STRUCTURE OF TOBACCO MOSAIC VIRUS

Radial Density Distribution in the Tobacco Mosaic Virus Particle

MEASUREMENTS of the equatorial scattering of X-rays by orientated gels of tobacco mosaic virus[1] have been used for calculating the mean electron density in the virus as a function of distance from the axis of the rod-shaped particle. Using a Geiger-counter diffractometer with monochromatic copper $K\alpha$ radiation, accurate, high-resolution recordings of the equatorial scattering have been obtained for values of $2\sin\theta/\lambda$ up to 0·06, and for $2\sin\theta/\lambda$ between 0·06 and 0·094 intensities have been estimated from photographs.

Over the angular range examined, the amplitudes of the intensity maxima are real since, for a helix such as tobacco mosaic virus[2], this part of the pattern is determined only by the cylindrically averaged density[3]. Sign relations between some of the maxima can be established from their regular periodicity in certain regions. Where this periodicity corresponds to a dimension about that of the particle diameter, it follows that the amplitude changes sign at the zeros separating the maxima[4]. Radial density distributions were calculated for the sign combinations consistent with these sign relations, and all but two sets were found to be improbable since they would require an unreasonably large diameter for the particle and unlikely density values. Unambiguous determination of the correct set of signs was made from the changes in the equatorial X-ray scattering produced by lead bound to the virus.

When tobacco mosaic virus is treated with lead acetate, lead is specifically bound, and the virus (in concentrated solution) remains soluble with up to about one lead atom added per 17,000 molecular weight of virus. The differences in X-ray scattering from orientated gels of normal and lead-substituted tobacco mosaic virus were used to calculate the radii at which the lead is fixed and to establish the signs of the amplitudes. Equal amounts of lead are found to bind at radii of 25 A. and 84 A.

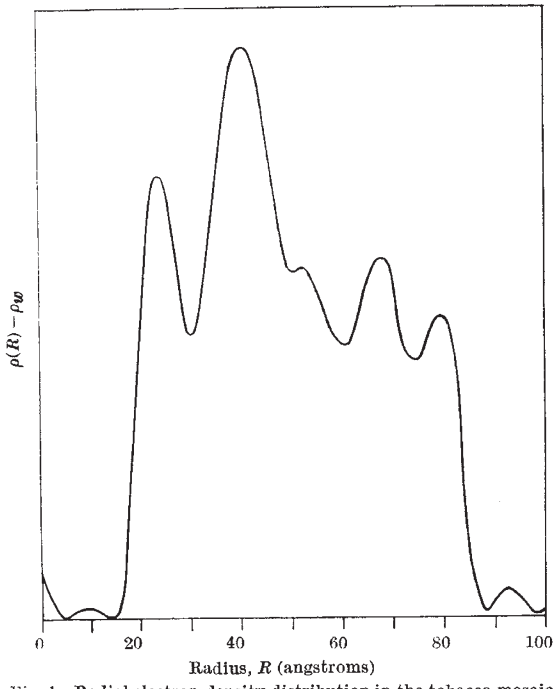

Fig. 1. Radial electron-density distribution in the tobacco mosaic virus particle plotted as a function of distance from the axis of the particle. Ordinate values are proportional to the mean density in excess of that of water

Using the signs so determined, the Fourier–Bessel transform of the equatorial amplitudes has been calculated to give the radial density distribution in the virus particle. This is shown in Fig. 1.

The following features of this transform should be noted: (1) The tobacco mosaic virus particle is hollow. A hole of radius about 19 A. extends along the axis of the particle. (2) The effective radius of the virus in solution is about 84 A., which is appreciably greater than the value 75 A.[1] obtained from the inter-particle distance in dry paracrystals. This difference is consistent with the results of Franklin and Klug[5], who found that there are rather deep indentations in the virus surface which follow the pitch of the helix in such a way that the particles can intermesh in the dry paracrystals. (3) There is a region of high density at a radius of 24 A. and one of higher density at 40 A. The peaks of smaller density at about 67 A. and 79 A. are also significant, but the other minor peaks are diffraction effects from the termination of the Fourier–Bessel integral.

Electron microscope studies[6] have shown that the ribonucleic acid in tobacco mosaic virus is located near the particle axis. From the present work alone it is not possible to decide at what radius the ribonucleic acid is located. This question is resolved by comparison of this density distribution for the normal virus with that for the ribonucleic acid – free virus protein, described by Dr. R. E. Franklin in the following communication.

Details of this work, which was supported in part by a grant from the U.S. National Science Foundation, will be described elsewhere.

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Location of the Ribonucleic Acid in the Tobacco Mosaic Virus Particle

In the rod-shaped particle of tobacco mosaic virus, the protein is in the form of sub-units set in helical array about the long axis of the particle[1]. Electron microscope studies[2] have indicated that the virus nucleic acid may form an axial core. In this com-