

THE OCCURRENCE AND RATES OF REPRODUCTION OF
VARIOUS MALE STERILITY GENES

by

F. K. VAN DER KLEY

Laboratory of Field Crop Husbandry of the Agricultural University, Wageningen.

(Received for publication February 9, 1955)

1. INTRODUCTION

In a previous publication (1954) a survey was given of the great number of species of plants in which individuals are known that completely or almost completely fail to produce viable pollen as a result of their genetical constitution; such plants are said to be male sterile (MS). It was also pointed out (1954) that nearly all known types of male sterility (MS) are caused by one or a few recessive nuclear factors. Cytoplasmatically inherited types of MS, known in cross fertilizing plants and hybrid species only, were all modified by nuclear factors (cf. KOOPMANS, 1952-1955).

It was shown by LEWIS (1941) that this is mainly a consequence of the rate of reproduction of the different MS genotypes, although the mutability of plasm factors also plays a role. This will be discussed and further outlined by deriving some formulae, showing the relation between the frequencies with which the various MS genotypes and MS plasmotypes occur in cross fertilizing and self fertilizing populations, their relative fertilities and the frequencies with which they are induced by mutations. The importance of these formulae in theoretical genetics and in plant breeding will be discussed.

The relative fertility (symbolized by q_r) of $r\%$ MS plants in a given population is defined as the ratio between the average number of seeds produced per plant and the number of seeds produced under the same circumstances by the normal

fertile individuals. The percentage of cross fertilization occurring in a population is symbolized by b . All percentages mentioned relate to the total number of plants, occurring in one generation of the population under discussion.

2. FERTILITY OF MS PLANTS

Since MS plants, as a rule, only produce seeds after cross pollination, their relative fertility will be higher in populations which show a higher percentage of cross fertilization. This may be quantitatively

expressed in the formula: $q_r = \frac{b(x_r + 1)}{100}$. In this formula $x_r (\geq 0)$

represents the excess of viable pollen, on an average occurring (in the presence of $r\%$ MS plants) on the stigmas of normal fertile plants. Since $x_r = x_0 \cdot F(100 - r)$, it may be estimated to be equivalent to x_0 in natural populations, in which usually only a small percentage of MS plants occur. The value of q_r corresponding with x_0 is symbolized by q . The magnitude of q and x_0 depend on the amount of viable pollen, produced on an average per plant, the number of plants per unit of area (LEWIS 1941), and the possibilities of successful pollination. The amount of viable pollen and the pollination chances depend on the type of male (or hermaphrodite) and female (or hermaphrodite) flowers, respectively (FRANKEL 1940), as well as on the external circumstances. Drought (high temperature combined with low relative moisture of air) and rain are the more important limiting factors in the production and dispersion of viable pollen (SUNESON 1951). In fact the relative fertility of MS plants, occurring in *self fertilizing plants*, is always smaller than one. In the case of the tomato the fruitset of MS plants is 5-10% of that of the normal fertile plants (RICK 1945). So one might estimate the relative fertility of the MS plants to be 0.05-0.10. For MS barley plants, q -values of about 0.25 were published by SUNESON (1951). For sorghum STEPHENS (1945) reported also q -values of about 0.25. Since in *cross fertilizing plants* no significant differences between MS and normal fertile plants have yet been reported, it is probable that q may be about one (see BAUMAN a.o. 1953).

3. RATES OF REPRODUCTION OF PLASM FACTORS CAUSING MS

A population in a given year is supposed to contain $p\%$ of MS individuals. In the absence of mutations in the following generations

(1, 2, n) this percentage will be pq , pq^2 , pq^n , respectively. It is obvious that, under the circumstances supposed, in *self fertilizing populations* ($q \ll 1$) the plasmatocal MS plants are ousted from these populations in geometric progression (see figures 1 and 2). In practice, however, in every generation $p\%$ more than the above calculated number of MS plants might be produced by mutations. Since MS plants cannot be identified before bud-stage (v. D. KLEY 1954, 1955), all mutations are expected to take place before MS plants can be counted. So the population (at flowering time of its plants) will eventually contain a percentage of MS plants that may be estimated best as the limit value of the decreasing geometric progression:

$$p + pq + pq^2 + \dots + pq^n = \frac{p}{1-q} \%.$$

The amount of this percentage MS plants, expected in every self-fertilizing population occurring in practice, is shown for increasing values of q in Table 2.

