

CHLOROPHYLL DEFICIENCIES IN RICE (*ORYZA SATIVA*).

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1. Introduction.

DURING the last thirty years numerous cases of chlorophyll deficiencies have been examined genetically and their inheritance recorded. A classified account of these is set out by De Haan (1933) in his monograph on the subject. He has actually described the chlorophyll characters individually and adopted definite nomenclatures as *viescens*, *xantha*, *chlorina*, etc., to specify particular types and the same have been followed in this paper.

Most of these characters are inherited in a Mendelian fashion and are found to be recessives to the normal green, barring a single instance of a dominant albino in maize (Kempton, 1924). Non-Mendelian inheritance involving the plasm with the plastids has also been recognised in several instances. The inheritance where the pollen also transmits the plastids with the plasm into the egg, has been recorded. Variegated plants conforming to this type of inheritance usually give green and chlorotic (white or yellow) progeny and only very rarely variegated progeny only. To the latter category belongs the variegated *Humulus* which transmits the variegation only through the mother and gives entirely variegated progeny without green or white plants. Recently Robb (1933) has recorded maternally inherited variegated oat plants giving only striped progeny with occasional green plants.

Among cereals, chlorophyll defective types have been recorded in maize, barley, rye, oats, sorghum, *ragi* (*E. corocana*) and wheat. The investigation of this character has progressed furthest in maize for which as many as 73 genes have been identified as controlling the formation and development of chlorophyll. The least worked crop with regard to this character is wheat which is considered to be comparatively more stable.

The chlorophyll deficient types occur as mutants, the mutating rate varying with different crops and seasons. Influence of external agencies

like X-rays and hybridity are known to enhance their frequency. Thus Stubbe (quoted by De Haan, 1933) found the mutation frequency for this character raised by 400% in *Antirrhinum majus* by exposure to X-rays. In rice, a similar experience has been encountered in the X-rayed progenies of certain pure lines (unpublished records of Paddy Breeding Station, Coimbatore). Hybrid generations have been noted to give a greater percentage of chlorophyll defective seedlings than pure lines.

The presence of chlorophyll defective characters is unfavourable from the economic point of view, as apart from the lethal or semi-lethal effect of the character in the homozygous condition, it has been shown that plants heterozygous for such characters may be less vigorous than the homozygous green plants. Mangelsdorf (quoted by Codd, 1934) who studied the effects of two lethal recessive seed factors on the height of maize found normal green plants to be the tallest, those heterozygous for one factor slightly shorter and those heterozygous for both the factors the shortest. Data regarding heterozygosity and yield in rice with respect to the various chlorophyll characters reported in this paper are being collected. In naturally cross-fertilised plants, like maize, these recessives are preserved in the heterozygous condition and are accumulated every time a new mutation occurs but are readily brought to light when the stock is selfed. In self-fertilised species, like rice, the danger is very much less as the genes responsible get eliminated by continuous in-breeding so that the few mutations that repeatedly occur in pure lines must be due to frequent mutation.

2. Previous Work.

Rice being a self-fertilised crop may not throw out as many mutants as a cross-fertilised crop like maize when selfed. But still a survey of the seed-beds of different varieties of rice, consisting of pure lines and hybrid progenies, for several years at the Paddy Breeding Station, Coimbatore, has shown that rice cannot be regarded as a stable crop for chlorophyll character, like wheat. Nevertheless, the reported cases of chlorophyll deficiencies in rice must be considered rather few. Literature on the Mendelian inheritance is confined to the albino, xantha, virescent, a few chlorina and one or two variegated plants. Morinaga, S. (1927) was the first to report about the albino and yellow seedlings both of which he found were controlled by duplicate factors. Ramiah (1931) also found that two recessive genes were responsible for the production of albinos. He also isolated for the first time a virescent yellow type of rice which gave both 3:1 and 15:1 ratios of normal green to virescent seedlings. Morinaga, T. (1932) recorded white seedlings to behave as simple recessives to green. He has also recorded the simple inheritance of yellow seedlings (xantha) which perish within two

or three weeks after germination. A few simple recessive forms distinguished by a greenish yellow colour of the leaf in both seedling and mature stages, designated as chlorina have also been reported by the same author. Kadam and Patankar (1934) working on Zinya rice have confirmed the observations of Morinaga and Ramiah regarding the inheritance of albinos. They have also recorded the presence of lethal yellows giving 3 : 1 and 15 : 1 ratios of green to yellows in certain segregating families. These yellows perish earlier like the albinos and are apparently different genetically from those reported by Morinaga, T. Recently Kadam (1935) has recorded the occurrence of a virescent white mutation where the first leaves always start without chlorophyll but later become green, the pigment developing from the tip downwards. Codd (1934) has described an albino involving three factors which in the homozygous recessive condition produced white seedlings. Among Mendelian variegated chlorophyll deficiencies two cases have been reported. Mitra and Ganguli (1934) reported the inheritance of white striped and albino plants. They found the white striped plants segregating into 3 striped and 1 albino, while in crosses with normal green they obtained a 3 : 1 ratio of green to striped plants. The white striped character in this case is described as persisting up to maturity, the mature seeds also showing a lighter colour than those of normal plants. Morinaga, T. has also recorded the simple inheritance of a few variegated forms.

As regards non-Mendelian inheritance of chlorophyll deficiencies in rice not many cases have been reported. Imai (1928) has recorded two types of green and white variegations. When self-fertilised one type gave almost exclusively green and albino progeny, conforming to the ordinary non-Mendelian inheritance. The other type belonged to a special class and gave on self-fertilisation 30.7% variegateds, 64.5% albino and 4.8% green progeny. This condition where the variegateds reappear in great numbers in the progeny has been explained to be due to the unstable plastids, which may be phenotypically green, mutating to white or green, quite out of control of genetic factors. An ordinary non-Mendelian green and yellow variegation yielding green and yellow seedling progeny has also been reported by Imai. Recently Morinaga, T. has also recorded the maternal inheritance of a green and white variegation.

