NATIONAL INSTITUTE OF GENETICS

(JAPAN)

ANNUAL REPORT

No. 2.

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(MISIMA, SIZUOKA-KEN, JAPAN)

1952

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Contents

Addendum

GENERAL STATEMENT

In 1951 the equipment of the Institute improved, and all its research activities made good progress. The main building which had been rented from the Fuji Industrial Company was purchased for the exclusive use of the Institute. Two new small buildings, one for breeding rats and mice and the other for silkworm culture, were completed and are in use. The land which had belonged to the Ministry of Education was legally transferred to the Institute. Also a piece of land 4,418 tubo (3.61 acres) in size was rented in the neighborhood as a nursery for rare varieties of cultivated trees and shrubs, as well as for the site of staff residences.

The library has been expanded by the addition of several back series and numerous current numbers of periodicals and many new books. Dr. R. GOLDSCHMIDT has continued to send reprints, journals and books newly acquired by him to bring the library which was formerly his own up to date. These new publications are very valuable, especially as our subscriptions to current journals are regretably limited.

Prof. S. MAKINO of Hokkaido University was appointed part-time member of the Institute. He is currently on leave for one year to study cytology in the United States. Research assistants M. OGAKI and S. KAJI resigned and were replaced by S. TSUDA and K. TUTIKAWA respectively. The number of regular members of the Institute has been raised from 33 to 38, by the addition of 5 field laborers.

S. MATSUMURA was awarded the Genetics Prize by the Genetic Society of Japan for his investigations on pentaploid wheat. T. KOMAI was elected corresponding member of the American Society of Human Genetics.

A number of research grants were received during the year by our staff. These have been of great aid to our research programs. The Ministry of Education granted from the Scientific Research Fund the following sums to our members to aid their respective researches:—

K. OGUMA and coworkers (including T. KOMAI, K. TUTIKAWA):

Breeding and reservation of strains of rats and mice suited for medical research purposes—¥730,000;

T. KOMAI and coworkers (including K. SAKAI and M. KIMURA): Researches in population genetics—¥500,000,

(Individual research items: T. KOMAI: Researches in population genetics with insects and a land-snail as materials, K. SAKAI: Competition between plants of different genotypes in a population, M. KIMURA: Theoretical researches on population genetics);

Y. TANAKA and coworkers (including M. TSUJITA): Fundamental and applied genetics of the silkworm—¥350,000,

(Individual research items: T. TANAKA: Phenogenetics of the silkworm, M. TSUJITA: Embryological and physiological genetics of the silkworm);

S. MATSUMURA: Radiation genetics of wheat and barley—¥40,000;

S. MATSUMURA: Breeding of wheat strains resistant to rust by means of the D-genome substitution—¥40,000.

The following researches were supported by the grants from the Scientific Experiment Fund of the Ministry of Education:—

S. MATSUMURA and coworkers: Breeding of triploid sugar-beet strains—¥100,000;

M. TSUJITA and coworkers (including B. SAKAGUCHI): Studies on lethality and failure of fertilization in the silkworm—¥50,000.

The Ministry of Education also gave the following extra-budgetary sums to the Institute:—

Expense for construction of constant temperature room used for the preservation of silkworm eggs and *Drosophila* strains—¥1,100,000;

Expense for purchasing an ultra-thin sectioning microtome—¥216,000.

The Ministry of Agriculture and Forestry granted from its fund for promoting investigations on techniques in agriculture, forestry and fishery to

K. SAKAI: Investigation on the efficacy of the bulk-breeding method—¥100,000.

Y. TAKENAKA gave from November 5 to 12 a series of lectures on genetics in Kanazawa University.

Among the large number of visitors was Prof. H. J. MULLER

of Indiana University. Prof. MULLER spent a week from April 8 to 15 in Japan on his trip back from India to the States. After an extremely busy two-and-half day program in Tokyo, being received in audience by the Emperor, attending a welcome party sponsored by the Japan Academy, delivering a public lecture to a large audience and visiting Tokyo University and the Sericulture Experiment Institution, he came to Misima on the 11th at about 10 o'clock in the morning. He heard reports of four geneticists from outside the Institute on the recent outcomes of their studies. He next gave a lecture on recent advances in genetics to an audience which consisted of the members of the Institute and many other biologists who had come to hear the well-known geneticist from all parts of Japan. He then went around the Institute and inspected the work of the members. In the evening he left Misima, and went to Atami, where he dined with the five senior members of the Institute (Fig.). He took a night train from Atami to Hiroshima with Drs. W. J. SCHULL of A.B.C.C., KIHARA and KOMAI. After inspecting the work in progress at the A.B.C.C. and giving a lecture at Hiroshima University, he stopped over at Kyoto on his way back, and gave another lecture in Kyoto University. On the whole, Dr. MULLER'S visit was highly beneficial not only to the Institute, but also to genetics and biology in Japan at large.

SCHULL, SINOTÔ, KIHARA, MULLER, OGUMA, KOMAI, TANAKA.

ABSTRACT OF DIARY IN 1951

January 15. A 4,418 tubo (3.61 acres) plot of land at Sironouti, Yata, in Misima was rented to be used as a nursery of useful plants and site of residences of the staff.

January 27. Third meeting of Misima Geneticists' Club.

February 24. Fourth meeting of Misima Geneticists' Club.

March 3. Board meeting of Association for the Propagation of the Knowledge of Genetics.

March 4. Committee meeting of the Genetic Society of Japan, Joint meeting of the National Committee of Genetic Researches and the National Committee of Researches in Plant and Animal Breeding of the Japan Science Council.

March 20. The land 24,524 tubo (20.01 acres) in extent has legally become the property of the Institute.

March 21. A part of the main building, 764.32 tubo in floor area, was purchased from the Fuji Industrial Company.

April 1. The number of regular members of the Institute was raised from 33 to 38. The office of the Genetic Society of Japan was moved from Tokyo University to the Institute.

April 11. Dr. H. J. MULLER visited the Institute and gave a lecture (see the foregoing report). The joint meeting of the National Committee of Genetic Researches and the National Committee of Researches in Plant and Animal Breeding of Japan Science Council. Fifth meeting of Misima Geneticists' Club. Meeting of Sizuoka Plant and Animal Breeders' Club.

May 11. Sixth meeting of Misima Geneticists' Club.

May 14. Fifth meeting of the Board of Councillors.

June 15. Seventh meeting of Misima Geneticists' Club.

July 31. Miss Carlyn HALDE's lecture on dermal diseases caused by parasitic molds.

November 18. Eighth meeting of Misima Geneticists' Club.

December 19. Meeting for interim reports on the fundamental studies for the improvement of tobacco plants.

December 22. The remaining part of the main building, 401.34 tubo floor area, was purchased. Ninth meeting of Misima Geneticists' Club.

STAFF

Department and Laboratory Heads

Kan OGUMA, D. Agr., Director, and Head of the Second Department
Yoshimaro TANAKA, D. Agr., D. Sc., Head of the First Department
Taku KOMAI, D. Sc., Head of the Third Department

Part-time Staff

Hitoshi KIHARA, D. Sc., Professor of Kyoto University
Yosito SINOTÔ, D. Sc., Professor of Tokyo University
Sajirô MAKINO, D. Sc., Professor of Hokkaido University

Laboratory Heads

Yô TAKENAKA, D. Sc.
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Tôru ENDÔ
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Sumiyoshi SUGIO, Head of General Business Section
Masao MIYAZAWA, Head of Finance Section
Naomi MATSUBARA
Hiroko NAKANO
Junzô KADOWAKI
Typist, Telephone operator, Chauffeurs, Field laborers, Janitors, etc.—14.

Misima Branch of Hatano Tobacco Experiment Station
Masao TANAKA, Head
Flora A. LILIENFELD, Ph. D.
Seiji IMAI
Assistants—3.

Whole-Japan Association of Poultry Genetics
Kan OGUMA, President
Yoshimaro TANAKA, Director of Researches
Také NAKAMURA, Managing Director

Association for Propagation of the Knowledge of Genetics
Kan OGUMA, President
Yô TAKENAKA, Managing Director
Seiji MATSUMURA, Managing Director

COUNCIL

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Kiyoshi MASUI, Emeritus Professor of Tokyo University, Professor of Nagoya University
Bungo MIYAZAWA, President of Woman's College of Anjô University
Toshitarô MORINAGA, Head of the Department of Physiology and Genetics of Agricultural Technique Institute
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Masanori NAKAIZUMI, Professor of Tokyo University
Yusuké SUMIKI, Professor of Tokyo University
Yûshi UCHIMURA, Professor of Tokyo University
Yasuké YAMAGUTI, Professor of Ibaraki University

RESEARCH PROGRAM FOR 1951

Tanaka Laboratory

Unstable genes—TANAKA

Selection and stability of genes—TANAKA

Genetic study of the dominant retarded silkworm—TANAKA

Genetic analysis of the recessive retarded silkworm—TANAKA

Photoperiodic effect on the diapanse of a wild silkworm *Antheraea pernyi*—TANAKA

Matsumura Laboratory

Radio-genetic studies on wheat—MATSUMURA and FUJII

Agropyrum as a close relative of *Triticum*—MATSUMURA

Nullisomics found among the progeny of pentaploid hybrid wheat —MATSUMURA

Breeding of triploid sugar beet—MATSUMURA, MOCHIZUKI (Kyoto Univ.), et al.

Mutation in *Nicotiana* by X-ray irradiation—KIHARA, MATSUMURA and FUJII

Breeding of strain of wheat resistant to rust—MATSUMURA and HIRATSUKA (Tokyo Univ. of Education)

Triticale—ENDÔ

Furusato Laboratory

Breeding of *Citrus* varieties—FURUSATO and MIYAZAWA

Production and breeding of polyploid plants—FURUSATO

Biochemical genetics of flower colors—ENDÔ and MIYAZAWA

Oguma Laboratory

Origin of sex-chromosomes—OGUMA

Phylogeny of animals and plants based on karyotype analysis—OGUMA, SINOTÔ and TAKENAKA

Genetics of right- and left-handedness in plant organs—KIMURA

Theoretical studies of population genetics—KIMURA

Origin of the plants of the genus *Lycoris* and their distribution —KIHARA and LILIENFELD

Cytogenetics of rat and mouse—OGUMA and TUTIKAWA

Takenaka Laboratory

Collection and preservation of varieties of useful plants—TAKENAKA

Origin of sex-differentiation in higher plants—TAKENAKA

Cytogenetics of some fungi—SINOTÔ and ITÔ

Komai Laboratory

Genetics of microcephaly in man—KOMAI, KISHIMOTO (Nagoya Univ.) and OZAKI (Inst. Public Health)

Japanese pedigrees of typical brachydactyly—KOMAI

Genetics of coat colors in cats, and the problem of origin of tortoiseshell male—KOMAI

Population genetics of the lady-beetle *Harmonia*—KOMAI

Genetics of the butterflies *Colias* and *Neozephyrus*—KOMAI

Population genetics of the land-snail *Bradybaena*—KOMAI

Sakai Laboratoay

Genetics of fruit-crops—SAKAI and GOTOH

Competition between plant individuals having different genetic constitutions—SAKAI and GOTOH

Theoretical and experimental studies on selection in plant breeding—SAKAI

Genetic study of competitive capacity of plant individuals—SAKAI

Genetic studies on flowering shrubs—GOTOH

Tsujita Laboratory

Virus infecting silk-producing insects—TSUJITA and SAKAGUCHI

Lethal eggs and sterility in silk-worm—TSUJITA and SAKAGUCHI

Manifestation of gene effects—TSUJITA and SAKAGUCHI

Developmental genetics of silk-worm—TSUJITA and SAKAGUCHI

Minute structures of chromosome—TSUJITA and SAKAGUCHI

Cytogenetics of silk-worm, especially polyploids—TSUJITA

Research Students and their Research Items:

Kôzô NAKAMURA: Polyploidy in plants

Yasuo SUZUKI: Breeding of polyploid plants

Seizô TSUDA: Genetics of useful molds

Kyôzo WATANABE: Hybridization between local races of newts

Tôru IWATA: Relation between chromosome number and speciation in plants

RESEARCHES CARRIED OUT IN 1951

A. HUMAN GENETICS

(Report by Taku KOMAI)

1. Japanese Pedigrees of Typical Brachydactyly

Three kindreds of typical brachydactyly have been discovered recently in Yokosuka, at a village near Matumoto (Nagano Pref.) and in Asiya (Hyogo Pref.). These include respectively 10, 18 and 6 patients besides a few doubtful cases. The abnormality consists of marked degeneration of the middle phalanges of *all* fingers and toes. This has been confirmed by X-ray photos of the hands and feet of some patients. Each kindred shows peculiarity in the details of the abnormality. The patients in the Matumoto kindred show abnormality almost identical to that in the patients in DRINKWATER's English pedigree and in ILTIS' American pedigree. The inheritance is monogenic, the abnormal character being dominant with perfect penetrance.

2. Genetic and Aetiological Studies on Microcephalic Idiots

Since last year, materials have been gathered for study of this severe congenital defect. So far nearly 60 cases have been obtained. Anthropometric and psychological tests have been conducted and pedigrees followed for nearly all of them. The patients are idiots of the extreme degree, the mental age being 2 at best. This abnormality is apparently due to a recessive gene. Complications, however, seem to exist. There are some cases which seem to be caused by simple developmental haphazard, without any relation to heredity. The present study will be nearly completed by the end of this year. It is expected that some data of general interest will be disclosed.

B. CAT GENETICS

(Report by Taku KOMAI)

Inheritance of Common Color Types and the Origin of Tortoiseshell Male

Census of cat populations have been conducted in Misima and Gotemba, as well as in several towns in Hokkaido, and the results have been analyzed with respect to the frequency and the location of the genes for

the common colors. Undisputable evidence has been obtained by this procedure of the sex-linkage of the gene for orange color and of the presence of the genes for tabby and black in an autosome. Among Japanese cats the frequency of the gene for orange is much higher than among the cats in London, the former being as high as 25–40 per cent as compared with the 10.7 per cent given as SEARLE's figure for the latter.

Fourteen specimens of tortoiseshell males have been examined, besides data on their mothers and litter mates. It has become clear that a tortoiseshell male can be produced by either a tortoiseshell mother, or by an orange or a black mother. Sections of testes of two of these specimens have been examined. They show characteristics of testes of perfect sterility, but nothing suggesting an intersexual gonad. These findings do not accord with the working hypothesis formally proposed by the writer. It is more plausible that the cause of the production of this kind of abnormal individual lies in the germ cell of the father, instead of that of the mother. If crossing-over takes place between the X and Y chromosomes in the spermatocyte of the father, the gene for the orange color O or its allele O^+ may be transferred from X to Y. Reciprocally, the gene-complex for fertility of the male may be transferred from Y to X. The son which receives such a crossover Y will become tortoiseshell and sterile. This hypothesis postulates a gene-complex for fertility in Y whose presence has never been demonstrated in any mammalian Y chromosome. This postulate has been made from the analogy of the construction of the Y chromosome in *Drosophila*, and it does not seem to be very improbable, if applied to the case in a mammalian cell.

C. SILKWORM GENETICS

1. *Genetical Interrelationship between Modifiers of Multilunar, Multistars and Knobbed in the Silkworm*

(Report by Yoshimaro TANAKA)

When two characteristics of skin, either multilunar (L) and multistars (ms), or multilunar and knobbed (K), or multistars and knobbed, coexist in the same individual, both characters exactly coincide in arrangement of composite spots and protuberances. For example, if L spots develop in each of the 4th to the 8th larval segments, the coexisting knobbed is also found in exactly the same segments. In any segment where an L spot is unpaired, the knob, if K gene is present, is invariably one-sided.

This fact seems to indicate that these characters have common modifiers which determine the arrangement of spots and knobs. The present

study, however, has disclosed that there is no ground for this supposition, as shown by the following findings:

a) There are characteristic arrangement patterns in the offspring for each of the three characters in question.

b) These characteristic patterns reappear in the offspring, whenever the major genes, *L*, *ms*, and *K*, are segregated in F_2 and later generations.

It is evident, therefore, that the coincidence in arrangement of these spots and knobs when they occur in the same individual is not of a genetic nature, but is due to a similarity in the developmental mechanism of these characters which are all related to the skin, especially to the dermal pigment.

2. *Modifiers of the Genes for Multilunar, Multistars and Knobbed Characters*

(Report by Yoshimaro TANAKA)

Studies on the numbers and kinds of modifiers of these three characters have not yet been completed. The following list is therefore a tentative one.

a) Modifiers controlling the arrangement types of multilunar

L_{10} Produces *L* spots in segments 4–10
L_9 Produces *L* spots in segments 4–9
L_8 Produces *L* spots in segments 4–8 (the standard type)
L_{4s} Suppresses *L* spots in segment 4
L_{6s} Suppresses *L* spots in segment 6
L_{7s} Suppresses *L* spots in segments 6 and 7

b) Modifiers controlling the arrangement types of multistars

ms_{4-10} Produces star spots in segments 4 and 6–10
ms_{6-10} Produces star spots in segments 6–10
ms_{6-9} Produces star spots in segments 6–9
ms_{8-10} Produces star spots in segments 8–10
$ms_{8,9}$ Produces star spots in segments 8 and 9
ms_8 Produces star spots in segment 8 (apparently $+^p$ type)
ms_0 Produces no star spot

c) Modifiers controlling the arrangement types of knobbed

K_8 Produces knobs in segments 2,3,5,8 (the standard type)
K_9 Produces knobs in segments 2,3,5,8,9
$K_{6,7}$ Produces knobs in segments 2,3 and 5–8
K_{10} Produces knobs in segment 10 (irrespectively of other segments)

3. *Unstable Genes or Polygenes?*

(Report by Yoshimaro TANAKA)

MATHER's theory of polygenes had been devised primarily to explain the effect of selection. The author's hypothesis of unstable genes also stands on the basis of effective selection. It seems therefore desirable to examine whether the polygene theory could be applied to the case in silkworm. I find some difficulties in explaining the results thus far obtained on the basis of the polygene hypothesis in connection with the following points:—

a) According to the polygene theory, the variation in F_1 of a cross between two inbred strains is nearly the same in extent as in the parents; in F_2 it suddenly increases and attains a maximum value; then it gradually decreases in later generations.