In *cross fertilizing populations* ($q \approx 1$), MS plants which occur can maintain themselves, also if mutations fail to complete their number. Since in every generation mutations may be supposed to occur with about the same frequency, the relative number of MS plants will increase in consecutive generations. This increase will occur up to a limit, at which all pollen available in the population is completely employed. The value of this theoretical maximum of the number of MS plants, expected in every cross fertilizing population may depend strongly on the excess of pollen (x_0) which is produced in the population if MS plants fail to occur.

4. RATES OF REPRODUCTION OF DOMINANT MS GENES

In a population $p\%$ monofactorial dominant MS plants are supposed to be caused by mutation. It follows from the Laws of Probability that among these mutated plants ($p - p^2/200$)% heterozygous and $p^2/200\%$ homozygous plants can be expected. The former will produce approximately $pq/2\%$ heterozygous MS plants; the percentage of heterozygous MS plants ($p^2q/200\%$) produced by the latter may be neglected. Since in populations occurring in practice p has only low values, these and other terms $p^2/200$ are negligible. In the absence of repeated mutations it follows that p , $(q/2)p$, $(q/2)^2p$ $(q/2)^np\%$

heterozygous MS plants, respectively, will be expected to occur in the generations 0, 1, 2, . . . n, after the presupposed rate of mutation. In fact under the circumstances mentioned monofactorial dominant MS individuals can maintain themselves in a population if they are at least twice as fertile as the normal plants in the population. This conclusion, which was already reported in cross-fertilizing plants by LEWIS (1941), is also valid for self-fertilizing species of plants. This may be obvious, since the transport of nuclear factors from one generation to another in normal plants is carried out to the same degree by pollen and ovaria, and since in MS plants one of these possibilities fails to occur. No indications are known, however, of q-values greater than one. In natural populations therefore only a slight percentage of monofactorial dominant MS plants will occur. If in every generation p% of MS individuals are induced by mutations, these populations (cross-fertilizing as well as self-fertilizing ones) at flowering time of its plants will eventually contain:

$$p + \left(\frac{q}{2}\right)^p + \left(\frac{q}{2}\right)^2 p + \dots + \left(\frac{q}{2}\right)^n \cdot p \% = \frac{2p}{2-q} \% \text{ of MS plants.}$$

The amount of this percentage is shown, for increasing values of q, in Table 2.

5. RATES OF REPRODUCTION OF RECESSIVE MS GENES

A. General

According to § 4, p% heterozygously mutated plants corresponds with about $p^2/200\%$ homozygously mutated ones. Regarding monofactorial recessive inherited MS the former are fertile, the latter MS. After self-pollination the former will produce $\frac{p}{2} \left(\frac{100-b}{100}\right) \%$ of heterozygous fertile (abbreviated by HF) and $\frac{p}{4} \left(\frac{100-b}{100}\right) \%$ of MS plants and after mutual cross fertilization $2 \cdot p/2 \cdot p/100 \cdot b/100\%$ of HF and $2 \cdot p/4 \cdot p/100 \cdot b/100\%$ of MS ones. From cross fertilization between the HF and the homozygous fertile (normal) plants $2 \cdot p/2 \cdot b/100\%$ of HF individuals will result. The number of HF and MS progeny produced by the $p^2/200 \%$ MS plants is negligible. In the first generation after the mutation pre-supposed consequently

$\frac{p(100 + b)}{200}$ % of HF and $\left(\frac{p(100 - b)}{400} + \frac{p^2b}{200 \times 100} \right)$ % of MS plants may be expected. The extent of both percentages and of its components depends strongly on the value of b.

B. *Self-fertilizing plants*

After neglecting cross-fertilization of the HF and normal plants the last mentioned percentages amount to $p/2$ and $p/4$, respectively. The former will produce $p/8$ % of MS and $p/4$ % of HF offspring; the latter will produce $p/4$ % of HF individuals. From this it is obvious that nearly all recessive MS genotypes are caused by mutation and by segregation of self pollinated HF plants only. The transport of recessive genes from one generation to another is carried out, however, by the HF individuals as well as by the MS plants. Considering these arguments the percentages of MS and HF individuals in consecutive generations can be calculated.