3. *Materials for the Study.*

At the Paddy Breeding Station, Coimbatore, where a large number of pure lines and hybrid progenies of rice are being grown every year the authors have had ample opportunities to come across a number of these chlorophyll mutants which either occurred spontaneously in pure lines or appeared in the progenies of heterozygous individuals. The different kinds of mutants,

including both Mendelian and non-Mendelian types were isolated and their inheritance studied by making suitable crosses between these and other types of known genetic constitution. To avoid confusion the Mendelian and non-Mendelian inheritance of the chlorophyll characters are treated separately. The material used, description of the character and its inheritance are dealt with separately under each head. A few general observations regarding the occurrence of chlorophyll deficiencies are recorded at the end.

4. Mendelian Inheritance.

(a) *Albinos (rw)*.—The study of albinos in rice was started at the Paddy Breeding Station, Coimbatore, as far back as 1916–17 and the presence of duplicate factors for this character was recorded by the senior author (1931). Besides definite 3 : 1 and 15 : 1 ratios of green to white, more complicated ratios were also obtained which do not conform to Mendelian inheritance. For instance one family was found to give 457 greens and 262 whites suggesting the presence of a two factor (9 : 7) or a three factor (43 : 21) inheritance. But when all the green plants were carried forward to the F_3 generation the segregation of whites in the various families did not conform to any of the two expectations. While 72 families bred true to green, the rest of the families segregated for green and white giving different ratios of green to white. There were only about 10 families which approached to 3 : 1 ratio, others giving very much more of whites. The behaviour of another segregating family was still more anomalous considered from the point of Mendelian inheritance. It gave in the F_2 , 1233 greens and 99 whites suggesting a 15 : 1 ratio of green to white. But when the F_3 generation was raised from all the F_2 plants, the results did not support a two factor inheritance. 976 families bred true to green and 200 alone segregated for green and white giving all sorts of ratios. The presence of such a large number of pure breeding greens is incompatible with a dihybrid segregation. Karper (1934) found similar fluctuations in the percentage of white seedlings in sorghum, which did not conform to Mendelian ratios. He also found that these white seedlings did not come out in patches in the heads as would be expected if they were of the ordinary non-Mendelian character but were distributed at random. He believed, therefore, that the white seedlings probably had some connection with the cytoplasmic disturbance caused by Mendelian factors. It may be that a similar cause operates in rice bringing about unconformable ratios. This point will be pursued further.

(b) *Virescent Seedlings (vv)*.—Virescent seedlings were first isolated by the senior author (1931) in the year 1922 in the progenies of an artificial cross of *white sirumani*. By study of artificial and natural crosses of this type with normal green, he found that duplicate factors controlled the

inheritance of this character. This character was originally described as yellow and represented by the symbol *c*. Hereafter this character will be described as virescent yellow and indicated by the symbol *v*, in conformity with the nomenclatures proposed by De Haan.

(c) *Chlorina varieties*.—Chlorina forms are found to occur commonly in rice and these show variation in the depth of chlorophyll pigment they contain. Plants with all gradations from dark to light green and yellowish green colour of foliage have been isolated. The inheritance studies of these forms are under way.

Several strains with yellowish green leaf were isolated from a variety known as *krishnakatukkulu*, at Maruteru (*Madras Agricultural Station Reports*, 1925–26 and 1928–29) and these were compared with typical green forms in regard to flowering duration, yield and other characters. It was found that the yellow forms flowered earlier and yielded better than the normal greens. The following table brings out the relation existing between the colour of foliage and flowering :—

Colour of foliage	October										Total
	Dates of flowering										
	21	22	23	24	25	26	27	28	29		
Yellowish green	1	9	11	12	11	4	48
Green	9	9	7	3	3	31
Dark green	7	4	2	1	1	..	15
Total ..	1	9	11	21	27	15	5	4	1	..	94

Morinaga, T., however, found his chlorina forms to be of slower growth and of less productivity than the normal greens. Those are probably genetically different from the chlorina forms of *krishnakatukkulu*.

(d) *Green and White striped seedlings (gw gw)* (Plate XXX, Fig. 1).—This is a seedling character found occurring for the first time in the seed-bed of one of the artificial cross-progenies of *sirumani*, a Tanjore variety of rice. The first leaf of this plant starts practically white with a tinge of green colour at the tip which later extends downwards along the region of the midrib presenting a striped appearance of green and white. The second and occasionally the third and fourth leaves also start similarly but with more green areas which gradually widen out till the leaves become green. Later formed leaves are practically green so that the seedling after 15 to 20 days' growth

in the nursery appears normal green. The mutant plant, although of slightly slower growth than the greens in the earlier stages, later pulled up and came to maturity at the same time as the normal greens. The seeds of this plant when sown in the following season yielded a progeny resembling the parent seedling. This true breeding type has since then been included in our pure line cultures at Coimbatore. Although there is slight variation in the distribution and development of chlorophyll in the different seedlings the essentially striped nature is conspicuously seen at the earlier stages in all young plants.

In the seed-beds of this type, during the season of 1931-32 a few green seedlings were noticed which were more vigorous than the rest, presumably resulting from cross-pollination with a green type. One of these was isolated and grown as an F_2 generation in the following season. Besides the natural crosses, artificial crosses were also made between a normal green and this green and white striped type during 1932-33 and the F_1 plants which were all green were also grown as F_2 in the season of 1934-35 for study of the inheritance of this character. The segregation of green and striped seedlings in the F_2 families is set down below:—

Segregation of "Green and White striped" plants in F_2 families.

Family Number	Green (Gw)	Green and white striped (gw)
3708 (Natural cross)	518	158
4560 (Artificial cross)	1747	623
Total for two families	2265	781
<i>Calculated 3 : 1</i>	2285	761
		Dev. S. E. = 0.84

The foregoing results are in close agreement with the expected Mendelian ratio where a single gene is involved so that the green and white striped character may be regarded as a simple recessive to normal green.

