All experiments were carried out at temperatures between 21 and 24 degrees C.

By referring to the graphs (Fig. 1), it will be seen that for amoebas from the acid culture, beginning at a hydrogen-ion concentration above pH 6.0, the rate of locomotion increased to a maximum at pH 6.6, then fell abruptly to a minimum at $pH 7.1-7.6$; while for amoebas from the alkaline culture, beginning with a hydrogen-ion concentration below pH 8.0, the rate increased to a maximum at pH 8.0-7.6, then fell abruptly to a minimum at pH 7.1-6.6, which was almost the same as that for amoebas from the acid culture at pH 7.1-7.6.

The decrease in the rate of locomotion which occurs when an amoeba is transferred from a slightly alkaline or acid solution to a neutral solution, strongly indicates that there is in this solution, a marked change in the permeability of.the membrane to the salts. If an increase in permeability to the salts does take place, they will enter and react with the protoplasmic proteins, causing an increase of the internal osmotic pressure, and consequently an increase in the water content of the amoeba, and a decrease in the rate of locomotion.

* This investigation was suggested by Professor S. O. Mast, and carried out under his direction. Further, he has furished valuable aid in this presentation of the results. For these favors ^I am greatly indebted to him.

¹ Bruce Fellow, Johns Hopkins University.

Clark, W. M., The Determination of Hydrogen-Ions, Williams & Wilkins, 1922. Collett, M. E., J. Exp. Zool., 29, 1919.

Pantin, C. F. A., J. Mar. Biol. Assn. United Kingdom, 8, 1923. Saunders, J. T., Proc. Cambridge Phil. Soc. (Biol. Sect.), 1, 1924.

Schaeffer, A., Sci., 44, 1916.

Taylor, Monica, Quart. J. Micr. Sci., 69, No. 1, 1924.

POLLEN ABORTION IN CHROMOSOMAL TYPES OF DATURA

BY A. F. BLAKESLEE AND J. L. CARTLEDGE \mathbb{R}^{13}

STATION FOR EXPERIMENTAL EVOLUTION, CARNEGIE INSTITUTION OF WASHINGTON, COLD SPRING HARBOR, N. Y., AND UNIVERSITY OF PITTSBURGH, PITTSBURGH, PENNA.

Communicated April 12, 1926

For an exact determination of the chromosomal constitution of a plant, a cytological investigation is essential. The size and condition of the mature pollen grains, however, may often give an indication of at least the chromosomal group to which the plant belongs. The relatively high proportion of abortive grains in our Datura mutants^{1,2} in comparison with normals, together with their peculiar breeding behavior, earlier suggested their similarity to the mutants of Oenothera in which abnormal chromosomal numbers had been established.

The present paper presents the results of a more detailed study of the proportion of abortive grains in the pollen of different chromosomal types. Flowers to be examined were collected in the morning, generally before the anthers had opened. The pollen was taken out of the anther with a needle and distributed in a drop of 45 per cent acetic acid slightly colored with iodine. This medium stains the contents of the grains but leaves the cell walls practically uncolored. Grains were recorded as abortive which were empty and shrivelled. There is usually no difficulty in distinguishing bad from good grains. Counts were made of the two kinds of grains in a series of different fields of the microscope under lower power. The abortive grains tend to collect at the edges of the drop. Their distribution was made more uniform by stirring. with the needle and the counts were made more representative of the actual condition in the flower by examining, in succession, fields from one side of the preparation to the other. For each flower a total of at least 500 grains were-counted. The first plants tested in a series were called the (a) plants and consisted of representatives from each type; those tested the second day were called (b) plants, etc. When a plant in the series under investigation had no flower at the proper stage for counting, either pollen from this plant was counted at another time or another plant of the same type was substituted in the records as indicated in the accompanying tables. Low temperatures greatly increased the number of aborted grains. Mosaic disease may affect the pollen before the plant shows outward signs of being infected. By taking records at different times on the same plant, however, as well as by using a number of individuals of each type, it was hoped to average out in large measure the influence of environmental factors.

