THE STRUCTURE OF TOBACCO MOSAIC VIRUS

I. X-RAY EVIDENCE OF A HELICAL ARRANGEMENT OF SUB-UNITS AROUND THE LONGITUDINAL AXIS

by

J. D. WATSON*

The Medical Research Council Unit for the Study of the Molecular Structure of Biological Systems, Cavendish Laboratory, Cambridge (England)

INTRODUCTION

Tobacco Mosaic Virus (TMV) is a well known structure. It has a molecular weight of about $4 \cdot 10^7$ and is rod shaped with a diameter of 150 A and a length of 2800 A. Like other plant viruses, it contains both ribonucleic acid (6%) and protein (94%). In liquid solution, the virus may aggregate lengthwise and form regions of parallel orientation in which the particles are arranged in hexagonal close packing at equal distances from one other. No regularity of arrangement exists in the direction of the particle length; the oriented regions appear to be liquid crystalline. Upon drying, the oriented arrangement of liquid solutions is retained and it is possible to obtain oriented dry specimens.

X-rays were first used to investigate the structure of TMV by BERNAL AND FANKUCHEN[1]. They obtained highly oriented X-ray photographs containing a very large number of distinct reflexions. By varying the inter-particle distance, they were able to show that the X-ray pattern arose not only from the regular arrangement of the virus particles in a hexagonal lattice but in addition from the presence of a complex structure within each virus particle. The repeat distance along the fibre axis was found to be 68 A, *i.e.* much shorter than the length of the particle; they concluded that each virus particle contains a large number of equivalent sub-units. In this paper we shall deal with the internal structure of TMV and shall present newly-obtained X-ray evidence indicating that the internal regularity is based on a division of the virus into crystallographically equivalent sub-units helically arranged around the longitudinal axis of the particle.

EXPERIMENTAL METHODS

The TMV was obtained in the form of purified suspensions from Dr. R. MARKHAM of the Molteno Institute. Liquid suspensions were oriented by flow in thin capillary tubes of borosilicate glass, while oriented dry suspensions were obtained by controlled evaporation in the simple evaporation cell of BERNAL AND FANKUCHEN[1]. The X-ray photographs were taken with a rotating anode tube

* This investigation was initiated while the author was a Merck Fellow of the National Research Council (U.S.A.) at the Molteno Institute, Cambridge.

References p. 19.

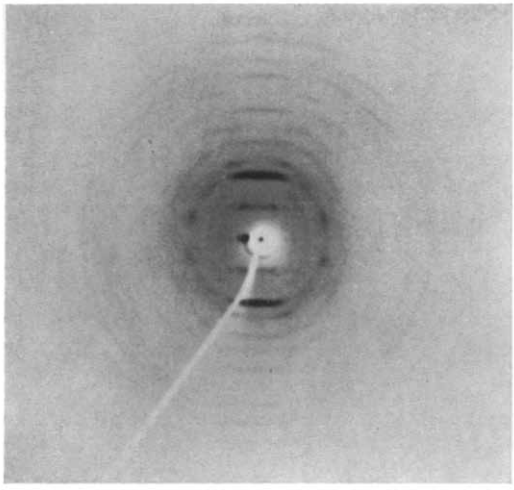

Fig. 1. X-ray photograph of dry specimen of TMV; fibre axis vertical. Cu Kα radiation, D = 10 cm; flat film.

constructed in this laboratory by Mr. D. A. G. BROAD. This tube produces an X-ray beam approximately 20 × stronger than that of conventional sealed-off tubes, and it was possible to obtain high resolution photographs in 2–3 hours.

EXPERIMENTAL RESULTS

X-ray photographs of a well oriented dry specimen are shown in Figs. 1, 2, 3 and 4. Photographs which are very similar, except in respect of the equatorial reflexions, are obtained from liquid preparations in which the particles are not in immediate contact but instead are separated by various quantities of water. The equatorial reflexions, as first noted by BERNAL AND FANKUCHEN, indicate an hexagonal close packing of the TMV rods and have positions determined by the virus concentration. In the wet preparations, which have interparticle distances up to 300 A, there is no reason to suppose a regularity in the direction of the particle length. In addition, it is most probable that a given particle has random orientation about its longitudinal axis and that this random arrangement will persist on drying. The equatorial reflexions thus represent the projection of randomly rotated, hexagonally-arranged rods. This random rotation tends to mask internal structure and accordingly it is found that all of the equatorial reflexions out to 5 A appear to arise from the scattering of the particle as a whole.

