GENETICAL STUDIES OF MONOSOMIC TYPES OF *NICOTIANA TABACUM*

H. P. OLMO

University of California, Berkeley, California

Received September 6, 1934

INTRODUCTION

In organisms having two sets of chromosomes that pair normally, bivalents being regularly formed at the first metaphase of meiosis, it is sometimes possible to obtain types that lack a chromosome, yet exhibit no other marked irregularities in chromosomal behavior. Such individuals are monosomics ($2n-1$) and, as a rule, are abnormal only in the sense that some specific chromosome is without a homolog.

Since monosomism destroys the original duality of one chromosome pair, an unbalanced genetical system is set up, capable of variation, as reflected both in the immediate individual and its progeny. Reports of types derived apparently from monosomic individuals, in many cases markedly deviating from normal, are prevalent in the literature of polyploid plants. Such variants, many of which have higher or lower chromosome numbers, fragments, or structural chromosomal rearrangements, are mentioned in numerous papers (see especially NISHIYAMA 1931, 1933; R. E. CLAUSEN 1930, 1931; POWERS 1932; HAKANSSON 1932). Few studies, however, have been exclusively devoted to the genetics and cytology of monosomic forms. Obviously processes that may modify chromosome number and structure are not without practical importance, since they may serve as a means of inducing variation and obtaining improved types of cultivated plants.

In common with many other polyploid plant genera, monosomic types have arisen spontaneously in *Nicotiana*. AVERY (1929) reports their occurrence in the 9-paired species *N. alata* var. *grandiflora*. In *N. tabacum* var. *purpurea* a form known as "fluted" or haplo-F has arisen spontaneously in cultures in the frequency of about 1:150 (CLAUSEN and GOODSPEED 1926a). Monosomic types have been isolated in designed experiments by backcrossing F_1 hybrids to one of the parental types with lower chromosome number. In this way CLAUSEN and GOODSPEED (1926b) obtained the derivative "corrugated" from the *sylvestris-tabacum* hybrid. LAMMERTS (1932), working with the allied species *N. rustica*, used the same method in isolating seven different monosomic types. GOODSPEED and AVERY (1933) have recovered monosomics in progeny from X-rayed *Nicotiana*.

MATERIAL AND METHODS

The seven monosomic ($2n-1$) types dealt with in this paper are those of *Nicotiana tabacum* var. *purpurea*. This particular variety of tobacco is a highly homozygous strain, having been inbred continuously for over 27 years at the UNIVERSITY OF CALIFORNIA.

According to the theory advanced by GOODSPEED and CLAUSEN (1928), the polyploid species *N. tabacum* ($2n=48$) has arisen by interspecific hybridization between two twelve-paired species, followed by a doubling of the chromosome number (amphidiploidy).

With the exception of haplo-F and haplo-C, of whose origin we shall speak in a later paragraph, all the monosomics have been obtained by interspecific hybridization and repeated backcrossing of selected F_2 derivatives to the normal *purpurea* variety. Hybrids are readily obtained between *tabacum* and *sylvestris* or *tomentosa*. The F_1 hybrids *sylvestris-tabacum* and *tomentosa-tabacum* are completely self-sterile when their own pollen is applied and typically show $12_{II}+12_I$ at first metaphase.

Seed of either the *sylvestris-tabacum* or *tomentosa-tabacum* hybrid may be obtained by backcrossing to *tabacum*. The progeny grown from seed of the *sylvestris-tabacum* backcross comprises a highly diversified collection of derivatives, which may be grouped into three general classes: (1) almost completely sterile, aberrant forms; (2) plants which resemble *tabacum*, but which are also highly sterile and give no progeny on self-fertilization; (3) *tabacum*-like forms that are somewhat fertile and produce in the course of a few generations plants identical with the original *tabacum* parent (GOODSPEED and CLAUSEN 1922). By cytological examination of the more fertile types, some are found to be monosomics. The process of backcrossing the partially fertile derivatives having a number of univalents to *tabacum* can be continued until other monosomics are isolated in succeeding generations.

