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A Study on the Nature of Genetic Divergence in Rice from Assam and North East Himalayas

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Summary. A representative group of 190 rice types collected from North-East India along with four standard varieties, three of which were *indicas* and one *japonica*, was studied to understand the nature of genetic divergence. Preliminary grouping was done by canonical analysis and the resultant 42 groups were further classified using the D^2 statistic.

The final grouping resulted in nine divergent clusters. The three *indica* standards were found in three different clusters indicating the wide available variability among them. The *japonica* standard formed a separate group by itself. A majority of the North-East Indian types formed clusters with *indicas*, whereas some were intermediate and still others were closer to *japonica* or *indica*, thus indicating a series of intergrades bridging *indica* and *japonica*.

Height followed by leaf area was found to be important for primary and 100-grain weight, followed by amylose content for secondary differentiation. It appears that natural selection as well as human selection might have operated for characters differentiating rice types in Assam and North Eastern Himalayas. Geographical distance was not found to be related to genetic divergence. The study suggests that *O. sativa* contains innumerable but divergent forms, and its classification into definite varietal groups on an arbitrary basis such as isolation barrier, sexual affinity or geographic distribution would be far from reality.

India is known to be at least a secondary centre of origin of rice, *Oryza sativa* L. Studies made by the Central Rice Research Institute on a rich collection of rice genotypes obtained from the Jaypore tract of Orissa State have provided useful data of phylogenetic value (Govindaswami and Krishnamurty, 1958). Another region of the country containing a wide range of valuable germplasm is Assam and the North Eastern Himalayas. A systematic collection of both primitive and existing cultivars of rice of this region, initiated by the Indian Agricultural Research Institute a few years ago, is being studied for characteristics both of theoretical and applied value (Sharma *et al.*, 1971). This collection contains a wide range of phenotypes resembling various grades of the *indica* and *japonica* subspecies of *O. sativa*.

In the past, attempts have been made by several workers to classify *O. sativa* and to understand the probable factors responsible for subspecific differentiation by studying, for example, geographical distribution, sexual affinity and taxonomic and biochemical differences (Terao and Mizushima, 1939; Matsuo, 1952; Oka, 1953a; Ghosh and Bhaduri, 1966; Siddiq *et al.*, 1972; Sampath and Mohanty, 1954). It is now possible to effectively classify biological populations on the basis of genetic divergence measured by Mahalanobi's D^2-statistic and also to identify factors influencing the genetic divergence (Rao, 1952; Murty *et al.*, 1965a; Murty and Arunachalam, 1966 and Morishima and Oka, 1960).

Attempts at studying the genetic divergence through an effective quantitative approach were few and information on the efficiency of the metric characters for differentiation is not adequate for the rice crop. It was found worthwhile, therefore, to study the nature of genetic divergence in a fairly large number of collections of rice and to assess the importance of a set of quantitative characters related to yield and quality in genetic differentiation.

Material and Methods

A representative group of one hundred and ninety types of rice, collected from North-East India by the Rice Botanist, Hyderabad, under a PL-480 Scheme, was chosen for classification in addition to three typical *indicas*, IR-8, Basmati 370 and NP 130, and one tropical *japonica*, Tainan-3. The places of collection and the number of types from each of them are given in Table 1.

The crop was raised at IARI, New Delhi during June-September (the kharif season) of 1970 under a uniform fertilizer level of 60, 30 and 30 kilograms per hectare of nitrogen, phosphorus and potash, respectively. Each variety was grown in three rows with a spacing of 9″ between rows and 6″ between plants, planting a single seedling in each hole. Discarding the two peripheral rows, the middle row was used for observations to avoid border effects and outcrossing with adjacent types. The material was grown in a randomized complete block design with the standards replicated after every twenty types. Ten plants were selected at random from the middle row and their identity was maintained throughout the study.