This conclusion was reached by comparing the observed reflexions with those to be expected from an hexagonal array of structureless solid rods. The theoretical diffraction pattern is calculated from the Fourier transform of an infinitely long solid cylinder. This transform is equal to $2 J_1\left(\frac{\pi D}{d}\right) \Big/ \frac{\pi D}{\mathrm{d}}$, where J_1 is a first-order Bessel function, D is the diameter of the cylinder, and $1/d$ is the distance in reciprocal space. Maxima in the diffraction pattern will thus appear where $J_1\left(\frac{\pi D}{d}\right)$ has a pronounced maximum or minimum. When the rods are arranged in hexagonal close packing (as in our case), the X-ray pattern can only reveal those regions of the transform near a lattice point. Thus, in general, many photographs, each at a different interparticle distance, will have to be taken to obtain the complete transform. For our purpose, however, the relevant region of the transform can be obtained from a single photograph if the interparticle distance is relatively large so that the lattice points

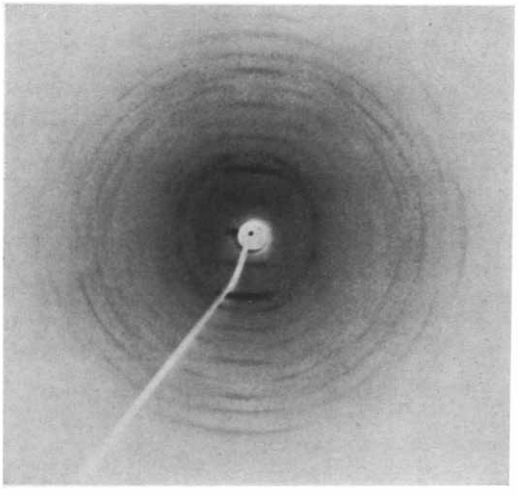

Fig. 2. Same photograph as in Fig. 1, but with a longer period of development to bring out the higher order reflexions.

References p. 19.

are closely spaced. Thus by observing the diffraction pattern of a 10% solution of TMV in which a = 450 A, it has been possible to sample accurately the transform of regions of reciprocal space where $1/d > 1/150$ A. Experimentally, maxima have been found at approximately 90 A, 50 A, 37 A, and 29 A (the pattern rapidly fades out beyond this reflexion), and null points at approximately 128 A, 70 A, 42 A, and 33 A. The corresponding theoretical maxima are at 91 A, 56 A, 40 A and 31.8 A, and null points at 125 A, 67 A, 42 A and 35 A. The agreement between the experimental and theoretical values is thus very good; hence it is the simplest hypothesis to believe that observed scattering arises from the particle as a whole and not from internal structure.

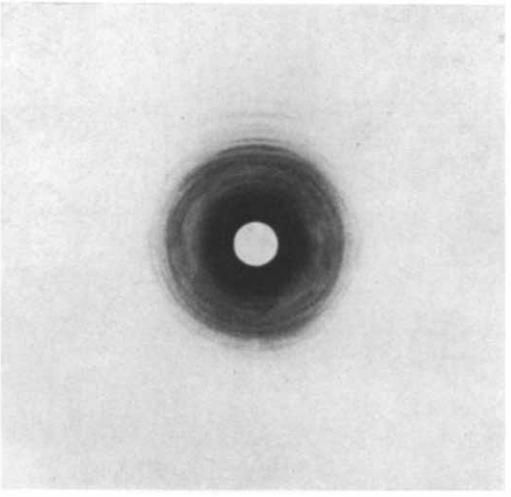

Fig. 3. Same TMV specimen but with fibre axis tilted 30° from vertical toward beam. Cu Kα radiation, 3 cm cylindrical camera.