By the method described above, it is theoretically possible to obtain twelve different monosomics of *tabacum*, types lacking one of the twelve *tabacum* chromosomes homologous with those of *tomentosa*. For convenience and distinction, these twelve haplo-types are to be designated A to L and may be appropriately called the "*tomentosa*" monosomics of *tabacum*. Four of these, A, B, C, and F, are considered in the present study.

In like manner, by backcrossing the F_1 *tomentosa-tabacum* hybrid, it is theoretically possible to obtain another series of twelve *tabacum* monosomics, in which the monosome is homologous with one pair of the chromosomes constituting the species *sylvestris*. This series is to be labeled M to X and constitutes the "*sylvestris*" monosomics of *tabacum*. Of these, haplos N, Q, and R have been selected for study.

Haplo-C has been the subject of a previous paper by CLAUSEN and GOODSPEED (1926b). Its lineage dates from 1915, when an *F*₁ *macrophylla-sylvestris* hybrid was backcrossed to the normal *macrophylla* parent. *Macrophylla* is a broadleaved, dwarf variety of the *tabacum* species. Several years later this monosomic of *N. tabacum* var. *macrophylla* was backcrossed a number of times to the *purpurea* variety, and the monosomic of the latter was isolated. This is the monosomic C dealt with in the present study.

Haplo-F and its derivatives have been more extensively investigated than any other monosomic type of *tabacum*. It is the F chromosome that carries the coral and mammoth complexes (CLAUSEN 1931). Because of the very characteristic waviness of the flower limb, this type has been described as "fluted" (CLAUSEN and GOODSPEED 1926a). The mechanism responsible for the occurrence of "fluted" has been attributed to non-conjunction of the F chromosome. Thus CLAUSEN (1931) has observed that occasionally at first metaphase there are $23_{II} + 2_I$ instead of the normal 24_{II} .

Because of its mode of origin, haplo-F was from the time of its inception a genetically homogeneous type. This was not the case with the other monosomics, which, as already noted, were isolated by interspecific hybridization and selection. The facility with which monosomics may be obtained by this method is somewhat lessened because, once isolated, they must be backcrossed a number of times to the normal *purpurea* so as to reduce the quantity of genetic material contributed by the alien species to a minimum.

MORPHOLOGY OF THE MONOSOMIC TYPES

Since the effect of chromosomal removal is a complex one, disturbing the genetic balance in its entirety, the morphological changes exhibited by these types are largely the result of genic deficiencies, which alter the interrelationships and factor balance previously associated with a normal phenotype. The removal of any one chromosome in *N. tabacum* var. *purpurea* produces rather general morphological changes. The flowers of the seven haplo forms are pictured in figure 1. Some of the features which most markedly distinguish each monosomic type from the normal strain are as follows:

Haplo-A: Reflexed corolla limb. Anthers are exerted.

Haplo-B: The leaf auricles are attenuated and narrow. The corolla limb is flat and intensified crimson in color.

Haplo-C: Large pendant flowers, the throats of which are light pink.

Haplo-F: The expanded flower limb is undulated and the entire inflorescence telescoped.

Haplo-N: Similar to haplo-F, but the flower limb is not fluted.

Haplo-Q: Plant of slender growth habit. The flower has a narrow throat and small limb.

FIGURE 1.—Typical flowers of the monosomic types and the normal *purpurea* strain.

Haplo-R: Flower has a very broad limb and is coral pink in color. The leaves are corrugated.

Seed Production

The chances of a monosomic individual's establishing itself under natural conditions and successfully competing with the normal phenotype would partly depend upon its fertility. The normal strain of *purpurea* yields approximately 4000 seeds per capsule. Every monosomic type investigated produces a small amount of seed in comparison with the normal strain. The average number of seeds from typical capsules of haplos A, F, and N is, by actual count, less than one-sixth of the number maturing in the normal *purpurea*. Even the types comparing most favorably—namely C, Q, and R—produce only about one-third of the normal seed yield.