(e) *Green and Yellow striped seedlings (gy gy)* (Plate XXX, Fig. 2).—This type was first noted to occur during 1934-35 in the seed-bed of one of the single plant progenies of a short duration variety known as *vellai kar*. The seedlings which showed this character are similar to the green and white striped seedlings described before but the green stripes in this case develop over an yellow instead of a white background as in the other case. The leaves turn green sooner so that after about 8 to 10 days from germination the type becomes indistinguishable from normal green. These seedlings

were noted in the nursery at a rather late stage and hence it was not possible to take counts of the striped and green seedlings in that population. However, seeds from 20 plants of this segregating family were sown separately for study of the behaviour of this character in inheritance. The results were rather peculiar in that only one out of twenty families bred true to the chlorophyll deficient type, 18 were pure greens and only one family segregated for the two types. Counts of green and striped plants are noted below:—

Family Number	Green	Green and yellow striped
5555/10	320	150
Calculated 2 : 1	313	157 $\frac{\text{Dev.}}{\text{S. E.}} = 0.7$

The counts indicate more a 2 : 1 ratio of green to the chlorophyll deficient character than anything else. Here it may be mentioned that out of 478 seeds sown in this family 470 or 98.3% of them germinated thus precluding the possibility of defective germination or seed lethality interfering with ratios. There was also no apparent spikelet sterility noticed in the parent. No satisfactory explanation can at present be given about this peculiar inheritance, but definite crosses have been made with this type which may throw light on this question.

(f) *Yellow and White striped seedlings (vv gw gw WW)* (Plate XXX, Fig. 3).—This character also is confined to the seedling which starts with its first and second leaves and sometimes one or two later leaves also marked by yellow stripes on a white background which gradually turns into yellow and later the whole seedling becomes indistinguishable from greens. The plants are weak and slow growing in the early stages but after they turn green, which is about a fortnight from germination, they become fairly normal. A few of the seedlings under adverse conditions perish at the earlier stages. This type was first separated out as a double recessive in an artificial cross between a green and white striped plant and a virescent yellow isolated by Ramiah (1931). The details of segregation and the proportion in which this type occurred in F_2 are given later in the paper (Tables VII and VIII).

(g) *Lutescent seedlings (ll)* (Plate XXX, Fig. 4).—This is an entirely new character in rice being defined as the opposite of virescent yellow. Lutescent seedlings are normal green first but afterwards the chlorophyll gradually disappears and the plants ultimately die off. This character has been recorded in comparatively few families of flowering plants.

In one of the pure line cultures, P. 67, this character was found segregating in the season of 1934-35. One week after germination when the seedlings had put on two leaves, they looked green but two days later a few among them were noticed to lag behind in point of growth and turn pale. This condition continued until about a month when the affected seedlings became absolutely pale and withered. Counts of segregating types in the family showed the abnormal plants to be nearly one-fourth of the population thereby showing the simple recessive nature of the lutescent type to the normal green.

Family Number	Green	Lutescent
P. 67	148	44
<i>Calculated 3:1</i>	<i>144</i>	48 $\frac{\text{Dev.}}{\text{S. E.}} = 0.67$

Twenty green plants in this F₂ family were carried forward to the F₃ generation to confirm the inheritance of this character. It was found that 6 out of 20 families bred true to greens and 14 segregated for both types as should be expected if a single factor difference conditioned the expression of this abnormal character. The ratios of green to lutescent plants in the segregating families given below also amply confirm the simple inheritance of this character:—

Family Number	Green	Lutescent
P. 67 (Total of 14 families)	2086	674
<i>Calculated 3:1</i>	<i>2070</i>	690 $\frac{\text{Dev.}}{\text{S. E.}} = 0.70$

(h) *Lethal Yellows (yy) (Xantha)* (Plate XXX, Fig. 5).—In two of the several families grown during 1934-35 for the study of dwarfism in rice, these yellows appeared along with normal greens. The leaves of these plants are of a faint yellow colour and do not develop chlorophyll and therefore the plants perish after about 8 to 10 days' growth in the nursery. These are evidently genetically different from yellow seedlings recorded by Morinaga which are reported to live up to 2 to 3 weeks after germination. They probably contain slightly more chlorophyll. Counts of seedlings in the two segregating families, given below, indicate that this chlorophyll deficient factor is a simple recessive to green.

Family Number					Greens	Lethal yellows
424	373	122
466	298	112
Total of 2 families					671	234
<i>Expected 3:1</i>					679	226 $\frac{\text{Dev.}}{\text{S. E.}} = 0.63$

(i) *Zebra marked seedlings* (Plate XXX, Fig. 6).—The markings on this type of chlorophyll deficiency resemble closely those described in the seedling Zebra of maize (Stroman, 1924). The leaves show horizontal bands of white and green, the bands in some places being irregular. The bands which are more marked in the seedling stage, persist for about a month after transplanting and later disappear, the plant then becoming normal green. This type was found occurring for the first time in seed-beds of one of the Chingleput varieties of rice sown in 1934-35 for purposes of pure line selection. A few of these seedlings were isolated and grown to maturity. All the plants have been found to be true breeding. Artificial crosses between this type and the normal green have been made for ascertaining the inheritance of this character. This is the first record of the occurrence of this character in rice although in maize where the inheritance of this character has been worked out, both mono and digenic segregations with normal greens have been recorded.

5. *Inter-Crosses between Mendelian Types.*

With a view to study the inter-relations of the different chlorophyll deficient types, crosses between the various types described above were undertaken. The albino, virescent yellow and the green-white striped seedlings being the more commonly occurring types, they were chosen for a beginning of this study and inter-crosses between them were made and studied up to the F_3 generation. The crosses were made reciprocally in each case and it was found that reciprocal crosses behaved identically in all cases. Although the three types behaved as simple Mendelian recessives to green independently, crosses between any two among them gave green F_1 plants segregating into greens and the parental forms in the ratio of 9:3:4 in the F_2 generation showing the interaction of two factors. The following table gives a summary of the crosses made and their behaviour:—

Parents of crosses	Albino (heterozygous)	Green and white striped
Green and white striped	F ₁ green F ₂ ratio 9 : 3 : 4	
Virescent	F ₁ green F ₂ 9 : 3 : 4	F ₁ green F ₂ 9 : 3 : 4

N.B.—For details of F₂ figures see Tables I, IV and VII.