As mentioned above, very similar non-equatorial reflexions are obtained from both dry and wet virus preparations. These reflexions are thus independent of the interparticle arrangement and must have their origin in the diffraction pattern of a single particle. Accordingly, it is profitable to consider the non-equatorial diffraction pattern as an expression of the Fourier transform of a *single* TMV particle. Especially relevant are the reflexions on or near the meridian (Table I), for these reflexions show a series of features which appear to be similar to those recently shown by COCHRAN, CRICK AND VAND[2] to be characteristic of helical structures. This suggests that the basic structural plan of TMV is a super helix in which the residues composing the helix are of the same order of size as the molecules of globular protein.

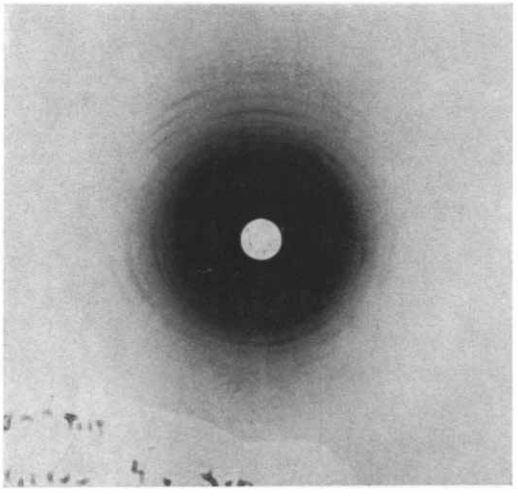

Fig. 4. Same photograph as in Fig. 3, but with a longer period of development to bring out the high order reflexions. An arrow points to the 31st-order meridional reflexion.

The most pronounced helical feature is the tendency of the meridional reflexions to split. These reflexions are the strongest in the X-ray pattern and indicate a layering of electron density within the virus. The fact that these reflexions are split suggests that the layers of electron density are not exactly perpendicular to the longitudinal axis, but instead are slightly tilted away. Two distinct groups of meridional reflexions occur: (1) a group near the origin located on the layer lines of order $3n (n = 1, 2, 3, \ldots)$; these become increasingly off meridional as n increases, and (2) a group in the vicinity of the 31st layer line, located on the layer lines of order $(3n + 1)$; these become noticeably off meridional as n decreases below 7. The presence of these

References p. 19.

TABLE I

MERIDIONAL REFLEXIONS FROM TOBACCO MOSAIC VIRUS (DRY SPECIMEN)

	A *Longitudinal axis of TMV perpendicular to X-ray beam*		*B* *Longitudinal axis of TMV tilted 30° from perpendicular position to X-ray beam*	
Order	*Position*	*Intensity*	*Position*	*Intensity**
1	—	—	(a)	
2	—	—	(a)	
3	Slightly off meridional	Medium	(a)	
4	—	—	(a)	
5	—	—	(a)	
6	meridional	very very strong	(a)	
7	very off meridional	strong	(a)	
8	—	—	(a)	
9	slightly off meridional(?)	weak	(a)	
10	very off meridional	weak	(a)	
11	—	—	(a)	
12	meridional	very weak	off meridional	medium
13	off meridional	very very weak	off meridional	weak
14	—	—	—	—
15	meridional	medium	meridional(?)	medium
16	slightly off meridional	weak	off meridional	medium strong
17	—	—	—	—
18	meridional	strong	off meridional	very strong
19	off meridional	very very weak	off meridional	weak medium
20	—	—	—	—
21	meridional	very weak	meridional(?)	weak medium
22	meridional	very weak	meridional	medium strong
23	—	—	—	—
24	meridional	medium	off meridional	very strong
25	—	—	meridional	very very weak
26	—	—	—	—
27	meridional	weak	off meridional	strong
28	—	—	meridional	very very weak
29	—	—	—	—
30	meridional	very very weak	off meridional	weak
31	—	—	meridional	strong
32	—	—	—	—
33	—	—	—	—
34	—	—	meridional	very very weak
35	—	—	—	—
36	—	—	off meridional	weak
37	—	—	meridional	weak
38	—	—	—	—
39	—	—	off meridional	—
40	—	—		

* The intensity measurements in A and B are not to be compared.
(a) Not visible due to heavy blackening of photograph near origin.

two groups of meridional reflexions is incompatible with the existence of a helix with an integral screw axis, and suggests the presence of a non-integral screw, that is, a helix which does not repeat after a single turn. It seems plausible to propose a helix* which

* A helical structure for TMV has previously been proposed by K. DORNBERGER-SCHIFF[3]. It bears only superficial similarity to our structure since its pitch is 68 A and its diameter 300 A.