Ten characters, namely, amylose content of the endosperm, L/B ratio of grain, panicle density (number of grains present in the primary panicle), apiculus hair length (cms), phenol reaction (1-negative, 6-highly positive), alkali spreading, one hundred grain weight (gms), leaf colour (1-pale green, 5-dark green), height and leaf area (sq. cms.) were studied. Amylose was estimated by the rapid calorimetric method described by Williams *et al.* (1970). The seven-point scale recommended by Little *et al.* (1958) was adopted to grade alkali spreading

Table 1. *Geographic distribution of 194 collections of rice chosen for classification*

Sl. No.	Place of collection	Number of types	Number of preliminary groups in which found	Number of final groups in which found
1.	North Lakhimpur (plain)	11	8	3
2.	Sibsagar (plain) (IARI 5785)	1	1	1
3.	Kamrup (plain)	11	8	3
4.	Mikir Hills and North Cachar Hills	69	24	7
5.	Garo Hills	47	20	4
6.	Khasi and Jantia Hills	34	16	5
7.	Research Station (Shillong Hills)	15	11	5
8.	Kohima Hills (IARI 6640, IARI 6642)	2	2	2
9.	North India (NP 130, Basmati 370)	2	2	2
10.	The Philippines (IRRI) IR-8	1	1	1
11.	Taiwan (Tainan-3)	1	1	1
	Total:	194		

of the kernels. Panicle density was expressed as the distance occupied by a single grain. The leaf area was computed by multiplying the product of length and maximum breadth of the boot leaf by the factor 0.69.

Analyses of variance and covariance were done on individual observations. Since computation of D^2 values for ten characters in 194 varieties would be unwieldy, preliminary grouping was carried out by canonical analysis (Rao, 1952) (See Fig. 1). Even though the two *indica* varieties, NP 130 and Basmati 370, were included in two different groups, they were treated as separate comparison. Based on the procedure described by Rao (1952) the values of D^2 between the preliminary groups were calculated. Following Tocher's method as given in Rao (1952), the final grouping was made and confirmed again by canonical analysis (Figs. 2a & 2b).

Results

The present study revealed some interesting results on (a) the nature of differentiation on the basis of genetic divergence in a large collection of rice from the Assam region, (b) the metric characters responsible for such differentiation and (c) inter-relationships in a set of quantitative characters influencing yield.

The analysis of variance based on individual plant values (Table 2) indicated that the populations under study differed significantly for all the characters. This implied that it would be worthwhile to classify the populations on the characters chosen. The inter-relationships among the characters were studied using total correlation coefficients (Table 3). It was found that amylose content was negatively correlated with 100-grain weight which showed positive significant correlation with panicle density and negative correlation with height. It was also interesting to note that leaf area was highly negatively correlated with panicle density and positively with height. The L/B ratio showed significant positive correlation with the phenol reaction. Little or no association was noted among the other characters.

The preliminary grouping of the 194 collections prior to D^2 analysis was based on principal component or canonical analysis (Fig. 1). Since the number of D^2 values for a large collection becomes quite large (in this case $1/2\,(194 \times 193) = 18721$), it would be practically impossible to classify them using the D^2 values. Hence it was thought proper to form preliminary groups using the mean values of the first two canonical vectors and then to work with these groups for final classification. Preliminary grouping will be efficient only if the first two canonical roots account for most of the total variation (say 90% or more). It was found that the first two canonical roots accounted for 95% of the total variation (Table 4), showing that the preliminary grouping based on the first two vectors would amply serve the purpose. The 194 collections could thus form 42 groups initially (Table 5). The number of the preliminary groups which included some collections from each centre is given in Table 1. It was found that the collections 5785 (from Sibsagar) and 6640 (from Kohima Hills), and the collection 6642 (from Kohima Hills) occupied distinct groups, in addition to the varieties NP 130, Basmati 370, IR-8 and

Table 2. *Analysis of variance for ten characters in 194 collections of rice*

	Degrees of freedom	Amylose content	L/B ratio	Panicle density	Hair length in μ	Phenol reaction	Alkali spreading	100-grain weight	Leaf colour grade	Height	Leaf area
		Mean sums of squares									
Varieties	193	437.583**	1.862**	0.017**	0.026**	24.736**	22.633**	1.359**	1.372**	4397.746**	936.937**
Error	1746	1.255	0.013	0.001	0.002	0.279	0.777	0.002	0.191	0.653	126.029