FIGURE 2.—Capsules of the seven monosomic types and the normal strain of *N. tabacum* var. *purpurea*.

The reduced seed yields are perhaps largely explainable on the basis that the capsules are merely reduced in size, in common with other morphological changes accompanying monosomism (figure 2). However, there are indications that a large number of ovules or young zygotes must abort before reaching maturity.

Pollen Production and Morphology

Striking are the differences existing between the pollen grains of most of the haplo types when viewed microscopically. The pollen of each monosomic type, with the possible exception of haplo-A, is dimorphic. Two general classes of pollen may be distinguished, one consisting of large and apparently morphologically normal grains, the other composing a majority of the total number, which are considerably smaller and have characteristic densely granular deposits within them (figure 3). In addition there is a small and variable number of aborted grains, appearing shriveled and almost devoid of plasma.

TRANSMISSION OF THE MONOSOMIC CONDITION

Progenies from the cross monosomic ♀ × normal ♂ and from the reciprocal combination were grown at the University Farm, Davis, and also at the UNIVERSITY OF CALIFORNIA, Berkeley, during the summer of 1933 for the purpose of obtaining the transmission ratios of the monosomic

condition through egg and pollen respectively. From four to six populations, consisting of approximately 35 to 70 plants each, were grown from a single cross.

FIGURE 3.—Pollen of haplo-N. The smaller grains with the granular deposits are assumed to be nullosomic for the N chromosome. Mounted in xylol-balsam. $\times 300$.

Through the Egg

The summarized data presented in table 1 show that the number of monosomic plants obtained in the progeny largely depends upon the particular chromosome that has been removed from the genom. Since the number of plants dealt with forms a reasonably large random sample, the differences existing in the transmission ratios are undoubtedly significant, especially since the results obtained for each population of a given type were fairly consistent.

Of the seven types, haplos A, Q, and R are outstanding in their high transmission of the monosomic condition. In haplo-A, 83.2 percent of the

TABLE 1
Transmission of the monosomic condition; monosomic as female parent.

MONOSOMIC SERIES	TYPE	NORMAL	MONOSOMIC	TOTAL	PERCENT* MONOSOMIC
"tomentosa"	A	40	243	292	83.2
	B	117	160	284	56.3
	C	62	153	226	67.7
	F	92	162	264	61.4
"sylvestris"	N	112	99	217	45.6
	Q	48	209	262	79.8
	R	41	175	223	78.5

* A small percentage of the total number were plants classified as "aberrant."

progeny are plants having only 47 chromosomes; in Q 79.8 percent; and in R 78.5 percent. The highest transmission reported in *N. rustica* (LAMMERTS 1932) was 75 percent. Five of the seven monosomics for which he reported transmission ratios showed a percentage varying from 56 to 75 for the number of functional (n-1) gametes, assuming that all or practically all the seed germinated and eventually produced mature plants.

Theoretically, one might expect gametes having 23 and 24 chromosomes in equal numbers. With the single exception of haplo-N, all the types produce a preponderance of 23-chromosome gametes. In general, this phenomenon has been attributed by various workers to the failure of the univalent chromosome to be regularly incorporated in the daughter nuclei during megasporogenesis. Differential fertility and survival are factors that cannot be neglected.