In the case of the albino which is lethal in the homozygous condition it was necessary to use green plants heterozygous for this character as parents in crosses.

On the strength of the evidence presented in the foregoing table the different types may be factorially represented as under :

WW VV Gw Gw .. Green
 ww VV Gw Gw .. Albino
 WW vv Gw Gw .. Virescent yellow
 WW VV gw gw .. Green and white striped.

The behaviour of the different crosses is treated separately.

(a) *Albino (Heterozygote Ww VV Gw Gw) × Virescent Yellow (WW vv Gw Gw)*.—A number of crosses were made between the above types during the year 1932–33 and an F₁ generation raised in 1933–34. All the F₁ plants were green and they segregated into green, virescent yellow and albinos in the F₂ generation (Table I).

TABLE I.

Family Number	Green	Virescent yellow	Albino
4519	1284	447	594
4539	1204	410	552
Total of 2 families	2488	857	1146
<i>Calculated 9 : 3 : 4</i>	2526	842	1123

P = between 0.50 and 0.60

The figures in the above table provide a close fit to a 9 : 3 : 4 ratio showing the interaction of two factors.

A number of plants in each of the green and virescent yellows of the F₂ generation was carried forward and the F₃ progenies were studied. The results are arranged in Tables II and III.

TABLE II.

F_3 progenies from green and virescent yellow F_2 plants of Table I, showing their theoretical and actual proportions.

F_2 Phenotype	F_2 Genotype	F_3 Segregation	Found	Expected	Deviation
Green ..	1. WW VV Gw Gw	All green	12	8	+ 4
.. ..	2. Ww VV Gw Gw	3 green 1 albino	14	17	- 3
.. ..	2. WW Vv Gw Gw	3 green 1 virescent	15	17	- 2
.. ..	4. Ww Vv Gw Gw	9 green 3 virescent 4 albino	35	34	+ 1
$P = \text{between } 0.5 \text{ and } 0.3.$					
Virescent yellow ..	1. WW vv Gw Gw	Virescent	7	9	- 2
	2. Ww vv Gw Gw	3 virescent 1 albino	19	17	+ 2
$P = \text{between } 0.5 \text{ and } 0.3.$					

TABLE III.

Segregation in F_3 progenies of the cross Albino (Heterozygote) \times Virescent Yellow.

F_2 Genotype	Green	Virescent yellow	Albino	
Ww Vv Gw Gw				
Total for 35 families	4,449	1,444	1,955	$P = \text{between } 0.7 \text{ and } 0.5.$
Calculated 9 : 3 : 4	4,413	1,471	1,961	
Ww VV Gw Gw				
Total for 14 families	2,030	..	681	$\frac{\text{Dev.}}{\text{S. E.}} = 0.13$
Calculated 3 : 1	2,033	..	678	
WW Vv Gw Gw				
Total for 15 families	2,268	813	..	$\frac{\text{Dev.}}{\text{S. E.}} = 0.18$
Calculated 3 : 1	2,311	770	..	
Ww vv Gw Gw				
Total for 19 families	2,678	954	$\frac{\text{Dev.}}{\text{S. E.}} = 0.17$
Calculated 3 : 1	2,724	908	

The behaviour of the F_3 progenies amply confirms the F_2 behaviour.

(b) *Albino (Heterozygote Ww VV Gw Gw) × green and white striped (WW VV gw gw).*—This cross was also made in 1932–33 and the F_1 plants resulting therefrom were all green. F_2 populations raised from these plants in 1934–35 showed segregation of green, green and white striped and albinos in the ratio of 9:3:4. The counts of segregation in the F_2 families are noted in Table IV.

TABLE IV.

Segregation in F_2 families of crosses between Heterozygous green (Ww VV Gw Gw) × Green and white striped (WW VV gw gw).

Family Number	Green	Green and white striped	Albino
4559	1279	425	610
4561	1518	564	690
Total of 2 families ..	2797	989	1300
Calculated 9:3:4	2860	954	1272

$P = \text{between } 0.2 \text{ and } 0.1$

The F_3 behaviour of a few green and green and white striped plants carried forward from the F_2 population is in close agreement with a two factor inheritance. The details of F_3 behaviour of these plants are set down in Tables V and VI.

TABLE V.

F_3 progenies from F_2 plants of Table IV showing their theoretical and actual proportions.

F_2 Phenotype	F_2 Genotype	F_3 Segregation	Found	Expected	Deviation
Green	1. WW VV Gw Gw	All green	7	6	+1
„	2. WW VV Gw gw	3 green 1 striped	11	12.5	-1.5
„	2. Ww VV Gw Gw	3 green 1 albino	13	12.5	+0.5
„	4. Ww VV Gw gw	9 green 3 striped 4 albino	25	25	0
				$P = 0.95$	
Green and white striped.	1. WW VV gw gw	All striped	4	4	0
	2. Ww VV gw gw	3 striped 1 albino	8	8	0

TABLE VI.

Segregation in the F_3 families of the cross Albino (Heterozygote $Ww VV Gw Gw$) \times Green and white striped ($WW VV gw gw$).

F_2 Genotype	Green	Green and white striped	Albino	
$Ww VV Gw gw$				
Total of 20 families	1,562	513	684	$P = \text{between } 0.95 \text{ \& } 0.90$
Calculated 9 : 3 : 4	1,552	518	689	
$WW VV Gw gw$				
Total of 7 families	786	245	..	$\frac{\text{Dev.}}{\text{S. E.}} = 0.94$
Calculated 3 : 1	773	258	..	
$Ww VV Gw Gw$				
Total of 7 families	806	..	284	$\frac{\text{Dev.}}{\text{S. E.}} = 0.8$
Calculated 3 : 1	817	..	273	
$Ww VV gw gw$				
Total of 4 families	287	94	$\frac{\text{Dev.}}{\text{S. E.}} = 0.12$
Calculated 3 : 1	286	95	

N.B.—Counts for all the families are not given as many of the seed-beds were badly damaged by depredations of field rats.

