

premeiotic interphase. Attempts to induce incorporation of label into sporocytes of excised whole or chopped up anthers submerged in medium containing H^3 -TdR have been unsuccessful.

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3. Further studies on disjunction at anaphase I of the chromosomes of a trivalent configuration.

It was reported in the 1965 M.G.C.N.L. that progeny of 21 chromosome plants carrying reciprocal maize-Tripsacum interchange chromosomes appeared to show a deficiency of 21 chromosome plants from non-disjunctive distribution for the distal region of the maize chromosome 2 short arm. The preliminary results were consistent with the interpretation that a tendency existed for trivalents destined to have non-disjunctive distribution to orient so that only the 2^I chromosome was directed toward the basal position. After addition of data from the 1966 season there is no significant difference in numbers of 20 and 21 chromosome progeny from non-disjunction as compared to disjunction and, therefore, no cause to suspect non-random metaphase I orientation of trivalents:

<u>disjunction</u>	<u>non-disjunction</u>
20 chrom. progeny - 430	260
21 chrom. progeny - 448	251

(Correction for estimated 8% non-disjunction of maize centromeres is included).

Frequencies of disjunction and non-disjunction for distal chromosome 2S from the trivalent described above have been studied from two lines of descent, one which had been outcrossed to L289 and the other repeatedly backcrossed to a Coop chromosome 2 tester. These have been found to differ significantly in non-disjunctive frequency (19% and 37% respectively) although each was internally homogeneous.

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1. Evidence for the inheritance of acquired characters.

The R gene conditions aleurone pigment in the endosperm of maize. When R is removed from a heterozygote with its allele Rst (such R alleles are symbolized R¹, one generation with Rst), less pigment is produced. This phenomenon is called paramutation and has been reported on by the Wisconsin Maize Laboratory over the past ten years.

In Vol. 40 (under Defiance College) we reported that when RR^{st} heterozygotes were given environmental treatments LL or LD (constant light or 12 hr. light and 12 hr. darkness, respectively) for the first four weeks of seedling development, differences in amount of pigment could be observed in the testcrosses of treated plants. LD environments conditioned more cells to form pigment; LL conditioned fewer pigmented cells. Our evidence now shows that these differences in R expression are found in the generation following the administration of LD and LL treatments--the differences are male transmissible.

Inbred W22 plants, RR^{st} , were raised under growth chamber conditions, LL and LD, for the first four weeks of plant development (70°F; light supplied by 14, 200W, cool white, fluorescent tubes supplemented by 12, 60W incandescent bulbs; in a 4' x 8' Percival Growth Chamber) in 1965. Plants so treated were removed to the field in June for the completion of their life cycle. Treated plants were sibbed or selfed to produce the seeds to be used in 1966; at the same time the treated plants were testcrossed to colorless inbreds. The testcross-kernels were scored by matching them against a set of standard kernels ranging in classes from 0-22, colorless to completely pigmented, respectively.

Table 1 shows that R^1 expressions from RR^{st} plants which received LD conditions are darker than those which had received LL conditions the previous year. The testcross scores represent R^1 alleles from W22/W23 hybrid background (R^1r) produced in 1965; this R^1r hybrid was testcrossed onto inbred W23 in 1966. The differences represented in Table 1 required that such differences accompany the R^1 allele through the pollen in 1965 in the W22/W23 hybrid; another pollen transmission was again required to account for the score differences in Table 1, in 1966. Thus the differences resulting from the LL and LD treatments in 1965 have survived two passages through the pollen.

Differences attributed to the LD and LL conditions are shown within a different subline in Table 2. R^2R^2 segregates from R^2R^{st} plants which had received LD and LL treatments show that darker phenotypes result from the LD conditions the previous year; LL cause R^2 to produce fewer pigmented cells. This difference can also be seen when the R^2 (Table 3) allele is transmitted through the female, and thus is present in the endosperm cells in two doses. Where R^2R^2 segregates are pollinated with rr to produce the triploid endosperm R^2R^2r , fewer kernels are found which show a mosaic phenotype on ears resulting from the plants whose R^2 allele traces back to the LD treatment the previous year. On the other hand, nearly twice as many kernels show a pigment mosaic in the endosperm when the R^2 allele which is present traces back to the LL treatment.

Table 4 shows that the effects of LL and LD environments on R^1 from RR^{st} heterozygotes, reported in 1965, are again repeated in a test conducted in 1966. LD conditioned darker R^1 phenotypes than the LL environment; mixed treatments show that it was the environment which the plants received during the third and fourth weeks of development that determined the phenotype which R^1 produced in the testcrosses.