** Significant at 1% level.

Table 3. *Total correlation coefficient matrix for ten characters in rice*

Characters	Amylose content	L/B ratio	Panicle density	Hair length in μ	Phenol reaction	Alkali spreading	100-grain weight	Leaf colour	Height	Leaf area
1. Amylose content		0.0110	−0.0880	−0.1972[1]	−0.0245	0.0636	−0.2082[2]	−0.1378	−0.0444	−0.0074
2. L/B ratio			0.1528	−0.1207	0.3142[2]	−0.0129	−0.0530	−0.1379	−0.0206	−0.0343
3. Panicle density				0.0985	0.0848	−0.0800	0.3016[2]	−0.0712	−0.2215[1]	−0.3636[2]
4. Hair length in μ					−0.1052	0.0085	0.1544	0.0886	−0.0297	−0.0539
5. Phenol reaction						0.0661	−0.0695	−0.1157	−0.0470	−0.2235[1]
6. Alkali spreading							−0.0692	0.0312	−0.0080	0.0091
7. 100-grain weight								0.1208	−0.2114[1]	−0.1735
8. Leaf colour									0.0007	0.1942[2]
9. Height										0.3452[3]
10. Leaf area										

[1] Significant at 5% level. — [2] Significant at 1% level. — [3] Significant at 0.1% level.

Table 4. *The first two canonical vectors for the classification of 194 collections of rice*

Grouping	Canonical vector	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8	X_9	X_{10}
Preliminary	1	−0.0043	−0.0030	−0.0092	−0.0016	−0.0039	−0.0004	−0.0490	+0.0007	+0.8698	−0.4906
	2	−0.2563	−0.0514	+0.0512	+0.0237	−0.0298	−0.0150	+0.9616	−0.0102	+0.0489	−0.0073
	Canonical root 1:			Value =	238712.9	Contribution to total variation = 90.2%					
	Canonical root 2:			Value =	13848.5	Contribution to total variation = 5.2%					
Final	1	−0.0085	−0.0077	−0.0082	−0.0028	−0.0154	+0.0008	−0.0611	+0.0004	+0.8688	−0.4907
	2	−0.3712	−0.0674	+0.0563	+0.0393	−0.0239	+0.0195	+0.9209	+0.0054	+0.0611	+0.0022
	Canonical root 1:			Value =	85456.1	Contribution to total variation = 93.7%					
	Canonical root 2:			Value =	3951.5	Contribution to total variation = 4.3%					

X_1 = Amylose %; X_2 = L/B ratio; X_3 = Panicle density; X_4 = Hair length; X_5 = Phenol reaction; X_6 = Alkali spreading; X_7 = 100-grain weight; X_8 = Leaf colour; X_9 = Height; X_{10} = Leaf area.