TABLE 1

Indicating, in column 2 and 3 respectively, the percentages of HF and MS plants, occurring in consecutive generations (column 1) of a self-fertilizing population, if mutations are supposed to occur in generation 0 only, thus inducing p % of HF and $p^2/200$ % of MS plants.

Generation	% HF individuals	% MS individuals
0	$y_0 = p \cdot (1)$	$p^2/200$
1	$y_1 = \frac{p}{2} \cdot (1)$	$\frac{1}{2}y_0$
2	$y_2 = \frac{p}{2^2} \cdot (1 + q)$	$\frac{1}{2}y_1$
3	$y_3 = \frac{p}{2^3} \cdot (1 + 2q)$	$\frac{1}{2}y_2$
4	$y_4 = \frac{p}{2^4} \cdot (1 + 3q + q^2)$	$\frac{1}{2}y_3$
n	$y_n = \frac{2^n}{p} \cdot \left(1 + \frac{n-1}{p}q + \frac{(n-2)(n-3)}{1 \times 2}q^2 + \frac{(n-3)(n-4)(n-5)}{1 \times 2 \times 3}q^3 + \dots \right)$	$\frac{1}{2}y_{n-1}$

It is clear from Table 1 and the figures 1 and 2 that monofactorial

recessive MS plants are ousted from a self-fertilizing population, unless in every generation new mutations induce MS. If these mutations produce $p\%$ of HF plants in every generation, the population will eventually contain percentages of HF and MS plants, fluctuating round constant values. At flowering time of the plants these percentages may be estimated best at $\frac{4p}{2-q}\%$ and $\frac{p}{2-q}\%$, respectively.

The amounts of these percentages are shown, for increasing values of q , in Table 2.

These estimations have been made after splitting up the expected percentage of HF plants $[y] = y_0 + y_1 + y_2 + \dots + y_n$ in its components $F(p)$, $F(pq)$, \dots and $F(pq^n)$, that appeared to be series of decreasing geometric progressions. In fact is $F(p) = p + p/2 + p/2^2 + \dots + p/2^n = 2p$, as is obvious from Table 1.

Furthermore:

$$\begin{aligned} f(pq) &= \frac{pq}{2^2} + \frac{2pq}{2^3} + \frac{3pq}{2^4} + \dots + \frac{(n-1)pq}{2^n} + \dots = \\ &= \left[\frac{pq}{2^2} + \frac{pq}{2^3} + \frac{pq}{2^4} + \dots + \frac{pq}{2^n} + \dots \right] + \\ &\quad + \left[\frac{pq}{2^3} + \frac{pq}{2^4} + \dots + \frac{pq}{2^n} + \dots \right] + \\ &\quad + \left[\frac{pq}{2^4} + \dots + \frac{pq}{2^n} + \dots \right] + \\ &\quad + \dots \left[\frac{pq}{2^n} + \dots \right] = \\ &= \left[\frac{pq}{2} \right] + \left[\frac{pq}{2^2} \right] + \left[\frac{pq}{2^3} \right] + \dots + \left[\frac{pq}{2^n} \right] + \dots = \frac{q}{2} f(pq). \end{aligned}$$

Also:

$$\begin{aligned} f(pq^2) &= \frac{pq^2}{2^4} + \frac{(1+2)pq^2}{2^5} + \frac{(1+2+3)pq^2}{2^6} + \\ &\quad + \dots + \frac{(1+2+\dots+(n-3))pq^2}{2^n} + \dots = \\ &= 1 \cdot \left[\frac{pq^2}{2^4} + \frac{pq^2}{2^5} + \frac{pq^2}{2^6} + \dots + \frac{pq^2}{2^n} + \dots \right] = \\ &\quad + 2 \cdot \left[\frac{pq^2}{2^5} + \frac{pq^2}{2^6} + \dots + \frac{pq^2}{2^n} + \dots \right] + \\ &\quad + 3 \cdot \left[\frac{pq^2}{2^6} + \dots + \frac{pq^2}{2^n} + \dots \right] + \end{aligned}$$

$$\begin{aligned}
 & + (n-3) \cdot \left[\frac{pq^2}{2^n} + \dots \right] = \\
 = & \frac{pq^2}{2^3} + \frac{2pq^2}{2^4} + \frac{3pq^2}{2^5} + \dots + \frac{(n-3)pq^2}{2^{n-1}} + \dots = \frac{q}{2} f(pq).
 \end{aligned}$$