References p. 19.

repeats after three turns since this could give a pseudo repeat after $^1/_3$ of the identity repeat of 68 A; this nicely accounts for the strong reflexions near the origin on the layer lines of order $3n$. The group of strong reflexions on the $3n + 1$ layer lines, we believe, arises from the presence of $3n + 1$ residues every 68 A, or $n + {}^1/_3$ residues per turn of the helix. By far the strongest reflexions of order $3n + 1$ occur on the 31st layer line, and it is simplest to assume that 31 residues comprise an identity repeat.

The theoretical X ray pattern to be expected from a non integral 3-turn helix can be calculated from the Fourier transform of a discontinuous helix. This transform has recently been derived by COCHRAN, CRICK AND VAND[2]. These authors consider the situation for a series of atoms repeated at regular intervals on an infinite helix. Of interest in our case is the value of the transform when the axial distance between successive turns is P, the axial distance between successive atoms is p, and the structure is so formed that it repeats in a distance c. In this case the transform is restricted to planes in reciprocal space which are perpendicular to the axis of the helix and occur at heights $\varrho = l/c$ where l is an integer. COCHRAN *et al.* show that on the lth plane (layer line) the transform has the value $\mathrm{F}(R, \varphi, l/c) = f \sum_n J_n(2\pi Rr) \exp [i(n\psi - n\varphi + n\pi/2 + 2\pi l z/c)]$; $(R, \varphi, l/c)$ are the cylindrical co-ordinates of a point in reciprocal space, f is the atomic scattering factor, J_n is the Bessel function of order n, r is the radius of the helix on which the set of atoms lies, the axes in real space being chosen so that one atom lies at $(r \cos \varphi, r \sin \varphi, z)$, where $\varphi = 2\pi z/P$. For a given value of l the sum $\sum_n$ is to be taken over all integral values n, which are solutions of the equation $n/P + m/p = l/c$, m being any integer. This function has two important features: (1) only certain Bessel functions can contribute to a particular layer line; and (2) for small values of $2\pi Rr$, (F) decreases rapidly as n increases—this is a consequence of the form of a Bessel function. Thus layer lines with low-order Bessel functions will tend to have reflexions nearer to the meridian than layer lines with high-order Bessel functions. In fact a truly meridional spacing can occur only on layer lines which involve Bessel functions of zero order, that is at reciprocal spacings of multiples of $1/p$ A.

Though this transform is derived for a helix composed of single atoms, COCHRAN *et al.* demonstrate that it can easily be applied to the situation in which the single atom is replaced by a group of atoms, since for each atom within the group, P, p, and c are the same, n being the only variable. The *helical* configuration defined by P and p of every set of atoms is *in itself* enough to enable us to make general predictions about expected X-ray intensities. They can thus predict that reflexions will be absent if the contributions of all sets of atoms to it are very small, while on the average it will be strong if all sets of atoms make a large contribution. It is to be expected that some reflexions predicted strong by the Bessel function argument will be weak owing to phase cancellation, but we should not expect this factor to make a weak reflexion strong. We should emphasise that this transform enables intensity predictions to be made without detailed assumptions concerning relative atomic positions. It should therefore serve a useful function by allowing the rapid testing of proposed helical structures without detailed structure factor calculations—thus COCHRAN AND CRICK[4] were able to show that the X-ray pattern of poly-γ-methyl-L-glutamate is in striking agreement with the transform of the α-helix of PAULING, COREY AND BRANSON[5].