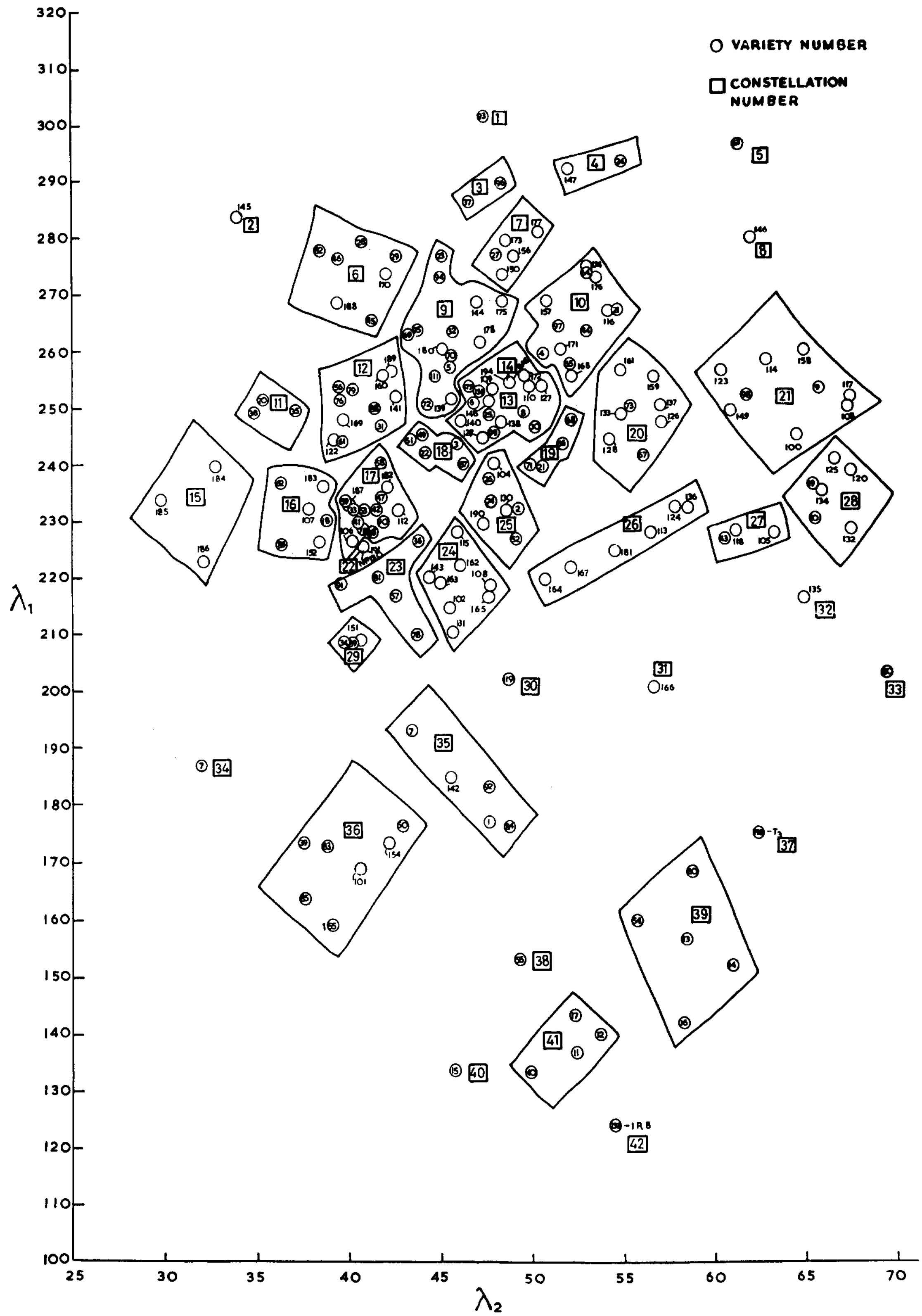

Fig. 1. Preliminary grouping of 194 rice collections using first two canonical vectors