This is not the case with the unstable genes governing the arrangement types of *L*, *ms* and *K* characters. To give an instance, the cross between two strains having different *L* arrangement types, both intensely inbred, has often shown variability which is highest in F_1, and decreases gradually in F_2 and later generations. The 0 type of *ms* marking is another example. Although it is an established strain, it sometimes segregates only in a negligible percentage in F_2 of the cross with the 8–10 type, and often it does not appear at all. In other crosses the 0 type occurs as early as F_1, and in still others appears first in F_3.

b) In contradiction to the expectation of the polygene theory, no arrangement type characteristic to *L*, *ms* and *K* becomes fixed, nor does it breed true even after a considerable number of generations of selection by inbreeding. The strains throw more or less different types in each generation, from which it is possible to breed a new type by selection.

4. *Appearance of a Recessive Retarded Strain from a Dominant Retarded Strain in the Silkworm*

(Report by Yoshimaro TANAKA)

In a strain which was produced by X-ray irradiation and presumably involves a deficiency and an inversion in chromosome II, the two characters *p* (plain marking) and *Y* (yellow blood) are inherited together as if they were completely linked. The heterozygotes are characterized by retarded development, small body size and small cocoon. The homozygotes mostly pass through the embryonal stage, but perish as larvae or pupae. The lethal action of this aberration therefore is apparently rather weak. This fact suggests that the deficiency in this strain is comparatively small. I mentioned in former papers (1934, 1935) that no cros-

sing-over occurs between *p* and *Y* in this strain. Later, however, I ascertained the occurrence of a small amount, about 1.7%, of crossing-over between them. I shall tentatively designate this dominant character for retarded development by the symbol *Rt*.

In the second season of 1951, 3 cultures from the cross $+/+ \times Rt/+$ were reared. One of them segregated + and *Rt* in a 1 : 1 ratio, while two produced two to three times as many + as *Rt*. A differential mortality was out of the question, because there was no marked difference in the total numbers between hatched and grown larvae. It can be inferred from the results in later generations that the dominant character for retarded development changed to a similar but recessive one in a part of the germinal cells of the male parent.

In the next generation of normals from the culture in which normals and retarded had segregated in a 1 : 3 ratio, both types were produced almost exactly in a 3 : 1 ratio. These normals were again mated among themselves, and 3 cultures were reared. One lot gave normals only, while the other two segregated normals and recessive retarded (designated by the symbol *rd*) in a 3 : 1 ratio.

What was the cause of the production of this recessive retardation strain from the dominant retarded strain? Two considerations seem possible.

a) A new recessive mutation occurred independently from the original dominant character for retarded.

b) The chromosome aberration which had caused the dominant retardation changed in length or position through some segmental interchange, and became a recessive character as in the case of the position effect of "hairy" in *Drosophila*.

For the moment I cannot decide which is the correct explanation, but I am inclined to adopt the second view, because there is a very close similarity between the two retarded types, except for the reversed dominance relations. If this is established, the present case seems to be the first example of position effect found in the domestic silkworm.

5. *Changes of the Long-Day Effect to a Neutral One in the Photoperiodism of a Wild Silkworm, Antheraea pernyi*

(Report by Yoshimaro TANAKA)

The author (TANAKA, 1950) has proved that photoperiodism plays the most important role in determining the hibernating character of the Chinese tussar silkworm, *Antheraea pernyi* GUER. When the larva is exposed throughout its life to the short-day treatment, below 14 hours per day, it becomes a hibernating pupa without exception. If it is exposed to a long-day treatment, over 15 hours per day, it invariably gives

a non-hibernating pupa. The intermediate day-length, between 14 and 15 hours per day exerts no positive effect; it shows a neutral behavior as to photoperiodism, and both hibernating and non-hibernating pupae are produced. Constant light and constant dark do not, contrary to expectation, behave as extreme cases of long-day and short-day respectively; their effects are similar and neutral.

In order to find how the long-day effect changes into the neutral one under the constant exposure to light, the larvae were treated with a short-day exposure (8 hrs) through I to IV instars, and only V instar was exposed to different light conditions. The results are as follows:

Lot No.	Day-length in V instar	Hibernating pupae, on the average
23–24	16 hrs per day	41.9%
25–26	18 ,,	52.3 ,,
27–28	20 ,,	83.8 ,,
29–30	22 ,,	88.7 ,,
31–32	24 ,, (constant light)	95.4 ,,

The increase of the percentage of hibernation in the classes from 16 hrs upwards to 24 hrs shows a decrease of the long-day effect or non-hibernation-inducing effect exerted upon the larvae in the last instar counteracting the short-day or hibernation-inducing effect imposed on them in I to IV instars. Thus we know that the long-day effect changes somewhat gradually to a neutral effect, although there is a remarkable gap between 18 and 20 hours.

6. *Studies on the So-called Multi-allelic E-series in the Silkworm*

(Report by Mitsuo TSUJITA)

A. Studies on the new multi-star-marking gene E^{Ms}

E^{Ms} is a new gene belonging to the multiple-allelic E-series of the silkworm. E^{Mc} has originated apparently by mutation of E^{Ms}, though it could be due to some change in chromosomal structure. TSUJITA and SAKAGUCHI are now studying the action of these genes in relation to the other alleles of the same series, such as E^{H}, E^{Kp}, E^{D}, E^{El}, E^{Ca}, E^{N}, E, from the embryological and genetical points of view. A general summary of the experimental results follows:—

1) Both E^{Ms} and E^{Mc} have a markedly lethal action. Embryos homozygous for E^{Ms} have supernumerary abdominal legs on the 10th and 11th segments, and die in the later embryonal stages or immediately after hatching. The embryos homozygous for E^{Mc} also die in later embryonal stages or immediately after hatching; they have thoracic legs and thoracic setae on all segments, and are incapable of blastokinesis.

2) Embryos of the heterozygotes E^{Ms}/E^{D}, E^{Ms}/E^{N}, E^{Ms}/E^{Ca} and those of heterozygotes E^{Mc}/E^{D}, E^{Mc}/E^{N}, E^{Mc}/E^{Ca} die in the pigmentation period. Supernumerary legs, or fusion of segments, or deformity of some internal organs, may be observed in the lethal embryos.

3) It may be noted that the percentage of lethal embryos is different in reciprocal crosses between normal and E^{Ms} or E^{Mc}. When the mother is of the former type, the percentage of lethal embryos becomes much higher than in the reciprocal cross. The cause of this difference, however, remains to be clarified.

4) Very few individuals with a combination of the characters peculiar to each type have been obtained by mating a normal female with a male heterozygous for E^{Ms} or E^{Mc} in combination with other genes of the same series. However, whether this is due to genetic recombination cannot be ascertained until the suceeding generation are examined.

5) In short, it appears that E^{Ms} and E^{Mc} are genes participating in the formation of the larval structure in the early developmental stages, and that they have a pleiotropic effect like other genes of the E-series.

B. Larvae of the genotype $\dfrac{E^{H}E^{Kp}}{+\ +}$

Fifteen genes E, E^{Kp}, E^{Ca}, E^{Cr}, E^{El}, E^{D}, E^{H}, E^{Nc}, E^{Np}, E^{Ds}, E^{Ms}, E^{Mc}, E^{Ns}, E^{N}, E^{A} are located at the end of chromosome VI. It has been shown that they form a multi-allelic series, although some workers have expressed their scepticism of this interpretation. Most of the genes produce extra-legs or extra-semilunar patterns or both on two or three abdominal segments of the larva.

In a previous investigation, TSUJITA and SAKAGUCHI (1951) obtained individuals trisomic with respect to chromosome II. During 1951, experiments were carried out to obtain individuals trisomic with respect to chromosome VI. This aim has not been attained, but some other interesting facts, as described in the following paragraphs, were found. Males heterozygous for the genes E^{H} and E^{Kp} from the allelic series mentioned above were dusted with B.H.C. powder, or treated with radiation of high frequency waves. These treated males were mated with normal females. As controls heterozygous males which had not been treated either with B. H. C. or radiation were mated with normal females. Among the progeny of the former cross a small number of individuals with combined E^{H} and E^{Kp} types were found. Some such exceptional larvae, however, were also obtained from the control lot. Therefore, it seems that this apparent change in genetic constitution can occur without any relation to B.H.C. dusting or radiation.

Breeding tests of the individuals with the combined characters have disclosed that they are due to the recombination of E^{H} and E^{Kp} i.e.

$\frac{E^H E^{Kp}}{+\ +}$. These larvae have a phenotype which is more than the combination of the characters peculiar to E^H and E^{Kp}, representing a new type characterized by the presence of extra abdominal legs on the first and second abdominal segments as well as of extra-semilunar patterns on the first abdominal segment. They are thus easily distinguished from the $\frac{E^H +}{+ E^{Kp}}$ larvae.

From the cross wild $(+) \times \frac{E^H E^{Kp}}{+\ +}$ a few E^H and E^{Kp} larvae always segregate, obviously by recombination.

Embryos of the genotype $\frac{E^H E^{Kp}}{E^H E^{Kp}}$, have extra-legs which develop almost to the same size as the normal abdominal legs. Under a definite environmental condition these embryos die immediately before the pigmentation period. The phenotypes of $\frac{E^H E^{Kp}}{E^H +}$ and $\frac{E^H E^{Kp}}{+ E^{Kp}}$ show a distinction in that the extra-leg development is more pronounced in the former combination than in the latter. The phenotype of the $\frac{E^H E^{Kp}}{+\ +}$ larvae can hardly be distinguished from that of E^{Kl}. E also shows a very similar phenotype.

The gene E^H has a slight lethal effect in the heterozygous state, while the effect is somewhat stronger in the homozygote. The gene E^{Kp} has little lethal action both in heterozygote and homozygote. The lethal action of the genotype $\frac{E^H E^{Kp}}{+\ +}$ is stronger than that of types $\frac{E^H}{+}$, $\frac{E^{Kp}}{+}$, or $\frac{E^H +}{+ E^{Kp}}$. There is little difference in the intensity of lethal action between the $\frac{E^H E^{Kp}}{E^H E^{Kp}}$ and the $\frac{E^H}{E^H}$ individuals. In the degree of lethal effect, the genotype $\frac{E^H +}{+ E^{Kp}}$ is almost the same as the genotype $\frac{E^H E^{Kp}}{+ E^{Kp}}$.

From the facts presented above*, it seems that the genes belonging to the E-series behave as either allelic or tightly linked genes, and it is likely that the E "locus" is not a point but has a stretch of some extent. Perhaps it consists of several genes with similar effects arranged in close sequence at the end of chromosome VI. This kind of gene group has been called by various names (comp. KOMAI 1950); MULLER (1948) has called it "semi-allelic genes". The fact that the phenotype of $\frac{E^H E^{Kp}}{+\ +}$ is

* According to ITIKAWA (1951), some $E^A E^{Nc}/+$ individuals due to recombination between E^A and E^{Nc} were obtained.

clearly different from the phenotype of $\frac{E^{H}+}{+E^{Kp}}$ should be regarded as another good example of position effect which was demonstrated first in Bar in *Drosophila melanogaster*.

7. "*Lethal Yellow*" *Gene in Bombyx and its Relation to* "*Lemon*"

(Report by Mitsuo TSUJITA)

The lethal yellow gene in the silkworm is recessive. The larvae homozygous for this gene show a distinct yellow body color directly after the first moulting and die within a few days because of their inability to feed. The yellow color is due to the pigment "xanthopterine-B", contained mostly in the pigment granules of the hypodermal cells.

In order to make clear the relation between this lethal yellow and "lemon" which has a similar phenotypic effect, 9 batches of F_1 hybrids between the homozygous lemon (*lem/lem*) and the heterozygous lethal yellow (*+/ly*) were examined. All larvae hatched from 3 of these batches were normal, while normals and lemons were found in the ratio 1 : 1 among the larvae hatched from the other 6 batches. No lethal larvae were obtained from sib-matings of normal individuals produced in the former as well as in the latter batches, but among the lemon larvae in one of the latter batches about 25% were dead in the egg. Although it might appear strange that we could not find any lethal yellow larvae immediately after the 1st moulting, the reason is easy to see. The full-grown embryo, which is of a yellowish brown color, cannot chew up the chorion to hatch out, because of the incomplete differentiation and insufficient hardening of the mandibles. If such an embryo is released by cutting the chorion, it emerges as an apparently normal larva and moves about actively, but it cannot eat mulberry leaves and soon starves to death. The death of the full-grown embryo in this case is similar to the case reported by TSUJITA (1951) of the death of the larvae immediately after the 1st moulting.

The characteristic dead eggs may be called "lethal yellow eggs". These eggs resemble the eggs of the red-larva strain not only in their external features in the pigmentation period, but also in the appearance of the embryo inside the chorion. They are, however, easily distinguishable from the latter by their inability to hatch.

A few batches in back-cross F_1 lemon × lethal yellow, produced only normal larvae, while the other batches (amounting to about 2/3 of the total) segregated normal, lemon and lethal yellow eggs in the ratio 2 : 1 : 1. Also, in the back-cross lethal yellow × F_1 lemon, the larvae of three types segregated in the ratio normal 2 : lemon 1 : lethal yellow 1.

It is well known that lemon is recessive to normal (OGURA 1922). The recessiveness of lethal yellow to wild has been ascertained by SUZUKI (1950). The experimental results described above clearly show that lemon is dominant to lethal yellow. Therefore, I could draw the following conclusions: i) The three genes +, *lem*, and *ly* form a multi-allelic series, and ii) their dominant-recessive relation is $+ > lem > ly$.

The reciprocal crosses between $+/ly$ and lem/ly give somewhat different results:— When the female is $+/ly$ and the male lem/ly, the embryo homozygous for *ly* becomes a normal black-colored young larva and hatches out, but in the reciprocal cross, the young larva in the egg, which is colored yellowish brown, cannot hatch out. It is thus clear that the stage of death is controlled by the genetic constitution of the mother used in the crosses. Therefore, it may be said that inheritance of the lethal yellow character represents another case of maternal inheritance in the silkworm. And this special genetic behavior seems to be based on a difference in the substances within the eggs participating in the formation of pigments, such as melanin and xanthopterine-B, as well as on the interaction between them. For the confirmation of this point the aid of biochemist is to be sought for.

The embryo and the 1st-instar larva, homozygous for the gene *ly* are sensitive to environmental factors, as pointed by UMEYA (1951). For example, of the newly hatched larvae of the lethal strain ($+/ly$) reared in a chamber kept at high temperature and low humidity, more individuals die before the 1st moulting than when they are reared at relatively low temperature and high humidity.

8. *Sterility in the Silkworm due to an Abnormality in the Bursa Copulatrix*

(Report by Mitsuo TSUJITA)

TSUJITA and SAKAGUCHI are now working on the genetics of sterility found in the Nf_1 strain. The results obtained last year are summarized below:—

The females of this strain produce almost as many eggs as those of the normal strain. More than 90 percent of these eggs, however, are not fertilized; the percentage is often even below 1.

The results of the reciprocal crosses between the normal (N) and the sterile strain (Nf_1) are as follows:

$$Nf_1 \times Nf_1 = \text{sterile}$$
$$N \times Nf_1 = \text{fertile}$$
$$Nf_1 \times N = \text{sterile}$$

Judging from these results, it is clear that the sterility is due to some defect in the female. Therefore, the structure of the internal sexual organs, i.e. bursa copulatrix, ductus bursae, ductus seminalis, ductus tortuosus, glandula receptaculi, in these abnormal females has been examined; and we have found an abnormality existing in the bursa copulatrix.

The bursa copulatrix of such a female after copulation contains a spermatophore, but the passage of this organ to the ductus seminalis is choked with fibrous stuff which hinders spermatozoa bundles or a single spermatozoon entering the receptaculum seminis. Variation may be seen in the amount of this fibrous stuff. When it is large, complete obstruction occurs, but when it is small, some spermatozoa may migrate into the receptaculum seminis. It is evident that the very low fertilization rate of this strain is due to the presence of this substance. This fibrous stuff may be found filling the whole space between the wall of the spermatophore and the cuticular layer of the hypodermis, but it is most abundant in the cavity in the proximal portion of the bursa copulatrix. Occasionally, even the ductus bursae or the ductus seminalis is filled with this stuff.

As for the nature of this fibrous material, our studies have shown that it is a product of the hypodermis of the bursa copulatrix. The cuticular layer of the flat hypodermal cells is composed of a compact aggregation of fibrous bodies running parallel in a transverse direction. Mitochondria seem to participate in the formation of these bodies.

As to the origin of the fibrous stuff in the lumen of the organ, it is possible that it is liberated from the apical layer of the fibers composing the cuticular layer, or it may be newly secreted from the apical portion of the cuticular layer. At present, the first explanation seems to be the more plausible one.

Genetical analysis of this sterility is now under way.

9. *On the Relation of Penetrance of a Gene (or a Gene-set) Causing Malformation to Environmental Conditions*

(Report by Mitsuo TSUJITA)

The present report deals with some effects of the environment upon the expression of the malformation in an inheritable crippled silkworm strain. The deformity appears on the dorsal and ventral sides of several segments ranging both anteriorly and posteriorly from the 5th abdominal segment. The shape and degree of the malformation vary markedly from individual to individual.

In our previous papers on the effect of the gene causing this malformation (OMURA 1950; TSUJITA 1951), it has been stated that: i) In the control lot under ordinary treatment of the eggs, the penetrance of the abnormality is about 50–70%, while under the immersion treatment with diluted hydrochloric acid 20 hours after laying, the percentage rises to 80–100%. ii) However, when the eggs are treated in an early stage with a low temperature (15°C) to slow down the development, almost all of the larvae hatched from them become normal.

For the purpose of accurately determining the sensitive period, TSUJITA, in cooperation with T. TAKASU of the Sericultural Experiment Station in Tokyo, examined the abnormality among larvae hatched from eggs kept at low temperatures (15° and 20°C) in an early stage of development for period of 1,3,5 and 7 days.

A summary of the results obtained is presented below.

(1) Eggs first kept at a temperature of 25°C for 10–15 hours after oviposition, were subsequently incubated at 15°C for 3 days. They were then kept in a cold room at 5°C for 60 days. After such refrigeration they were subjected to treatment by dilute hydrochloric acid. The rate of abnormal larvae hatched from these eggs was very low.

(2) When the incubation period at the temperature of 15°C was extended to 5–7 days, few abnormal larvae were produced.