That the viability of monosomic zygotes may be somewhat less than normal is suggested by the seed germination data. The average number of seeds germinating in the cross monosomic ♀ × normal ♂ is about 84 percent—10 percent lower than when the seed from a normal plant pollinated with monosomic pollen is sown. Such a result might be expected if those zygotes having an unbalanced chromosome number are less viable than zygotes having all 48 chromosomes. Monosomics of *purpurea* also seem to be slightly less vigorous than their normal sibs. That they are usually retarded in time of development is borne out by the successful practice of selecting the later-developing seedlings of a progeny, so that the monosomic type may be perpetuated by growing only a small number of plants. Whereas haplos Q and R, for instance, ordinarily produce about 78 or 79 percent of monosomic offspring, this percentage may be increased to 100 if only the seedling plants that are somewhat delayed in growth are selected for preservation. Moreover, it is among such groups of retarded individuals that most of the plants classified as "aberrant" have

been discovered. There is reason to believe, therefore, that the actual number of functional ($n-1$) gametes is much higher than that found indirectly by counting the number of monosomic plants, because of a decreased adaptability to environmental conditions brought about by the change in genic balance. "Functional" gametes are herewith defined as those producing mature seeds.

LAMMERTS (1932) suggested that the differences which he noted in some of the female transmission ratios of different monosomic types in the theoretically amphidiploid species *N. rustica* might be attributable to a differential lagging of the monosome, so that some univalents were more liable to be eliminated than others.

It should therefore be possible to demonstrate here, for example, that elimination of the unpaired chromosome is much more frequent in such a type as haplo-A, which gives approximately 83 percent of functional ($n-1$) gametes, than in a type like haplo-B, where about 56 percent of ($n-1$) eggs are functional, if relative viability of the seed is neglected.

As a measure of the frequency of univalent elimination during microsporogenesis, the number of microcytes or micronuclei can be counted in the tetrad stage, and the approximate number of n and ($n-1$) gametes calculated (NISHIYAMA 1931). By employing iron aceto-carmines smears, one can readily observe the number of microcytes and micronuclei. In table 2 each group of observations pertains to the results obtained by smearing anthers from one flower. Usually counts were made of from 150 to 200 tetrads from a single slide. In haplos A and B the slides were prepared from material collected over a period as long as two months, although adherence to any collection schedule was neglected. The results vary considerably from slide to slide.

On comparing the averages of the number of microspores calculated to be deficient for a monosome, one sees that the variation between the different monosomic types is insignificant and incapable of explaining the large excess of monosomic plants actually obtained in some haplo types. Thus as shown by table 3, haplo-A produces over 83 percent of monosomic progeny, whereas the calculated number is about 77 percent. From the previous considerations on the relative viability and survival of the types with unbalanced chromosome number, this discrepancy would be even larger.

For the moment, if we make allowance for the lower germination percentages obtained in the cross monosomic ♀ × normal ♂, the transmission ratios through the egg would be converted as shown in table 3. The differences in germination percentages reported are assumed to have resulted solely from the mortality of ($2n-1$) zygotes. The average decrease in seed viability in column 2 was obtained by subtracting the observed germina-

TABLE 2
Frequency of univalent elimination in various monosomic plants.

MONOSOMIC TYPE	PLANT NUMBER	MICROCYTES AND MICRONUCLEI PER TETRAD				RATIO (n-1):n	PERCENT (n-1)
		0	1	2	2+*		
A	34240P1	26	55	35	0		
		47	93	92	0		
	34240P2	65	45	89	4		
		51	27	69	3		
		41	22	25	2		
		39	15	37	1		
		53	22	37	1		
		322	279	394	11	3057:923	76.8
B	34244P7	63	43	75	7		
		49	25	47	2		
		41	30	54	4		
		37	12	35	3		
		36	16	29	0		
		226	126	240	16	1790:578	75.6
N	34256P2	46	32	56	8		
		79	56	94	13		
		125	88	150	21	1114:338	76.7
R	34264P6	35	25	45	3		
	34264P8	49	28	41	0		
		52	40	51	2		
		44	28	44	3		
		180	121	181	8	1447:481	75.0

* Tetrads containing more than two microcytes or micronuclei and omitted from the calculations in determining ratios and percentages of (n-1) gametes.

tion percentage of each haplo type from the average percentage of the reciprocal crosses. The data presented in table 3, though limited, indicate that differential lagging cannot account for such excesses of monosomic plants.