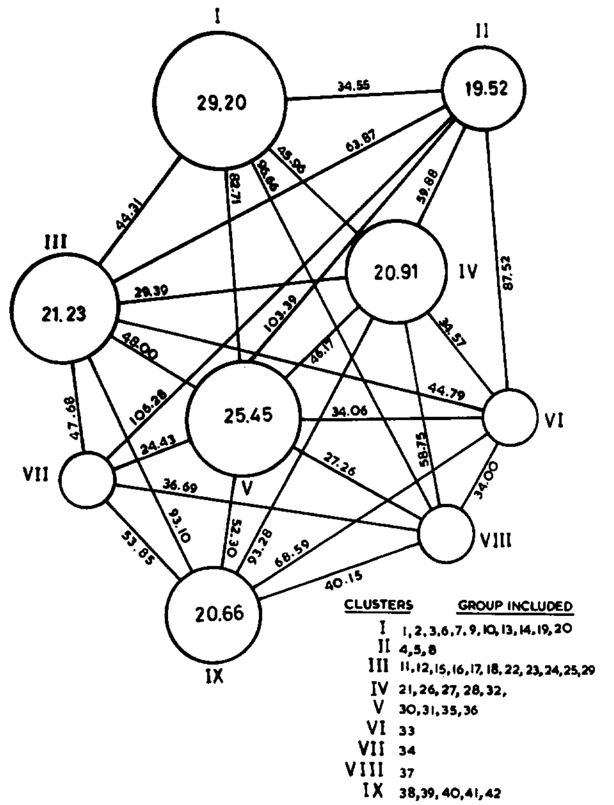

Fig. 2a. Classification of 194 collections of rice by D^2 statistic

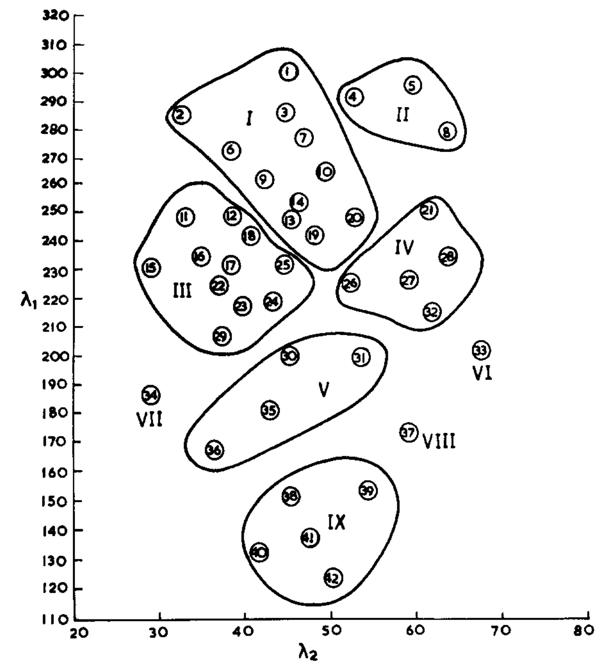

Fig. 2b. Disposition of 194 collections of rice in λ_1—λ_2 chart

Tainan 3, in the preliminary classification. On the other hand, the centres of collection, North Lakhimpur, Mikir Hills and North Cachar Hills, Garo Hills, and Khasi and Jantia Hills, were good sources of genetic variability because each of them provided a number of distinctly different groups both at the preliminary and at the final analysis. Thus it would appear that the present material will be of use in projecting our observations on the source and nature of variability in rice in the regions of Assam and North-East Himalayas.

A final grouping was obtained by computing the D^2 values for all the possible two-way combinations of these preliminary groups and by using Tocher's method of classification (cf. Rao, 1952). It was found that the 42 groups could be coalesced further into nine clusters (Fig. 2a, b). The number of preliminary groups and the number of cultigens included in each cluster, with the places of their collection, are shown in Table 5. The distribution by place of the collections in the final group (Table 1) confirmed our earlier observations on them based on preliminary grouping.

It was interesting to observe that Tainan-3, IARI-5804 and IARI-6593 formed not only unique and distinct preliminary groups (nos. 37, 34 and 33 re-

Table 5. *Final classification of 194 collections of rice by multivariate analysis*

*Cluster	Preliminary groups		+ Serial number of places of collection	Total number of collections
	Total number	Serial number of the groups		
I	11	1, 2, 3, 6, 7, 9, 10, 13, 14, 19, 20	1 to 9	70
II	3	4, 5, 8	4, 6, 7	4
III	11	11, 12, 15, 16, 17, 18, 22, 23, 24, 25, 29	1, 3, 4, 5, 6, 7, 9	66
IV	5	21, 26, 27, 28, 32	3 to 8	25
V	4	30, 31, 35, 36	4 to 6	14
VI	1	33	4	1
VII	1	34	1	1
VIII	1	37	11	1
IX	5	38, 39, 40, 41, 42	4, 7, 10	12
Total:	42			194

* See Figs. 1 and 2; + as in Table 1.