In the same way:

$$\begin{aligned}
 f(pq^3) &= \frac{pq^3}{2^6} + \frac{4pq^3}{2^7} + \frac{10pq^3}{2^8} + \dots + \frac{pq^3(n-3)(n-4)(n-5)}{2^n \cdot 1 \times 2 \times 3} + \dots = \\
 &= 1 \cdot \left[\frac{pq^3}{2^6} + \frac{pq^3}{2^7} + \frac{pq^3}{2^8} + \dots + \frac{pq^3}{2^n} \right] + 3 \cdot \left[\frac{pq^3}{2^7} + \frac{pq^3}{2^8} + \frac{pq^3}{2^9} + \dots + \frac{pq^3}{2^n} \right] + \\
 &+ 6 \cdot \left[\frac{pq^3}{2^8} + \frac{pq^3}{2^9} + \dots + \frac{pq^3}{2^n} \right] + \dots = \\
 &= \frac{pq^3}{2^5} + 3 \cdot \frac{pq^3}{2^6} + 6 \cdot \frac{pq^3}{2^7} = \frac{q}{2} f(pq)^2.
 \end{aligned}$$

Since in general it can be derived that $f(pq^n) = \frac{q}{2} f(pq^{n-1})$, consequently:

$$\begin{aligned}
 y &= f(p) + f(pq) + f(pq^2) + \dots + f(pq^n) = \\
 &= 2p + \left(\frac{q}{2}\right) \times 2p + \left(\frac{q}{2}\right)^2 \times 2p + \dots + \left(\frac{q}{2}\right)^{n-1} \times 2p + \dots = \frac{4p}{2-q}
 \end{aligned}$$

The same result can be obtained with the aid of matrices.

The estimation of the percentages of MS plants can be carried out in the same way, although it is evident that it has to be $\frac{1}{4}$ of the percentage of HF plants.

C. Cross-fertilizing plants

After substituting $b = 100$, the percentages of HF and MS plants mentioned at the end of section 5A appear to be equivalent to $p\%$ and $p^2/200\%$, respectively. In the absence of mutations, in every subsequent generation the same percentages can be calculated. The constancy of the former is apparently due to the failure of segregation in cross-fertilizing populations.

As the monofactorial recessive MS plants preponderantly result from mutual fertilization of fertile heterozygotes, their part in a cross-fertilizing population must also be constant. These conclusions are not in agreement with LEWIS' view (1941) that monofactorial recessive MS individuals should be ousted from cross-fertilizing populations as quickly as the monofactorial dominant inherited types. LEWIS' conclusion (1941), however, is inconsistent with the practical experiences of many plant breeders and geneticists that in cross-fertilizing populations recessive genes are usually kept for a long

time in the population under the protection of the dominant alleles.

In fact it is concluded that monofactorial recessive inherited MS plants maintain themselves in cross-fertilizing populations, even when mutations fail to occur in every generation. If, however, these do occur to the same extent in every generation, the theoretically expected number of MS plants in consecutive generations will increase to the percentage discussed in section 3 and corresponding with the complete employment of all pollen occurring in the population.

6. REPRODUCTION OF INTERACTING FACTORS CAUSING MS

It follows from the Laws of Probability that the majority of mutated plants is expected to contain only one or a few interacting factors that can together cause MS. Consequently these plants will reproduce themselves to the same degree as the plants containing none of these factors. In fact in consecutive generations the frequency of genes, each partially responsible for the occurrence of MS, will be constant or increasing. According to section 5C this will also be the case with the expected percentage of MS plants, occurring in cross-fertilizing populations. The percentage of MS plants will increase in relation to the frequency of MS inducing mutations and the number of interacting factors required to induce MS.

From this it is obvious that all types of cytoplasmic inherited MS known in cross-fertilizing plants will be caused by interaction of cytoplasm and nuclear genes.

In self-fertilizing populations MS plants are largely produced by segregating heterozygous fertile individuals. The more factors required to interact to cause MS, the more the number of HF individuals, which can produce MS plants after selfing, will decrease and the lower the percentage of MS individuals generated by each of them. From this it is clear that in self-fertilizing plants only one bifactorial inherited and no polyfactorial inherited type of MS is known (V. D. KLEY 1954).