We shall now consider the exceptional instance of egg transmission in which the number of functional (n-1) gametes was below the expected value of 50 percent, as determined by counting the number of monosomic plants in the progeny. Again according to table 1, one type, haplo-N, produced 45.6 percent of monosomic plants—considerably below that obtained for any other type. But, as shown in table 3, this fact may well be explained by the selective elimination of (2n-1) zygotes, which fail to germinate. This appears all the more probable if we compare the germina-

TABLE 3

Corrected transmission ratios of the monosomic types compared with the expected percentages, as calculated from the frequency of univalent elimination during microsporogenesis.

MONOSOMIC TYPE	AVERAGE DECREASE IN SEED VIABILITY	PERCENTAGE OF MONOSOMIC PROGENY (TABLE 1)	CORRECTED PERCENTAGE OF (2n-1) PLANTS	CALCULATED PERCENTAGE (TABLE 2)
A	4.2	83.2	87.4	76.8
B	20.1	56.3	76.4	75.6
C	3.5	67.7	71.2	..
F	6.6	61.4	68.0	..
N	25.1	45.6	70.7	76.7
Q	2.5	79.8	82.3	..
R	5.2	78.5	83.7	75.0

tion percentages with the number of monosomic plants surviving. Thus the populations of haplo-B and haplo-N, which produce the smallest proportion of monosomic plants, also manifest the lowest seed viability. If this is a logical explanation, the number of (2n-1) zygotes in haplo-N is approximately 71 percent. Seed viability and ultimate survival thus appear to be important factors in interpreting the transmission ratios, and one is led to conclude that all the monosomics of *tabacum* discussed herein produce an excess of (n-1) egg cells.

Through the pollen

Only a very small percentage of (n-1) pollen grains succeed in fertilizing the ovules of normal plants. The tabulated results are collected in table 4. The highest number of monosomic plants was obtained in the case of haplo-F, where over 7 percent of the progeny were 47 chromosome plants. Haplo-A, which has been shown to transmit the monosomic condition so readily through ovules, produces only a few monosomic plants when used as male parent.

TABLE 4

Transmission of the monosomic condition, normal ♀ × monosomic ♂.

MONOSOMIC TYPE	POPULATION NUMBER	NORMAL	MONOSOMIC	ABERRANT*	TOTAL NUMBER PLANTS
A	33208	47	2		49
	33209	45	4	1	50
	33210	48	3		51
	33211	43	1		44
	Totals	183	10	1	194
	Percent	94.3	5.2	0.5	
B	33212	49	1	1	51
	33213	41	2	2	45
	33214	41	1		42
	33215	40	2	1	43

TABLE 4 (Continued)
Transmission of the monosomic condition, normal ♀ × monosomic ♂.

MONOSOMIC TYPE	POPULATION NUMBER	NORMAL	MONOSOMIC	ABERRANT*	TOTAL NUMBER PLANTS
	Totals	171	6	4	181
	Percent	94.5	3.3	2.2	
C	33216	44			44
	33217	45		1	46
	33218	48			48
	33219	43			43
	Totals	180		1	181
	Percent	99.4	0.0	0.6	
F	33220	39	5	3	47
	33221	40	4	3	47
	33222	27	3		30
	33222	11	1	3	15
	33223	51	1		52
	Totals	168	14	9	191
	Percent	88.0	7.3	4.7	
N	33224	51	2		53
	33225	55		2	57
	33226	52	4	1	57
	33227	46		4	50
	Totals	204	6	7	217
	Percent	94.0	2.8	3.2	
Q	33228	52			52
	33229	51		1	52
	33230	49	1	1	51
	33231	45		2	47
	Totals	197	1	4	202
	Percent	97.5	0.5	2.0	
R	33232	53	1	1	55
	33233	44	2		46
	33234	48			48
	33234	1		1	2
	33235	46		1	47
	33235	2			2
	Totals	194	3	3	200
	Percent	97.0	1.5	1.5	

* The occurrence and cytology of aberrant plants in offspring of these monosomic types are discussed by the author in a companion paper (1935).