Table 6. *Intra- and inter-cluster average D^2 values in the nine clusters formed by 194 collections of rice*

Cluster No.	I	II	III	IV	V	VI	VII	VIII	IX
I	852.61 (29.20)	1193.50 (34.55)	1963.21 (44.31)	2112.20 (45.96)	6840.99 (82.71)	5253.63 (72.48)	7129.63 (84.44)	9343.26 (96.66)	16659.83 (129.07)
II		380.97 (19.52)	4079.38 (63.87)	3585.85 (59.88)	10689.79 (103.39)	7659.76 (87.52)	11295.00 (106.28)	13348.38 (115.54)	22452.66 (149.84)
III			450.73 (21.23)	864.05 (29.39)	2304.46 (48.00)	2006.11 (44.79)	2273.48 (47.68)	4017.66 (63.39)	8668.08 (93.10)
IV				437.15 (20.91)	2131.96 (46.17)	1194.97 (34.57)	3131.98 (55.96)	3451.45 (58.75)	8700.97 (93.28)
V					647.66 (25.45)	1160.33 (34.06)	597.17 (24.43)	742.90 (27.26)	2735.35 (52.30)
VI							1779.46 (42.18)	1155.88 (34.00)	4704.41 (68.59)
VII								1346.26 (36.69)	2899.51 (53.85)
VIII									1612.32 (40.15)
IX									426.96 (20.66)

Figures in parenthesis are the D-values.

Table 7. *The mean values of ten characters for nine clusters obtained by multivariate analysis in rice*

Cluster No.	Amylose content	L/B ratio	Panicle density	Hair length in μ	Phenol reaction	Alkali spreading	100-grain weight	Leaf colour	Height	Leaf area
I	27.1	2.8	0.2	0.3	2.4	5.0	1.9	3.2	155.9	43.9
II	14.4	2.8	0.2	0.3	2.8	6.3	2.2	3.2	168.9	53.0
III	26.8	2.8	0.2	0.3	2.3	5.1	1.6	3.1	134.8	43.8
IV	19.8	2.5	0.2	0.3	1.4	5.0	2.6	3.3	133.9	46.8
V	26.3	2.7	0.2	0.3	2.4	4.1	2.0	3.1	109.0	38.6
VI	4.8	3.2	0.3	0.3	1.0	5.3	2.8	3.9	118.6	37.7
VII	25.3	3.6	0.2	0.2	1.0	3.4	1.3	2.2	109.3	33.0
VIII	19.3	2.0	0.2	0.7	1.0	6.0	2.6	3.6	101.3	34.7
IX	27.6	2.8	0.2	0.3	4.6	5.4	2.4	3.3	79.9	34.2

spectively) but also final groups (cluster VIII, VII and VI respectively). Basmati 370, collection 6640 from Kohima Hills and collection 5785 from Sibsagar were included in cluster I, while the other collection 6642 from Kohima Hills was found in cluster IV and NP 130 collected from the same place as Basmati 370 was found in cluster III. This pattern of grouping was clearly brought out in the preliminary classification too. However, IR-8 occupied a distinct position both in the preliminary and in the final grouping.

The intra- and inter-cluster average D^2 and D values are presented in Table 6. It can be seen that, in general, the divergence among the collections studied was substantial, giving rise to large intra-cluster-D values. The three clusters I, III and IV were formed from collections from the same regions (Table 5), but the inter-cluster distance between I and III was almost equal to that of I and IV, indicating the availability of large genetic diversity in the material from these regions. The maximum divergence was found between cluster IX, containing IR-8 among others, and cluster II, containing IARI-5904B, 6187, 10404 and 10415 ($D = 149.8$). The minimum was found between cluster V, containing collections from hilly regions, and Tainan-3 (cluster VIII) ($D = 27.3$). The intra-cluster divergence was maximum in I ($D = 29.2$) and least in II ($D = 19.5$). It was almost of the same magnitude in clusters II, III, IV and IX.