The plants tested were grown well-spaced under good garden conditions and appeared true to type. For the most part they belonged to our highly inbred line ¹ and were. closely comparable genetically. It has been pointed out³ that our first haploid in line 1 was called Haploid 1A and that the types derived from it form line 1A and should be completely homozygous and alike in gene constitution (barring new point mutations). All the balanced chromosomal types tested in 1925 and shown in tables 4 and 5 were in line 1A as also the majority⁴ of the $(2n + 1)$ types tested in 1924 and shown in tables 2 and 3. Most of the types tested in 1923 and shown in table ¹ were in line 1.6

Unbalanced Chromosomal Types.—The distinction between Primary and Secondary $(2n + 1)$ types has been given in earlier publications.^{6,7} Spinach has been provisionally listed as the 12th Primary. Although it is a 25 chromosome type occurring occasionally in the offspring of triploids and as a spontaneous mutant it is peculiar in breeding behavior. Its chromosomal constitution has not been definitely determined. It is possible that the 12th Primary is not viable. Divergent is apparently

in the group with Spinach. Wiry is apparently a tertiary type related to Poinsettia and Rolled.8 Nubbin, Pinched and Hedge form a group of mutants with peculiar relationship to the Secondaries-Strawberry and Mutilated-and to the two Secondaries of Rolled.

Table ¹ shows the averages for the 1923 records. Table 2 gives the detailed records for 1924 and table 3 the summaries for 1924 and the

TABLE ¹

SUMMARY OF AVERAGE PERCENTAGES OF ABORTIVE POLLEN GRAINS IN $(2n + 1)$ TYPES: RECORDS OF 1923

For each type, 4 flowers from each of 3 different plants were examined and a minimum of 500 grains were counted, making a total of 6000 grains for each type. Counts were made in series (a) on $9/6$, $9/10$, $9/13$, $9/16$; in series (b) on $9/7$, $9/11$, $9/14$, $9/17$; in series (c) on $9/8$, $9/12$, $9/15$, $9/18$. On two dates no flowers on selected Poinsettia and flowers from other plants were substituted; for same reason on one date another plant was substituted for Elongate. Capital letters are used for Primaries, small letters for Secondaries and Tertiaries.

averages for the two years. It will be observed that although there is a considerable variation. between the different individual counts, in all cases diploids are better than Primaries and Secondaries show a higher percentage of bad grains than their respective Primaries.

Balanced Chromosomal Types.---It is usually possible to determine the balanced group to which a plant belongs by an examination of its pollen. Pollen of a diploid is relatively good with the grains practically all of the same size; pollen of tetraploids is distinctly larger with a slightly

-

 $\ddot{}$

 \cdot

 $\hat{\mathcal{A}}$

 \mathcal{S}

TABLE 2

 \sim

 $\hat{\mathcal{A}}$ \sim \sim

l,

 $\hat{\mathcal{A}}$

GENETICS: BLAKESLEE AND CARTLEDGE PROC. N. A. S.

 $\hat{\mathcal{L}}$

 $\frac{1}{\sqrt{2}}$

higher proportion of bad grains; pollen of triploids is characterized by a high proportion of bad grains and a wide diversity in size of the good grains; pollen of haploids is largely bad but the good grains are the same size as in diploids. Photographs have been published elsewhere⁹ of the pollen of diploids, triploids and tetraploids.

TABLE ³

SUMMARY OF TABLE 2 SHOWING AVERAGE PERCENTAGES OF ABORTIVE POLLEN GRAINS IN $(2n + 1)$ TYPES; RECORDS OF YEAR 1924 WITH AVERAGES FOR 1923 For each type, except as otherwise noted, a total of 8000 grains were counted.

* For Polycarpic, only ⁵ flowers from two plants were examined, making a total of 2500 grains counted.

Table 4 gives the detailed counts and table 5 the summaries for the balanced types. Plant 20745(4) is ^a graft from our first haploid A and is the origin of line 1A. The four triploids were. grafted clones of a single individual. The tetraploids were determined'by Miss Rachel Haynes to have 48 chromosomes each. They were probably all true tetraploids since in all cases they showed more of the 24-24 than of the 25-23 distribution.¹⁰

TABLE ⁴

PERCENTAGES OF ABORTIVE POLLEN GRAINS IN BALANCED CHROMOSOMAL TYPES. RECORDS OF YEAR 1925

For each type 4 flowers from each of 4 different plants were examined, except as noted, and a minimum of 500 grains from each flower were counted.

* No flowers on selected plant this date; flower from another plant of same type substituted in records.