It is concluded that the LD and LL environments are capable of conditioning heritable changes in R expressions and that these changes are determined sometime during the third and fourth weeks of seedling development. While it may be objected that the environments above affect only the paramutation process, it must be pointed out that the changes in the endosperm pigment mosaic attributed to the RRst combination are to be found when R is made heterozygous with any of its alleles (see below). The change in mosaic pattern, called paramutation, is simply a more extreme mosaic with greater standard deviations among pollen samples from a single plant. Our data in MGCNL 40 showed that R from either the RR or Rr combinations showed tassel mosaicism and thus variation in R expression, depending on the tassel sectors from which the gametes originated. The RR and Rr combinations differ from RRst heterozygotes by showing a much narrower range of variation for R mosaicism from a single tassel. To argue therefore, that LD and LL effects are to be found only in the presence of paramutation is not meaningful because now it appears that no conditions exist in which the R expression is free of paramutation (mosaicism) when testcrossed.

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Table 1
Growth Chamber Treatments, Spring 1965

	LD	LL
	17.56	15.44
	15.92	12.62
	15.78	15.80
	16.94	13.62
	19.10	13.94
	18.64	15.28
	17.30	15.50
	17.08	15.44
Pooled \bar{X}	17.29	14.71

Testcross scores of R¹ from hybrid R¹r background (Inbred W23, rr, x Inbred W22, RRst). Plants scored above were raised under greenhouse conditions in 1966. Scores represent ear means based on 50 kernels/ear.

Table 2
Growth Chamber Treatments, 1965

LD	LL
5.52	2.62
8.00	1.88
11.20	5.28
5.26	3.10
5.86	3.08
6.40	3.58
5.88	3.34
7.96	2.84
8.94	3.10
9.22	1.40
\bar{X} 7.42	3.02

Testcross scores of R^2R^2 segregates from seeds tracing back to LL and LD treatments of R^2Rst the previous year. Above scores are ear means based on 50 kernels/ear from testcrosses made in the field in 1966. Endosperm genotypes are rrR^2 .

Table 3
Growth Chamber Treatments, 1965

LD		LL	
Mosaic	Total	Mosaic	Total
3	113	35	252
3	246	69	254
17	347	40	233
15	278	47	382
11	344	32	308
15	212	11	252
7	224	12	189
39	313	13	262
47	350	26	174
38	360	19	259
2	130	41	347
2	294	46	296
2	336	42	337
3	132	28	269
2	253	41	271
3	286		
<u>209</u>	<u>4218</u>	<u>502</u>	<u>4085</u>
5.0%		12.3%	

Numbers of mosaic kernels/ear on R^2R^2 segregates tracing back to R^2Rst which received LD and LL treatments and had been self pollinated the previous year.

Table 4
Growth Chamber Treatments, Spring of 1966

	LD	LL	Field	LL-LD	LD-LL	t-Test Comparisons	P
Ear means	17.14	8.38	13.98	15.36	11.58	LD vs LL	<.001
based on	18.52	8.34	14.56	17.04	11.70	LL-LD vs LD-LL	<.001
50-kernel							
samples/ear.	15.78	9.92	16.38	16.20	13.70	LD vs Field	<.05
Fall, 1966.	13.60	9.98	13.56	15.92	9.36	LL-LD vs Field	<.05
	17.20	11.78	9.58	15.60	11.22	LD-LL vs Field	<.20
	17.26	11.78	14.52	16.52	13.82	LL vs Field	<.01
Pooled \bar{X}	16.58	10.03	13.76	16.11	11.90		

Testcross data for R^1 expressions from RR^{st} heterozygotes given environmental treatments during the first four weeks of seedling development in 1966. A repeat of experiments performed in 1965.

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2. Selection for different states of R^9 when transmitted through the female.

In MGCNL 40 we reported that it was possible to select heritable light and dark phenotypes from among testcross kernels when R^1 was removed from the R^1R^{st} heterozygote. Such differences in phenotype, following paramutation, suggest that the R alleles have different heritable states which are reflected in different degrees of mosaicism in the endosperm of testcross kernels. In advanced stages of paramutation, when R is introduced through the pistillate parent and is represented in endosperm cells by two chromosomes with R , one can observe many near colorless kernels. In Vol. 38 we reported that the lightest and darkest of such phenotypes (when R^6 was introduced through the female parent) did not respond to selection.

It was noted, in 1965, that upon self-pollination of R^9R^9 homozygotes (nine generations with R^{st}) the upper halves of ears produced 20% more kernels with mosaic patterns of pigment in the aleurone than did the lower halves of ears. Kernels from the upper half of the ear were grown out along with kernels from the lower half in an effort to check for the heritability of these mosaic sectors in the female inflorescence. Table 5 shows the percentage of mosaic kernels observed in the upper and lower halves of ears in 1965; 1966 results show nearly the same numbers of mosaic kernels were found in both groups of progeny from each of the