7. IMPORTANCE IN PLANT BREEDING AND GENETICS

In the preceding pages, MS plants, apart from their genotype and cytoplasm, in the absence of repeated mutations failed to maintain themselves to a considerable degree in *self-fertilizing populations*.

In arable crops this actually prevents the commercial use of MS, previously discussed (1954, 1955).

Since dominant MS genotypes and MS plasmtypes in the figures 1 and 2 appeared to be ousted more quickly than recessive MS genotypes,

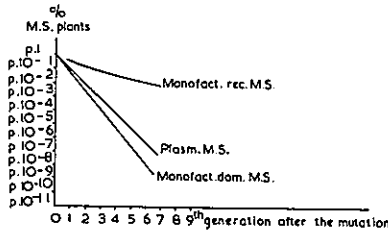


Fig. I

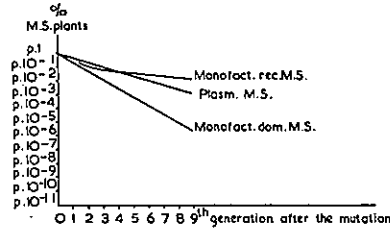


Fig. II

The ordinates (with logarithmic scale) indicate the percentages of MS plants, expected to occur in a self-fertilizing population. The abscissae show the number of generations that has been passed since the first origin of MS plants. Mutation to and remutation from MS plants are supposed to occur in the population with the same frequencies. In figure 1 the relative fertility of the MS plants is 0.1; in figure 2 it is 0.5.

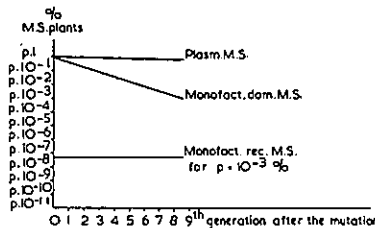


Fig. III

Fig. 3. The ordinates (with logarithmic scale) show the percentage of MS plants, expected to occur in a cross-fertilizing population. The abscissae show the number of generations that has been passed since the first origin of MS plants. Mutation to and remutation from MS plants are supposed to occur in the population with the same frequencies. The relative fertility of MS plants is supposed to be equivalent to that of the normal fertile ones. The percentage of monofactorial recessive MS plants in every generation is expected to be equivalent to $p^2/200$

the latter have been used in trials, carried out by SUNESON (1951), in order to overcome the objection mentioned. Results applicable in practice have, up to now, been obtained with the aid of artificial

TABLE 2

Percentages of MS plants (with relative fertilities q), in the long run expected to occur in natural populations at flowering-time of plants. In every generation $p\%$ of heterozygous or of MS individuals are supposed to be induced by mutations, which occur before flowering-time of plants. Percentages of MS types not mentioned, will be discussed in the text.

Method of inheritance of MS	Formula valid in	Expected percentage of MS plants	Relative fertility of MS plants										
			0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	0.99	
Cytoplasmatic	All populations	$\frac{p}{1-q}$	1.11p	1.25p	1.43p	1.67p	2.00p	2.50p	3.33p	5.00p	10.0p	100.0p	
Monofactorial dominant	All populations	$\frac{2p}{2-q}$	1.05p	1.11p	1.18p	1.25p	1.33p	1.43p	1.54p	1.67p	1.82p	1.98p	
Monofactorial recessive	Self-fertilizing populations only	$\frac{p}{2-q}$	0.52p	0.55p	0.59p	0.62p	0.66p						

pollination only in the case of some horticultural crops, e.g. tomatoes (RICK 1945). In order to obtain the MS breeding material desired, its frequencies in natural populations are of considerable importance. The relative fertility (q) of this MS material usually being small, the expected frequencies of various types of MS, shown in Table 2, appear to be small in self-fertilizing populations.

In fact the actually expected frequencies are strongly dependent on the values of p , which are usually unknown. They might be estimated, however, with the aid of the formulae given, after calculating the relative fertilities of sufficient numbers of MS plants, found in populations with known percentages of intercrossing.

Further, the occurrence of various non-allelomorphic genes causing MS (v. D. KLEY 1954) will increase the total frequency of MS genotypes. The types of MS not mentioned in Table 2, in sections 2, 5C and 6 proved to be able to increase in cross-fertilizing populations. This increase was shown to be possible up to a limit, depending on the amount of pollen available in the population.