(c) *Virescent yellow* ($WW vv Gw Gw$) \times *Green and white striped* ($WW VV gw gw$) seedlings.—*Virescent yellow* ($WW vv Gw Gw$) when crossed

TABLE VII.

Segregation in F_2 families of the cross between *virescent yellow* ($WW vv Gw Gw$) \times *Green and white striped plants* ($WW VV gw gw$).

Family Number	Green	Virescent yellow	Green and white striped and yellow and white striped
4552	570	187	220
4554	937	312	404
4555	1332	449	575
Total of 3 families	2839	948	1199
Calculated 9 : 3 : 4	2806	935	1246
	$P = \text{between } 0.2 \text{ and } 0.3$		

on to green and white striped plants (WW VV gw gw) yielded green F₁s which in the F₂ generation segregated into green, virescent yellow and green and white striped plants in the ratio of 9 : 3 : 4. In this cross it was possible to distinguish the double recessive type which, in the beginning, is characterised by yellow and white stripes on leaves soon changing to green. (This type has been described already earlier in the paper.) For purposes of counts in the F₂, this was included in the green and white striped class as after some time the two types overlap and become indistinguishable causing

TABLE VIII.

F₃ progenies from F₂ plants of Table VII showing their theoretical and actual proportions.

F ₂ Phenotype	F ₂ Genotype	F ₃ Segregation	Found	Expected	Deviation
Green	1. WW VV Gw Gw	All green	12	11	+1
"	2. Ww VV Gw Gw	3 green 1 green and white striped	22	22	0
"	2. WW Vv Gw Gw	3 green 1 virescent yellow	18	22	-4
"	4. WW Vv Gw gw	9 green 3 green and white striped 1 yellow and white striped 3 virescent yellow	47	44	+3
<i>P = between 0.9 and 0.8</i>					
Green and white striped.	1. WW VV gw gw	All green and white striped	23	22.5	+0.5
	1. WW vv gw gw	All yellow and white striped			
"	2. WW Vv gw gw	3 green and white striped 1 yellow and white striped	22	22.5	-0.5
<i>P = between 0.9 and 0.8</i>					
Virescent yellow ..	1. WW vv Gw Gw	All virescent	15	15.3	-0.3
"	2. WW vv Gw gw	3 virescent 1 yellow and white striped	31	30.7	+0.3
<i>P = between 0.8 and 0.1</i>					

a little difficulty in classification. However, in early stages, a few days after germination, this type is very easily identified. Table VII gives the results of F₂ behaviour of three families.

It is seen from the table that the striped plants are slightly in defect of the expected proportion. This is because the double recessive plants are of delayed germination and some of the seedlings, which are very weak at the early stages owing to lack of chlorophyll, perish. A few from each of the genotypes of the F₂ were carried forward and the behaviour of the different F₃ progenies is arranged in Tables VIII and IX.

TABLE IX.

*Segregation in the F₃ families of the cross between virescent yellow
× Green and white striped plants.*

F ₂ Genotype	Green	Green and white striped	Virescent yellow	Yellow and white striped
WW Vv Gw gw				
Total of 22 families	2257	963 (including yellow and white striped plants)	754	
Calculated 9:4:3	2236	993	745	
			<i>P = between 0.5 and 0.3</i>	
WW VV Gw gw				
Total of 18 families	2946	934		$\frac{\text{Dev.}}{\text{S. E.}} = 1.3$
Calculated 3:1	2910	970		
WW Vv Gw Gw				
Total of 18 families	3423	..	1124	$\frac{\text{Dev.}}{\text{S. E.}} = 0.45$
Calculated 3:1	3410	..	1137	
WW Vv gw gw				
Total of 22 families	2986	..	$\frac{1025 \text{ Dev.}}{1003 \text{ S. E.}} = 0.8$
Calculated 3:1	3008	..	
WW vv Gw gw				
Total of 31 families	5355	$\frac{1702 \text{ Dev.}}{1764 \text{ S. E.}} = 1.7$
Calculated 3:1	5293	

It is seen from a study of the foregoing three sets of crosses that three pairs of factors (Ww, Vv, Gw gw) are concerned in the development of chlorophyll

in rice. The inter-crosses have also established that the three factor pairs undergo ordinary Mendelian segregation and recombination and are inherited independently of each other without any linkage.

6. *Non-Mendelian Inheritance.*

Variiegated plants have been found to occur in rice fields at the Paddy Breeding Station, Coimbatore, every year in the different cultures. They are of three kinds, *viz.*, (1) green and white variegation where the leaves, culms and even panicles are marked green and white; (2) green and yellow variegation, the latter being present when the plant is young and later fading into white as the plant matures; and (3) green and yellow variegation where the yellow areas do not change colour with time. All these plants exhibit a large variation in point of intensity of chlorophyll deficient areas so that there may be plants with a preponderance of green or chlorophyll deficient areas or with an even distribution of the two. There is again variation in the parts affected. Chlorophyll deficient areas are found most commonly on leaves and culms but are also found to extend to the panicles and the individual florets. Sometimes variegation is confined only to the leaves, or to the culms or even, as it very occasionally happens, to panicles and spikelets only. Variiegated plants often bear apparently pure green tillers or *vice versa*. Occasionally entirely chlorotic tillers arise due to bud mutation in leaf axils of green or variegated tillers (Plate XXXI, 2). A comprehensive study of variegation was started in 1931-32 and for this purpose several variegated individuals occurring spontaneously in the various cultures were isolated. When variegated plants were selfed they gave perplexing ratios of green and chlorotic plants which did not conform to Mendelian inheritance. To see if the abnormalities were distributed at random on the several ears of the plant, the individual tillers were marked as green and variegated and the seeds from individual tillers were sown separately. In some plants even the sub-branches of individual panicles were separated and sown. In some cases the individual florets also were marked as variegated or green by means of charts and they were collected separately and sown for study of their progeny. Crosses were made between variegated and green plants reciprocally and their progeny studied to obtain a knowledge of the inheritance of variegation. The results obtained in the three types of variegation are set down separately.

