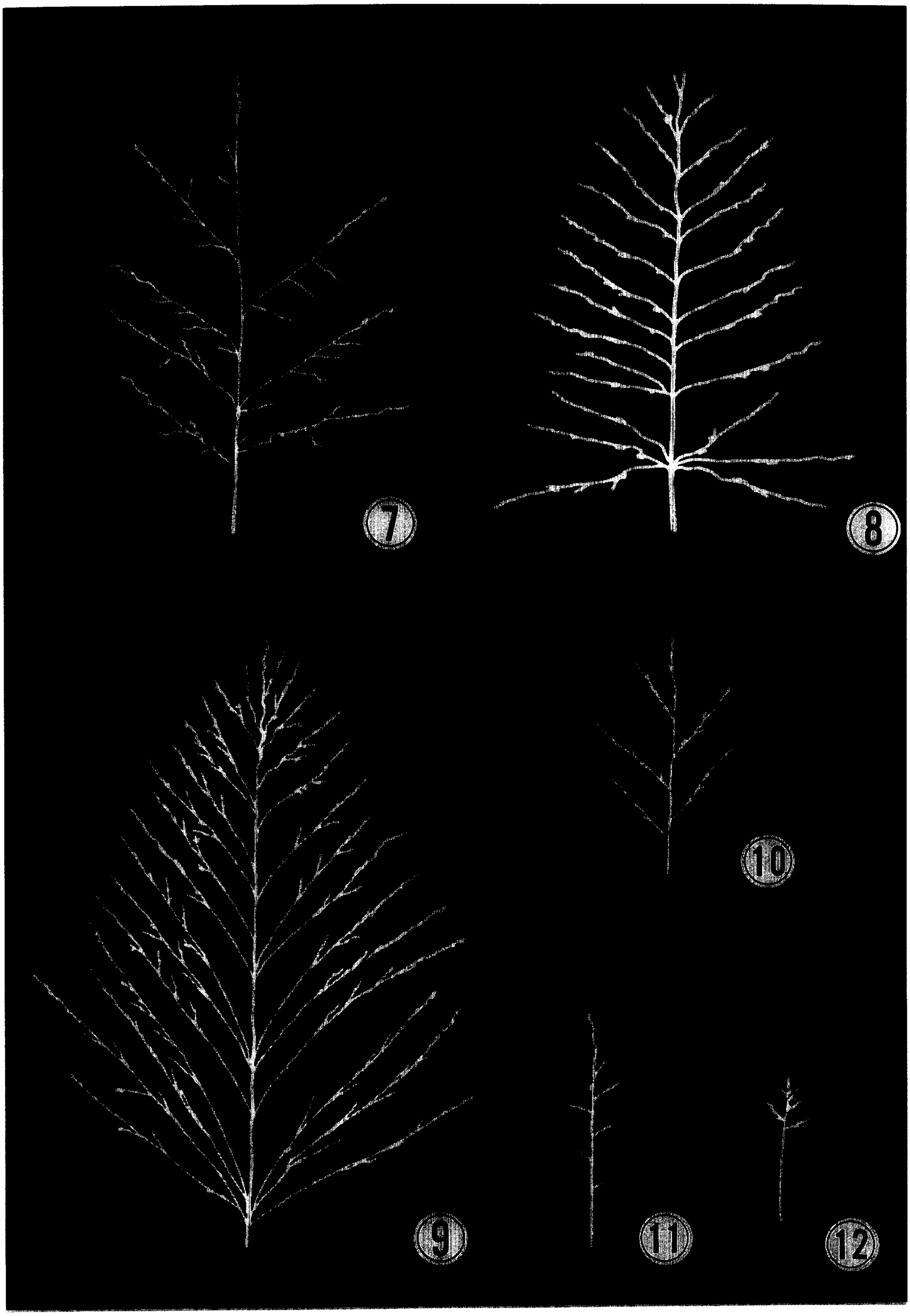
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ger in *O. australiensis*, *O. latifolia*, and *O. alta* than in other species. Diameter of neck node of the panicle was slightly bigger in *O. latifolia*, *O. grandiglumis*, and *O. australiensis* than in other species, the largest being *O. grandiglumis* and the smallest being *O. perrieri*. The number of primary branches was abundant in *O. australiensis* and *O. grandiglumis* ; it was approxi-

Table 1. Materials used for experiment in the present study.