There is a large variability in the number of monosomic plants in different populations of the same cross. According to table 4, population 33220 segregated 5 monosomic plants out of a total of 47, whereas in population 33223, grown from the same seed lot, only one plant of the 52

was monosomic. The average differences between populations of any two monosomic types may be less significant than they appear. It seems probable, however, that, as in ovule transmission, certain differences are traceable only to the degree of unbalance caused by the absence of any specific chromosome.

A very low transmission of the monosomic condition through the pollen is characteristic of all the *purpurea* monosomics used in this study. This corroborates the findings of CLAUSEN and GOODSPEED (1926a), who reported only about 2 percent of functioning pollen grains of the 23 chromosome class in haplo-F. In the *macrophylla* derivative "haplo-C" the same authors (1926b) reported a pollen transmission of 3.3 percent, whereas in the present study the haplo-C *purpurea* was the only one of the seven types which failed to transmit the monosomic condition when used as male parent.

No correlation appears to exist between the transmission of monosomism through the ovules and pollen of the same haplo type. Thus haplo-F produced approximately 7 percent of monosomic plants as male parent, and 61 percent transmission was found through the ovules, whereas haplo-C failed to transmit through pollen yet gave rise to approximately 68 percent of monosomic plants when fertilized with normal pollen.

A large proportion of the functioning pollen grains must contain a chromosomal complement that has been the outcome of structural or numerical chromosomal rearrangements originating in the mother plant. The fact that such modified gametes are frequently pollen-transmitted accounts for the comparatively large number of off-type plants, which can be classified as neither monosomic nor normal (table 4).

DISCUSSION

Of the seven monosomic types reviewed in the present paper, each is readily distinguishable from the normal strain by a complex of characters, which are typically inherited as a unit. Each complex is general in nature, reflecting changes in the physiology of the whole plant rather than strictly localized ones.

The monosomic types of *N. tabacum* var. *purpurea* are somewhat retarded in development, besides being slightly less vigorous than the normal strain. The proportion of monosomic plants in a progeny may be increased by preserving only plants that are retarded in the seedling stage of development. LI (1927) showed that haplo-IV flies of *Drosophila melanogaster* were retarded in all three developmental stages and emerged two to three days later than normal sibs. AVERY (1929) described a monosomic form of *Nicotiana glauca* var. *grandiflora* ($2n = 18$) as being less vigorous than the diploid, as is the case reported by KIHARA (1932) in *Pharbitis nil* ($2n = 30$).

In fatuoid oats ($2n=42$), as illustrated by NISHIYAMA (1933), only a slight change occurs in the phenotypic appearance of plants monosomic for the *c* chromosome. POWERS (1932), working with some strains of cultivated wheats derived from interspecific crosses, stated that 41 chromosome plants were indistinguishable from the normal diploid. Obviously the character and extent of the underlying physiological changes may vary according to the genic content of the particular chromosome removed relative to the rest of the complement. Thus the removal of a chromosome in polysomic or polyploid forms has little effect, because of the compensation afforded by another chromosome or chromosomes performing the same or similar functions.

