CHROMOSOME NUMBER AND MORPHOLOGY IN NICOTIANA VI. CHROMOSOME NUMBERS OF FORTY SPECIES[1]

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In the University of California Botanical Garden over 60 species and varieties of the genus *Nicotiana* have been under investigation, together with species of such related genera as *Petunia, Fabiana, Salpiglossis* and *Nierembergia*. Morphological, distributional and cytogenetic evidence indicates the desirability of recognizing among the races of *Nicotiana* under observation, the following 40 species. The list is arranged in order of date of description.

glutinosa L.
paniculata L.
rustica L.
tabacum L.
tomentosa Ruiz & Pavon
undulata Ruiz & Pavon
longiflora Cav.
plumbaginifolia Viv.
bonariensis Lehm.
repanda Willd.
suaveolens Lehm.
Langsdorffii Weinm.
alata Link & Otto
glauca Grah.
acuminata (Grah.) Hook.
solanifolia Walp.
rotundifolia Lindl.
corymbosa Remy
Miersii Remy
Cavanillesii Dun.
trigonophylla Dun.
cordifolia Phil.
wigandioides Koch & Fint.
megalosiphon van Heurck & Müll.
attenuata Torr.
Bigelovii S. Wats.
nudicaulis S. Wats.
caudigera Phil.
pampasana O. Kuntze
sylvestris Speg. & Comes
Stocktoni Brandg.
Sanderae hort.
Debneyi Domin
Raimondii Macbride
nesophila Johnston
tomentosiformis Goodspeed
4 unnamed Australian species

The haploid chromosome numbers characteristic of these 40 species are 9, 10, 12, 16, 20, 22, 24 and 32, and in the following table the species are arranged under these various chromosome number classes.

For the sake of completeness, chromosome numbers of species earlier published by the author and by others are included in table 1 along with those first reported in the above list. Our representatives of the species listed have received detailed taxonomic study to assure nomenclatorial accuracy. For reasons to be discussed elsewhere, it appears desirable to distinguish *plumbaginifolia* from *longiflora, caudigera* from *acuminata, Raimondii* from *glauca* and *nesophila* from *Stocktoni*. The status of *wigandioides* and *tomentosiformis* has already been commented upon (Goodspeed[2,3]).

As indicated in footnote 2 to table 1, separate discussion of the *Nicotiana* species peculiar to Australia proper, Lord Howe Island and Rarotonga will be forthcoming. It should be noted, however, that decision to recog-

TABLE 1

CHROMOSOME NUMBERS OF *Nicotiana* SPECIES[1]

9	10	12	16	20	22	24	32
alata bonariensis Langsdorffii Sanderae	longiflora plumbaginifolia	acuminata attenuata caudigera Cavanillesii cordifolia corymbosa glauca glutinosa Miersii pampasana paniculata Raimondii solanifolia sylvestris tomentosa tomentosiformis trigonophylla undulata wigandioides	suaveolens and 3 unnamed species[2]	megalosiphon[2]	rotundifolia[2]	Bigelovii Debneyi[2] nesophila nudicaulis repanda rustica Stocktoni tabacum	unnamed species[2]
4	2	19	4	1	1	8	1

[1] Expressed as number of pairs of chromosomes and based upon counts in P. M. C. and in root-tips.
[2] Australasian species concerning the cytotaxonomy of which an article by Miss Helen-Mar Wheeler is in preparation.

nize as new species 4 races allied to *suaveolens* and obtained from the wild state came only after thorough comparative study of all available herbarium material of types. Of special interest are two 32_{II} races, one of which represents an instance of polyploidy within the species, being a replica of typical *suaveolens* on a large scale, while the other is apparently a distinct species.

With the exception of *N. sylvestris* and *paniculata*, all the species listed above give evidence, from herbarium specimens or in the living state, of being more or less polymorphic. As a result, named varieties of many of them are recognized (cf. Millán[4]), but often, particularly in botanical gardens, varieties, and in some cases minor ones, are given species designations. It might be noted in this connection that a considerable number of varieties of *tabacum, rustica, Bigelovii, acuminata, longiflora* and *Cavanillesii* examined show no variation in chromosome number.