We can similarly apply this transform to our proposed helical structure for TMV, which for convenience we shall assume to contain 31 residues per repeat. If the helical structure is correct, the location of the reflexions along the various layer lines must

References p. 19.

agree with the transform restrictions; that is, no reflexions should be found in those regions of reciprocal space in which the appropriate Bessel functions have very small values. The Bessel functions which should contribute to a given layer line can be calculated from the formula $n/P + m/p = l/c$, in which m and n take integer values only. For our helix with $P = 22.6$, $p = 2.2$ and $c = 68$, this equation becomes $l = 3n + 31m$. Solutions of this equation for $l = 0$ to $l = 40$ are given in Table II. Only two values of n for a given l are given since the difference between successive values of n is always 31.

TABLE II

COMPARISON OF CALCULATED AND OBSERVED POSITIONS OF THE NEAR MERIDIONAL REFLEXIONS FOR TMV

Layer line	*Lowest two values of n allowed by theory*	*Value of $2\pi Rr$ when J_n has its first maximum*	*Spacing corres. to $\frac{2\pi 75}{X}$*	*Obs. position of reflexion nearest to meridian*
0	0	0		—
1	—10, 21	11.5	41 A	30 A
2	11, —20	12.6	37	27
3	1, —30	1.8	262	Very near non meridional
4	— 9, 22	10.5	45	21
5	12, —19	13.8	34	25
6	2, —29	3.0	157	meridional(?)
7	— 8, 23	9.5	49	30
8	13, —18	14.9	32	20
9	3, —28	4.1	115	meridional or near meridional
10	— 7, 24	8.5	55	36
11	14, —17	16.9	30	15
12	4, —27	5.2	91	meridional or near meridional
13	— 6, 25	7.5	63	40 (very weak)
14	15, —16	17.0	28	5
15	5, —26	6.3	75	very near non meridional
16	— 5, 26	6.3	75	near meridional
17	—15, 16	17.0	28	15
18	6, —25	7.5	63	meridional or near meridional
19	— 4, 27			
20	—14, 17			
21	7, —24			
22	— 3, 28			
23	—13, 18			
24	8, —23			
25	— 2, 29			
26	—12, 19			
27	9, —22			
28	— 1, 30			
29	—11, 20			
30	10, —21			
31	0, 31			
32	—10, 21			
33	11, —20			
34	1, —30			
35	— 9, 22			
36	12, —19			
37	2, —29			
38	— 8, 23			
39	13, —18			
40	3, —28			

References p. 19.

We also indicate in Table II the value of $2\pi Rr$ at which the lower order Bessel function has its first maximum*. This value, together with a value for r, allows us to predict where the first reflexion on a given layer line can occur. (Naturally it may actually fail to appear owing to phase cancellation.) Since the diameter of TMV is 150 A, r cannot assume a value greater than 75 and so the innermost reflexions cannot occur closer to the meridian than $\frac{2\pi 75}{X} = \frac{1}{R}$. We thus include in Table II the lowest possible value of $1/R$ for a given r. These should be compared with the observed positions which are also tabulated in Table II. The agreement can be seen to be good, as in no case is a reflexion found in a region forbidden by the Bessel function argument. In fact, the initial reflexions systematically appear slightly beyond the predicted region and may suggest that the outermost regions of each TMV particle only slightly contribute to the