TABLE ⁵

SuMMARY OF TABLE 4 SHOWING AVERAGE PERCENTAGES OF ABORTIVE POLLEN GRAINS IN BALANCED CHROMOSOMAL TYPES; RECORDS OF 1925

 $Discussion$.---From the data presented, it is evident that a large part at least of the pollen abortion in Datura is brought about by abnormalities in chromosomal constitution. Probably the most potent immediate cause of premature death in pollen is chromosome deficiency. The condition is clearest in the pollen of haploids'1 in which the 12 chromosomes undergo a "reduction" into $6 + 6$, $5 + 7$, $4 + 8$, etc. Apparently all grains with less than the complete haploid complement abort and the small percentage of normal grains which are found have obtained the normal number of chromosomes by non-reduction of the $1n$ mothercells. No $(2n-1)$ types have been discovered in the more than 300 offspring of haploids where one would expect them if any of the pollen

grains or ovules were capable of functioning with any single one of the 12 chromosomes absent. Moreover, rather extensive sowings from sectorial deficiencies¹² have failed to secure $(2n-1)$ offspring. Deficiencies also may be brought about by non-disjunction and detachment. Thus in diploids and Primary $(2n + 1)$ types the non-disjunction found would lead to about 0.4 per cent of $(n-1)$ grains.⁷ If the amount of detachment in diploids approaches that found in the mother-cells of triploids,'3 deficiencies brought about by non-disjunction and detachment would more than account for the pollen abortion found in normals.

While the lack of a single chromosome apparently causes the abortion of all of the gametophytes affected, the presence of an extra chromosome in $(2n + 1)$ types does not. Non-disjunction is apparently no more common in such types⁷ than in normals and the excess of aborted grains over those produced by diploids may be attributed to the unbalance produced by the extra chromosome which renders the grains less viable. The reduction in viability of pollen grains apparently depends somewhat upon which chromosome is extra. It is not to be expected that a given extra chromosome will have the same unfavorable effect upon the different stages of growth. There is in fact no close relationship between the amount of bad grains and either the viability of the zygotes or the extent to which the extra chromosome is transmitted through the pollen. Thus Rolled has a low percentage of bad grains and is one of the least frequent types in the offspring of triploids. Cocklebur has a relatively high percentage of bad grains for a Primary but transmits its extra chromosome through the pollen to a greater extent than any other mutant. When the unbalance is increased in the $(2n + 2)$ Globe or in double $(2n + 1 + 1)$ chromosomal types the amount of pollen abortion is also increased.

Triploids"3 doubtless owe their high proportion of bad grains to the unbalance brought about by more than a single chromosome.

Secondaries in all cases show a greater average amount of abortion than their respective Primaries. In Secondaries^{6,7} we appear to have the extra chromosome deficient for one half while double for the other half of the chromosome. There is evidence that the gametophytes with this chromosome alone in a set are non-functional since no types have been discovered in which this double-half chromosome has replaced a normal member of the disome. Whenever the double-half chromosome goes to one pole in disjunction, the two normal chromosomes capable of taking part in formation of the Primary type should go to the other pole. The proportion of their Primaries thrown by the several Secondaries, therefore, might be an indication of the relative frequency of separation of the two normal chromosomes from the double-half member. If deficiency for one half of a chromosome together with excess of the other half causes pollen abortion, we should then expect that Secondaries which throw a high proportion of their own Primaries would have relatively bad pollen. A comparison of tables in this paper with those in an earlier publication⁶ suggests a general relation between the number of Primaries thrown by a given Secondary and the amount of bad pollen which it shows. In the exceptional case of Polycarpic which throws few of its Primary Rolled, and still has a large amount of'bad grains, it is possible that the unbalance of this particular double-half chromosome which makes Polycarpic our weakest mutant may be responsible for an increased abortion of its $(n + \frac{2}{2})$ gametes. It will not be desirable, however, to attempt a too close comparison between pollen abortion and breeding behavior of Secondaries until a larger accumulation of data has been secured in more strictly comparable material.

Pollen of tetraploids shows only slightly more abortive grains than do diploids. Abnormalities in distribution of chromosomes are frequent¹⁰ but the unbalancing effect due to the loss of or addition of a single chromosome is less.