Genus	Section	Species	2n	Genome	Geographical distribution	Growh habit	No. of strains. investigated
Oryza							
	Oryzae						
		sativa L.	24	AA	Asia	perennial	1
		rufipogon Griff.	24	AA	Asia, America	annual-perennial	16
		meridionalis Ng	24	AA	Australia	annual	2
		longistaminata A. Chev. et Roehr.	24	AA	Africa	perennial	2
		glaberrima Steud.	24	AA	Africa	annual	4
		breviligulata A. Chev. et Roehr.	24	AA	Africa	annual	4
		punctata Kotschy et Steud.	24, 48	BB, BBCC	Africa	annual-perennial	2
		minuta J.S. Presl. ex Chandl.	48	BBCC	Asia	perennial	1
		eichingeri A. Peter	24	CC	Africa	perennial	1
		officinalis Wall. wx Watt.	24	CC	Asia	perennial	1
		latifolia Desv.	48	CCDD	America	perennial	1
		alta Swallen	48	CCDD	America	perennial	1
		grandigumis (Doell) Prod.	48	CCDD	America	perennial	1
		australiensis Domin	24	EE	Australia	perennial	1
	Angustifoliae						
		brachyantha A. Chev. et Roehr.	24	FF	Africa	annual-perennial	1
		perrieri A. Camus	24	Unknown	Malagasy	perennial	1
		tisseranti A. Chev.	24	Unknown	Africa	perennial	1

Explanation of figures*

Fig. 1. *O. sativa* (T414 ; cultivated rice), well-developed secondary branch, representing cluster 1**.
Fig. 2. *O. rufipogon* (W0149 ; perennial type), well-developed secondary branch, representing cluster 1.
Fig. 3. *O. meridionalis* (W1299 ; annual type), poorly developed secondary branch, representing cluster 2.
Fig. 4. *O. longistaminata* (W1441 ; perennial type), large panicle and poorly developed secondary branch, representing cluster 4.
Fig. 5. *O. glaberrima* (W0492 ; cultivated rice), poorly developed secondary branch, representing cluster 2.
Fig. 6. *O. glaberrima* (W0502 ; cultivated rice), well-developed secondary branch, representing cluster 1.
Fig. 7. *O. breviligulata* (W0828 ; annual type), well-developed secondary branch, representing cluster 1.
Fig. 8. *O. grandiglumis* (W1197), long panicle and large number of primary branch, representing cluster 3.
Fig. 9. *O. australiensis* (W0008), long panicle and large number of primary branch, representing cluster 3.
Fig. 10. *O. minuta* (Y22), small panicle and poorly developed secondary branch, representing cluster 2.
Fig. 11. *O. branchyantha* (W1405), small panicle and poorly developed secondary branch, representing cluster 2.
Fig. 12. *O. perrieri* (W1529), the most inferior in panicle components having least similarlity with other strains, representing cluster 5.

* magnification is ×0.25 in all figures.
** see Fig. 13.

Table 2. Morphological characters concerning growth and differentiation of panicle in *Oryza* plants.