(a) *Green and White Variegation.*—Seven plants of this type were isolated in the course of last three years and they were all selfed and the seeds from each tiller were sown and studied separately. Table X gives a summary of the description of the plants and the nature of their selfed progeny.

TABLE X.

Progeny from Green and White Variegated Plants.

Year of isolation of plant	Variety or progeny from which isolated	Appearance of the plant (tillerwar)	Selfed progeny		
			Green	Variegated	Albinos
1932—33..	Co. 2	Variegated and green tillers (variegated tillers showed striping on leaves, culms and sometimes on panicles)	Green
.. ..	Co. 3	Do.	Green
1933—34..	GEB. 24	(i) Variegation on leaves and spikelets	Green
		(ii) Variegation on rachii and spikelets	Green	..	3
		(iii) Thin white streaks on edges of leaves	Green
.. ..	967	(i) Apparently green tillers	Green	Variegated	Albinos
		(ii) Variegated tillers	Green	..	Albinos
1934—35..	578	(i) White stripes on leaves	Green
		(ii) White stripes on leaves and spikelets	Green
		(iii) Broad stripes of white and green	Green
.. ..	1048	The leaves of the entire plants were green but all the panicles and spikelets showed variegation	Green
..	5518 (<i>Gobi kar</i>)	(i) Green—Sub-branches of panicles sown separately			
		(a)	15
		(b)	18
		(c)	23
		(d)	20
		(e)	21
		(f)	17
		(g)	11
		(h)	20
		(i)	14
		(ii) Green—Sub-branches			
		(a)	21
		(b)	20
		(c)	22
		(d)	23
		(e)	20
		(f)	26
		(g)	17
		(h)	14
		(i)	16
		(iii) Green	Green
		(iv) Variegation on spikelets			
		(a)	47
		(b) No variegation on spikelets	58

TABLE X—(contd.)

Year of isolation of plant	Variety or progeny from which isolated	Appearance of the plant (tillerwar)	Selfed progeny			
			Green	Variegated	Albinos	
1934—35..	5518 (<i>Gobi kar</i>)	(v) Variegated—Sub-branches	(a)	19
			(b)	21
			(c)	3	..	13
			(d)	12
			(e)	17
			(f)	16
			(g)	18
			(h)	17
		(vi) Variegated—variegation on spikelets No variegation on spikelets	(a)	39	2	22
			(b)	54	..	6
		(vii) Variegated—Sub-branches	(a)	25
			(b)	23
			(c)	23
			(d)	17
			(e)	23
			(f)	26
			(g)	20
			(h)	10
		(viii) Variegated		20	3	16

(N.B.—In earlier years, actual counts were not recorded, but it was noted that segregation did not conform to Mendelian ratios.)

It is seen from the foregoing table that plants of Co. 2, Co. 3, 578 and 1048 although showing variegation, yielded only green progenies. GEB. 24 gave only three whites in the progeny of the whole plant which may be due to either plastid or genic mutation. The plant isolated from the family 967 on selfing gave green, albino and a few variegated progeny and the ratios of the three types did not conform to any of the Mendelian expectations. Detailed observations were made on the plants isolated from 5518 (*Gobi kar*). In this case not only the individual heads were sown separately but the sub-branches in each head of a few tillers in the variegated and green classes were also sown separately to see if there was any difference in the distribution of various types of seedlings on the panicle.

It is seen from the data in Table X that green tillers give only green progeny and that variegated tillers give mostly white or green progeny only. Occasionally a few variegateds are also present in the progeny of the variegated plants. It is also observed that the distribution of the albino and green seedlings on the different ears of the variegated plants is not at random as would be expected if Mendelian factors are concerned. They are distributed in patches, *i.e.*, certain heads give only albinos and certain

others only greens (Plate XXXII). This is in accord with the view that the character is transmitted not through the nucleus but through the plasm and the plastids. The direct correlation that is found between the appearance of the maternal tissue and the kind of seedlings which it produces, in sorghum and maize, does not apply with equal force to this kind of variegation in rice. This disparity may be explained to be due to differences in hereditary constitution between the sub-epidermal tissue from which the female gametes originate and the epidermal tissue. For example certain variegated plants like those of Co. 2, Co. 3, etc., do not yield albino or variegated progeny but give only greens on selfing, and this may be explained to be due to the sub-epidermal tissue from which the female gametes arise being normal in respect of the plasm and the plastids they contain while the epidermal tissue alone is affected.

To see if the character is transmitted through the pollen, reciprocal crosses were made between variegated and green plants. Pollen collected from flowers in a region devoid of chlorophyll was used to fertilise normal green flowers. Conversely, crosses were made with pollen from normal green flowers being used to fertilise flowers situated in the chlorophyll deficient areas of the panicle. The results are as follows:—

Parents	Number of flowers crossed	Nature of F ₁ progeny		
		Green	Variegated	Albino
5518 Variegated ♀ × green ♂	16	13	..	3
5518 Green ♀ × variegated ♂	10	10

It is seen from the above, that pollen from variegated plants has no part in transmitting the character, while the egg, if it has the abnormal plastids, transmits the character to the progeny. That all the F₁ seeds of the variegated ♀ × green ♂ did not give rise to albinos or variegated seedlings may be due to the fact that all of them were not borne on chlorophyll deficient or transitional tissue.

(b) *Green and Yellow Variegation, the Yellow Fading to White.*—These plants on selfing produce green and yellow seedlings instead of greens and albinos as in the previous case. The yellow seedlings are faintly coloured and perish like the albinos in about a week's time from germination. The behaviour of the several plants when self-fertilised is given in Table XI.

TABLE XI.

Progeny from Green and Yellow (the latter fading to White) Variegated Plants.