Characteristic of the monosomic types is a very high transmission of the monosomic condition via the egg. The percentage of $(2n-1)$ plants obtained in the progenies of haplo type ♀ $\times$ normal ♂ ranged from approximately 45.6 percent in haplo-N to as high as 83.2 percent in haplo-A. This range in variation is less pronounced if the viability of the seed is considered. If the decrease in seed viability is caused by the mortality of monosomic zygotes, then the number of functional $(n-1)$ eggs is always well above 50 percent (table 3). Yet even after such a correction, the difference between such types as haplo-A and haplo-F amounts to approximately 20 percent. One cannot logically state that the number of monosomic plants obtained in the progeny is an accurate measure of the number of $(n-1)$ egg cells originally produced. For this reason we have purposely defined "functional" egg cells as those which produce mature seed. At present, no data are available giving the approximate percentage of $(n-1)$ egg cells that are formed, and which become fertilized. NISHIYAMA (1928) determined the number of functional $(n-1)$ female gametes in two different monosomic spelt wheats ($20_{II}+f$) and ($20_{II}+g$) to be 71 and 72.7 percent respectively. This would indicate that the specific chromosome left in the univalent condition is not influential in determining the relative frequency in which $(n-1)$ egg cells are produced. In the latter case, however, the removal of a chromosome would not be expected to produce so profound a change in balance as occurs in *N. tabacum*, theoretically an amphidiploid.

If NISHIYAMA's (1928) conclusions in regard to univalent elimination in monosomic spelt wheats are applicable in the present instance, then the frequency of univalent elimination calculated from pollen mother cell tetrads should be approximately the same as the percentage of monosomic plants obtained in the progeny, after allowing for reduced viability. Of the four monosomic types thus analyzed, the percentage of $(n-1)$ microspores ranged from approximately 75 to 77 percent (table 2). Although admittedly the variability between individual counts is sometimes very large, the averages indicate that the frequency of univalent elimination

is practically the same, regardless of the specific chromosome left in the univalent condition. The haplo types such as N, C, and F, therefore, might show a lower ratio of transmission either because of differential fertility, or a differential production of $(n-1)$ eggs. As yet we have no method of testing such an assumption. But any explanation for an excess of monosomic plants over the calculated number is not forthcoming, unless it be that univalent elimination occurs more frequently during megasporogenesis.

Whereas in monosomic hexaploid wheats and oats the results of KIHARA (1924), HUSKINS (1928), NISHIYAMA (1931, 1933), POWERS (1932), and others, demonstrate that 20-chromosome pollen is usually only at a slight disadvantage in competition with 21-chromosome pollen, the situation is much different in *N. tabacum* monosomics, where the highest number of $(n-1)$ microspores effective in fertilization was approximately 7 percent in haplo-N. In haplo-C the monosomic condition was not pollen-transmitted. Judging from the frequency of univalent elimination during microsporogenesis, the ratio of $(n-1)$ to n microspores is probably about the same in all of the types—namely, in the ratio of approximately 3:1. In 41 chromosome fatuoid oats, NISHIYAMA (1931) found the ratio to be 6:1. The same author (1928) reported a ratio of $(n-1)$ to n egg cells in two 41 chromosome spelt wheats to be 3:1. KIHARA'S (1924) results with emmer-spelt derivatives with 41 chromosomes approximated a 3:2 ratio. From these reports it appears that such ratios may vary widely, depending on the species or hybrid concerned. Possibly, too, environmental conditions may cause marked deviations in the ratio of $n:(n-1)$ gametes.

SUMMARY

Seven monosomic $(2n-1)$ types of *N. tabacum* var. *purpurea* are described. With the exception of haplo-F, all were obtained by interspecific hybridization and repeated backcrossing of the more fertile derivatives to the normal strain.

Characteristic of the types studied is a slight reduction in the vigor of growth accompanying a retardation in the rate of development.

All the types are markedly less fertile than the normal *purpurea* strain.

The pollen of each monosomic type except, possibly, haplo-A, is dimorphic.

The transmission of the monosomic condition through ovules is high, ranging from 45.6 percent in haplo-N to 83.2 percent in haplo-A. If seed viability and ultimate survival of the plants be considered, the number of functional $(n-1)$ eggs is always well above 50 percent.

The highest transmission of the monosomic condition through the pollen was recorded in haplo-N, where only 7 percent of the progeny were mono-

somic. In the cross normal ♀ × haplo-C ♂ no monosomic plants were recovered.