Characters	Panicle length (mm)	Rachis length (mm)	Length of primary branch (mm)	Internode length of rachis (mm)	Length of secondary branch (mm)	Internode length of primary branch (mm)	Diameter of neck node of panicle (mm)	No. of primary branches	No. of nodes in primary branch	No. of secondary branchrs per primary branch	No. of nodes in secondary branch	Percentage of develoment of secondary branches(%)
Oryza sativa	220.6	139.0	92.4	16.6	20.7	11.0	1.83	9.6	8.4	2.15	3.2	25.2
O. rufipogon	159.6	108.0	60.8	18.0	12.2	9.2	1.50	6.7	6.6	0.96	2.4	11.3
O. meridionalis	180.5	145.1	44.7	13.4	10.2	6.9	1.49	8.6	6.5	0.33	2.9	4.5
O. longistaminata	286.7	247.6	47.8	17.4	4.8	6.7	1.88	14.0	7.2	0.05	2.0	0.4
O. glaberrima	186.7	124.9	70.9	16.1	14.3	10.2	1.72	8.8	7.1	1.20	2.7	13.2
O. barthii	209.4	123.8	89.4	19.9	19.5	12.2	1.71	7.6	7.3	1.17	2.7	12.9
O. punctata	225.9	152.8	112.4	30.9	17.4	12.6	1.59	5.9	9.0	2.70	3.6	29.2
O. officinalis	204.6	156.6	87.6	25.3	13.6	12.1	1.52	7.2	7.3	1.89	3.1	24.5
O. eichingeri	124.0	73.3	63.5	33.3	12.9	8.9	0.97	3.2	7.1	2.50	3.1	34.7
O. minuta	125.9	84.6	51.5	19.3	7.4	6.3	0.98	5.4	8.3	2.30	2.9	27.9
O. alta	307.0	217.2	155.1	24.1	15.1	14.7	1.95	10.0	10.6	4.30	3.7	39.0
O. latifolia	298.8	244.4	158.8	20.0	16.6	14.6	2.37	13.8	10.9	4.39	4.7	39.0
O. grandiglumis	269.2	248.6	75.2	10.0	10.7	11.9	2.52	26.0	6.4	0.96	2.6	13.0
O. australiensis	372.8	337.5	115.8	13.5	16.3	15.8	2.33	26.3	7.3	1.96	2.8	25.5
O. brachyantha	126.1	93.1	18.8	13.3	—	6.0	1.11	8.0	3.1	—	—	0.0
O. tisseranti	148.0	130.0	29.3	14.5	11.8	5.0	0.70	10.0	5.9	0.92	4.0	12.6
O. perrieri	24.5	24.5	1.7	4.6	—	1.2	0.68	6.3	1.4	—	—	0.0

Table 3. Variation of panicle components with the change from perennial type to annual ones in Asian race of *O. rufipogon*.

Characters	Panicle length (mm)	Rachis length (mm)	Length of primary branch (mm)	Internode length of rachis (mm)	Length of secondary branch (mm)	Internode length of primary branch (mm)	Diameter of neck node of panicle (mm)	No. of primary branches	No. of nodes in primary branch	No. of secondary branchrs per primary branch	No. of nodes in secondary branch	Percentage of develoment of secondary branches(%)
Perennial	186.2	120.6	76.9	18.0	15.8	9.6	1.56	7.8	8.0	2.10	3.1	26.9
Intermediate	159.5	97.4	58.7	17.2	12.8	9.1	1.57	6.7	6.3	0.91	2.7	10.7
Annual	132.2	88.8	48.3	16.2	9.3	8.2	1.31	6.1	6.0	0.32	2.4	5.0

mately three times that in *O. sativa* and *O. glaberrima*, the cultivated rices. *O. eichingeri* had the smallest number of primary branches. The number of nodes in the primary branch was the highest in *O. latifolia*, which was very closely follwed by *O. alta* ; the lowest was in *O. perrieri* ; in all other species except *O. brachyantha* it ranged from 5.9 to 9. The number of secondary branches per primary branch was considerably great in *O. alta* (>4) and *O. latifolia*, and in *O. minuta*, *O. eichingeri*, *O. punctata*, and *O. sativa* it was >2 ; in the rest of the species it was <2 and in *O. longistaminata* it was only 0.05. The number of nodes in the secondary branch varied according to species, from 2.0 to 4.7, *O. latgfolia* having the highest number and *O. longistaminata* the lowest ; however, *O. tisseranti* closely followed *O. latifolia*. The percentage of development of secondary branches in *O. alta*, *O. latifolia*, and *O. eichingeri* was above 30 ; in *O. longistaminata* it was only 0.4 and in *O. brachyantha* and in *O. perrieri* it was completely lacking.

In Asian race of *O. rufipogon*, the dimension of panicle components as a whole was smaller in the annual type than in the perennial type and the difference was very conspicuous in the case of secondary branches (Table 3).