Year of isolation of plant	Variety of progeny from which isolated	Appearance of the plant (tillerwar)	Selfed progeny			
			Green	Variegated	Yellow	
1932-33..	T. 243	1. Green	Green	..	Yellow	
		2. "	"	
		3. Variegated	"	
		4. "	"	
		5. "	"	..	Yellow	
		6. "	Green	
		7. "	"	..	1 yellow	
		8. "	"	The tiller died out	out	
" ..	<i>Gobi kar</i>	1. Green	18	..	46	
		2. "	4	..	44	
		3. "	38	1	38	
		4. "	Yellow	
		5. "	Yellow	
		6. "	9	1	..	
		7. Variegated	53	..	44	
		8. "	52	..	66	
		9. "	Yellow	
		10. "	Yellow	
1933-34..	4597	Green tillers (a)	Green	..	Yellow	
		Variegated tillers (b)	Green	..	Yellow	
" ..	5599	Green tillers (a)	Green	..	Yellow	
		Variegated tillers (b)	Green	..	Yellow	
1934-35..	6136	(i) Apparently green—Sub-branches	(a)	11
			(b)	14
			(c)	5
			(d)	13
			(e)	11
			(f)	9
			(g)	11
			(h)	9
			(i)	18
			(j)	12
			"	(ii) Variegated—Spikelets variegated Spikelets green	(a)	40
	(b)	68		
	"	(iii) Variegated—Sub-branches	(a)	7
			(b)	6
			(c)	9
			(d)	14
			(e)	11
			(f)	11
			(g)	6
(h)			13	
(i)	11			
(j)	11			

TABLE XI—(contd.)

Year of isolation of plant	Variety of progeny from which isolated	Appearance of the plant (tillerwar)	Selfed progeny		
			Green	Variegated	Yellow
1934—35..	6135	(iv) Variegated—Spikelets variegated (a)	10
		Spikelets green (b)	120
" ..		(i) Variegated—Spikelets variegated	20	..	36
		Spikelets green	23	..	1
		(ii) Variegated—Spikelets variegated	31	..	1
		Spikelets green	25
		(iii) Variegated—(most of the spikelets also show variegation)	27
		(iv) Apparently green—(but rachii and some spikelets are variegated) Sub-branches (a)	3	..	9
		(b)	5
		(c)	12
		(d)	12
		(e)	7
		(f)	3	..	2
		(g)	6
		(h)	3
	(v) Variegated (more yellow areas than green. Rachii also green)				
	Spikelets variegated	4	
	Spikelets green	1	..	38	

The behaviour of these plants on selfing is very similar to the green and white variegated plants except that in these plants lethal yellows instead of whites as in the previous case are segregated along with greens. The correspondence between the appearance of the parental plant and the nature of the seedling progeny is not very close, as variegated tillers are found to give rise to exclusively green progeny and green tillers to exclusively yellow progeny. The point that the seeds giving the different type of seedlings are distributed on the plant in patches is clearly brought out by the different tillers giving rise to exclusively one type of seedlings.

Parents	Number of flowers crossed	Nature of F ₁ progeny		
		Green	Variegated	Yellow
6135 Variegated ♀ × green ♂ ..	22	7	..	15
6135 Green ♀ × variegated ♂ ..	17	17

To obtain a knowledge of the inheritance of this variegation in artificial crosses, reciprocal crosses were made as in the previous case and the results are set down as above. It is clear from the above table that the male genetes do not transmit the variegation to the progeny.

(c) *Green and Yellow Variegation* (Plate XXXI, Fig. 1).—This type of variegation where green and yellow areas are found on rice plants has not been noted with as much frequency as the other two types. For the first time two plants of this type were isolated during 1934–35 and grown separately. The selfed seeds of the two plants were sown and the results are given in Table XII.

TABLE XII.

Year of isolation of plant	Variety of progeny from which isolated	Appearance of the plant (tillerwar)	Selfed progeny			
			Green	Variegated	Yellow	
1934–35..	T 445	(i) Variegated (more green areas)	21	..	27	
		(ii) Leaves apparently green (peduncle and rachii variegated)	77	
		(iii) Leaves apparently green (peduncle and rachii variegated)	86	
		(iv) Variegated—Sub-branches	(a)	7
			(b)	9
			(c)	8
			(d)	17
	(e)		8	
	(v) Variegated	(f)	8	
		(g)	7	
		(h)	11	
		(i)	92	
		(j)	92	
	..	(vi) Variegated (mostly yellow)	(k)	5	..	30
			(l)	5	..	30
		(vii) Variegated—Sub-branches	(a)	13
			(b)	12
(c)			11	
(d)			10	
(e)			6	
(f)			14	
..	5517	(i) Variegated—Sub-branches	(g)	17
			(a)	7	..	6
			(b)	15
			(c)	9	2	9
			(d)	5	..	6
			(e)	7
			(f)	6	1	3
			(g)	6	..	11
			(h)	16
			(i)	3	3	3
(j)	13	..	3			
(k)	6	..	2			

TABLE XII—(Contd.)

Year of isolation of plant	Variety of progeny from which isolated	Appearance of the plant (tillerwar)	Selfed progeny		
			Green	Variegated	Yellow
1934—35..	5517	(ii) Apparently green—Sub-branches			
		(a)	14
		(b)	20
		(c)	15
		(d)	10
		(e)	16
		(f)	21
		(g)	17
		(h)	16
		(i)	12
			(iii) Practically yellow (except for a fine streak of green on the flag-leaf)	31	2
	(iv) Variegated	102	
	(v) Variegated (flag-leaf almost yellow)	80	1	12	
	(vi) Variegated	124	3	28	
	(vii) Apparently green	138	
	(viii) Variegated	23	1	48	
	(ix) Apparently green	142	
	(x) Apparently green	128	
	(xi) Variegated	110	