(3) When low temperature treatment was began 20 hours after oviposition and continued as in the preceding experiment, more malformed larvae were produced than in the foregoing cases. Furthermore, delaying the beginning of the treatment with low temperature (15°C) until 25 hours after oviposition hardly reduced the rate of malformed individuals in comparison with the control lot.

(4) In the case in which the temperature was changed from 15°C to 20°C, a higher percentage of malformation was obtained than in the case of 15°C.

(5) Lastly, when the eggs were immersed in dilute hydrochloric acid 20 hours after oviposition, and incubated at 15° or 20°C for 1,3,5 and 7 days respectively, almost the same tendency as that described above was recognized, although on the whole, more malformed larvae were produced than in the lot treated with the refrigeration-immersion method. Even in a lot in which the eggs were treated with dilute hydrochloric acid 20 hours after oviposition and incubated at a low temperature for several days, a number of abnormal larvae appeared.

It has been confirmed, by the results presented above, that the most sensitive period of the gene causing the malformation to environmetal factors, especially temperature or stimulation by hydrochloric acid immersion, is of very short duration, from 10 to 25 hours after oviposition. This period exactly corresponds to the early stages of the embryo

formation, i.e. the time during which cleavage nuclei migrate under the egg shell, form an epithelial layer, and some of them begin to invaginate and differentiate into the blastoderm.

Also, we have obtained results which suggest a correlation between the temperature in the pupal stage and the percentage of abnormality in the next generation. We shall, however, defer the detailed report on this point to the time of completion of these experiments.

10. The Effect of Centrifugal Force upon the Development of Silkworm and Eri-Silkworm Eggs

(Report by Bungo SAKAGUCHI)

A. Induction of malformations

Experiments are now in progress to study the malformations induced by centrifuging, as a preliminary to an investigation of the embryological genetics of various malformations. One to 40 hours after oviposition, eggs were subjected to centrifugal force of 4,000 R.P.M. for 10–15 minutes, or of 10,000 R.P.M. for 15–30 seconds. All eggs were placed 10 cm from the axis of rotation.

The results obtained with the silkworm (*Bombyx mori*) were similar to those with the eri-silkworm (*Attacus ricini*). In this report mainly the results of experiments with the silkworm are described.

When eggs were centrifuged, 20 hours after oviposition, the induced malformations amounted to 28%, which was the maximal value. This seems to show that the stage 20 hours after oviposition which corresponds to the time of blastoderm formation is the critical one. When eggs before or after this stage are treated, the rate of malformation is more or less reduced according to the variation in the time factor. Examination of the embryos in dead eggs has shown that the earlier the stage when the centrifugal force was applied, the more abnormal embryos were produced.

The induced malformations included segmental malformations, i.e. fusion of several segments apparently restricted to the superficial part of the body, defects in some organs, twisting of the longitudinal axis of the larval body, duplications of some organs, and asymmetry of thoracic and abdominal organs.

Genetically abnormal strains give more abnormal larvae by treatment than the normal strain. The abnormality tends to be localized around the fifth, sixth and ninth segments. There is some resemblance between the types of malformations induced by centrifugal force in the normal strain and those in certain genetically malformed strains. The type of

deformity bears a close relation to the direction of the centrifugal force upon the eggs.

B. Embryological observations

When eggs are subjected to the centrifugal force 5 and 10 hours after oviposition, deformity appears in various organs of the developing embryo. For instance, thoracic legs, mandibles and antennae are formed at abnormal sites. This seems to be due to the fact that the predetermined regions of the organs are thrown into confusion by the centrifugal force, and that abnormal differentiation proceeds in this confused state. The eri-silkworm embryo has shown more abnormalities than the silkworm embryo.

In one of the eggs treated 5 hours after oviposition a dwarf embryo was formed at the region opposite to the micropyle; i.e., near the posterior pole, lying parallel with the shorter axis of the egg. In another embryo, some organs showed striking abnormalities; for instance, the mandibles had the cutting margins turned outside, and they were fused with each other at their bases. Thus the direction of the mandibles was reversed as compared with that in the normal condition.

In another egg treated 5 hours after oviposition, an imcompletely double embryo was formed, apparently by splitting of the longitudinal axis of the embryonal body. Also, embryos having duplicated organs have been found. These results seem to indicate that the ooplasm has a certain regulating power in the formation of the embryo, as well as in the differentiation of organs. This tendency is more marked in the eri-silkworm than in the silkworm.

It is interesting that in eggs treated one hour after oviposition, appendages like mandibles, antennae, thoracic legs, etc., developed independently of one another, until the pigmentation period. This observation suggests that the development of such organs proceeds to a certain degree independently in each of the segments. This tendency was recognized more clearly in the silkworm embryo than in the eri-silkworm embryo.

D. GENETICS OF POLYMORPHISM IN SOME INVERTEBRATES

(Report by Taku KOMAI)

1. The Lady-beetle Harmonia

Population samples of the variable lady-beetle *Harmonia* have been obtained from ten localities of Hokkaido. This collection has been made under the expectation that some samples might show evidence of their

resemblance to the population on the Asiatic Continent. None of them, however, did. But two samples from Kenbuti near Kamikawa collected at different seasons showed considerable difference in composition, reminding one of the situation in another polymorphic lady-beetle *Adalia bipunctata* reported by TIMOFÉEFF some years ago from a suburb of Berlin. More materials are being sought from the same locality.

A more recent sample from Suwa shows a distinct directional change in composition which has been continuous since 1920. An attempt to explain this change in relation to climatic change is under way. Also, experimental studies on the differential viability of various color types of this species under low temperature are in progress.

2. *The Lycaenid Butterfly Neozephyrus*

The Lycaenid butterfly *Neozephyrus taxila japonicus*, which is rather common in the mountainous districts of Japan, shows a great sexual difference in the color of the wings. Moreover, the female is tetramorphic: 1. dark-brown without any marking, 2. with orange patterns on the forewing, 3. with bluish suffusion on the forewing, 4. with both orange and bluish markings. These four forms are apparently due to a set of triple-allelic genes, something like the four blood-types in man, i.e., the genes producing the markings in the second and third forms are both dominant over the gene producing the plain form, while the fourth form is the heterozygote of these dominant genes. Ten population samples from different localities sustain this view. In nearly all of these samples, however, the second and third forms are somewhat lower, and the first and fourth forms higher in frequency than could be expected on this view. This is probably due to a relatively lower viability of the dominant homozygotes, as compared with the dominant heterozygotes and recessives.

3. *The Pierid Butterfly Colias*

Colias hyale poliographus is one of the commonest butterflies in the fields of Japan. As in most of the other species of the same genus, the female shows two color forms, white and yellow. The white form is commoner than the yellow form over the whole range of this species in Japan. S. AÉ, a student in Kyoto University, has performed breeding experiments on this butterfly under KOMAI's direction. He has found that these two forms among the females are due to a set of allelic genes, *W* and *w*, of which the dominant gene *W* shows its effect only in the female; all males are yellow, irrespective of their genic compositions. Thus, the genetic behavior of this species is essentially the same as that of the allied American species, *C. chrysotheme* studied by GEROULD and HOVANITZ. A difference may be found in the fact that, while in the American species

the dominant homozygote *WW* is apparently lower in viability than either the heterozygote *Ww* or the recessive homozygote *ww*, in the Japanese species the recessive *ww* seems to be more handicapped in natural selection than either *Ww* or *WW*. Several population samples from various localities in Japan and Korea suggest the existence of a geographic gradient in the incidence of these genes.

4. *The Land-snail Bradybaena*

The common small land-snail *Bradybaena similaris* has four color forms—yellow-plain, yellow-striped, brown-plain and brown-striped. The basic genes of these forms are triple-allelic: the yellow-plain is the recessive form; both the striped and brown are dominant forms; while brown-striped is due to the combined effect of the two dominant genes. More than 80 samples from different localities in Japan show a different relative incidence of these genes. They also indicate the strong effect of isolation on the differentiation of local populations. Comparison of samples of living and dead shells from one of these localities suggests a relatively higher viability of the recessives and the dominant heterozygotes over the two dominant homozygotes. Experiments are under way, using a refrigerator to test the relative suscestibility to low temperature of these forms.

E. GENETICS OF SOME CEREALS

(Reported by Seiji MATSUMURA)

1. *Radiation Genetics in Einkorn Wheat*

Dormant seeds of *Triticum monococcum* were exposed to X-radiation of 180KVP, 3mA, 16cm, without a filter. The doses ranged from 5,400 to 13,500*r* units. The higher the dosage, the greater was the delay in the germination of irradiated seeds and the growth of the seedlings. The frequency of chromosome aberrations increased in a parabolic relation to the dose.

At the same dose (8,100*r*) and target distance (16cm), but with varying kilovoltage (80–180KVP) and time of exposure, the aberration frequency decreased with the increase of wave length.

As to the relation between the aberration frequency and the dose or wave length, the results of previous experiments at 30–90KVP (MATSUMURA 1951) have been confirmed. These facts can be explained on the basis of the difference in ionization distribution within nuclei and chromosomes.

The mutation rate of chlorophyll abnormalities among the seedlings of the X_2 generation seems to depend not only upon the X-radiation dosage,

but also upon the wave length. The final decision on this relation will be deferred until after observation of the mature plants has been made.

Dormant seeds of the same species were also exposed to short electric waves and supersonic waves. Few irregularities were observed in the meiosis of the treated plants. Among the progeny obtained by selfing of the treated plants, however, there have been found some abnormal plants—highly sterile or dwarfish or haploid. The mechanism of the production of these abnormalities awaits further investigation.

2. *Nullisomic Dwarfs in Vulgare Wheat and Gigas-plants in their Offspring*

Dwarf plants possessing 20_{II}-chromosomes occasionally appear among the offspring of pentaploid wheat hybrids. These plants are nullisomics, deficient in a chromosome pair from the D-genome. The seven different kinds of nullisomics may be called a~g-dwarfs. Dr. SEARS recently obtained all the 21 possible nullisomics in *Triticum vulgare* (Chinese Spring). He has been working on the study of crosses between his own nullisomics, XV–XXI, and the author's a~g-dwarfs. His results show that Nulli-XVI corresponds with the g-dwarf. The author's crossing experiments, however, show that chromosome XVI can correspond to no other chromosome than the f-chromosome, as the hybrid Nulli-XVI × f-dwarf is highly sterile (fertility, 2.94%) and has chromosome conjugations mostly of the type $1_{III}+18_{II}+1_I$ and 20_{II}, while Nulli-XVI × g-dwarf has a relatively high fertility (73.04%) and the chromosome configuration is of the type $19_{II}+2_I$+frag. (The fragment has been derived undoubtedly from the g-dwarf used in the cross.) Among the F_2 of the former hybrid, most of the plants are dwarfish; only a few have normal height and the chromosome configuration, $20_{II}+1_I$. Among the F_2 of the latter hybrid, on the other hand, many plants are of normal height and only a few are dwarfish.

The hybrids between Nulli-XVI and a~e-dwarfs usually have the chromosome conjugations $19_{II}+2_I$, $1_{III}+18_{II}+1_I$, $18_{II}+4_I$, $1_{III}+17_{II}+3_I$ etc. and high fertility. But the hybrids of Nulli-I, -III and -VII with a~g-dwarfs are of lower fertility, in spite of showing similar chromosome conjugations. This must be due to the fact that in the former hybrids the A- and B-genomes are complete, and only two of the D-chromosomes are without partners, while in the latter hybrids either the A- or B-genome, and also the D-genome, are lacking in one chromosome.

In the hybrids between Nulli-I or -VII and a~g-*gigas*-plants, the chromosome configurations of $1_{IV}+18_{II}+1_I$, $1_{III}+18_{II}+2_I$, $19_{II}+3_I$ and $20_{II}+1_I$ have been observed. The hybrid Nulli-I × c-*gigas* was highly sterile (fertility, 4.94%), while the hybrids between Nulli-I and other *gigas*-plants had 65–87% fertility. Furthermore, the hybrid Nulli-VII × a-*gigas* showed

a markedly higher fertility (84.60%) than the hybrids between Nulli-VII and other *gigas*-plants, whose fertility was 20–45%. From these results it is assumed that the supernumerary chromosome α in the a-*gigas* is the same as SEARS' VII. The hybrid Nulli-VII × a-*gigas* is expected to show a higher fertility after the recovery of the chromosome in which the A- or B-genome of SEARS' nullisomic is lacking.

3. *Studies on Agropyrum, a Genus Related to Triticum*

Of the hybridization experiments between *Triticum* spp. and *Agropyrum* spp., the one between *T. polonicum* (AABB) and *A. glaucum* ($2n=42$) has been successful. This hybrid has been cytologically examined. Meiosis shows 5–10 gemini with the mode at 7. Often 1–2 trivalents are found and rarely 1 tetravalent occurs. It is inferred from these facts, as well as from earlier results (MATSUMURA 1949), that the genome of *A. glaucum* which is homologous with one of the *Triticum* genomes is the B-genome. The hybrid is perennial and vigorous, but completely sterile, and matures very late.

4. *Morphologically Different Twins found in the Progeny of a Hybrid Wheat*

(Reported by Tarô FUJII)

Twin plants of $2x:2x$-chromosome set are morphologically identical. In the F_2 of a hybrid between Nulli-VII ($2n=40$) and a-*gigas* ($2n=42$) a pair of twin plants was obtained. They both had 41 chromosomes, but one of them was awnless and the other tip-awned. In the selfed progeny of each of these plants there appeared many normal plants with 21_{II} and $20_{II}+1_{I}$ besides a few dwarfs, whose chromosomes should be 20_{II}. The offspring of the awnless twin were all awnless. The tip-awned twin showed relatively lower fertility and a lower percentage of heading. Its progeny segregated as to the awn character in the monohybrid ratio, 1 awnless : 2 tip-awned : 1 awned, independently of chromosome numbers. This shows that the tip-awned twin must have been heterozygous as to the awn character.

The origin of these twins can be explained in two ways:

1) One fertilized egg (awnless homozygote) was divided into two embryos in an early stage and a minute deficiency of the awn gene occurred simultaneously.

2) The egg cell and one synergid were fertilized by 2 pollen grains, one with the gene for awnless and the other with a minute deficiency of the awn gene.

The first hypothesis seems to be more probable than the second.

F. GENETICS AND CYTOLOGY OF *NICOTIANA*

1. Cytogenetic Studies on the Genus Nicotiana II

(Report by Yô TAKENAKA)

A. On the meiotic chromosomes of ten wild and one cultivated species of the genus Nicotiana

Seed of eight species, namely *Nicotiana longiflora, N. paniculata, N. tomentosiformis, N. trigonophylla, N. undulata, N. suaveolens, N. Gossei* and *N. rotundifolia,* were received, together with other wild species, from Prof. R.E. CLAUSEN, through Dr. F.A. LILIENFELD, one of the collaborators in our Institute. Three other species of the same genus were obtained from Japanese sources. Seeds of *N. nudicaulis* were obtained from the Kagoshima Tobacco Laboratory, Japan Monopoly Corporation. *N. alata* is found growing wild, since about 20 years ago, in the fields of Kônô-Gakuen near Misima. *N. rustica* is being cultivated in the Hatano Tobacco Experiment Station.

The behaviour of chromosomes and the number of gemini were observed in the meiosis of the pollen mother cells of these eleven species.

The bivalent chromosome numbers are as follows:—*N. alata* 9, *N. longiflora* 10, *N. paniculata* 12, *N. tomentosiformis* 12, *N. trigonophylla* 12, *N. undulata* 12, *N. nudicaulis* 24, *N. rustica* 24, *N. suaveolens* 16, *N. Gossei* 18 and *N. rotundifolia* 22. These numbers agree with those given by previous authors, such as GOODSPEED, RESENDE, TENOVSKY and WHEELER. The meiotic figures have been found to be very regular, except that it has been difficult to count 24 gemini in the Ist metaphase of *N. nudicaulis,* since some chromosomes present figures resembling quadrivalents.

B. Cross between N. glutinosa and N. sylvestris

In the summer of 1950, 266 flowers of *N. glutinosa* were pollinated by *N. sylvestris* and gave 34 capsules. The reciprocal cross, 418 flowers of *sylvestris* pollinated by *glutinosa,* gave no capsules. Almost all of the seeds were abortive, and only 22 plants were obtained in the spring of 1951. Twenty of these showed the typical features of *glutinosa* and grew to maturity in the same manner, like the control *glutinosa* plants. Of the remaining two plants, one was wholly *sylvestris,* and the other was very dwarfish, looking like a haploid *sylvestris* produced by androgenesis, although the leaf shape showed some features of *glutinosa.* This dwarf plant died before blooming so that its meiosis could not be examined; its root tips showed 24 chromosomes. This shows, at least as far as the roots are concerned, that the plant was not a haploid *sylvestris.* It may have been a hybrid between *glutinosa* and *sylvestris.*

The production of relatively many plants of the *glutinosa* type in the cross described above may be due to the considerable dissimilarity between

the genomes of *glutinosa* and *sylvestris*, which made the nuclear fusion extremely difficult, so that the *glutinosa* egg cells developed parthenogenetically by chromosome doubling, after activation by the pollen hormones of *sylvestris*. Or it is possible that parthenogenetic development was induced through fusion of an egg cell with the synergidal cell in the same embryo-sac. For the production of the *sylvestris* type plants, it may be assumed that one sperm nucleus with a doubled chromosome number or two fused sperm nuclei developed androgenetically into a *sylvestris* embryo within a *glutinosa* embryo-sac.

C. Hybrid between N. glauca and N. plumbaginifolia

Pollinations of many flowers of *N. glauca* with pollen of *N. plumbaginifolia* gave only 6 capsules in the summer of 1950.

Many F_1 plants were obtained from this cross. Although they were generally intermediate between the two parents as to external characters, the shape of leaf and branch approached those of the father and, on the contrary, the height of the plant came nearer to that of the mother. The flower size was intermediate and the flower colour was at the start light yellow resembling that of *glauca*, changing to pale white approaching that of *plumbaginifolia* at the end of the flower life. Leaves, flowers and branches of the plants were very numerous, the growth was extremely exuberant and the flowering period very long. In short, the plant showed typical heterosis.

The somatic chromosome number, as expected, was 22, containing 12 chromosomes of *glauca* and 10 of *plumbaginifolia*.

