PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES

Volume 10 APRIL 15, 1924 Number 4

INHERITANCE IN NICOTIANA TABACUM. V. THE OCCURRENCE OF HAPLOID PLANTS IN INTERSPECIFIC PROGENIES

BY ROY E. CLAUSEN AND MARGARET C. MANN

DIVISION OF GENETICS, DEPARTMENT OF AGRICULTURE, UNIVERSITY OF CALIFORNIA

Communicated February 18, 1924

When two constant species of *Nicotiana* are crossed, the hybridization, if successful, gives a uniform F_1 exhibiting unmistakable hybrid characteristics. There have, however, been sporadic reports of the production of occasional plants in interspecific hybridization in *Nicotiana* which differ from the expected hybrid type. Manifestly some of these results have been due to error, dependent particularly on the use of parent species one or both of which have not been constant; but it is difficult to explain all the reports in this way.

During the season of 1923 two plants were obtained which were outstanding exceptions to the general rule of uniformity of F_1 interspecific progenies. Both occurred in F_1 progenies of *Nicotiana Tabacum* ♀ × *N. sylvestris* ♂. As a rule this cross gives a uniform, vigorous, nearly completely sterile F_1 hybrid which is a replica *on an enlarged scale* of its particular *Tabacum* parent (cf. Goodspeed and Clausen, 1917 *a* and *b*). Two such hybrid progenies grown in 1923 gave the usual results, except that in each population one exceptional plant appeared which was a replica *on a reduced scale* of its immediate *Tabacum* parent. Both of these plants had 24 chromosomes. Since the chromosome number in *Tabacum* is $n = 24$ (White, 1913) and in *sylvestris* $n = 12$ (Goodspeed, 1923), the exceptional plants were evidently *Tabacum* haploids.

One of these exceptional plants appeared in an F_1 of *N. Tabacum* var. *purpurea* ♀ × *N. sylvestris* ♂. Among 58 plants grown, 57 were of the expected hybrid type. The exceptional plant was obviously a reduced replica of *purpurea.* It exhibited all the differential characters peculiar to *purpurea;* but the expression of the characters was somewhat exaggerated. This exaggeration of *purpurea* characters was particularly evident in the leaf base, which in *purpurea* is sharply constricted almost to the midrib.

In the haploid the constriction was more pronounced, so that the leaves had a distinct short petiole. The haploid was about three-fourths the height of *purpurea,* the leaves were smaller, the branches more slender, and the flowers distinctly smaller as is shown by the measurements recorded in the accompanying table. Since floral measurements are so remarkably constant in *Nicotiana,* this difference is of particular significance. The haploid, although somewhat less vigorous than *purpurea,* bloomed profusely, but no seeds were produced. The pollen seemed to be completely defective; the grains were exceedingly variable in size, and most of them were shrivelled and devoid of contents. Numerous attempts to secure seed by application of *purpurea* pollen failed. The capsules were retained slightly longer; but ultimately they were cast before reaching maturity. Examination of immature capsules failed to disclose the presence of developing ovules.

GARDEN NUMBERS	DESCRIPTION	NUMBER OF PLANTS MEASURED	COROLLA LENGTH	COROLLA SPREAD
23.050	*sylvestris*	50	85.3	42.5
23.014	*purpurea*	49	49.3	36.0
23.083	*purpurea* ♀ × *sylvestris* ♂	48	59.0	44.1
23.083P57	*purpurea* haploid	1	40	25
23.131	*macrophylla* derivative, normal type	23	44.8	38.0
23.132	*macrophylla* derivative × ♂ *sylvestris* ♂, normal type	27	55.1	39.9
23.132P11	*macrophylla* derivative, normal type haploid	1	39	28

The second exceptional individual was produced under somewhat less favorable conditions for demonstration. The *Tabacum* parent was a fifth generation *macrophylla* derivative obtained by back crossing an F_1 of *N. Tabacum* var. *macrophylla* ♀ × *N. sylvestris* ♂ to *macrophylla,* after which the partially fertile progeny were selfed for five consecutive generations. The derivative line was selected for an aberrant type, called "corrugated" on account of its bullated leaves, which when selfed always yields a dimorphic progeny consisting of approximately two-thirds corrugated and one-third normal plants identical in appearance and genetic behavior with *macrophylla.* From a fifth generation corrugated ♀ × *N. sylvestris* ♂ an F_1 of 50 plants was grown, 49 of which were distributed approximately equally into the two expected classes, a normal red-flowering type identical with the typical F_1 *macrophylla-sylvestris* hybrid, and a white-flowering type corresponding to the corrugated derivative. The exceptional plant was strikingly different from the plants of both of these two classes. It was a reduced replica of *macrophylla,* evidently corresponding to the normal plants of the selfed progeny of the corrugated parent. It exhibited the same general resemblance to *macrophylla* as has been described for the *purpurea* haploid and *purpurea*. As compared with *macrophylla*, the size was somewhat reduced, the leaves were smaller and thinner, the branches more slender, and the flowers smaller as shown by the measurements in the accompanying table. The haploid was somewhat less vigorous than *macrophylla;* but it was by no means a weakling. When lifted and transferred to the greenhouse at the end of the season it continued to grow and blossom; but it set no seeds. The pollen was totally defective.