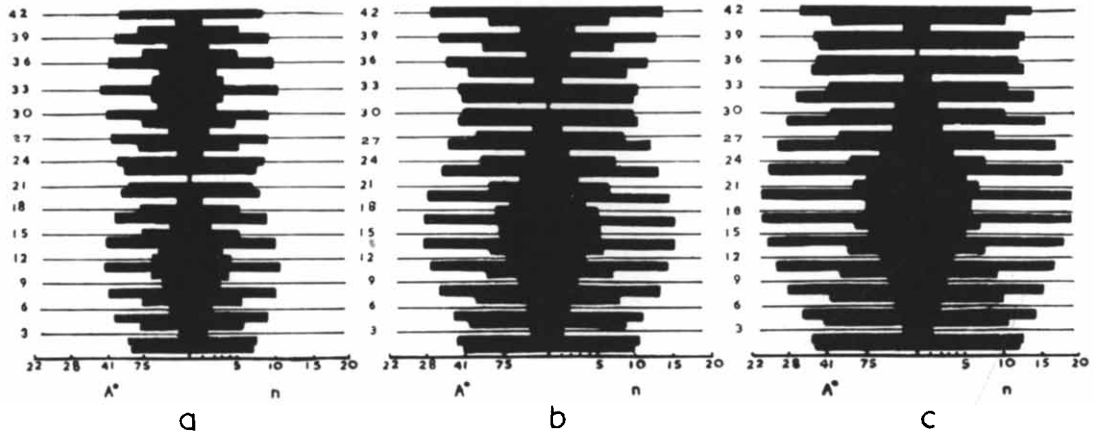

Fig. 5. Diagrammatic illustration of the forbidden regions in reciprocal space in which X-ray reflexions cannot occur. The forbidden regions are darkened and are presented for helices repeating after 3 turns and containing (a) 22, (b) 31, and (c) 37 residues per repeat of 68 A. The numbers on the left-hand margin of each diagram refer to the layer-lines along the fibre axis. The horizontal scale is described in two ways. On the left-hand side, the numbers refer to spacings in reciprocal space, while those on the right-hand side refer to the order n of the lowest order Bessel Function which contributes to a given layer line. For convenience the vertical scale has been compressed approximately six-fold and so the horizontal and vertical distances are not equivalent.

observed scattering. We should note that for very low order Bessel functions the innermost reflexions may occur very near the meridian. Thus it may be possible to observe splitting of these reflexions only under the most favourable conditions of particle orientation. It was therefore pleasing to obtain several photographs from a very well-oriented specimen which indicated a definite splitting of the 3rd and 15th order meridional reflexions. As yet we have been unable to observe splitting of the 6th, 9th or 12th meridional reflexions.

It is pertinent to compare the 31 residue helix with related helices containing 3 turns and $3n + 1$ residues per repeat. This we have done in Fig. 5, in which are illustrated diagramatically the forbidden regions of 3-turn helices containing 22, 31 and 37 residues. While all of the diagrams are roughly similar, they can be seen to differ

* The shape of Bessel Functions is such that they have very low values except in the immediate vicinity of maxima or minima.

References p. 19.

markedly in the location of the layer-lines to which the very low order Bessel functions contribute. It can be seen that a J_0 Bessel function contributes to the layer-line corresponding to the number of residues per identity repeat, and that accordingly the location of the first truly meridional reflexion moves away from the origin as n increases. Thus by observing the position of the true meridional reflexions it should be possible theoretically to determine the exact number of residues per repeat. Unfortunately, our X-ray diagrams were obtained from slightly disoriented specimens, and it is impossible to distinguish a layer-line to which a J_0 Bessel function contributes from one to which a J_1 Bessel function contributes. Experimentally it is thus impossible to determine n unambiguously. The general appearance of our diagrams, however, can be seen to be more similar to the pattern expected from the 31 residue helix than to the patterns expected from the 22 or the 37 residue helices, and so it appears probable that n is of the order of the magnitude of 10.

The data, however, are precise enough to make highly improbable any helical structure other than a non-integral one containing 3 turns and $3n + 1$ sub-units in 68 A. For instance, it might be argued that our failure to split the 6th order meridional reflexion indicates the presence of a six-fold screw axis. This would be a most improbable suggestion as it fails to account for either (1) the size of the absence regions near the meridian in the vicinity of the origin on the $3n + 1$ and $3n + 2$ layer lines, or (2) the tendency of the higher order $3n$ reflexions to spread away from the meridian, or (3) the presence of the meridional reflexion on the layer lines of the order $3n + 1$ in the region around $n = 10$. It seems most probable that our failure to split the meridional reflexion on the 6th order layer line is due to inadequate particle orientation.

As we are unable to determine the exact number of sub-units, we can only place approximate limits to their molecular weight. It ranges from M.W. 27,000 for 37 sub-units per 68 A to a M.W. of 45,000 for 22 sub-units per 68 A. Correspondingly, the number of sub-units per infective particle has a value between 900 and 1500. It should be emphasized that these figures refer to the size of the crystallographically detectable sub-unit and that this unit itself may also be composed of still smaller sub-units. The X-ray data are only able to place an upper limit to the size of the basic repeating unit.