The meiosis of the pollen mother cells was highly irregular, as is generally observed in hybrids between distantly related species. In the first metaphase, many univalents were observed besides 1–4 bivalents, but the partners of the bivalents seemed to be only partially homologous, because their connection was loose. In the first anaphase, chr mosome bridges were very frequently observed, and some of them were carried over to the IInd anaphase or the tetrad stage. There were also new chromosome bridges which appeared only in the IInd division. The IInd division was carried through in most of the pollen mother cells, but was observed to break down in a few of them. In the tetrad stage, many mother cells held four microspores in each cell, a few cells held only one, two or three microspores and some of the mother cells contained a few small microspores besides the microspores. Because of the irregular meiosis, this hybrid did not give even a single seed.

2. *Cytogenetic Studies on the Genus Nicotiana III*

(Report by Yô TAKENAKA and Flora A. LILIENFELD)

By crossing two commercial varieties of *N. tabacum*, Bright Yellow and Odaruma, with *N. sylvestris*, one of the original parents of *N. tabacum*,

triploid hybrids were obtained in 1950.

Morphologically the hybrids could scarcely be distinguished from *N. tabacum*. However, they blossomed ten days earlier than *N. tabacum*. Because of this feature they could become important under conditions which require early maturing tobacco varieties.

The meiosis was studied in pollen mother cells. As expected, the chromosome conjugation was $12_{II}+12_{I}$, the univalents representing the *tomentosa* set. From the occurrence of trivalents it could be concluded that several of the *tomentosa* chromosomes are semihomologous with the *sylvestris* chromosomes. Most of the nuclear plates showed the configuration $3_{III}+9_{II}+9_{I}$. According to expectation based on the irregular behaviour of the chromosomes after first metaphase, only a few seeds were obtained.

3. *Mutations in Tobacco Induced by X-rays*

(Report by Seiji MATSUMURA and Tarô FUJII)

Dormant seeds of *Nicotiana tabacum* (Bright Yellow) were subjected to X-ray treatments. In the first experiment, the seeds were exposed to unfiltered radiation at 90KVP, 3mA, 15cm, of intensity of 216 *r*/min for 10–60 minutes. The dosage applied ranged from 2,160 to 12,960 *r* units. There were no striking differences in germination rate of seeds or in morphological characters of mature plants between untreated and variously irradiated plants.

In the second experiment, the seeds were irradiated with harder X-rays at 180KVP, 3mA, 11.2cm, without filter, of 480 *r*/min intensity. The dosage was 5,000–50,000 *r*. At the highest dosage the germination rate of the irradiated seeds was reduced, from the 82.4% of untreated seeds, to 65.6%. The higher the dosage above 20,000 *r*, the more delayed and uneven were the germination of treated seeds and the growth of the seedlings. Among the mature plants from seeds irradiated at 15,000 *r* and at higher dosage, various kinds of abnormalities appeared, such as narrow leaf, crêpe leaf, white spotting, etc. In some of the plants the capsules dropped after flowering. At 50,000 *r*, about 40% of the X_1-plants showed such abnormalities. Chromosome aberrations, such as $1_{IV}+22_{II}$ and 24_{II} +frag. etc., were observed in the meiosis of these plants. The relation of aberration frequency to dosage is not clear, because of the small number of anthers examined.

44 offspring were bred from the selfing of X_1-plants in the first experiment. In 15 of them mutants in morphological characters appeared, such as: early and late maturity, vigorous, early bolting, dwarf habit, broad leaf, narrow crêpe leaf, spotted leaf, etc. Some of the mutations showed characters useful for breeding purposes.

4. *Studies on the Relative Weight of Mid-rib in Nicotiana tabacum Leaves*

(Report by Kan-Ichi SAKAI, Kanji GOTOH and Shinya IYAMA)

The proportion of mid-rib volume to the total volume of a tobacco leaf is not only important to the tobacco industry but also interesting to the students of quantitative characters in plant genetics. With the purpose of analyzing the genes controling this character, our first attempt was made to examine the differences of that proportion in various tobacco varieties as well as its correlation with some other leaf characters. The mid-rib proportion was determined by the ratio of mid-rib weight to total leaf weight.

Five individuals were taken at random from each of twenty-four tobacco varieties and from three F_1 hybrids. From each individual four leaves, from the third to the sixth leaf upwards, were collected. Two leaves, the third or the fourth and the fifth or the sixth were measured as to their mid-rib proportion as well as their shape and size immediately after harvesting. These two and the remaining two leaves were then dried at room temperature and again the mid-rib weight and total weight of dry leaves were determined.

Results of the analysis of variance of the data are as follows:

Variation due to	d.f.	Mid-rib proportion	
		Fresh leaf	Dry leaf
Variety	26	85.79**	78.13**
Individual	108	3.62	2.04

Variation due to	d.f.	Leaf size[1]	Leaf shape[2]
Variety	26	778708**	365.68**
Leaf	243	45390	29.98

** Exceeds the 1 percent point.

1) (Length of mid-rib)×(Width of leaf).

2) (Width of leaf)/(Length of mid-rib).

The correlation coefficients between the mid-rib proportion of dry leaves and that of fresh leaves as well as size and shape of leaves are as follows:

	Mid-rib proportion of dry leaves
Mid-rib proportion of fresh leaves	+0.913**
Leaf-size	+0.282
Leaf-shape	−0.455*

* Exceeds the 5 percent point. ** Exceeds the 1 precent point.

The conclusion that the mid-rib proportion in dry leaves is highly correlated with that in fresh leaves offers valuable information for our future work.

G. GENETICS OF *CAPSICUM*

1. Genetic Studies on some Fruit Characters in Capsicum annuum

(Report by Kan-Ichi SAKAI)

Comparative studies were made in *Capsicum annuum* on some fruit characters of F_1 hybrids and their parents. The experiment consisted of two parts: 1. comparison between the effects of different paternal genotypes on F_1 hybrids derived from a common mother-plant, and 2. study of the behavior of genes for fruit characters. The number of progeny obtained from selfing and crossing in these two experiments approached one hundred, and the experiments were combined in order to apply the simple lattice design with four replications.

Though data obtained on the average weight of a fruit, number of fruits per plant and the total weight of fruits per plant are still under examination, the following results can be considered as established:

(1) The total weight of fruits per plant exhibits heterosis in some combinations and not in others.

(2) The smaller number of fruits per plant behaves in most cases as an incompletely dominant character.

(3) Also, small fruit size is partially dominant over large fruit size.

Further discussion and criticism will follow after the necessary computations have been completed.

2. Decline of Fruit Productivity by Artificial Selfing in Capsicum annuum

(Report by Yasuo SUZUKI)

With four strains representing three varieties of *C. annuum*, the writer made comparative studies on fruit productivity by means of open-pollination and artificial selfing. The experiment was conducted by the split-plot design with three replications. Data obtained were analyzed by using the variance-analysis method. Significant differences between open pollination and selfing have been found in the total number of fruits, the total weight of ripe fruits, the topweight, and in the total weight of ripe and unripe fruits. The writer, however, has failed to find any significant difference between the treatments in respect to the number of ripe fruits, plant weight excluding fruits, and in the average weight of fruit. Variety-treatment interactions in these four characters except plant weight, the total weight of ripe fruits, and the total number of fruits were also non-significant. The *t*-test of data has shown that the decline of character due to selfing in all but the average weight of fruit was apparent only in

the Chinese variety. Thus the rate of increase in the yield characters has proved to be apparently different between varieties with smaller and those with larger fruits, the increase in the former varieties being 3 to 9 per cent, while that in the latter bearing large fruits such as the Chinese variety ranged from 35 to 60 per cent. The increase was apparent in the number of fruits and in the other characters, except the average weight of fruits. Quantitative differences in yield characters between open- and self-pollinated lots in this experiment are possibly due to heterotic genes which would segregate within the same variety. Further experiments will be conducted in 1952.

H. GENETICS OF EGGPLANT

(Report by Kanji GOTOH)

1. Studies on Developmental Processes of Fruits in Eggplants

The fruit-shape in eggplants is roughly classified into spherical, oval and long. The purpose of this investigation is to clarify the developmental processes of these different fruit-shapes.

Two varieties and several F_1 hybrids between these two and other varieties with different fruit-shapes were examined. From seven days after anthesis the longitudinal and horizontal diameters of the developing fruits were measured on every fourth day until they became almost constant.

The data show that the so-called fruit-shape expressed by the ratio of these two diameters became stabilized from 15 to 23 days after anthesis. The regression equations and the regression coefficients concerning the developmental process in all the F_1 and the varieties were computed from data transformed into logarithms on each diameter. The regression coefficients thus obtained are all statistically significant. Then the differences between the regression of F_1 and that of its parents, as well as the difference between the regressions of the parents themselves were analyzed by joint regression methods.

A comparison between these regression equations suggests that in some cases differences in increments of longitudinal or horizontal diameter had already been established before the measurements, since their differences were statistically significant. In one case, the differenc of regression coefficient in horizontal diameter between on F_1 hybrid and its parent was found to be statistically significant.

In addition, the growth curves of these dimensions suggest the existence of inherent turning-points. When the growth of fruit attains turning-

points, the ascending tendency of growth rate begins to decline. Consequently, it is conceivable that all growth curves have two turning-points, one before anthesis and the other at a certain period after anthesis. Also it is likely that differences found in the shape of fruits are due to integrated effects of the genes acting in different periods partitioned by these two turning points. Hence, the genetic analysis of fruit-shape has to be conducted with reference to each of these three stages.

2. *Regression Analysis of Fruit-shape and -size Genes with the Aid of F_1 Hybrids in Eggplants*

In eggplants the shape and size of fruits are highly variable. An investigation was undertaken to analyze the role of genetic factors concerned in the variability of these quantitative characters. Five varieties, apparently different in their fruit characters, and their F_1 hybrids were grown in a randomized block arrangement. Measurements of these characters were made simultaneously, when the fruit seemed to have completed development about a month after anthesis. Arithmetically calculated data were obtained on fruit-shape and -size. The shape was expressed by the ratio between the length and width of the fruit, and the size, by the weight per fruit. Genotypic variance, variance due to dominance and covariance between F_1 and its variable parent were calculated in each of the five constant parent groups. By means of constant parent regression analysis, mathematical models of the action and effect of fruit-shape and -size genes were obtained.

By this means it has been found that there are arithmetically cumulative action with slightly negative dominance of the genes for shape, and logarithmically cumulative action of the genes for size.

3. *Studies on Combining Ability in Eggplant Varieties*

This experiment was undertaken to ascertain whether general or specific combining ability existed in eggplants. 10 varieties and 15 F_1 hybrids between them were examined by replicated yield trials in a randomized block arrangement, and the results were tested statistically.

The yield of the F_1 hybrids was, as a whole, superior to the mean yield of their parents. In 14 combinations, the F_1 hybrids outyielded the lower-yielding parents and in 5 combinations they even outyielded the higher-yielding parents, the difference being statistically significant.

The increase in yield of the F_1 hybrids over the mean yield of their parents ranged from 12% for the Minden × Sendai-naga No. 1 to 70% for Burma × Sendai-naga No. 1. The F_1 hybrids between the variety Turuboso-sen-nari and any other variety were very vigorous and showed higher yielding ability as compared with other combinations. This suggests

that the variety Turuboso-sen-nari has a high general combining ability. Hybrid vigor obtained in hybrids between Turuboso-sen-nari and Sendai-naga No. 1 or Sinkuro, etc. also suggests that some of the varieties have specific combining ability.

All F_1 hybrids from these combinations outyielded the higher-yielding parents and the differences were highly significant.

Furthermore, it has been shown that the high yielding varieties do not necessarily have high combining ability, and that the increase in yield of the F_1 hybrids outyielding the higher yielding parent is largely due to an increase in the number of fruits per plant.

I. CYTOLOGY AND GENETICS OF SOME FLOWERING PLANTS

1. Karyological Studies on Narcissus I

(Report by Yô TAKENAKA)

Karyological studies, especially karyotype analyses, on the genus *Narcissus* have been carried out, and somatic chromosome numbers of 58 clones including forms, garden and wild-growing varieties, belonging to 10 species, have been determined as given below.

(1) Group of *Narcissus Tazetta* L.

Mont cenis 20, Maestro 20, Jaune Sprene 30, Batharst 20+1 fragment, Paper White 22, Grand Monarque 32, Runa 32, White Pearl 32, Sicily White 32+1 fragment, Gloriosa 17, and var. *chinensis* 30 and 32.

The basic haploid chromosome number of this species is 10. Diploid, triploid and aneuploid plants were observed.

In one garden variety, "Gloriosa", 17 somatic chromosomes were counted in the root tips, suggesting its hybrid origin from a cross between *N. Tazetta* with 10 and another species with 7 as the haploid chromosome number. The latter parent may have been *N. poeticus*, judging from the appearance of this variety.

(2) Group of *N. poetaze* hort.

Klondyke 17, Aspasia 17, Triumph 24, Alsace 24, and Erbira 24.

This plant is considered to be a horticultural species originating from the hybridization between *N. poeticus* var. *ornatus* and *N. Tazetta*. The chromosome complex of his group consists of one chromosome set of *N. Tazetta* and one or two sets of *N. poeticus*.

(3) Group of *N. poeticus* L.

Almira 14, Ornatus 21, King of England 21, Pheasnt's Eye 21, and var. *plenus* 14.

The basic haploid chromosome number is 7, diploid and triploid clones have been found in this group.

(4) *N. Jonquilla* L.

Jonquill Single 14.

The basic haploid chromosome number is 7.

(5) Group of *N. odorus* L.

Odorus Regulosus 14, Campernella Common 14 and Odorus Giganteum 28.

The somatic cells of this group have 14 chromosomes as the basic diploid chromosome number. A tetraploid clone has been found.

(6) Group of *N. incomparabilis* L.

Gloria Mundi 14, Sir Watkins 21, Fire Flame 21, Bedouin 21, Will Scarlet 28 and Bernadio 28.

The basic haploid chromosome number is 7.

Diploid, triploid and tetraploid garden varieties have been found in this group.

(7) Group of *N. Barrii* hort.

Barbara Holms 21, Conspicuous 21 and Barrii Seagull 21.

It is considered that this species arose from a cross between *N. incomparabilis* and *N. poeticus.*

Three clones examined were all triploid.

(8) Group of *N. Leedsii* hort.

Minnie Hume 14, Amabilis 21 and White Lady 21.

This horticultural species is said to have originated from *N. incomparabilis*×*N. poculidormis.* Three clones examined were diploid or triploid.

(9) Group of *N. Pseudo-Narcissus* L.

William Gold Ring 14, Vanilla 14, Princeps 14, Golden Spur 14, Cervantes 14, J.B.M. Cum 21, Emperor 21, Victoria 21, Empress 21, Van Waveren's Giant 21, Madam Plemp 21+1 fragment, Silver Spur 28, King Alfred 28, Glory of Noordwijk 28, Madame de Graaff 31, Tresserve 36. Of the clones belonged to var. *pleno,* Silver Wing 14, Orange Phoenix 13+1 fragment, Double van Sion 14 and Sulpher Phoenix 14.

The basic haploid chromosome number in this group has been observed to be 7. This group constitutes an euploid series of $2x$, $3x$, $4x$, and $5x$, with the addition of a few aneuploid plants and two clones with a chromosome fragment.

(10) *N. Bulbocodium* L.

Only one clone was examined; the somatic chromosome number was 42, consisting of 6 basic 7-chromosome sets.

2. *Cytogenetic Studies on the Sex in Cannabis sativa L. I*

(Report by Yô TAKENAKA)

One spontaneous autotetraploid female plant was found among about 300 hemp plants from seeds sown in our garden in spring of 1950. In

November of the same year, this plant gave 105 seeds, all of which were supposed to be triploid.

The seeds were sown in our garden in the early spring of 1951. Many seedlings withered because of lack of proper care during the long hot season, but 50 plants grew to maturity and consisted of females, intersexes and males in the ratio of 21 : 25 : 4. The intersexes ranged gradually from practically wholly female plants with only a few male flowers to predominantly male plants.

The somatic chromosome complement of hemp is known to consist of 20 chromosomes; i.e., 18a + 2X in the female and 18a + X + Y in the male. Accordingly, the tetraploid female should have 36a + 4X, and consequently, plants with 27a + 3X and 27a + 2X + Y could have been expected as the result of free pollination of the tetraploid female. Root-tips of seven plants among the offspring were cytologically examined. Almost all cells showed thirty chromosomes as expected. In the triploid females the X-chromosome could not be identified, but in the triploid intersexes one large chromosome of a J-shape rather than a V-shape was infrequently distinguished from the other chromosomes.

The meiosis of the triploid intersexes was examined by BELLING's aceto-carmine method. In the zygotene and pachytene stages, some chromosomes were found to be arranged in juxtaposition, by threes. Also, in the diplotene stage, three chromosomes were frequently gathered in a group, though not necessarily parallel with one another. In diakinesis, four to six trivalent chromosomes were found; rarely fewer than four. Their number in the Ist metaphase was usually six. Accordingly, most of the nuclear plates of that stage had the chromosome configuration $6_{III} + 4_{II} + 4_{I}$. One of these trivalents showed frequently difference of size among its three elements, the complex usually forming a straight line by the end-to-end union of the chromosomes, though it was occasionally V-shaped. This tripartite chromosome may represent the sex-chromosome's complex. The chromosome separation at the Ist anaphase is not so irregular as is usual in other triploids, though rarely a few chromosomes may be located outside of both polar groups. Accordingly, at least one complete autosome set goes to each pole, and the sex chromosomes separate as X—XY, or XX—Y. The chromosomes split in the stage from the IInd metaphase to anaphase, and go to the poles, except for a few which are irregularly distributed outside of the spindle at the Ist division. The number of microspores of the tetrad stage was mostly four in each mother cell. In addition, one or two small microspores might be found. The relative frequency of the cases (4 microspores) : (4 microspores + one small microspore) : (4 microspores + 2 small microspores) found in each mother cell is about 160 : 27 : 4. Most of the pollen grains appeared normal. As mentioned

above, since the meiosis of these triploids is not so irregular as in many other sterile triploids, an abundance of seeds could be harvested from the triploid females and intersexes.