Discussion

We investigated panicle structure of 17 species of the genus *Oryza*, which included cultivated, wild, annual, and perennial species, from the viewpoint of growth and differentiation. Viewed from the external gross rorphology, we divided panicle components into two groups : (I) that reflecting, externally, the growth of the panicle ; (II) that reflecting, externally, the differentiation in the panicle. As the plant growth, which is a function of the cell number, cell length, and cell breadth, is externally reflected by the length and breadth of an organ we included the length and diameter of the panicle components as the characters related to growth. And, as the external manifestation of the organ-level differentiation of a plant part is reflected by the types, number in each type, structure, and configuration of the organs we included the number of each of the panicle components as characters related to differentiation in the panicle. From these perspectives, no study has yet been carried out on the structure of panicle in the genus *Oryza*. The most important feature we could clarify is that in Asian race of perennial type *O. rufipogon*, secondary branch was well developed but in American race of perennial type of this species the secondary branch was poorly developed. This was the main difference between Asian and American race of perennial type *O. rufipogon*. A new species of annual type, *O. meridionalis*, as named by Ng *et al.*[15], and the annual type of *O. rufipogon* had more or less similar panicle type with poorly developed secondary branch. But, the panicle or rachis was slightly longer and the primary branch was more plentiful in *O. meridionalis*. In *O. longistaminata*, however, secondary branch was not well developed, though it was a perennial type. The reason may be that it propagates mainly by its well-developed, plentiful rhizome and thus in continuation of its generation the necessity of producing secondary branches to bear seeds might be very negligible.

In respect of growth and differentiation of the panicle components in species having CCDD genome, viz., *O. latifolia*, *O. alta*, and *O. grandiglumis*, we observed a clear-cut difference. The former two species had more or less similar type of panicle with long panicle, long and well-spread primary branches and well-developed secondary branches. In the latter one, *O. grandiglumis*, the panicle was considerably smaller, with short rachis, primary branch, and secondary branch, but with a greater number of primary branches having a very low percentage of secondary branch development. The panicle components related to growth in *O. australiensis* did not show much difference with those in *O. latifolia* and *O. alta*, but those related to differentiation showed a considerable difference : the number of primary branches was higher but the number of nodes in the primary and secondary branch and the number of secondary branches was lower in *O. australiensis* than in *O. latifolia* and *O. alta*.

The Asian race of *O. rufipogon*, which is considered to be the ancestor of *O. sativa*[2,3,16], is usually of two types-the annual and the perennial, depending on the life cycle. The perennial type is considered to be primitive and the annual type to be the evolutionary recent form of the primitive perennial one[18]. The two types are generally adapted to two