It is most likely that the protein component within each sub-unit is present in the form of folded polypeptide chains of the α-type. Several independent pieces of evidence suggest this conclusion. The most compelling is that of FRASER[6] using polarised infra-red radiation. He finds that the dichroism and frequency of the absorption bands are those of α-polypeptide chains preferentially oriented perpendicular to the longitudinal axis. The X-ray evidence supports this interpretation as the TMV X-ray pattern is dominated by 10 A reflexions, a feature generally interpreted by protein crystallographers to indicate the presence of a polypeptide chain. The strongest group of these 10 A reflexions is found near the meridian and supports the conclusion that the polypeptide chains lie largely at right angles to the particle axis. It is suggestive that the pitch of our helix (22 A) is just twice the thickness of a folded α-chain, and we think it probable that each sub-unit contains two layers of α-chains.

DISCUSSION

The preceding X-ray evidence indicates a division of the TMV particle into a large number ($\approx$ 1200) of crystallographically equivalent diffracting groups which for con-

References p. 19.

venience we call sub-units. These sub-units have been called equivalent, but of course the resolution of the X-ray photographs is only about 5 A and so it is possible to imagine minor differences among them. If such differences exist, however, they must be such as not to affect the systematic arrangement of the units into a regular helix.

We are unable to draw any conclusions about the ribonucleic acid (RNA) component since its small percentage (5%) makes its detection difficult, especially in view of the lack of oriented X-ray diagrams from isolated RNA. We do not mean to suggest that the RNA plays an unimportant role in the structure, in fact we would guess otherwise. It may be useful, therefore, to consider the structure of the two viruses in which the position of the nucleic acid has been tentatively located. These are Turnip Yellow Mosaic Virus[7], a plant virus containing RNA, and T2[8], a bacterial virus containing DNA. In both of these viruses the nucleic acid appears to be located in the interior and surrounded on the outside by the protein component. Since Turnip Yellow Mosaic Virus and T2 are very dissimilar viruses, it is tempting to speculate that the nucleic acid of all viruses forms a central core which is surrounded by a protein shell. If TMV is built on this basis, the RNA would form a central core 35 A in diameter corresponding to its percentage composition of 6%. It may be pertinent to enquire whether the RNA also tends to repeat its structure at fixed intervals along the fiber axis. The available X-ray evidence, however, can only be used to demonstrate a periodicity in the protein component. It is possible that only the protein component repeats its pattern every 68 A, while the RNA consists of non-repetitive polynucleotide chains 2800 A in length.

We should note that the molecular weight of TMV (about $4 \cdot 10^7$) as deduced from physical chemical measurements is in agreement with that of a solid rod with dimensions as observed in the electron microscope. The structure is therefore relatively solid and must not contain a large proportion of empty holes. In agreement with this supposition is the previously noted fact that the high-order reflexions ($d < 20$ A) are relatively unchanged by the presence of water. If TMV were a sponge-like structure containing a large number of empty regions with dimensions about 10 A, we should expect a change in the high-order reflexions following the introduction of water. On the contrary, the observed similarity in the high-order reflexions indicates that a large fraction of each crystallographic sub-unit is filled with virus protein or nucleic acid. The virus components within a crystallographic sub-unit are therefore in contact not only with the virus components of adjacent residues in the same turn of the helix, but also with virus components in adjacent turns.

This "close packing" of the virus material appears to us not to be without significance. It seems most probable to us that some stage in TMV formation involves aggregation of the sub-units. Since this process would involve the arrangement of similar units into a regular lattice structure, it may be equivalent to crystal formation. The rules of crystal growth may be applicable, and we should consider the conclusions of BURTON, CABREARA AND FRANK[9]. These authors conclude from theoretical calculations that crystals will grow faster if they contain screw dislocations and thus do not form a perfect lattice. The presence of screw dislocations increases the rate of crystal growth by permitting the perpetuation of "corners" into which the monomers can fit and allows crystal growth to occur at a constant rate uninterrupted by the formation of closed surfaces. The essential point in their argument is that the rate of crystal growth is greatly increased by the presence of "cosy" corners. We should not expect a linear aggregate to be formed by a linear end-to-end attachment since there would be only

References p. 19.

a single surface to attach to. Instead, we should expect the line of attachment of one monomer to another to be at an angle to the longitudinal axis, forming a helical structure in which each monomer is in contact not only with adjacent monomers on the same turn of the helix but also with monomers on adjacent coils. We should emphasise that a helical form in itself does not provide cosy corners since helices can be constructed in which the monomers on non-adjacent coils do not touch.