3. *Irregular Mitosis in some Clones of the Genus Colchicum*

(Report by Yô TAKENAKA)

From the observation of somatic nuclear divisions in root-tips of some clones of the genus *Colchicum*, the following facts have been confirmed:—

(1) Somatic chromosome numbers—*Paplium major* $2n=34$, *Autumnale alba* $2n=36$, *Ancrist* $2n=38$, *Purpurea* $2n=38$; one clone from the Botanical Garden of Hokkaido University had $2n=40$. The same clone, transplanted in 1927 into Dr. OGUMA's garden in Sapporo from the Botanical Garden of Hokkaido University and retransplanted in 1950 to our garden in Misima surprisingly showed $2n=38$.

(2) In general, the mitotic chromosome figures of all these plants showed stickiness, being "C-mitotic", and it has been difficult to determine exactly the metaphasic chromosome numbers, as the mitotic figures almost always show fragmentation and/or fusion of chromosomes.

(3) The clone transplanted to Misima from Dr. OGUMA's garden in Sapporo showed the greatest irregularities of all. This clone had produced normal flowers every autumn all through the 21 years from 1927, exactly like the original clone in the Botanical Garden of Hokkaido University. But in the autumn of 1950, all the plants in Misima had open degenerate flowers entirely lacking stamens and petals, though having normal pistils and corollae. Root-tips of one of these plants were fixed at the end of the summer, 1950. The sections showed various irregular mitotic figures.

(a) There were many necrotic cells in the cortex region apparently resulting from extremely abnormal diffusion or contraction of chromosomes. At the same time, abundant chromatin bodies of various shapes—chromosome clumps, fragments or chromatin granules—were spread out into the cytoplasm. (b) Some anaphasic figures showed unequal distribution of sister chromosomes to the poles. (c) The equatorial plates held mostly 38 chromosomes, but not infrequently various numbers of chromosomes from 34 to 41 were seen. The largest V-shape chromosome was usually represented twice in each nuclear plate, but there were sometimes three of them.

These findings, especially on the clone derived from Dr. OGUMA's garden, seems to allow the following conclusions:—

(1) The plants of the genus *Colchicum* are very strongly affected by environmental conditions, which is shown in the frequency of irregular nuclear divisions. Such a reaction may have some relation to the colchicine contained in the tissue of the plant.

(2) A new clone having a different chromosome number or a different karyotype, or both, may be produced from the original clone, as a consequence of various differentiations in the number or shape of the chromosomes in the meristem cells of a bulb, if such a change takes place even in a single cell, and also it takes the precedence in competition with many other cells. The abnormal clone described above seems to be an example of this kind.

(3) Series of very unusual chromosome numbers in this genus, reported by LEVAN (1940), such as $2n=38$, 40, 42 and 44, may have been derived from a single ancestral pattern.

4. *Progeny of Lycoris radiata*

(Report by Hitoshi KIHARA and Flora A. LILIENFELD)

Seeds of the triploid *Lycoris radiata*, obtained from selfing and from cross-pollination with pollen of the diploid *L. sanguinea*, were sown immediately after ripening. The results of self- and cross-pollinations are shown in the following table.

Table 1. Results of self- and cross-pollination experiments with *L. radiata*

	No. of inflorescences	No. of flowers	No. of fruits	No. of good seeds	No. of germinated seeds (%)
Self-pollination	94	—	—	43	3(6.9)
Cross-pollination	115	792	268	151	17(11.2)

The germination was not good, but all seedlings looked healthy and grew well. Chromosome counts were not undertaken, because the plants give roots only once a year.

5. *Genetics of Flower Characters in Zinnia elegans*

(Report by Kanji GOTOH)

In 1951, crossing between single and complete double as well as between non-petalous and many other types were undertaken. Selfing of F_1 hybrids was also made. The flower of F_1 hybrids between single and complete double flowers showed the following structures:—the basal part of the flower was constituted of 1~2 layers of florets with petals, while the tubular flowers occupied the remaining part except for the top having

some petalous florets. This type has been identified with "E type" which was realized in the writer's experiments conducted in 1950. Experiments are being continued.

6. *Sterility in Phaseolus multiflorus*

(Report by Akira MIYAZAWA)

Phaseolus multiflorus is known to be fully fertile in its natural habitat which is in cool mountainous districts like Nagano or Hakone. The plant transplanted from Hakone to the experimental garden in the institute exhibited high sterility. On September 2nd 1950, about 20% of pollen grains were found to be empty. Moreover, the ratio of empty pollen grains declined with the progress of the season. It was assumed that the high temperature of the very hot summer in Misima is the cause of this sterility.

The present report deals with observations of the meiotic behavior of this plant. In the maturation divisions of P.M.C.'s, various irregularities were frequently observed. At the first metaphase one or more univalent chromosomes were seen outside of the plate. Some chromosome bridges were found at the first anaphase, and some lagging chromosomes were observed at interphase. The polar views of the second metaphase showed 10–12 chromosomes in the nuclear plates, while the expected normal number should have been eleven in each plate ($2n=22$). In the tetrad stage the number of microspores was mostly four, but a few mother cells contained two, three or more than four. The size of the pollen grains was very variable. It seems that the E.M.C.'s behaved in a similar manner.

The phenomena described above seem to be analogous to the observations made in plants treated with high temperatures. These cytological findings support the author's previous hypothesis. However, the very high degree of sterility does not have a fully adequate counterpart in the meiotic behavior. Therefore, ecological factors should also be taken in consideration. This will be the subject of the investigations of this year.

7. *Paper Chromatographic Studies of Flower Color Variation*

(Report by Tôru ENDÔ)

The writer has made some introductory studies on chemico-genetics of flower color variation by paper chromatography, using six *Dahlia* varieties in 1951.

1% methanolic hydrochloric acid extracts of fresh petals were chromatographed on Tôyô filter paper No. 2 with *n*-butanol acetic acid-water (40–10–50 volume %). The results of this experiment are as follows:

Table 1

Flower color	Anthocyanin		Flavonoid	
	Cyanin ($0.25 \pm .06$)	Pelargonin ($0.34 \pm .04$)	Yellow ($0.39 \pm .09$)	Brown ($0.49 \pm .06$)
white	−	−	+	+
mauve	++	−	++	++
pink	+	+	+	+
vermilion	+	++	+	+++
purple	+++	+	+++	++
dark red	+++	+++	+	+++

Numbers in brackets stand for the R_f values and −, +, or +++ indicates the relative quantity of the pigments, − indicating none, +++ the maximum quantity contained.

As is illustrated in this table, there has been found a remarkable parallelism between the intensity of flower color tones and the amount of the component pigments. It was also found in this experiment that the pelargonin was always accompanied by fluorescent substances (light yellow fluorescence).

Similar experiments are now in progress with *Viola tricolor, Verbena hybrida, Impatiens Balsamina, Antirrhinum majus* and *Petunia hybrida.*

J. IMPROVEMENT OF SOME USEFUL PLANTS

1. *Improvement of Sugar Beets by Means of Induced Triploidy*

(Report by Seiji MATSUMURA)

Triploid beets are more vigorous, grow better and always show a higher yield, a higher sugar content and a higher resistance to diseases than the diploid Hon-iku No. 192, the most widely grown variety, according to comparative studies carried out on a large scale in various districts of Hokkaido. The triploid seeds, however, are inferior in germination rate. In order to solve this problem, various intervarietal triploid hybrids were obtained and compared with one another.

The germination rate of the tetraploid seeds is variable; it is very low in Hon-iku No. 48–4x, but relatively high in Hon-iku No. 398–4x and No. 402–4x. Therefore, the triploid combinations No. 398–4x × No. 162–2x and No. 402–4x × No. 399–2x are most promising.

For the large scale production of triploid seeds it was found advisable to plant 4x and 2x beets in the ratio of 3 : 1. In this way relatively many triploid plants were obtained.

2. *Genetics and Breeding of Citrus*

(Report by Kazuo FURUSATO)

A. Pathenocarpy and seed reproduction

Citrus Unshu has usually no seeds in the parthenocarpic fruits. This is due to pollen abortion which takes place in our climate in the early and middle parts of the flowering period of this variety. Therefore, even artificial self-pollination fails to produce seeds. However, when pollinated with good pollen of another variety (e. g. ***Citrus natudaidai*** or ***C. tamurana***), ***C. Unshu*** easily sets seeds. This indicates that ***C. Unshu*** can produce normal seeds, provided that good pollen is available. In fact, normal seeds of this variety can be easily obtained later in season, when its own pollen is well developed. The failure to yield good pollen is apparently due to the influence of the high temperature prevailing during most of the flowering period in our country.

Parthenocarpy without pollination occurs in ***C. Unshu***. Even when the pistils are cut off before the opening of the flowers, the same amount of fruits will be set as in natural condition.

B. Polyembryony

Studies on polyembryony in ***Citrus*** have shown that many additional embryos are formed from nucellar cells after the fertilization of the egg cell. The number of embryos per seed varies from species to species, and even among the seeds of the same variety.

In ***Citrus Unshu*** 20–30 large and small embryos were counted in one seed. This number is higher than that hitherto reported by other authors. This difference is due to different methods used in counting the embryos. The embryos vary in size from very small to normal. The use of a microscope for counting will increase the number of embryos counted. The number of plants which developed was considerably less than that of the embryos.

When the seeds of ***C. daidai*** are sown in the soil, only 1–4 embryos develop into plants against 16 embryos on the average develop from one seed. When the embryo-culture method is used, seeds sown on agar show a better development of the embryos than when planted in the soil. However, not all of the embryos are able to develop.

As to the relation between polyembryony and the nature of the pollen parent, when polyembryonic varieties are pollinated with pollen of monoembryonic varieties, all seeds produced are polyembryonic, but when the reciprocal pollination is carried out, monoembryonic seeds are produced. Thus, the nature of the pollinator has no influence on the number of embryos produced. Further experiments will show whether some kind of maternal inheritance or influence has to be taken into consideration in this case.

3. *Induced Polyploidy in some Cultivated Plants and its Utilization*

(Report by Kazuo FURUSATO)

A. Polyploid watermelons (Citrullus vulgaris)

In order to breed new varieties of triploid watermelons, three newly induced tetraploids of the varieties I. K. (provisional designation) and Kanro were obtained. These new tetraploids were almost of the same type in morphological and ecological features as those obtained before. Tetraploid Kanro attracted my attention on account of the very vigorous growth of its vine. So I planted it mixed with some diploid varieties such as Yamato, Asahi, Miyako and others, hoping that new triploids might be produced by cross pollination. These triploids, if found, will be selected on the basis of yield, quality of flesh and disease resistance.

B. Grafting stocks for triploid watermelons

Triploid watermelons were grafted last year on di-, tri- and tetraploids and on calabash. In plants thus obtained the quality of fruit flesh and the development of empty seeds were examined. Grafting was tried also on other species, such as *Cucumis sativus* and *Cucurbita moschata*. When *Cucurbita* was used as the stock, many fruits were produced, but they contained many empty seeds. When cucumber was used as the stock, the yield was low, but the number of empty seeds was small.

C. Tetraploid melon (Cucumis Melo)

A tetraploid plant was obtained by colchicine treatment from Nara No. 1, one of our melon varieties. The fruits of this plant were flat, and had a thick flesh layer. Their appearance was not attractive, because of an overdeveloped hilum, but the thickness of the flesh and the deep coloring of the skin are desirable characters. Further attempts will be made to obtain a good tetraploid variety of melon.

D. Tetraploid race of Medicago denticulata

A tetraploid race obtained from *Medicago denticulata* had longer and thicker stems than the diploid race, but their number was smaller. The yield will be investigated in the field.

K. STUDIES ON SOME LOWER ORGANISMS

1. *Effect of X-ray Irradiation on Streptomyces griseus*

(Report by Seiji MATSUMURA and Tarô ITÔ)

The present study was undertaken in cooperation with the Fuji Plant, Kyôwa Hakko Co., in order to obtain by irradiation with X-rays a high-potency mutant of *Streptomyces griseus*, which is being used for the production of antibiotics.

The spore suspension, prepared in various concentrations (1.5×10^2/cc, 1.5×10^3/cc, 2.5×10^6/cc), was exposed to X-irradiation, operated at 180 KVP, 3 mA, without filter. The doses ranged from 5,000 to 150,000 r units. The logarithmic curve of survival ratio to dosage, appearing more or less linear at any concentration, confirmed that the organism was killed by the direct effect of one hit of X-rays.

Morphological mutations induced by the irradiation appeared as f. inst. yeast-like and grey-colored strains which were low-yielding. The irradiated cultures showed, in general, a very wide variation in the yield of the antibiotic substance, and at low X-ray dosage a variant was found which was 10 to 20% more potent than the untreated strain.

The stability in the yield of streptomycin was investigated by subculturing (from the view point of mass production). By subculturing a grey-colored type was found to revert gradually to the normal white.

These results give hope for the production of a high-yielding strain by X-ray treatments.

2. *On a Heterokaryon in Aspergillus candidus*

(Report by Seizô TSUDA)

In many species of Aspergillaceae, development of the perthecium occurs very rarely in nature, and multiplication of the fungus is usually through the production of conidia. Though these fungi do not form hybrids, a phenomenon analogous to hybridization has been found to occur. In this process, one or more nuclei migrate from one cell into another, and produce a heterokaryon. This phenomenon has been studied by SMITH and HANSEN (1932) on *Mucor*, and more recently by BAKER (1944) on *Penicillium*, by PONTECORVO (1946) and by SAKAGUCHI and ISHITANI (1951) on *Aspergillus*, among others.

The writer found in the fall of 1951 a case of heterokaryosis in a strain of *Aspergillus candidus*. From the culture of this heterokaryotic cell a morphologically different strain was segregated. This new strain was cultured repeatedly as many as ten times, and found to retain its morphological characteristic, no further segregation occurring. Accordingly, it was assumed that this strain had become a homokaryotic strain. In this newly segregated homokaryotic strain, the conidiophore was found to be relatively shorter, and the size of the conidiospore was somewhat smaller than in the heterokaryotic strain. The conidiophore was colored white, and the shape of the colonies was round.

It has been noticed that the heterokaryotic strain has a lamella, and the homokaryotic strain a hexenring. The culture media used was Ballg, 5° wort agar, and cultivation was carried out at 28–29°C.

These spores were stained with ROBINOW's Giemsa method (1941) after fixation and hydrolyzation by normal HCl at 60°C for 7 minutes. Observation of the preparations has revealed that the spores of the heterokaryotic strain contain many nuclei, from five to twenty in each, while the spore of the homokaryotic strain usually contains only two or three nuclei.

Cytological and enzymatic studies on these strains are now in progress.

3. *Studies on Neurospora crassa*

(Report by Tarô ITÔ)

A. Rate of production of fruit-body in different culture filtrates

Experiments have been conducted to study the mode of fruit-body formation in the filtrate of the culture of one of the mating types 4A and 8a, and in the filtrate of the mixture of these two types. The filtrate was prepared by passing a 72 hr. culture through a Seitz filter into an Erlenmeyer flask. WESTERGARRD and MITCHELL'S culture medium was added to this filtrate before inoculation.

Many more fruit bodies were formed in the culture medium containing the filtrate than in the control without the filtrate. The fruit-body formation was especially profuse in the culture medium to which the mixed culture filtrate had been added.

From the above result, it may be assumed that some substance or substances which promote conjugation and fruit-body formation are produced. The relative power of the three kinds of filtrates in producing this effect is in the order of (4A+8a)>4A>8a.

B. Growth promotion of culture medium filtrates of two mating types

In order to study the differences in physiological activities between the two mating types, 4A and 8a of *N. crassa*, the growth response of these types to the filtrates of their cultures was examined on the basis of the following presumptions :—

(1) There is no difference in promotion activity between the homotype and the heterotype; that is, the culture filtrate of either the 4A or 8a shows equal effect on the growth of either type.

(2) There are some differences in promotion activity between 4A and 8a, thus :—

a. The culture filtrate promotes the growth of its own strain.

b. Each culture filtrate promotes the growth of the other strain, that is, the filtrate of 4A promotes the growth of 8a and *vice versa*.

In the investigation, the rate of growth response induced by the filtrates was measured by weighing mycelia growth on each filtrate by the method described in the writer's previous report, and the results were analyzed by the variance analysis method.

It has been found that the 4A strain responds more vigorously to the 8a culture filtrate than the 8a strain to its own filtrate, while both strains hardly showed any differential growth response to the 4a culture filtrate.

4. *Studies on the Virus Infecting the Silkworm*

(Report by Mitsuo TSUJITA)

A. On a method of propagation of the virus infecting the silkworm

It is well known that the so-called polyhedral bodies contain infective virus, and that the caterpillars can be infected by eating mulberry leaves contaminated with the polyhedra. There is, however, another important method of propagation of this polyhedral disease. It consists in the transmission of the virus in a latent condition from generation to generation. This has been ascertained by the facts described in the following. Several egg batches of a silkworm strain highly susceptible to the virus were used in this experiment. Each of the batches was divided into two parts, and one of them was treated with diluted hydrochloric acid about 20 hours after oviposition. A special room was used for the incubation of the egg material and rearing of the larvae. The temperature and humidity in the room were variable, according to outdoor conditions in summer. The other half of each batch was placed first in a room at 25°C for 40 hours after oviposition, and then it was refrigerated for 60 days, or kept in a resting condition at room temperature. The eggs were incubated and reared in a thermostat at 25°C and 75 to 85% humidity.

Of the two lots mentioned above, the former produced jaundice-diseased larvae on the second day, and in some lots all of the young larvae died before the first moulting, or by the end of the second instar. On examination of the young larvae which died within twenty hours after emergence, a large number of polyhedral bodies were found, whereas in the latter lot only a small number of larvae died of the disease, and almost all of the apparently healthy larvae developed through pupal stages to emergence. It is scarcely possible that so many polyhedral bodies could have been produced within twenty hours after hatching if infection had entered from the outside of the eggs at the time of emergence of the larvae. This observation seems important because it indicates that the virus must have resided in the developing embryo, instead of coming from outside the shell. It is out of question that the virus had been transmitted from the female parent through the ooplasm, and multiplied in the functional cell in a later embryonic stage.

In short, whether the polyhedra are formed by multiplication and growth of the virus in tissue cells of the larval body or not, there is no doubt that this is controlled by environmental factors in the larval stage. This is also apparently true even for the pupal stage. This also suggests

that the virus in the latent state is activated by environmental stimuli, and muliplies and grows, causing the disease.