Other authorities for chromosome number determinations are cited by Tischler[5] and Gaiser.[6] The only species not in the above list (table 1) mentioned by them are *cerinthoides, noctiflora, petiolaris, Forgetiana, viscosa, Palmeri, angustifolia, Rusbyi* and *clarionensis*. The species referred to by others as *Rusbyi* is listed here as *tomentosiformis* (Goodspeed[2,3]). The designation *clarionensis* was never published (cf. Johnston[7]), this species being referred to here as *Stocktoni*. De Vilmorin and Simonet[8] reported *cerinthoides, Forgetiana* and *noctiflora* as possessing 9_{II} and *trigonophylla, solanifolia* and *petiolaris* as 24_{II}. Seed of what was grown by them under these designations (except *petiolaris*) was kindly supplied by M. de Vilmorin and when grown here gave the following results: "*noctiflora*" = typical, blue-pollened *Langsdorffii;* "*Forgetiana*" and "*cerinthoides*" = apparently derivatives of *Langsdorffii* × *alata;* "*solanifolia*" and "*trigonophylla*" = *rustica* varieties. *N. petiolaris* is a designation usually applied to certain *rustica* or *tabacum* varieties. Gaiser[6] lists "*angustifolia*" ($n = 10$) as reported by Clausen.[9] Although the taxonomic situation in regard to this species designation is confused, it is clear that the race referred to by Clausen is a *longiflora* variety. The following species for which Christoff[10] gives chromosome number determinations are also listed by Gaiser: "*viscosa* (?)" ($n = 24$), "*Palmeri* (?)" ($n = 12$), and "*solanifolia* Wolf—*cardiophylla* Ph."* ($n = 12$). There is no evidence as to the identity of Christoff's "*viscosa*" since if it had been an *attenuata* variety, as he suggests, the chromosome number should have been $n = 12$ rather than $n = 24$. Christoff refers "*Palmeri*" to *trigonophylla*.

Some 50 interspecific hybrids in *Nicotiana* have been obtained here and have included three amphdiploid types. To *digluta* ($n = 36$), an amphidiploid *glutinosa* × *tabacum* hybrid (cf. Clausen and Goodspeed[11]), can now be added the amphidiploid *glutinosa* × *tomentosa* hybrid, *diglutosa* ($n = 24$), and *disualovii* ($n = 40$), an amphidiploid *suaveolens* × *Bigelovii* hybrid. If the chromosome numbers of these three "species" are added to the series given in table 1, the complete list is 9, 10, 12, 16, 20, 22, 24, 32, 36 and 40 pairs.

Among by-products of recent cytogenetic investigations in *Nicotiana* carried on here are numerous aneuploid types in various species—*alata*, *Langsdorffii*, *sylvestris*, *paniculata*, *suaveolens*, *tabacum* and *rustica*. Tetraploid *Langsdorffii*, *sylvestris* and *tabacum* have been studied. Haplonts within all chromosome number classes doubtless occur; those at present known are in the 9_{II}, 12_{II} and 24_{II} groups, i.e., *glutinosa, tabacum, nudicaulis;* and *Langsdorffii* (Kostoff[12]). A variety of quantitative chromosome alterations have been established in stable derivatives of *tabacum* and *sylvestris* as products of treatment with high frequency radiation. A number of sesquidiploid forms have also been obtained (cf. Webber[13]).

The chromosome numbers of related genera have in a few cases been studied. *Petunia* species have for some time been known to possess 7_{II} and more recently a 9_{II} species has been reported by Ferguson and Coolidge.[14] This last is of obvious interest since a group of *Nicotiana* species shows this number and because hybrids between members of it and *Petunia* have been reported (cf., however, Kostoff[15]). The count of 22_{II} for *Salpiglossis sinuata* reported by de Vilmorin and Simonet[8] can be confirmed. For *Fabiana imbricata* and *Nierembergia frutescens*, the numbers, not before reported, are in each case $2n = 18$.

Evidence which has for some years been accumulating will make possible

* Concerning Christoff's "*solanifolia* Wolf—*cardiophylla* Ph." there is only the matter of the authority for *solanifolia* to be noted. He apparently misinterpreted "Wolf" for "Walp." on the herbarium sheet from which the seed was obtained, and this mistake is referred to because it has been perpetuated by Gaiser[6] where, in addition, the authority for *cardiophylla* is stated to be "Rh." instead of Ph.

a partially complete description of species origins and relationships in the genus *Nicotiana*, based upon morphological, cytogenetic and other studies. A few postulates which appear justified and are pertinent in the present connection may be mentioned: 1. Certain genetic groups characterized by similarity both in chromosome number and in certain basic morphological features have been recognized. The "alata group" includes *alata, Langsdorffii, Sanderae* and *bonariensis* ($n = 9$); *longiflora* and *plumbaginifolia* ($n = 10$); the "tomentosa group" ($n = 12$) consists of *tomentosa, tomentosiformis, glutinosa* and *wigandioides;* the "glauca group" ($n = 12$) of *glauca, Raimondii, paniculata, solanifolia, cordifolia* and *undulata;* the "corymbosa group" ($n = 12$) of *corymbosa* and *Miersii;* the "Cavanillesii group" ($n = 12$) of *Cavanillesii* and *pampasana;* the "acuminata group" ($n = 12$) of *acuminata, caudigera* and *attenuata;* the "repanda group" ($n = 24$) of *repanda, Stocktoni* and *nesophila*. The "suaveolens group," consisting of *suaveolens, Debneyi, rotundifolia* and *megalosiphon*, is a natural one despite the distinctions in chromosome number involved. 2. Certain, if not all, of the 24_{II} species are of allopolyploid origin. Thus *tabacum* ($n = 24$) may be traced to derivatives of hybrids between the "tomentosa group" ($n = 12$) and *sylvestris* ($n = 12$); *rustica* to derivatives of hybrids within the "paniculata group" ($n = 12$), *Bigelovii* obviously involves in its origin *attenuata* ($n = 12$) and probably *trigonophylla* ($n = 12$), while the origin of the "repanda group" and *nudicaulis* is not so clear, due perhaps to the absence of living descendants of their progenitors. The occurrence in our cultures of an amphidiploid between two 12_{II} species—*diglutosa*—lends some weight to the postulated amphidiploid origins just mentioned. That higher chromosome races of *Nicotiana* can be derived is indicated by our *digluta* and *disualovii* and by the results of Kostoff,[15] Lammerts[16–18] and Rybin.[19]