Many of the fibrous proteins appear to be constructed from the aggregation of globular proteins, *e.g.* fibrin, F-actin, and fibrous tropomyosin. We suspect that our preceding argument in favour of aggregation into super-helices should also apply to these structures and that it is the presence of super helices which is responsible for the long spacings of several hundred Angstrom units which have been observed with X-rays and the electron microscope. This possibility we hope to test by an examination of the appropriate X-ray patterns.

ACKNOWLEDGMENTS

During the course of this investigation, the author has benefited at numerous times from discussions with Mr F. H. C. CRICK. He is also indebted to Dr H. E. HUXLEY both for instruction in the technique of obtaining X-ray photographs and for having kindly taken several photographs with his low-angle camera. Professor Sir LAWRENCE BRAGG, Dr J. C. KENDREW and Dr M. F. PERUTZ have kindly read a preliminary version of this manuscript and have contributed many useful suggestions for revisions.

SUMMARY

On the basis of X-ray diffraction evidence, a helical structure is proposed for Tobacco Mosaic Virus. It is suggested that the virus contains a large number of equivalent sub-units helically arranged about the longitudinal axis. The proposed helix repeats after 3 turns in 68 A and contains $3n + 1$ sub-units per repeat. It is considered plausible that n is of the order of 10; thus the molecular weight of a sub-unit is approximately 35,000 and the number within an infective particle is approximately 1,200.

RÉSUMÉ

Le virus de la mosaïque du tabac, en se basant sur une étude par la diffraction des rayons X, semble avoir une structure hélicoïdale. Le virus contiendrait un grand nombre de sub-unités équivalents, disposées d'une manière hélicoïdale le long du grand axe. Cette structure hélicoïdale se répète après 3 tours en 68 A et elle contient $3n + 1$ sub-unités pour cette distance. Il est probable que n est de l'ordre de grandeur de 10; il s'ensuivrait que le poids moléculaire d'une sub-unité serait d'environ 35,000 et que leur nombre dans une particle infectante serait d'environ 1,200.

ZUSAMMENFASSUNG

Untersuchungen mit Röntgenstrahlen deuten auf eine spiralförmige Struktur des Tabak Mosaik Virus hin. Es wird vorgeschlagen, dass der Virus eine grosse Anzahl von gleichwertigen Untereinheiten enthält, die spiralförmig der Länge nach angeordnet sind. Die vorgeschlagene Spiralstruktur wiederholt sich nach 3 Drehungen innerhalb 68 A und besteht aus $3n + 1$ Untereinheiten per 68 A. Es erscheint möglich, dass n die Grössenordnung 10 hat und daher das Molekulargewicht der Untereinheit ungefähr 35,000 ist; ein infektiöses Partikel würde demnach aus ungefähr 1,200 solchen Untereinheiten bestehen.

REFERENCES

1 J. D. BERNAL AND I. FANKUCHEN, *J. Gen. Physiol.*, 25 (1941) 111.
2 W. COCHRAN, F. H. C. CRICK AND V. VAND, *Acta Crystal.*, 5 (1952) 581.
3 K. DORNBERGER-SCHIFF, *Ann. Physik*, 6 (1949) 14.
4 W. COCHRAN AND F. H. C. CRICK, *Nature*, 169 (1952) 234.
5 L. PAULING, R. B. COREY AND H. R. BRANSON, *Proc. Nat. Acad. Sci. Wash.*, 37 (1951) 205.
6 R. D. FRASER, *Nature*, 170 (1952) 491.
7 R. MARKHAM, The Size and Shape Factor in Colloidal Systems, *Discuss. Faraday Soc.*, 11 (1951) 221.
8 A. D. HERSHEY AND M. CHASE, *J. Gen. Physiol.*, 36 (1952) 39.
9 W. BURTON, N. CABREARA AND F. C. FRANK, *Phil. Trans. Roy. Soc.*, A 243 (1951) 299.

Received April 16th, 1953