Thus, the polyhedral viruses must be capable of lying latent within the silkworm through all its developmental stages. Such a virus is generally called by the name of "latent virus". The phenomenon that the pathogenic agents in the latent state are transmitted from parent to offspring, and the polyhedral disease develops through stimulation by environmental factors, should be distinguished from real cytoplasmic inheritance. Therefore, it is proposed to call this phenomenon "pseudo-cytoplasmic inheritance".

It has been shown by L'HÉRITIER (1948) that sensitivity to CO_2 in *Drosophila* is controlled by a kind of cytoplasmic unit called by him "genoid" or "sigma". This body is transmitted from parent to offspring through the ooplasm and possibly by the sperm also. However, it has, in the meantime, become fairly clear that this cytoplasmic unit is a symbiotic or parasitic virus, because it is contagious. The silkworm virus under discussion bears similarity to this genoid in many points.

ISHIMORI (1940) and YAMAFUJI (1949) claim that the virus in the silkworm can be artificially produced *de novo* by physical and chemical stimulus. Indeed, when the silkworm is refrigerated or injected or fed with various chemicals such as hydroxylamine, potassium nitrite or hydrogen peroxide, it often develops a polyhedral disease. Such an observation might tempt one to a belief in the spontaneous origin of this disease. However, since this virus is apparently transmitted from parent to offspring through ooplasm much as is sigma in *Drosophila*, it is more pausible that the virus is already present in the animal in a latent or dormant state, and that a physical or a chemical treatment may activate it to multiply and grow, and to start the disease.

B. On the multiplication and growth of virus in living cells

The virus particles which appear in the blood of the silkworm in early stages of jaundice disease are from 10 to 30 mμ in diameter. These seem to be virus units liberated from the tissue cells in which they have multiplied. The units multiply by duplication and development, and become *Rickettsia*- or *Diplococcus*-like granules 400–450 mμ in length and 100–150 mμ in width. Each of these granules contains one to several mature thin rod-shaped virus particles, each of which in turn consists of a number of units. The large part of the protein composing the polyhedra is produced in the course of reproduction and growth, probably by some activity of the virus. Consequently, various developmental stages of the virus are contained in each polyhedron. In some cases, rod-shaped particles and spherical particles about 50–100 mμ in diameter can be recognized in the polyhedra. WYCKOFF and SMITH (1951) observed similar virus particles liberated from polyhedra which had developed in the larva of the garden

tiger moth (*Arctia caja*), by dissolving them in dilute alkaline solution. They state that at least two different kinds of this disease may be found in certain Lepidoptera. As reported by BERGOLD (1950) and TSUJITA (1951), the silkworm virus has a kind of life cycle within the host cells. It seems that some primitive phase of this life cycle is transmitted as a latent virus or provirus to the next generation through the ooplasm.

L. THEORETICAL GENETICS

1. *Experimental Demonstration of the Theory of Variance Increase due to Competition in Plant Populations*

(Report by Kan-Ichi SAKAI)

In the 1951 issue of the report of this Institute, the writer advanced a theory postulating an increase of variance caused by competition between plants of different pheno- or genotypes in a heterogeneous plant population. The present report describes the results of an experiment with artificially mixed wheat populations undertaken for the purpose of demonstrating the theory.

Plants of three varieties of wheat, called A, B and C for convenience's sake, were individually space-planted in rows in four different mixtures; the three varieties were also planted without mixing. The experiment was conducted according to the complete randomized block design with four replications. Young seedlings were transplanted into the experimental field in the fall of 1950 so that plants of the varieties to be mixed were placed at random. Data were taken on the basis of the dry plant weight and the number of heads on plant.

(a) Effect of mixing varieties on plant characters.

According to the result of variance analysis, it was found that the plant weight as well as the number of heads of a given variety were significantly affected by the coexistence of another variety or varieties. It has been found that, with regard to competitive ability, $A \geqq B > C$.

(b) Estimation of increments due to competition.

In order to make such estimations, it is necessary to introduce the following premises for the uncertain or unknown part of the experiment:—

(1) Competition occurs only between neighbors in the same row.

(2) Increments in one plant due to two neighbors accumulate additively.

Estimation was made by the method of the least squares, with the result that all of the increments effected by competition in mixed populations, except in the A+B population, were significantly different from zero.

(c) Increase of variance due to interplant competition in mixed populations.

Taking three adjoining rows at random so that we may have approx-

imately a one-hundred plant population from each plot, variances were calculated and the variance of variances was analyzed. It was shown that, with regard to plant weight, the amount of variance in mixed and non-mixed populations differed significantly at the 5 percent level of probability. As the mixed plant population contains plants of different genotypes, the variance of any character in the population should naturally consist of three components; i. e. the environmental, the genotypical and the competitional. The question is: whether any variance due to competition actually exists in the mixed populations of the present experiment. In order to answer this question, the following analysis was made.

(d) Determination of variance due to interplant competition.

In order to determine any variance which would be attributable to the effect of interplant competition, comparison was made between the variance of the mixed population and the variance of an artificial population constructed from two or three groups of data obtained from non-mixed populations.

Differences between the corresponding two variances represent the variance due to competition between plants of different genotypes; that is, the variance due to competition and interaction between competition and the genotype. Analysis of variance made on this set of variance differences showed that the variance due to competition (including the competition-genotype interaction) differed highly signficantly according to the varieties mixed.

The extent of increase of variance is different according to the combination of varieties, being approximately zero in the A+B population, fairly large in A+B+C and B+C populations and very large in the C+A population.

With regard to the number of heads per plant, no significant increase of variance in mixed populations was observed, although there was a general tendency of increase of variance, approximately parallel to that concerning plant weight.

Thus the writer's theory of variance increase due to interplant competition in plant populations has been demonstrated to be valid by the experimental data. This suggests the necessity of a correction in the methods of biometrical investigations of some plant characters. Furthermore, the present theory presents interesting problems concerning plant evolution as well as plant breeding.

2. *Competition Studies with Six Varieties of Rice*

(Report by Kan-Ichi SAKAI)

Competitive ability has been studied in six varieties of rice-plant. The number of experimental plots in one block was thirty-six, covering all combinations between any two of the six varieties. 25 cm^2 space-planting

of individual plants was made according to the 6×6 simple lattice design with four replications. After harvesting, dry-plant weight, plant height, total weight of panicles, number of culms and panicles and length of the first panicle were determined on a plant basis.

By the analysis of variance, all of the characters studied showed highly significant differences among the varieties, separately grown or mix-planted. Average increments of characters of each variety surrounded by the other five varieties were calculated, and analysis of variance was again pursued to find which would be more effective in the role of the surrounding or the surrounded variety. As indicated in Table 1, this analysis has disclosed that the differences in increments due to competition tend to show higher significance in each variety when it behaved as a surrounded plant than as a surrounding plant.

Table 1. Analysis of variance of increments of characters of varieties due to intervarietal competition

Factors	d.f.	Plant weight	Plant height	Number of culms	Number of panicles	Weight of panicles	Length of panicle
Variety as a surrounder	5	76.5**	3.7	1.8*	1.4*	12.1	0.21
Variety as a surrounded one	5	112.9**	6.9*	4.4**	2.1**	57.7**	0.56
Error	25	16.3	2.5	0.6	0.4	4.9	0.23

* Exceeds the 5 percent point. ** Exceeds the 1 percent point.

A comparison of the competitive ability of various varieties when surrounded by other varieties is illustrated in Table 2. Here the standard error of the average increments of the varieties surrounded by five other varieties is taken as a unit.

Table 2. Distribution of six varieties of rice on the basis of competitive ability. Unit of scale: Standard error

Character	Standard error	Distribution of six varieties measured by the competitive increments on a standard error scale										
		−6.5	−5.5	−4.5	−3.5	−2.5	−1.5	−0.5	+0.5	+1.5	+2.5	+3.5
Total weight	1.65			A			T_1S	N	K			T_2
Plant height	0.64				T_2		KS	A	N	T_1		
Number of culms	0.30	A					T_1	SK	T_2N			
Number of panicles	0.25		A					T_1T_2	KSN			
Weight of panicles	0.90	A					S	NT_1			KT_2	

The average competitive ability of N, S, and T_1 are shown to be approximately zero, while the capacity of A, T_2 and K has a plus or minus value for more than one character. It is especially noticeable that the competitive ability of A, the only glutinous variety, called Asahi-mochi, for all characters except plant height shows negative value.

3. *Theoretical Studies on Selection in the Breeding of Autogamous Plants*

(Report by Kan-Ichi SAKAI)

(1) Selection of quantitative characters.

Quantitative characters in plants are often supposed to be controlled by a number of multiple genes, which have similar and additive effects. Though it is in many cases very difficult or even impossible to analyze the genotypical constitution of such characters on account of considerable fluctuation, they often provide good material for successful selection work. The present paper deals with a theoretical consideration concerning the effect of partial selection on quantitative characters in a hybrid population of autogamous plants.

Assumptions are made that the pairs of genes concerned are two, i. e. *Xx* and *Yy*, assorting independently of each other, and having the same and additive effects. The selection, accordingly, deals only with plus-genes.

Frequencies and selective values of genotypes involving four to zero plus-genes are given as follows:

Number of plus-genes	4	3	2	1	0
Genotypes and their relative frequencies in parentheses:	*XXYY* (a)	*XXYy*(b) *XxYY*(c)	*XxYy* (e)	*XXyy*(d) *xxYY*(f)	*xxYy*(g) *Xxyy*(h)	*xxyy* (i)
Selective valus of genotypes:	s_1	s_2	s_3	s_3'	s_4	s_5

Frequencies of any genotype in the nth generation can be computed from the formulae given below:

$$a_n=\left(s_1a_{n-1}+s_2\frac{1}{4}b_{n-1}+s_2\frac{1}{4}c_{n-1}+s_3\frac{1}{16}e_{n-1}\right)\Big/W_{n-1}$$

$$b_n=\left(s_2\frac{1}{2}b_{n-1}+s_3\frac{1}{4}\cdot\frac{1}{2}e_{n-1}\right)\Big/W_{n-1}$$

$$c_n=\left(s_2\frac{1}{2}c_{n-1}+s_3\frac{1}{4}\cdot\frac{1}{2}e_{n-1}\right)\Big/W_{n-1}$$

$$e_n=s_3\frac{4}{16}e_{n-1}/W_{n-1}$$

$$d_n=\left(s_3'd_{n-1}+s_2\frac{1}{4}b_{n-1}+s_3\frac{1}{4}\cdot\frac{1}{4}e_{n-1}+s_4\frac{1}{4}h_{n-1}\right)\Big/W_{n-1}$$

$$f_n=\left(s_{3'}f_{n-1}+s_2\frac{1}{4}c_{n-1}+s_3\frac{1}{4}\cdot\frac{1}{4}e_{n-1}+s_4\frac{1}{4}g_{n-1}\right)\Big/W_{n-1}$$

$$g_n=\left(s_4\frac{1}{2}g_{n-1}+s_3\frac{1}{4}\cdot\frac{1}{2}e_{n-1}\right)\Big/W_{n-1}$$

$$h_n=\left(s_4\frac{1}{2}h_{n-1}+s_3\frac{1}{4}\cdot\frac{1}{2}e_{n-1}\right)\Big/W_{n-1}$$

$$i_n=\left(s_5i_{n-1}+s_3\frac{1}{16}e_{n-1}+s_4\frac{1}{4}g_{n-1}+s_4\frac{1}{4}h_{n-1}\right)\Big/W_{n-1}.$$

Here W_{n-1} stands for the mean selective value in the $(n-1)$th generation which is formulated as,

$$W_{n-1}=s_1a_{n-1}+s_2(b_{n-1}+c_{n-1})+s_3e_{n-1}+s_{3'}(d_{n-1}+f_{n-1})+s_4(g_{n-1}+h_{n-1})+s_5i_{n-1}.$$

Since the selection is repeated during each of the successive generations, the total number of individuals in the nth generation is proportional to w_n, which will be expressed as:

$$w_n=W_0W_1W_2\ldots.W_{n-1}=\prod_{j=0}^{n-1}W_j \qquad (n\geq 1,\ w_0=1).$$

Let w_na_n, w_nb_n, ..., w_ni_n be A_n, B_n, ..., I_n, and the selective values be represented as $s_1=K_1$, $\frac{s_2}{2}=K_2$, $\frac{s_3}{4}=K_3$, $s_{3'}=K_{3'}$, $\frac{s_4}{2}=K_4$ and $s_5=K_5$, the following equations result:

$$A_n=\frac{K_2K_3}{2(K_2-K_3)}\left[L(1,2)-L(1,3)\right]+\frac{K_4}{4}L(1,3),$$

$$B_n=C_n=\frac{1}{2}K_3L(2,3),$$

$$E_n=(K_3)^n,$$

$$D_n=F_n=K_3\left\{\frac{K_2}{4(K_2-K_3)}\left[L(3',2)-\frac{(4^n-1)K_3{}^{n-1}}{3}\right]+\frac{4^{n-1}K_3{}^{n-1}}{3}\left(1-\frac{1}{4^n}\right)+\frac{K_4}{4(K_4-K_3)}\left[L(3',2)-\frac{(4^n-1)K_3{}^{n-1}}{3}\right]\right\}.$$

$$G_n=H_n=\frac{1}{2}K_3L(4,3),$$

$$I_n=\frac{K_4K_3}{2(K_4-K_3)}\left[L(5,4)-L(5,3)\right]+\frac{1}{4}K_3L(5,3),$$

where $L(i,j)$ stands for $\frac{K_i{}^n-K_j{}^n}{K_i-K_j}$.

Assuming the selective value of any genotype with a given number of plus-genes to be 1 or 0.1, the proportion of *XXYY* plants in some hybrid generations is presented in the following Table 3.

Table 3

Genotype	No. of plus genes	Selective values					
XXYY	4	1	1	1	1	1	1
XXYy, XxYY	3	1	1	1	1	1	0.1
XxYy	2	1	1	1	1	0.1	0.1
XXyy, xxYY	2	1	1	1	0.1	0.1	0.1
Xxyy, xxYy	1	1	1	0.1	0.1	0.1	0.1
xxyy	0	1	0.1	0.1	0.1	0.1	0.1
Proportion of	F_4	19.14	22.06	30.57	46.43	75.39	89.70
XXYY	F_5	23.46	29.93	39.48	81.86	93.38	99.93
in percent	F_6	24.90	33.15	42.05	98.77	99.61	100.00

It is noticeable from this table that the proportion of *XXYY* in later generations will be considerably affected according to whether the selection of *XXyy* and *xxYY* be possible or not.

(2) Effect of a single mass-selection during segregating generations of a hybrid population of autogamous plants.

In a single mass-selection conducted in one of the segregating generations of autogamous hybrid plants, the degree of efficacy of the selection for securing as many homozygous dominants as possible should be computed by taking into consideration the time of occurrence of the selection. A brief consideration will be here given.

Let the numbers of segregating generations before and after any single selection be n and m respectively, and the total number of segregating generations $N(=n+m)$, and also, let the selection coefficient of recessive genotypes be s, then the frequency of phenotypic dominants in the Nth generation, D_N, may be computed by the following formula,

$$D_N=t\left[\frac{1}{2}+\frac{1}{2^{N+1}}\right]^r=t\frac{1}{2^r}\left(1+\frac{1}{2^N}\right)^r,$$

where t is a function of s as given below and r stands for the number of corresponding gene pairs.

$$t=\frac{1}{1-(1-s)\left[1-\frac{1}{2^r}\left(1+\frac{1}{2^n}\right)^r\right]}.$$

The following table illustrates the percentage of phenotypic dominants in F_7 in a hybrid population which has been subjected to a single selection, taking all dominants and ten percent of all recessives in any of the F_2 to F_6 generations.

Table 4

Number of gene pairs	Without any selection	With a single mass-selection in				
		F_2	F_3	F_4	F_5	F_6
1	50.78	65.52	76.65	83.76	87.84	90.03
3	13.30	27.30	40.96	50.33	55.74	58.62
5	3.38	10.77	18.17	22.41	24.46	25.43
10	0.11	0.76	1.05	1.11	1.12	1.13
15	0.004	0.03	0.04	0.04	0.04	0.04

This shows that a single selection during cultivation of a hybrid bulk is effective in increasing the number of desirable dominant genotypes in the final population, and that the later the selection occurs, the greater the chances of the success.

4. *Fluctuations of Adaptive Values and the Frequency Distribution of Heterotic Genes in Natural Populations*

(Report by Motô KIMURA)

A. Long term distribution determined by random fluctuation

It is well known that in panmictic populations the superiority in adaptability of heterozygotes over their corresponding homozygotes will lead to the maintenance of more than two alleles or chromosome types in stable equilibrium (cf. WRIGHT 1949; BRIEGER 1950, etc.). Recent experiments on natural populations have revealed that adaptive values of many genotypes undergo both random and cyclic fuctuations, which are often characteristic of the coadaptation mechanism, that is, the mechanism of mutual adjustment of the gene contents of different chromosome types (cf. DOBZHANSKY 1950, 1951; FISHER and FORD 1947, 1950, etc.). The following is a result of mathematical investigations on these problems.

Let x be the relative frequency of a gene (or a chromosome type) A, and let $1-x$ be that of its allele (or a different chromosome type) A' in a panmictic and sufficiently large population. If the adaptive values of the three genotypes AA, AA' and $A'A'$ are respectively $1-s$, 1 and $1-t$, and the mutation rates of A to and from A' are respectively u and v, then the mean ($M_{\delta x}$) and the variance ($V_{\delta x}$) of the rate (δx) of change of the frequency of A per generation amount to

$$M_{\delta x} = -\bar{s}x^2(1-x) + \bar{t}x(1-x)^2 - ux + v(1-x)$$

and

$$V_{\delta x} = x^2(1-x)^2\{V_s x^2 - 2W_{st}x(1-x) + V_t(1-x)^2\},$$

where $\bar{s}$, $\bar{t}$ and V_s, V_t respectively denote the means and variances of selection coefficients, i.e. s and t, while W_{st} is a covariance between them.