Evidence is presented which indicates that univalent elimination may occur more frequently during megasporogenesis than microsporogenesis.

There appears to be no correlation between the transmission of the monosomic condition through the eggs and pollen of the same haplo-type.

ACKNOWLEDGMENT

The author wishes to acknowledge his indebtedness to Professor R. E. CLAUSEN, whose friendly advice and criticism were always welcomed throughout the course of this study.

LITERATURE CITED

- AVERY, P., 1929 Chromosome number and morphology in *Nicotiana*. IV. The nature and effects of chromosomal irregularities in *N. alata* var. *grandiflora*. Univ. California Pub. Bot. 11: 265-284.
- CLAUSEN, R. E., 1930 Inheritance in *Nicotiana tabacum*. X. Carmine-coral variegation. Cytologia 1: 358-368.
- 1931 Inheritance in *Nicotiana tabacum*. XI. The fluted assemblage. Amer. Nat. 65: 316-331.
- CLAUSEN, R. E. and GOODSPEED, T. H., 1926a Inheritance in *Nicotiana tabacum*. VII. The monosomic character "fluted." Univ. California Pub. Bot. 11: 61-82.
- 1926b Interspecific hybridization in *Nicotiana*. III. The monosomic *tabacum* derivative "corrugated" from the *sylvestris-tabacum* hybrid. Univ. California Pub. Bot. 11: 83-101.
- GOODSPEED, T. H. and AVERY, P., 1933 Inheritance in *Nicotiana tabacum*. XIII. The cytogenetics of "deformed," an X-ray derivative. Genetics 18: 487-521.
- GOODSPEED, T. H. and CLAUSEN, R. E., 1922 Interspecific hybridization in *Nicotiana*. I. On the results of backcrossing the F₁ *sylvestris-tabacum* hybrids to *sylvestris*. Univ. California Pub. Bot. 11: 1-30.
- 1928 Interspecific hybridization in *Nicotiana*. VIII. The *sylvestris-tomentosa-tabacum* hybrid triangle and its bearing on the origin of *tabacum*. Univ. California Pub. Bot. 11: 245-256.
- HAKANSSON, ARTUR, 1932 Zytologische Studien an compactoiden Typen von *Triticum vulgare*. Hereditas 17: 155-196.
- HUSKINS, C. L., 1928 On the cytology of speltoid wheats in relation to their origin and genetic behavior. J. Genet. 20: 103-122.
- KIHARA, H., 1924 Cytologische und genetische Studien bei wichtigen Getreidearten mit besonderer Rücksicht auf das Verhalten der Chromosomen und die Sterilität in den Bastarden. Mem. Coll. Sci. Kyoto Imp. Univ. Ser. B. 1: 1-200.
- 1932 Chromosomale Aberranten bei *Pharbitis Nil*. Kwagaku 2: 196-198.
- LAMMERTS, W. E., 1932 Inheritance of monosomics in *Nicotiana rustica*. Genetics 17: 689-696.
- LI, JU-CHI, 1927 The effect of chromosome aberrations on development in *Drosophila melanogaster*. Genetics 12: 1-58.
- NISHIYAMA, I., 1928 On hybrids between *Triticum spelta* and two dwarf wheat plants with 40 somatic chromosomes. Bot. Mag. Tokyo 42: 154-177.
- 1931 Genetics and cytology of certain cereals. II. Karyogenetic studies of fatuoid oats with special references to their origin. Jap. J. Genet. 7: 49-102.
- 1933 The genetics and cytology of certain cereals. IV. Further studies on fatuoid oats. Jap. J. Genet. 8: 107-124.
- OLMO, H. P., 1935 Cytological studies of monosomic and derivative types of *Nicotiana tabacum*. Cytologia, in press.
- POWERS, LeROY, 1932 Cytologic and genetic studies of variability of strains of wheat derived from interspecific crosses. J. Agric. Res. 44: 797-831.