The effect of the external environment upon pollen abortion is often marked but probably acts through changes in distribution of the chromosomes. Practically all the grains have been found to be aborted after treatment with cold. The internal environment of a plant with abnormal chromosomal constitution may have an influence upon the proportion of grains which abort. In sectorial chimeras¹² with the formula $(2n-1)$ we have always found considerably more than the 50 per cent abortive grains expected from the chromosome numbers. If our interpretation of the chromosomal constitution of these chimeras is correct, the internal environment of the deficient branches must have been responsible in some way for the increased abortion.

Summary.-It has been shown that the size and condition of the pollen grains give an indication of the chromosomal group to which a , plant belongs. In haploids the abortive grains (88 per cent) are due to deficiencies, the few good grains to non-reduction. In diploids the bad grains (1-2 per cent) may be due in part at least to non-disjunction and possibly to detachment of chromosomes. In Primary $(2n + 1)$ types the excess of bad grains over diploids is probably due to poor viability of $(n + 1)$ grains. Secondary $(2n + 1)$ types average more bad grains than their Primaries. The increase probably is brought about by the The increase probably is brought about by the abortion of grains with only the double-half chromosome in the set involved. Triploids have a high proportion (43 per cent) of bad grains due chiefly to unbalance from more than single extra chromosomes. Tetraploids show only slightly more bad grains (5 per cent) than diploids. Abnormal chromosomal distributions are more frequent in tetraploids but the unbalance of single chromosomes is less.

¹ Blakeslee, A. F., 1921, Genetics, 6, 241-264.

² Blakeslee, A. F., 1921, Amer. Nat., 55, 254-267.

³ Blakeslee, A. F., and John Belling, 1924, Jour. Hered., 15, 194-206.

⁴ Dwarf, Wedge, Mutilated, Sugarloaf, Polycarpic, Scalloped, Elongate, Nubbin, Pinched and Hedge belonged to line 1, not line 1A. Maple arose in an extract from the related lines ¹ and 2 and has been several times back-crossed to line IA. Wiry and Undulate arose in extracts from lines ¹ and 4 and have been back-crossed to line 1A.

⁵ Exceptions: Maple, derived from lines 1 and 2; Wiry, Elongate and Undulate derived from lines ¹ and 4.

⁸ Blakeslee, A. F., 1924, these PROCEEDINGS, 10, 109-116.

⁷ Belling, John, and A. F. Blakeslee, 1924; Ibid., 10, 116-120.

⁸ Belling, John, and A. F. Blakeslee, 1926, Ibid., 12, 7-11.

⁹ Blakeslee, A. F., 1922, Amer. Nat., 56, 16-31.

¹⁰ Belling, John, and A. F. Blakeslee, 1924, Amer. Nat., 58, 60-70.

¹¹ Blakeslee, Belling, Farnham and Bergner, 1922, Science, 55, 646-647.

¹² Blakeslee, A. F., and John Belling, 1924, Ibid., 60, 19-20.

¹³ Belling, John, and A. F. Blakeslee, 1922, Amer. Nat., 56, 339-346.

REMARKS ON PENETRATING RADIATION

BY EDWARD CONDON

DEPARTMENT OF PHYSICS, UNIVERSITY OF CALIFORNIA

Communicated April 15, 1926

The recent measurement by Millikan¹ and by Myssowsky and Tuwim² of the coefficient of absorption of the penetrating radiation which is the source of the small residual ionization always found in closed vessels, 3,4 has stimulated thought, 5.6 on the origin of this penetrating radiation. The extreme shortness of the estimated wave-length, 0.00038 A makes it apparent that the source of this radiation must lie in a radiative process involving the very smallest units of matter-the electron and the proton. In this brief note I desire to record a calculation whose result is in surprising agreement with the measurements, a result which because of the difficulties involved ^I can scarcely regard as more than coincidence. But perhaps it is not.

Let it be supposed that an electron is a sphere of negative electricity of uniform density ρ and radius r_0 . Suppose also that relative to r_0 the proton can be regarded as ^a point charge. A proton can thus have an equilibrium position inside the electron just as an electron was supposed to be in equilibrium inside a sphere of positive electricity in the atom of three decades ago which served for Lorentz classical theory of the Zeeman effect. Given such a "neutron" the work required to take the proton, to the surface of the electron is easily seen to be $e^2/2r_0$ and the work to take it to infinity against the Coulomb force is e^2/r_0 . Suppose one assumes