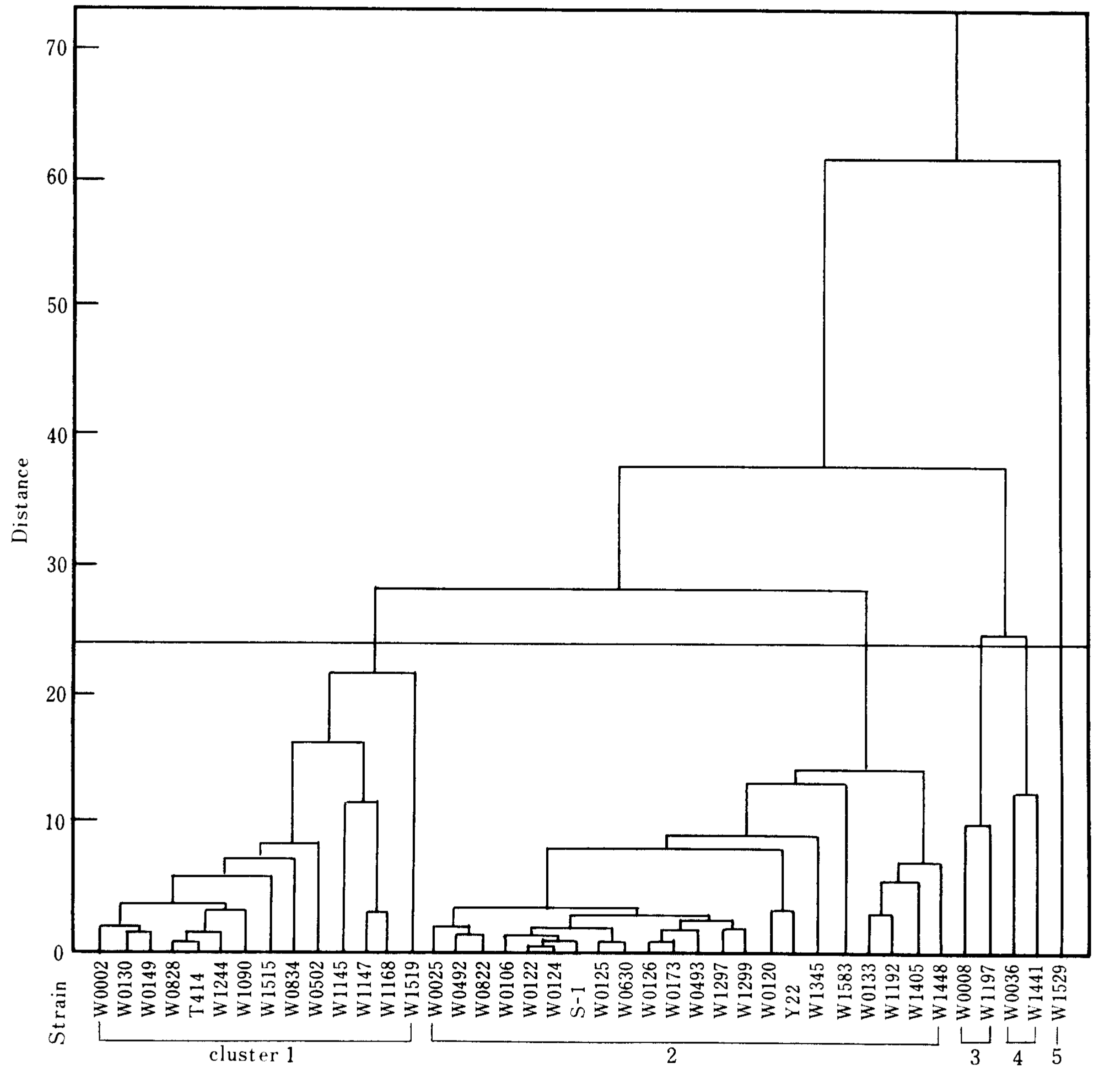

Fig. 13. Dendrogram showing 5 clusters based on 12 panicle characters concerning growth and differentiation of panicle in *Oryza* plants.

separate habitats. The annual type is adapted to upland or shallow water condition with disturbed environment and the perennial type grows usually in the wet region having deep water with relatively less disturbed environment[13,14]. This is because the annual type prefers r-adaptive strategy and the perennial one prefers K-adaptive strategy. However, as for the panicle components, our observation in this study clarifies that growth and differentiation is comparatively less in the annual type, with the consequence of small panicle and inferior panicle components, than in perennial ones. This would otherwise mean that there had been a reduction in respect of growth and differentiation of panicle of the perennial type during the course of its evolution to annual type.

On cluster analysis, the strain included in this study could be divided into 5 clusters based on characteristics of panicle components (Fig. 13). The cluster 1 was characterized with well-developed secondary branches and the cluster 2 with poorly developed secondary branches. The cluster 3 was characterized with long panicle and a large number of primary branches, while the cluster 4 had long panicle with poorly developed secondary branches. The cluster 5 was characterized with very short panicle and with very inferior panicle components.

In cultivated rice, *O. sativa,* the degree of development in the secondary branch is influenced by the environmental condition[4]. Our observation in this study substantiated this contention. Generally, in *O. glaberrima* and *O. breviligulata* there is little intranspecific variation[11,12] and in these two species the development of secondary branches in the panicle can hardly be seen. But, in our study, the strain W0502, representing *O. glaberrima*, and the strain W0834, representing *O. breviligulata*, had their position in cluster 1, having well-developed secondary branches and similar type of panicle as of Asian race of perennial type *O. rufipogon*. This, we consider, might be attributable to the difference between climatic elements of Japan and Africa, the day length and temperature, in particular.

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