Under these conditions, the probability density $\varphi(\tau, x)$ for the frequency

of A in the τ-th generation satisfies the following FOKKER-PLANCK equation (cf. WRIGHT 1945):

$$(1)\qquad \frac{\partial\varphi(\tau,x)}{\partial\tau}=\frac{1}{2}\frac{\partial^2}{\partial x^2}[V_{\delta x}\varphi(\tau,x)]-\frac{\partial}{\partial x}[M_{\delta x}\varphi(\tau,x)]\,.$$

Assuming that the means, the variances and the covariance of the selection coefficients are all constant for a long period and $W_{st}^2-V_sV_t<0$, then the solution; $\varphi(x)$, for the stationary state; $\partial\varphi(\tau,x)/\partial\tau=0$, becomes

$$(2)\quad \varphi(x)=C\{(x-\alpha)^2+\beta^2\}^{-A-1}(1-x)^{\frac{2}{V_s}\left\{\bar{s}+\frac{3V_s+2W_{st}}{V_s}u-v-V_s\right\}}$$
$$\times x^{\frac{2}{V_t}\left\{\bar{t}-u+\frac{2W_{st}+3V_t}{V_t}v-V_t\right\}}$$
$$\times\exp\left\{-2B\tan^{-1}\left(\frac{x-\alpha}{\beta}\right)-\frac{2u}{V_s}\left(\frac{1}{1-x}\right)-\frac{2v}{V_t}\left(\frac{1}{x}\right)\right\},$$

where
$$A=\frac{\bar{s}}{V_s}+\frac{\bar{t}}{V_t}+\frac{V_tV_{s+t}-(V_t-V_s)^2}{V_s^2V_t}u+\frac{V_sV_{s+t}-(V_t-V_s)^2}{V_sV_t^2}v\,,$$
$$B=\frac{1}{\sqrt{V_tV_s-W_{st}^2}}\left\{\left(1+\frac{W_{st}}{V_s}\right)\bar{s}-\left(1+\frac{W_{st}}{V_t}\right)\bar{t}\right.$$
$$+\frac{(W_{st}+V_t)V_sV_{s+t}-2(V_tV_s-W_{st}^2)(V_t-V_s)}{V_s^2V_t}u$$
$$\left.-\frac{(V_s+W_{st})V_tV_{s+t}+2(V_tV_s-W_{st}^2)(V_t-V_s)}{V_t^2V_s}v\right\},$$
$$\alpha=(W_{st}+V_t)/V_{s+t}\,,\qquad \beta=\sqrt{V_tV_s-W_{st}^2}/V_{s+t}\,,$$
$$V_{s+t}=V_s+2W_{st}+V_t$$

and $\tan^{-1}X$ takes a principal value. The value of C is chosen such that $\int_0^1\varphi(x)dx=1$. From the "ergodicity of stationary stochastic process", the formula (2) gives the long term distribution of gene frequencies in natural populations. Since u and v are usually expected to be much smaller than $\bar{s}$ and $\bar{t}$, the distribution curves centre around the equilibrium frequency; $\hat{x}=\bar{t}/(\bar{s}+\bar{t})$, as V_s and V_t tend to 0. So in this case the ratio $\bar{s}/\bar{t}$ is the determining factor for the frequency distribution. But if V_s and V_t are not negligible for $\bar{s}$ and $\bar{t}$, the ratios $\bar{s}/V_s$, $\bar{t}/V_t$ and the correlation coefficient (r_{st}) between s and t, as well as $\bar{s}/\bar{t}$, are all important for the distribution.

For cases of coadaptation, the values of r_{st} may be expected to be approximately -1. The estimation of the above mentioned parameters in natural populations would be an important task left for future experiments.

B. Process of the change of gene frequencies due to the cyclic and random fluctuations of selective values.

As the simplest model of coadaptation, let us consider the case in which one cycle consists of m generations and $\bar{s}=c_1 \sin(2\pi\tau/m)$, $\bar{t}=-c_2 \sin(2\pi\tau/m)$, where $c_1 \geq c_2 > 0$. To make the calculations simpler, let us assume further that there is a complete negative correlation between s and t ($r_{st}=-1$), that their coefficients of variation are equal in absolute value ($\sqrt{V_s}/|\bar{s}| = \sqrt{V_t}/|\bar{t}|$), and that the change due to mutations is negligible.

Putting $\sqrt{V_s}/c_1=\sqrt{V_t}/c_2 \equiv k(\tau)$, the mean and the variance of δx become respectively

$$M_{\delta x}=-x(1-x)\{c_2+(c_1-c_2)x\} \sin(2\pi\tau/m)$$

and

$$V_{\delta x}=x^2(1-x)^2\{c_2+(c_1-c_2)x\}^2 k^2(\tau) .$$

If the frequency x is transformed into z either by the relation:

$$z=\frac{1}{c}\log\left(\frac{x}{1-x}\right) \qquad (\text{if } c_1=c_2\equiv c)$$

or by the relation:

$$z=\frac{1}{c_2}\log x-\frac{1}{c_1}\log(1-x)-\frac{c_1-c_2}{c_1c_2}\log\left(\frac{c_2}{c_1-c_2}+x\right) \quad (\text{if } c_1>c_2),$$

the resulting variate z may be regarded as a scale for the gene frequency, changing continuously from $-\infty$ to $+\infty$ as x changes continuously from 0 to 1.

Under this scale, the mean and the variance of the rate of change per generation become simpler, being

$$M_{\delta z}=-\sin\left(\frac{2\pi}{m}\tau\right) \quad \text{and} \quad V_{\delta z}=k^2(\tau) \quad \text{approximately.}$$

So if the number of generations (m) in one cycle is large, the probability density $\phi(\tau, z)$ in the τ-th generation satisfies the equation:

$$(1) \qquad \frac{\partial\phi}{\partial\tau}=\frac{k^2(\tau)}{2}\frac{\partial^2\phi}{\partial z^2}+\sin\left(\frac{2\pi}{m}\tau\right)\frac{\partial\phi}{\partial z},$$

which represents a spatially homogeneous MARKOV process.

The solution of this equation is

$$\phi(\tau,z)=\frac{1}{\sqrt{2\pi}\sigma_\tau}\exp\left\{-\frac{\left[z-\frac{m}{2\pi}\cos\left(\frac{2\pi}{m}\tau\right)+\frac{m}{2\pi}-z_0\right]^2}{2\sigma_\tau^2}\right\}, \quad (\tau>0),$$

where $\sigma_\tau^2=\int_0^\tau k^2(\tau')d\tau'$ and z_0 is the value of z at the start ($\tau=0$). In every cycle, the mean value of z;

$$\bar{z}=z_0+\frac{m}{2\pi}\left\{\cos\left(\frac{2\pi}{m}\tau\right)-1\right\}$$

returns to its original value, z_0, while the variance increases by $\sigma_m^2 = \int_0^m k^2(\tau')d\tau'$. In a sufficiently large number of generations, the increase in variance will be counterbalanced by mutation or migration, and the probability distribution for a given generation would become independent of the inital condition (z_0), though I have not succeeded in obtaining the formula for that distribution.

From the comparison of the series of values between z and $\bar{s}$, it may be clear that there is a shift by $m/4$ generations between the periods of their maxima and also between their minima, so that the period at which the frequency of AA becomes maximum or minimum lags respectively by $m/4$ generations behind that at which its adaptability becomes maximum or minimum. This indicates that, against the cyclic change in the environmental conditions, the mode of adaptation due to the "coadaptation" mechanism is less effiicent than that due to the direct change of phenotypes.

5. *Process of Irregular Change of Gene Frequencies due to the Random Fluctuation of Selection Intensities*

(Report by Motô KIMURA)

In the mathematical treatment of the process of change by selection, it has commonly been assumed that the selection intensity is constant throughout many generations, though in practice the intensity must be subject to fluctuations. In the present investigation random fluctuation of the selection intensities is assumed to occur and the resulting MARKOV process is investigated.

Let x and $1-x$ be respectively the frequencies of a gene a and its allele A in a population which is assumed to be very large and panmictic. The rate of change of frequency of a per generation, if there is no dominance, is

$$\delta x = sx(1-x)\,,$$

while it is

$$\delta x = sx^2(1-x)\,,$$

if A is completely dominant over a. Here s stands for the selection coefficient of the gene a in the former case, while it stands for that of the recessive individual (aa) in the latter case.

If the frequency x is transformed into the variate z either by

$$z = \log\left(\frac{x}{1-x}\right) \quad \text{(for the case of no dominance)}$$

or by

$$z=-\frac{1}{x}+\log\left(\frac{x}{1-x}\right) \quad \text{(for the case of complete dominance),}$$

the rate of change of the value of z per generation becomes

$$\delta z=s$$

in either case. If the gene frequency in the population is measured by this z scale, it changes continuously from $-\infty$ to $+\infty$ as x changes from 0 to 1. The mean and the variance of δz are equal respectively to the mean ($\bar{s}$) and the variance (V_s) of the selection coefficient (s).

Thus, under the z scale, the process of the change of the gene frequency can be represented by a temporally and spatially homogeneous MARKOV process, the transition probability of which is

$$f(\tau,z|0,z_0)=\frac{1}{\sqrt{2\tau\pi V_s}}e^{-\frac{(z-\bar{s}t-z_0)^2}{2V_s\tau}}, \qquad (\tau>0),$$

and hence often called "GAUSS process" by mathematicians.

Therefore, if x_0 is the initial gene frequency ($\tau=0$), the probability; $\varphi_\tau(x)dx$ that x_0 changes into $x\sim x+dx$ through the selection extending τ generations, is:

$$\varphi_\tau(x)dx=\frac{1}{\sqrt{2\pi\tau V_s}}\exp\left\{-\frac{\left(\log\frac{x(1-x_0)}{x_0(1-x)}-\bar{s}\tau\right)^2}{2V_s\tau}\right\}\frac{dx}{x(1-x)}, \qquad (\tau>0),$$

for the case of no dominance and

$$\varphi_\tau(x)dx=\frac{1}{\sqrt{2\pi\tau V_s}}\exp\left\{-\frac{\left(\log\frac{x(1-x_0)}{x_0(1-x)}-\left(\frac{1}{x}-\frac{1}{x_0}\right)-\bar{s}\tau\right)^2}{2V_s\tau}\right\}\frac{dx}{x^2(1-x)}, \quad (\tau>0),$$

for the case of complete dominance.

This process should proceed indefinitely, if there were no disturbance by gene mutation, though in practice the advance will finally be checked by the opposed mutation pressure.

In the above discussion, it has been assumed that $\bar{s}$ and V_s are constant. If they change from generation to generation, they must be treated as functions of τ, so that $\bar{s}\tau$ and $V_s\tau$ in the above formulae must be replaced respectively by $\int_0^\tau\bar{s}(\tau')d\tau'$ and $\int_0^\tau V_s(\tau')d\tau'$.

6. *On "Effective Size of Populations"*

(Report by Motô KIMURA)

The concept of "effective size of population", which was introduced by WRIGHT (1931) and developed in his later papers, is fundamental in dis-

cussing the frequency distribution of genes in natural populations. Recently, the present writer attempted a mathematical study on this problem, and some of the results obtained are reported here.

Let us consider a sexually reproducing population of any diploid organism, in which the relative frequency of an autosomal gene A is x.

The effective size (N_e) of the population may be defined by the relation:

$$N_e \equiv x(1-x)/(2V_{\delta' x}) ,$$

where $V_{\delta' x}$ is the variance of the deviation ($\delta' x$) of the gene frequency due to random sampling of the gametes in one generation, (assuming that x is neither zero nor unity).

If, in each generation, the population is produced by the union of N_a male and N_a female gametes taken, as random samples, from all the gametes produced equally by N_A members of the previous generation, so that the generations never overlap and the population retains its number N_A for many generations, then the effective size is equal to its apparent or total number (N_A):

$$N_e = N_a .$$

But, there may be cases, in which the population in every generation emerges from any random portion of the previous generation, with the result that the number (N_b) of the effectively breeding individuals will become smaller than that (N_A) of the total population in any stage of the life cycle. In such case the effective size is equal to N_b and smaller than N_a:

$$N_e = N_b < N_a .$$

If there are changes in the number of the effectively breeding individuals, as well as in apparent size, the mean effective size over τ generations approximates to

$$\bar{N}_e = \tau \Big/ \left\{ \left(\frac{1}{N_a^{(\tau+1)}} - \frac{1}{N_a^{(1)}} \right) + \sum_{t=1}^{\tau} (1/N_b^{(t)}) \right\}$$

which is reduced to

$$\bar{N}_e = \tau \Big/ \sum_{t=1}^{\tau} (1/N_b^{(t)}) ,$$

if the change is cyclic such that $N_a^{(\tau+1)} = N_a^{(1)}$. Here it must be assumed that τ is not too large. Therefore, when there are fluctuations within a very wide range, the effective size is controlled much more by the smaller phase than by the larger.

If there is a great difference between the number of males (N_m) and the number of females (N_f), N_e is much smaller than the total number, as will be shown below: Let M and W be the mean and the variance in the number (J) of females which mate with one male respectively, so that $M = N_f/N_m$ and $W = \sum_{i=1}^{N_m} (J_i - M)^2/N_m$, then

$$N_e=4N_mN_f\Big/\left\{N_m\left(1+\frac{W}{M}\right)+N_f\right\},$$

assuming that the number of the females is larger than that of the males ($N_f>N_m$) and that a female never mates with more than one male, as may be the case in the harems of seals. Thus if N_f is very large, while N_m is much smaller, the effective size becomes approximately $4N_m$.

So far we have assumed that the frequency distribution in the number of surviving offspring produced by one parent corresponds approximately to the POISSON series.

In organisms which reproduce by apomixis or close inbreeding, the effective size is largely controlled by the variance (V) in the numbers of the surviving offspring per individual. For example, in the populations of self-fertilizing plants

$$N_e=N_aN_b/2\{(V/\bar{X}-1)N_b+N_a\},$$

where $\bar{X}$ and V are respectively the mean and the variance of the number of surviving seeds of any individual which belongs to any effective portion of the population from which the next generation starts. The formula reduces to $N_e=N/(2V)$, if $\bar{X}=1$ and therefore $N_a=N_b\equiv N$. In the following, the symbol N is used for designating the effective size when N_b coincides with N_a. In partially self-fertilizing plants, if λ is the probability that any ovule would be fertilized by a pollen randomly extracted from the whole population,

$$N_e=\frac{2(1+\lambda)N}{\lambda(4-\lambda)+(2-\lambda)^2V},$$

assuming that the population retains its size N for many generations. For a large population λ may safely be taken as the relative frequency of cross-fertilization.

In many higher animals and in perennial plants, generations overlap and situations may be more complicated, so that some extention of the above mentioned definition will become necessary.

If $\overline{\delta x}$ is the rate of change in gene frequency due to mutation and selection per one breeding season, the extended definition is:

$$N_e=x(1-x)/\{2(1+\alpha)V_{\delta' x}\},$$

where $V_{\delta' x}$ is the sampling variance of gene frequency which will be expected in periods during which a newly-born individual ends its life and is replaced by its offspring, while $(1+\alpha)\overline{\delta x}$ is the rate of change in gene frequency due to mutation and selection in the corresponding periods.

For example, if every newly-born individual keeps its original fecundity through n breeding seasons, and then is replaced by its offspring,

$$V_{\delta' x}=\frac{x(1-x)}{2Nn}\left[\left(1+\frac{1}{n}\right)^{2n}-1\right] \quad \text{and} \quad \alpha=\frac{1}{n}\left[\left(1+\frac{1}{n}\right)^{n-1}-1\right],$$

where Nn is the total number of breeding individuals in the population. So when n is large

$$N_e=\frac{Nn}{\left(1+\frac{e-1}{n}\right)(e^2-1)},$$

i.e., the effective size would be about $1/(e^2-1)$ or 1/6.4 of the total of breeding individuals in the population. On the other hand, the properties of large, uniformly distributed populations have been discussed in detail by WRIGHT (1946–1951). No doubt, "effective size" is a very important concept, but for the genes which influence—or have some relation to—the breeding behavior, routine extrapolation must be avoided, and new computations, fitted to each case, become necessary.

7. *On the Process of Decay of Variability due to Random Extinction of Alleles*

(Report by Motô KIMURA)

In a population of restricted size, the relative frequencies of genes undergo random changes from generation to generation owing to the random sampling of gametes in reproduction, so that a gradual decrease in genetic variability of the population is to be expected, unless variants are constantly supplied by mutation or migration. The process of such changes was studied by FISHER (1930) by means of a partial differential equation and also by functional equations. WRIGHT independently investigated this problem, first (1931) by the method of an integral equation in conjunction with his path coefficient technique, and later (1945) by a partial differential equation of a somewhat different kind. The attention of these authors, however, was restricted to the state of change, after the lapse of a sufficient number of generations, when the distribution curve would have reached a constancy of form and the frequencies of all heterallelic classes were decreasing approximately at the rate of $1/2N$. The present writer has attempted a more extensive analysis of the problem which includes the process before such a state is reached, and he has obtained some new results by calculating the moments of distribution.

Consider a population of effective size N, in which the initial frequencies of gene A and its allele A' are p and $q(=1-p)$ respectively. If $f_t(x)$ is the probability that the frequency of A will change to x after t generations, x may take any one of a series of values:

$$0,\ \frac{1}{2N},\ \frac{2}{2N},\ \cdots,\ 1-\frac{1}{2N},\ 1,$$

and the n-th moment of the distribution about zero as origin;

$$\mu_n'^{(t)}=\sum_{x=0}^{1} x^n f_t(x)\ ,$$

is, for a value of t which is large, and not smaller than the order of N,

$$\mu_n'^{(t)}=p-3pq\frac{n-1}{n+1}\lambda_1{}^t-5pq(p-q)\frac{(n-2)(n-1)}{(n+1)(n+2)}\lambda_2{}^t$$
$$-7pq(-5pq+1)\frac{(n-3)(n-2)(n-1)}{(n+1)(n+2)(n+3)}\lambda_3{}^t-9pq(14pq^2-7pq+p-q)$$
$$\times\frac{(n-4)(n-3)(n-2)(n-1)}{(n+1)(n+2)(n+3)(n+4)}\lambda_4{}^t+0(\lambda_5{}^t)\ ,$$

where $\lambda_1=1-\frac{1}{2N}$, $\lambda_2=1-\frac{3}{2N}$, $\lambda_3=1-\frac{6}{2N}$, $\lambda_4=1-\frac{10}{2N}$, $\lambda_5=1-\frac{15}{2N}$, etc., and the absence of any systematic pressure (i.e. mutation, migration and selection) is assumed.