A study of inter-cluster divergence revealed that clusters V, VI, VII and VIII were nearer to one other, and divergent from clusters IX, I, II, III and IV. Within the latter group of clusters, I and II were nearer to each other and cluster IX was highly divergent from the rest of the clusters.

The mean values from the characters studied are given in Table 7 for each cluster. The clusters V, VII, VIII and IX were composed largely of dwarfs and semi-dwarfs while the rest included talls and semi-talls. The mean leaf area was maximum in cluster II (53 sq. cms.), medium in clusters I, III and IV (44.47 sq. cms.) and low in clusters V to IX

(33.39 sq. cms.). Clusters IV, VI and VIII showed high test weight of grains and cluster VII the lowest. The amylose content of clusters I, III, V, VII and IX was near to that of typical *indica* varieties cultivated in the plains of India but it was below normal in the rest, the lowest (4.8%) being in cluster IV. Clusters I, III, IV, V and VII were medium for gelatinization temperature, as measured by alkali spreading values, while the other clusters were low for this character. In general, the cluster means (Table 7) indicated inter-cluster differences for amylose content, height and leaf area and lesser differences for alkali spreading, 100-grain weight and phenol reaction.

The component D^2's due to each character variable (the component D^2 being the square of the difference in the transformed uncorrelated mean values corresponding to that character variable) were ranked in descending order of magnitude, rank 1 being assigned to the highest value. The total of these ranks over all the possible 861 combinations (for 42 preliminary groups) would provide indirect information about the order of priority of the characters for classification. This order was found to be height, leaf area, 100-grain weight, amylose content, L/B ratio of the grain, phenol reaction, panicle density, alkali spreading, leaf colour and apiculus hair length.

The absolute magnitude of the coefficients in the first two canonical vectors would reflect to a good extent the importance of the characters for primary and secondary differentiation. It was observed that height, leaf area and 100-grain weight were important for primary differentiation and 100-grain weight, height, panicle density and amylose content for secondary differentiation (Table 4). Remarkable closeness was observed in the first two vectors and their contributions to the total variation in the preliminary and final grouping. Summing up, it was found that height, leaf area, 100-grain weight and amylose content were the important characters for classification and these observations were supported both by D^2 and principal component analysis.

Discussion

Of the two cultivated species of the genus *Oryza*, it is *O. sativa* which has been extensively studied with respect to its origin, distribution and subspecific differentiation. Nevertheless, the precise nature of differentiation of *O. sativa* is still not wholly understood. Early workers such as Kato *et al.* (1930) proposed to divide *O. sativa* into two varietal groups, 'tropical' and 'temperate', on the basis of a set of morphological characters, serological reactions and sexual affinity. On the basis of degree of crossability in these two varietal races, an intermediate group comprising varieties from Java and the adjoining islands was introduced by Terao and Mizushima (1944). The occurrence of groups within the subspecific *japonica* was shown later by Oka (1958a). Study of a partial world collection of rice by Mizushima (1948, 1950) revealed the existence of at least five different types. Oka (1958b) concluded, from a similar study, that morphological differences between the varietal groups, *japonica* and *indica*, overlapped and consequently were not of a distinct character.

In the present study using multivariate analysis, the rice collection from Assam was found to form nine distinct clusters, indicating that there are more than the known three groups in *O. sativa*. This is in good agreement with the findings of Mizushima (1948, 1950) and Jawahar Ram and Panwar (1970). Among the nine clusters, II, I and IX were highly divergent. Interestingly, the three *indica* standards, NP 130, Basmati 370 and IR-8, were included in separate clusters instead of forming a single group, showing that there was considerable divergence even among varieties belonging to the *indica* race.

A majority of the Assam types which are supposed to belong to the *indica* zone were classified, as expected, with the *indica* varieties in clusters I, III and IX, while some others formed distinct clusters divergent from the typical *indicas* and the *japonica* variety, Tainan-3. Some clusters were also found to be nearer either to clusters containing *indica* types such as NP 130 and Basmati 370 or to those containing *japonica* types. These observations lend adequate support to the existing views (Mizushima, 1948, 1950) that the extreme forms, *japonica* and *indica*, recognised by Kato are connected by a continuous series of intergrades and that there is no sharp line of demarcation between the *japonica* and *indica* groups (Hsieh and Oka, 1958).