[1] The investigations reported upon were supported by a grant from the Board of Research, University of California.

[2] Goodspeed, T. H., *Bot. Gaz.*, **93,** 340–341 (1932).

[3] Goodspeed, T. H., *Ostenia,* Montevideo, 309–314 (1933).

[4] Millán, A. R., *Rev. Fac. Agr. y Vet.*, **6,** 169–216 (1928).

[5] Tischler, G., *Tabulae Biologicae,* **4,** 1–83 (1931).

[6] Gaiser, L. O., *Bibliogr. Genetica,* **6,** 171–466 (1930).

[7] Johnston, I. M., *Proc. Calif. Acad. Sci.*, Ser. 4, **20,** 9–104 (1931).

[8] Vilmorin, R. de, and Simonet, M., *Compt. Rend. Acad. Sci.*, Paris, **184,** 164–166 (1927).

[9] Clausen, R. E., *Verh. V. Intern. Kongr. Vererbwiss., Zeitschr. indukt. Abst. u. Vererb.*, Supplb., **1,** 547–553 (1928).

[10] Christoff, M., *Genetics,* **13,** 233–277 (1928).

[11] Clausen, R. E., and Goodspeed, T. H., *Genetics,* **10,** 279–284 (1925).

[12] Kostoff, D., *Zeitschr. Zellforsch. u. mikr. Anat.*, **9,** 640–642 (1929).

[13] Webber, J. M., *Univ. Calif. Publ. Bot.*, **11,** 319–354 (1930).

[14] Ferguson, M. C., and Coolidge, E. B., *Am. J. Bot.*, **19,** 644–658 (1932).

[15] Kostoff, D., *Genetica,* **12,** 33–139 (1930).

[16] Lammerts, W. E., *Genetics*, **16**, 191–211 (1931).
[17] Lammerts, W. E., *Cytologia*, **4**, 38–45 (1932).
[18] Lammerts, W. E., *Ibid.*, **4**, 46–51 (1932).
[19] Rybin, W., *Ber. d. deutsch. bot. Ges.*, **47**, 385–394 (1929).

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*YOUNG'S MODULUS AND POISSON'S RATIO WITH REFERENCE TO GEOPHYSICAL APPLICATIONS**

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Scope of the Investigation.—The theory of elasticity furnishes the following relations among the constants describing the elastic behavior of an isotropic and homogeneous medium obeying Hooke's law:

$$V^2 = \frac{E}{\rho}\,\frac{(1-\sigma)}{(1+\sigma)(1-2\sigma)},$$

and

$$\left(\frac{V}{v}\right)^2 = \frac{2(1-\sigma)}{1-2\sigma},$$

where V is the velocity of a longitudinal elastic wave in an infinite volume of the material, v is the velocity of a transverse wave, E is Young's modulus, σ is Poisson's ratio and ρ is the density of the medium. In rocks, V and v can be determined by seismological methods. Assuming perfect elasticity and isotropy for rocks, E and σ can be calculated. Conversely, on the same assumption one can predict V and v, if he can measure E and σ by statical methods in the laboratory, at the range of stresses involved in the propagation of earthquake waves.

The validity of the underlying assumption can be tested. With the explosion-wave method V and v are measured in an exposed terrane and thence the elastic constants are calculated. These are then compared with the constants measured statically on specimens of rock from the same terrane and at the corresponding extremely low range of stress-differences. If the respective values do not agree, the rock is not ideally elastic or homogeneous, and corrections must be applied before the constants determined from V and v, measured seismologically, can be used for identifying the rock where hidden underground. In practice, the elastic coefficient useful in such diagnoses is cubic compressibility. Hence the geophysicist needs data concerning the statical compressibility of an extensive series of standard rocks at varying hydrostatic pressures and under the