Thus the probability of fixation of the gene A in the population in the t-th generation is

$$f_t(1)=p-3pq\lambda_1{}^t-5pq(p-q)\lambda_2{}^t-7pq(-5pq+1)\lambda_3{}^t$$
$$-9pq(14pq^2-7pq+p-q)\lambda_4{}^t+0(\lambda_5{}^t)$$

and the probability of extinction is

$$f_t(0)=q-3pq\lambda_1{}^t+5pq(p-q)\lambda_2{}^t-7pq(-5pq+1)\lambda_3{}^t$$
$$+9pq(14pq^2-7pq+p-q)\lambda_4{}^t+0(\lambda_5{}^t)\ ,$$

while the probability of coexistence of A and A' in the population; $\Omega_t=\sum_{0<x<1} f_t(x)$, is

$$\Omega_t=6pq\lambda_1{}^t+14pq(-5pq+1)\lambda_3{}^t+0(\lambda_5{}^t)\ .$$

From the above relations, the following formulae will be easily obtained:

(1) $\Omega_t>\Omega_{t+1}>\cdots>\Omega_\infty=0$

(2) $\lim_{t\to\infty}(\Omega_{t+1}/\Omega_t)=1-1/2N$

(3) $f_t(x)\sim 6pq(1-1/2N)^t$ $\quad(t\to\infty,\ 0<x<1)$

(4) $f_t(1)\sim p-3pq(1-1/2N)^t$ $\quad(t\to\infty)$

(5) $f_t(0)\sim q-3pq(1-1/2N)^t$ $\quad(t\to\infty)$

8. *Process of Recombination of Chromosome Segments in a Random Breeding Population*

(Report by Motô KIMURA)

(1) Case of "Introgressive hybridization" (cf. E. ANDERSON 1949)

In natural populations, chromosomes or gene blocks may often be introduced from the populations of allied species or subspecies through

hybridization, though in very low frequencies. If the hybrids are more or less fertile, the parts of the newly introduced chromosomes will spread in the population through repeated backcrossing and crossing-over, increasing or decreasing according to the degree of fitness of the group of genes that they contain, or to the chance survival or extinction in reproduction. The writer has investigated mathematically the behavior of such segments in a large and randomly breeding population and has derived some formulae regarding the frequency distributions of such segments, by solving integral equations of the finite difference type.

Consider a very large and randomly breeding population and let A be a type chromosome in the population while A' is an introduced chromosome which is homologous to A but differing in many alleles and having a genetical length of $100x_0$ units.

If the intial frequency (R_0) of A' in the population is very low ($R_0 \ll 1$), the composition of the population after n generations may be expressed approximately as:

$$(1-Q_n-R_n)AA\,;\quad Q_nA\alpha\,;\quad R_nAA'\,,$$

unless n is not very large. Here α is a chromosome produced directly or indirectly by crossing-over between A and A'. If the composition of the population at the start ($n=0$) is

$$(1-R_0)AA\,;\quad R_0AA'\,.$$

the frequency of AA' in the n-th generation is

$$R_n=(1-x_0)^nR_0\,.$$

The frequency of $A\alpha$ pairs in the same generation is

$$Q_n=\{nx_0+1-(1-x_0)^n\}R_0\,,$$

of which the frequency of the chromosome pair having heterozygous segment or segments of $100x\sim100(x+dx)$ is

$$Q_n(x)dx=\{n(n+1)(1-x)^{n-1}-n(n-1)(1-x)^{n-2}(1-x_0)\}R_0dx\,,\quad (0<x<x_0)\,.$$

For deriving these formulae it is assumed that the hybrid and its descendants have a normal fertility and only a single crossing-over is allowed to occur in the heterozygous segment. But this may not be the case in general. More usually the fertility may be lowered by hybridization and the introduced chromosomes will be subjected to natural selection. In such cases, the problem becomes very difficult to treat mathematically. But, particularly for the case in which the effect of reducing fertility is geometric; i.e., where the logarithm of fertility is proportional to the length of heterozygous segments, the present writer has succeeded in deriving a formula by solving an integral equation. This will be discussed in a later paper.

For the case in which the number of the chromosomes introduced into

the population is small, we must consider the chance disappearance of segments derived from them, as in the case of an individual gene. Let m be the number of A' at the start; then the chance that ν chromosomes having the whole or a part of segments of A' will survive to the n-th generation may be given by

$$\frac{1}{\nu!}\left[\frac{\partial^\nu}{\partial z^\nu}\varphi_n(z)\right]_{z=0},$$

if selection is absent. In this expression, $\varphi_n(z)$ is a generating function and satisfies the relation:

$$\varphi_n(z)=[F_0\{F_1(\cdots(F_{n-1}(z))\cdots)\}]^m,$$
$$F_k(z)=\exp\{-(1+x_k)(1-z)\} \text{ and } x_k=x_0/(1+kx_0).$$

The probability of the complete disappearance may be given by $\varphi_n(0)$. In the following table, values of $\varphi_n(0)$ are listed for several values of m and n when $x_0=0.3$. For instance, if a foreign chromosome is introduced into the population through an outcrossing with an allied species and if the cross-over value is 30%, the chance that all chromosome segments derived from it will have disappeared after 15 generations is about 71%.

Table 5

n \ m	1	3	5
1	0.273 (0.3679)*	0.020	0.002
3	0.474 (0.6259)	0.106	0.024
7	0.613 (0.7905)	0.231	0.087
15	0.708 (0.8873)	0.355	0.178

* Values in parentheses are the chance of disappearance of an individual mutant gene, the calculation of which we owe to R.A. FISHER (1930).

If, on the other hand, there is no crossing-over, the chance is about 89%.

(2) Change in high frequencies

If the initial composition of the population is

$$\frac{1}{4}AA;\ \frac{1}{2}AA';\ \frac{1}{4}A'A',$$

the frequency of chromosome α at the n-th generation ($n\geqslant 1$) may be

$$1-(1-x_0/2)^{n-1}[(2-x_0)/2]$$

while the frequency of A or A' chromosome may be equal to

$$(1-x_0/2)^{n-1}[(2-x_0)/4].$$

Thus the frequency of heterozygous pairs may be

$$H_n=1-2\left(1-\frac{x_0}{2}\right)^{2(n-1)}\left(\frac{2-x_0}{4}\right)^2,$$

and the mean length of their heterozygous segments may be

$$x_0\Big/\left\{2-\left(1-\frac{x_0}{2}\right)^{2(n-1)}(2-x_0)^2\right\}.$$

9. *Method of Mating-Operators and its Application to the Study of Partially Self-fertilizing Populations*

(Report by Motô KIMURA)

(1) Mating-operators

For a partially self-fertilizing population, it is not easy to trace mathematically the process of recombination of chromosome segments from generation to generation. To overcome this difficulty, the method of mating-operators has been introduced. Let H_n be the frequency of heterozygous chromosome pairs in a population of the n-th generation; then the random-mating-operator f_∞ is defined such that $f_\infty H_n$ represents the frequency of the heterozygous pairs after the population undergoes random mating of one generation, while the selfing-operator f_1 is defined such that $f_1 H_n$ represents the corresponding frequency after the population undergoes self-fertilization of one generation. Thus $f_1 f_\infty H_n$ represents the frequency of heterozgous pairs in the $(n+2)$-th generation when random-mating in the n-th generation is followed by self-fertilization in the $(n+1)$-th generation.

In a partially self-fertilizing plant population, if μ is the proportion of individuals fertilized by their own pollen, while $\lambda(=1-\mu)$ is the proportion in which they are fertilized by polleh randomly extracted from the population as a whole, then the frequency of heterozygous pairs in the n-th generation will be

$$H_n=(\lambda f_\infty+\mu f_1)^n H_0 . \tag{1. 1}$$

In expanding the right-side of (1. 1), we must notice that while the operators follow the distributive law;

$$(\lambda f_\infty+\mu f_1)(\lambda f_\infty+\mu f_1)=\lambda^2 f_\infty^2+\lambda\mu f_\infty f_1+\mu\lambda f_1 f_\infty+\mu^2 f_1^2 , \tag{1. 2}$$

they do not statisfy the commutative law;

$$f_1 f_\infty \neq f_\infty f_1 . \tag{1. 3}$$

For the calculation, the following relation is fundamental:

$$f_1^{\,t} f_\infty^{\,1+s+r} H_0 \geqq f_1^{\,t} f_\infty^{\,r} \underset{s,r}{(\Pi f)} H_0 \geqq f_1^{\,t} f_\infty^{\,r} H_0 , \tag{1. 4}$$

where $\underset{s,r}{\Pi f}$ denotes the product of s f_1 operators and r f_∞ operators in an

arbitorary order. The equality in the formula holds only when crossing-over is absent.

(2) Application to a partially self-fertilizing population

If the initial population is exclusively composed of individuals having AA' chromosome pair (genetical length of $100x_0$ units), we obtain by direct calculation,

$$(2.1) \qquad f_1{}^i f_\infty{}^r H_0 = 2^{-i}(1+ix_0) - 2^{1-i}\left(1-\frac{x_0}{2}\right)^{2(r-1)}\left(\frac{1-x_0}{2}\right)^2 \qquad (r \geq 1).$$

After expanding the right side members of (1. 1) and applying the fundamental inequality formula (1. 4) together with (2. 1), we obtain

$$\lim_{n\to\infty} H_n = \frac{2\lambda}{2\lambda+\mu}\left(1+\frac{\mu}{2\lambda+\mu}x_0\right) < 2\lambda(1+x_0)\,,$$

if x_0 is not too large.

In this limiting state, it is proved that the population contains only $\alpha\alpha$-heterozygote and $\alpha\alpha$-homozygote. Here α is the chromosome derived from A and A' through crossing-over. In some cultivated plants, for example in wheat, egg plant and pea, which reproduce almost exclusively by self-fertilization, the incidence of natural cross is very rare ($\lambda \ll 1$). In such cases, from the above formulae, the amount of heterozygosis in them may be expected to be correspondingly low.

10. Statistical Theory on the Pre- and Post-reduction of Chromosomes

(Report by Motô KIMURA)

By the progress in the chiasma-type theory and through tetrad analyses in lower organisms, it has been made clear that each locus in a given chromosome has its specific frequency of equational separation at the first division of meiosis. The purpose of the present investigation is to deduce mathematically the state of chromosome reduction from the experimental findings; i.e., (1) to obtain the frequency distribution of the length of pre- and post-reductional segments in the chromosome tetrads, and (2) to calculate the mean length of such segments for some genetically well-studied chromosomes.

1) For telomitic chromosomes with a genetical length of $100\,l$ units and without chromatid interference, the frequency distribution curve of the length (ξ) of post-reductional segments is given by the following formula, if multiple cross-overs are negligible in frequency:

$$\Phi(\xi) = \varphi'(\xi) + 2\varphi(l-\xi) - (l-\xi)\varphi''(\xi) - 1\,,$$

where $\varphi(\xi)$ is the recombination fraction between two genes which are 100ξ units apart. For the X-chromosome of *Drosophila melanogaster* (70

units in length), the above formula becomes

$$\Phi(\xi) = \cos 2\xi + 2\cos(1.4-2\xi) + (1.4-2\xi)\sin 2\xi - 1,$$

if $\varphi(\xi) = (\sin 2x)/2$ (cf. LUDWING 1935).

2) Taking the chromosome as the abscissa and assuming that $f(x)$ represents the *probability* of the post-reduction of a point x, then the mean length of post-reductional parts of the chromosome or chromosome segment ab is

$$L = \int_a^b f(x)dx,$$

which equals the area bounded by the curve $Y = f(x)$, the axis of x and the ordinates $x=a$, and $x=b$. The proportions (in percent) of the mean length of pre- and post-reductional segments calculated by the above method are listed for some genetically well-studied chromosomes as follows:

Table 6

Chromosomes	Source of data used for the calculation	Relative length of pre-reductional segment $(l-L) \div l$	Relative length of post-reductional segment $L \div l$
Neurospora crassa, sex-chromosome	C.C. LINDEGREN 1936	66.5%	33.5%
Sphaerocarpus Donnellii, squamifera-chromosome	E. KNAPP 1937	52.2%	47.8%
Drosophila melanogaster, X-chromosome	LUDWIG 1935	46%	54%
	CHARLES 1938	48%*	52%*
II-chromosome	LUDWIG 1935	48%	52%
Drosophila virilis X-chromosome	CHINO, 1941; DEMEREC & LEBEDEFF 1934	40.7%	59.3%
	FUJII 1941	40.0%*	60.0%*

* The values with the asterisks have been calculated on cytological maps, while all other values have been derived from genetical maps.

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ADDENDUM

1. The Misima Branch of Hatano Tobacco Experiment Station of the Japan Monopoly Corporation

As stated in the Annual Report No. 1, the Institute is cooperating in fundamental researches for the improvement of tobacco plants cultivated in Japan. A branch of the Hatano Experiment Station has been set up in the main building, and three researchers including Dr. Flora A. LILIENFELD are working on this project. Most of the botanical members of the Institute are participating in the work. In 1951, the following items were chosen for the main research topics:—

1. The nature of the so-called good quality in tobacco,
2. Physiology and ecology of various strains of cultivated tobacco plants,
3. Interspecific crosses,
4. Artificial induction of new mutants,
5. Virus infecting tobacco plants.

2. The Association for the Propagation of the Knowledge of Genetics (Idengaku Hukyû-kai)

This association was organized on May 23, 1947, and named the Genetics Research Institution (Idengaku Kenkyû-syo), with its office in the Laboratory of Animal Husbandry in Tokyo University. This is the fore-runner of the National Institute of Genetics. After the establishment of the Institute, the name of the Association was changed to the present one, and the office was moved into the Institute in November 1950. At that time, the primary object of the Association was redefined as the popularization of genetics. Its activity in 1951 consisted in:—

1. Manufacture and distribution of microscopical slides for cytological demonstration,
2. Distribution of seeds of hybrid plants,
3. Distribution of some mutant strains of *Drosophila*,
4. Editorial business of the popular journal "Iden".

3. The Whole-Japan Association of Poultry Genetics

This association was organized by poultry breeders of all districts of Japan with the object of producing breeds of high egg production. It has 271 regular members, 30 associate members and 50 special members. Since this object can hardly be realized without being guided by sound genetic principle, and without sufficient knowledge of the genes governing egg production, the whole work has been entrusted to the Institute. TANAKA has taken the responsibility of the whole project. He laid out the program, and has been looking after the work in operation. By the fall of 1951, all the equipment including a hatchery, a testing barn, 6 colony barns and a residence, had been completed, and the work was started, using 7 strains of single-comb White Leghorn and 3 strains of Plymouth Rock. Crosses were systematically made among these, and the progeny is being raised.

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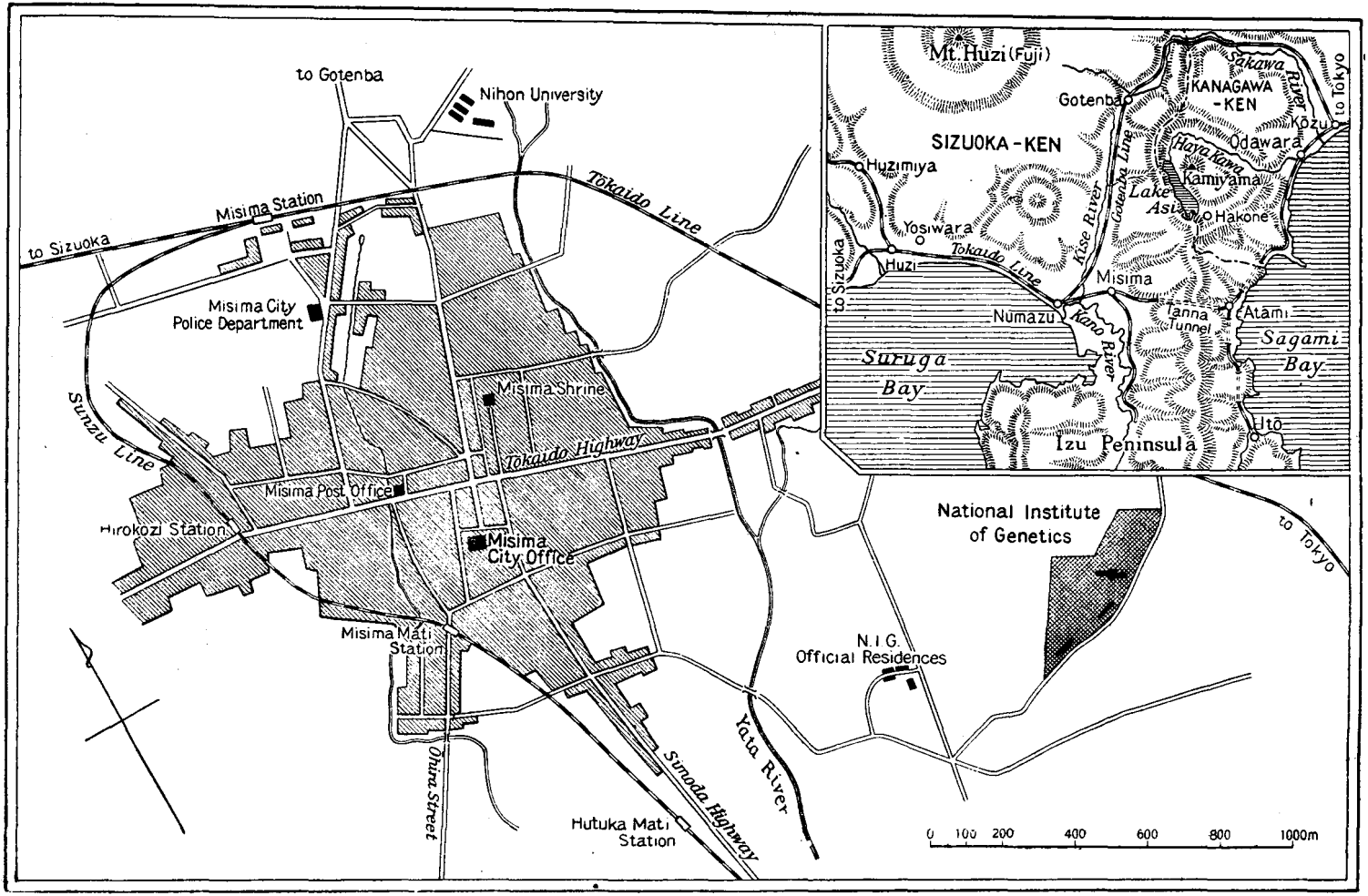
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