In this case the progeny of selfed plants consists of green and yellow seedlings and a few variegated plants of the parental type. The yellow seedlings are quite different from the yellows segregated in the No. 2 type of variegation. While yellow seedlings of the latter die out after 8 to 10 days from germination yellow seedlings produced by the green and yellow variegated plants live for a longer time. Though they are of equal growth and vigour with the green plants soon after germination, they lag behind and grow very slowly afterwards. Many of them perish after growing for a month or even more, but it looks possible to grow a few of them to maturity. Some of these plants have been planted out and they are growing still—now nearly three months from germination—although they remain very weak and pale. If these plants could set seed, we will have a pure chlorophyll deficient type which will be inherited only through the mother and this material should be of help in the study of plastid inheritance. The variegated plant of 5517 gives besides green and yellow seedling progeny, a few variegateds of the parental type, the last evidently arising from transitional

tissue of green and abnormal plastids. In this case also, the correspondence between the appearance of the parental plant and the nature of the seedling progeny arising therefrom is not close for variegated tillers and even variegated spikelets are noted to give green seedling progeny and green tillers and green spikelets to yellow progeny. In this case also as in the two foregoing, the different seedlings are distributed not at random, but in patches on the panicles thus showing that the nature of the sub-epidermal tissue from which the flowers take their origin, determine their distribution.

Artificial crosses made between this type of variegation and green plants have shown once again the maternal inheritance of this type. The following are the results of the crosses made :—

Parents	Number of flowers crossed	Nature of F ₁ progeny		
		Green	Variegated	Yellow
5517 Variegated ♀ × green ♂ ..	20	6	1	13
5517 Green ♀ × variegated ♂ ..	9	9
T. 445 Variegated ♀ × green ♂	7	2	1	4
T. 445 Green ♀ × variegated ♂	16	16

7. Discussion.

The occurrence and behaviour of the chlorophyll deficient characters in rice suggest several interesting features. Karper and Conner (1931) have found a striking similarity in the presence and mode of occurrence of chlorophyll characters between maize and sorghum. They have isolated chlorophyll deficient types in sorghum very much resembling those in maize and on that account suggest a parallelism of such characters in the two species. A similar parallelism may be said to exist in rice also. Characters described in this paper are very similar, if not identical, to those recorded in maize.

As regards the types of mutations that occur Demerec, Hutchinson and others have shown that chlorophyll mutations in maize are most apt to be those which hinder rather than enhance the development of this pigment and that therefore the mutations having the more pronounced detrimental effects would probably be of the most frequent occurrence. This was found to be the case in maize and sorghum where white seedlings were the most prevalent of the chlorophyll types (Karper and Conner, 1931). In the case of rice also, among the chlorophyll mutations so far met with, white seedlings are the most frequent. That the genes causing the production of

white seedlings are most unstable was also seen in the X-rayed progenies of rice varieties where white seedlings were found to be the more common of the several chlorophyll mutations. Hybridity also provokes the appearance of these whites in much larger numbers than other chlorophyll deficient types. Counts of mutants occurring in 150 F_3 families of an intervarietal cross gave 2.8% whites and 0.6% only of mutants like the yellows and striped plants.

Regarding the frequency of occurrence of chlorophyll mutants in rice, it was observed that in the several pure lines which are practically inbred through a number of generations, chlorophyll deficient types suddenly mutate to the recessive form. That these forms are not carried in the heterozygous state, which is known by the fact that they occur in inbred lines which did not show any chlorophyll deficient types through a number of generations, suggest that these are due to recent mutations and such mutations are fairly common to rice. This might suggest that the rate of mutation of this character is fairly high in rice.

Non-Mendelian variegations described in this paper strictly conform to the maternal type described for other species. The special type of non-Mendelian inheritance in rice referred to by Imai was not met with. Among the three types of variegation described, the last type where green and yellow areas are present, has not been recorded before. This type of variegation is interesting because it has given rise to an yellow progeny which shows some chances of survival whereas other types have given besides greens, lethal progeny only. If the yellows should reach maturity and set seed they would provide material for the study of the plastids which are believed to be concerned in the inheritance of variegation.

Summary.

Nine types of Mendelian chlorophyll deficiencies consisting of both unicoloured and variegated forms have been described and their inheritance discussed. Some of these like the "zebra-marked", lutescent and certain variegated forms are recorded for the first time in rice.

A beginning was made to study the inter-relationships of these types and all possible crosses were made with the albino, virescent yellow and the green and white striped as the parents and studied up to the F_3 generation. It was found that while each of the three different types behaved as a simple recessive to the normal green, crosses between any two of them gave green F_1 plants segregating in F_2 into green and the parental types in the ratio of 9 : 3 : 4 showing the interaction of two factors. The crosses have further shown that three pairs of factors (Ww , Vv and $Gw\ gw$) are concerned in the

development of chlorophyll in rice and that these factor pairs undergo ordinary Mendelian segregation and recombination and are inherited independently of each other without any linkage.

Three kinds of variegated plants were isolated and their inheritance studied from the selfed progenies and from the progenies of suitable crosses. It was found that the character was inherited only through the mother, the male parent having no effect in the transmission of the characters. This fact combined with the irregular segregation ratios obtained in selfed progenies and the non-random distribution of the different kinds of seedlings on the different tillers of the same plant have suggested that the plastids with the plasm rather than the nucleus are concerned in the inheritance of these variegations in rice.

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EXPLANATION OF PLATES.

PLATE XXX.

- | | |
|--|----------------------------------|
| FIG. 1.—Green and white striped seedling. | FIG. 4.—Lutescent seedling. |
| FIG. 2.—Green and yellow striped seedling. | FIG. 5.—Yellow seedling. |
| FIG. 3.—Yellow and white striped seedling. | FIG. 6.—“Zebra-marked” seedling. |

PLATE XXXI.

- FIG. 1.—Green and yellow variegated seedling.
 FIG. 2.—A normal plant showing an albino mutant tiller.

PLATE XXXII.

Photograph showing seedlings from three different tillers of a variegated plant of type 1.
 The middle two rows of albinos are from one tiller.

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Coloured Plates (Nos. XXX & XXXI) will appear in the
next issue.

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