Cytological studies were made of both plants, using smears of pollen mother cells stained in aceto-carmine. Normal *Tabacum* and *sylvestris* were also examined by this method, the results corroborating those of the previous observers. Before reduction occurs the chromosomes of the haploids are the size of one member of a pair in normal *Tabacum* pollen mother cells and are split longitudinally. In fact at an early stage they greatly resemble the somatic chromosomes of the diploid, but the short rods soon form 24 compact V's which appear almost spherical, and contrast markedly with the dumb-bell shaped dyads of the diploid at the time of reduction. Reduction is a rather haphazard process, few or many of the chromosomes passing to the poles, the rest remaining at the equator of the spindle. The following distributions have been observed: 4<15>5, 6<12>6, 7<12>5, 9<6>9, 8<11>5, 7<10>7, 8<10>6, 8<1>15. In one case a single giant spindle contained all 24 chromosomes. The chromosomes which remain at the equator often divide. The second division is somewhat more regular than the first, but lagging chromosomes frequently fail to reach either daughter nucleus, forming extra small nuclei which later form microcytes. The pollen mother cells divide to form 2–5 cells which differ greatly in size, except when two cells result. The latter may be the result of non-reduction; but if this is the case, a certain amount of normal *Tabacum* pollen should be present.

The haploid tobaccos resemble the haploid Daturas (Blakeslee, et al, 1922), in the random assortment of whole chromosomes at the first division, the formation of two pollen cells as a result of the division of certain pollen mother cells, and in the high percentage of bad pollen which they produce. The appearance of an occasional haploid plant may account for the production in some cases of sterile, maternal plants in addition to true hybrids in interspecific F_1 progenies.

Blakeslee, A. F., Belling, J., Farnham, M. E., and Bergner, A. D. "A Haploid Mutant in the Jimson Weed." *Science*, **55**, 1922, 646–647.

Goodspeed, T. H. "A Preliminary Note on the Cytology of Nicotiana Species and hybrids." *Svensk Bot. Tid.*, **17**, 1923, 472–478.

Goodspeed, T. H., and Clausen, R. E. (*a*) "Mendelian Factor Differences versus reaction System Contrasts in Heredity." *Amer. Nat.*, **51**, 1917, 31–46, 92–101.

Goodspeed, T. H., and Clausen, R. E. (*b*) "The Nature of the F_1 Hybrids between

Nicotiana sylvestris and Varieties of *Nicotiana Tabacum* with Special Reference to the Conception of Reaction System Contrasts in Heredity." *Univ. Calif. Publ. Bot.*, **5**, 1917, 301–346.

White, O. E. "The Bearing of Teratological Development in *Nicotiana* on Theories of Heredity." *Amer. Nat.*, **47**, 1913, 206–228.

ELECTRODYNAMICS IN THE GENERAL RELATIVITY THEORY

BY G. Y. RAINICH

DEPARTMENT OF MATHEMATICS, JOHNS HOPKINS UNIVERSITY

Communicated February 26, 1924

Several attempts have been made to include the electrical phenomena in the general relativity theory by substituting a more general space for the Riemann space (Weyl, Eddington; the expression for the Riemann tensor as dependent on the electromagnetic tensor suggested in a previous paper of the author[1] also requires a generalization of geometry). But perhaps this generalization is after all not necessary and it may be possible to include electromagnetism in the general relativity theory without breaking the frame of the Riemann geometry. This note deals with an attempt to work out some consequences of what may be considered as pretty well established relations.

1. We hold fast to the idea of the previous note that the curvature tensor must be determined by the electromagnetic tensor but instead of putting down an *a priori* expression we will start with the known energy relation

$$F_{ij} = \tfrac{1}{2}\{f_i^k f_{kj} - d_i^k d_{kj}\} \tag{1}$$

where F_{ij} is the contracted curvature tensor, f_{ij} the electromagnetic tensor and d_{ij} its dual; this relation does not give the explicit expression for the curvature, it is true, but we will try to obtain from it as much information as possible. Together with equation (1) we have to consider the Maxwell equations

$$f^j_{i,j} = 0, \qquad d^j_{i,j} = 0. \tag{2}$$

2. There are two points of view from which the system (1)–(2) can be considered. If we concentrate our attention mainly on the Maxwell equations (2) we may remark that the existence of the relation (1) deprives them of their linearity: in fact, if we consider the f_{ij} as the unknowns and try to introduce them in the second set of the equations (2) we notice that the d's can be expressed through the f's only with the aid of the components of the fundamental tensor g_{ij} and since the g's enter in the left part of (1) they depend on the f's so that the second set of (2) is not linear