The primary factors contributing to divergence were reported to vary from crop to crop (Murty and Tiwari, 1967; Arunachalam and Jawahar Ram, 1967; Murty and Arunachalam, 1967; and Jawahar Ram and Panwar, 1970). In general, days to 50 percent flowering, height and tiller number were considered to largely contribute to genetic divergence in grain crops. In the present study, plant height was the most important, followed by leaf area and test grain weight. As observed earlier, these two characters were found to be the major factors for primary differentiation, while 100-grain weight and amylose content were the most important for secondary differentiation. However, Jawahar Ram and Panwar (1970) reported that days to maturity was important in primary differentiation, and plant height followed by number of tillers was important in secondary differentiation. The character, days to maturity, could not be included in the present study as the experimental material consisted of types which would mature within 150 days because the crop season in Northern India, where the experiment was laid out, is short.

Genetic barrier, through chromosomal or genic differences, is one of the mechanisms of isolation contributing to subspecific differentiation in *O. sativa* (Sampath, 1966; and Siddiq and Swaminathan, 1968). Geographical isolation was reported to contribute equally to divergence in cultivated rice (Richharia and Misro, 1961; Oka, 1953 a, b, c, 1954a, b, c, d). Jawahar Ram and Panwar (1970) indicated that geographic distance was related to genetic diversity from a study of a small number of varieties from different geographic zones. The material for the present investigation was from North-Eastern India which, though small, represents an array of diverse eco-geographic regions with different altitudes and other environmental conditions. The study revealed that collections from both the hills and plains grouped together in different clusters. It appears, therefore, that differences due to varied altitudes would not have created the divergence in the rice varieties of this area. Further geographical diversity need not be related to genetic diversity (Murty *et al.*, 1965a; Timothy, 1963; and Murty and Arunachalam, 1967). It is possible that, at different times in the past, people of Assam belonging to different ethnic groups might have spread the material from a common source and, later, difficulties of terrain and inter-tribal rivalries might have acted as effective isolating mechanisms resulting in the preservation of diverse varieties.

This study has demonstrated the usefulness of forming preliminary groups from a large material by principal component analysis, and arriving at a final classification of these preliminary groups using the D^2-statistic. This would, of course, be possible only if the first two canonical roots account for most of the variation so that the two-dimensional scatter of varieties can be used to delineate preliminary groups. The final grouping provided more information than could be had from the preliminary grouping. The relative importance of the characters in differentiation remained essentially the same in the preliminary and final grouping, as revealed by the first two canonical vectors (Table 4).

It may be observed that natural selection could have operated on the characters, height and leaf area, found to be important for primary differentiation. For example, tall plants with stronger culms, found very frequently in the regions studied, might have been the product of natural selection so that they could stand adverse conditions such as floods. Leaf area was found to be highly correlated with height and hence would be expected to show a correlated response to selection.

On the other hand, 100-grain weight and amylose content, which were found to be important for secondary differentiation, would appear to have undergone artificial selection since the former is an important yield component while the latter, related to cooking quality, is a factor of consumers' preference. It is possible that conscious selection for higher grain weight resulted in unconscious selection of lax panicles with large grains, as indicated by the significant negative correlation of 100-grain weight with panicle density. Juliano (1971) concluded from an extensive study of a world collection of rice that the amylose content varied widely in different geographic regions. This was to be expected since the people of each region would prefer a particular quality of rice answering to their demands for cooking properties. For instance, people from India prefer a high amylose content which helps to make dry and flaky rice on cooking.

The results of this study indicate that North-Eastern India is a good repository of divergent varieties of rice which might profitably be used in future breeding programmes to augment the present-day yield and quality of rice in this country.

Acknowledgement

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Literature

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