Therefore it can be expected that in these populations MS breeding material can be successfully searched for. These expectations are supported by previously published practical experiences (1954).

8. SUMMARY

The percentages in which various male sterile (MS) genotypes and plasmtypes are expected to occur in self-fertilizing and cross-fertilizing populations occurring in nature, are discussed.

From Table 2 it is concluded that in general MS plasmtypes may occur with considerable frequencies in cross-fertilizing plants. The potential value of such material for practical breeding is high.

In self-fertilizing crops only low percentages of various types of MS plants are expected to occur. Various non-allelomorphic monofactorial recessive MS genotypes have been practically applied in the tomato.

Formulae, showing the relation between the frequencies just mentioned, the frequencies of mutations inducing MS, and the relative fertilities of MS plants are derived and summarized in Table 2. It is contended that the formulae given make it possible to estimate the mutability of various genes and cytoplasm.

9. SAMENVATTING

Tussen de frequentie waarmede diverse manlijk steriele planten in populaties van kruis- en zelfbevruchters voorkomen, hun relatieve vruchtbaarheid en de frequentie waarmede zij door mutatie ontstaan, werd een kwantitatief verband afgeleid (zie o.a. tabel 2). De afgeleide formules maken het mogelijk de mutabiliteit van diverse genen en van het plasmoon te berekenen. De samenhang der genoemde factoren werd berekend uit de in de grafieken 1 tot 3 aangegeven snelheden waarmede de diverse vormen van MS uit denkbeeldige populaties, waarin geen mutaties voorkomen, verdrongen worden. Afgeleid werd, dat bij gelijke mutabiliteit der diverse nucleo- en plasmafactoren in natuurlijke populaties van *kruisbevruchters* een aanzienlijk aantal plasmatisch steriele en monofactorieel recessieve MS planten verwacht mogen worden. In populaties van *zelfbevruchters* zijn bij een even grote mutabiliteit de kansen op het aantreffen der verschillende vormen van MS alle klein, vooral die op het aantreffen van een bepaalde vorm van recessief verervende MS. Van monofactorieel recessief verervende typen van MS zijn echter blijkens een vorige publicatie (v. D. KLEY, 1954) vele niet-allelomorphe vormen bekend.

De betekenis van deze conclusies voor de plantenveredeling werd besproken. Geconcludeerd werd, dat de vroeger (1954, 1955) besproken toepassingen van MS als hulpmiddel bij het kweken van heterosisrassen zich vooralsnog zullen moeten beperken tot kruisbevruchters en zelfbevruchtende tuinbouwgewassen.

LITERATURE CITED

- BAUMAN, L. F., ALEXANDER, D. E., JUGENDHEIMER, R. W., WOODWORTH, C. M., 1953, Experimental corn hybrids tested in 1952. Bull. Illinois Agr. Exp. Sta. 563: 19.
- FRANKEL, O. H., 1940. The significance of male sterility in the genetic system. Journal Genetics 40: 171-184.
- KLEY, F. K. VAN DER, 1954. Male sterility and its importance in breeding heterosis varieties. Euphytica 3: 117-124.
- KLEY, F. K. VAN DER, 1955. De betekenis van manlijke steriliteit voor de kweker van heterosiszaad. (with a summary: The importance of male sterility in the commercial production of hybrids) Med. Dir. Tuinb. 18: 11-20.
- KOOPMANS, A., 1952-1955. Changes in sex in the flowers of the hybrid *Solanum rybinii* × *S. chacoense*. I-III (Genetica, 26: 359-380, 27: 273-285.
- LEWIS, D., 1941. Male sterility in natural populations of hermaphrodite plants. New Phytologist 40: 56-63.
- RICK, C. M., 1945. Field identification of genetic male sterile tomatoplants for use in producing hybrids. Proc. Am. Soc. Hort. Sci. 46:277-283.
- STEPHENS, J. C. and QUINBY, J. R., 1945. The MS_2V_{10} linkage group in sorghum. J. Agr. Res. 70: 209-218.
- SUNESON, C. A., 1951. Male sterile facilitated synthetic hybrid barley. Agr. J. 43: 234-236.