INTERROD FORCES IN AQUEOUS GELS OF TOBACCO MOSAIC VIRUS

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ABSTRACT The lateral separation of virus rod particles of tobacco mosaic virus has been studied as a function of externally applied osmotic pressure using an osmotic stress technique. The results have been used to test the assumption that lattice equilibrium in such gels results from a balance between repulsive (electrostatic) and attractive (van der Waals and osmotic) forces. Results have been obtained at different ionic strengths (0.001 to 1.0 M) and pH's (5.0 to 7.2) and compared with calculated curves for electrostatic and van der Waals pressure. Under all conditions studied, interrod spacing decreased with increasing applied pressure, the spacings being smaller at higher ionic strengths. Only small differences were seen when the pH was changed. At ionic strengths near 0.1 M, agreement between theory and experiment is good, but the theory appears to underestimate electrostatic forces at high ionic strengths and to underestimate attractive forces at large interrod spacings (low ionic strengths). It is concluded that an electrostatic-van der Waals force balance can explain stability in tobacco mosaic virus gels near physiological conditions and can provide a good first approximation elsewhere.

INTRODUCTION

The nature of the forces that stabilize liquid crystalline gels formed from long, cylindrically symmetrical rods is of considerable interest in both physics and biology. Such gels form spontaneously in aqueous solutions of cylindrical rods such as tobacco mosaic virus (TMV), in the filament lattice of striated muscle and in the array of collagen fibrils in cornea. More than forty years ago, Bernal and Fankuchen (1941) suggested that the stability of these systems was the result of a balance of long-range forces: repulsive electrostatic, and attractive van der Waals forces. If such a force balance is the basis of stability in these systems, one would expect that the interrod spacing at equilibrium would depend on the concentration of shielding ions in the solution (through the ionic strength, *I*) and the charge on the rods (through the pH). Variations of either of these parameters would be expected to change the electrostatic force while having little effect on the van der Waals force. The result would be a shift in the equilibrium separation. Changes qualitatively similar to those expected were found for the TMV system (Bernal and Fankuchen, 1941) and for the filament lattice in vertebrate cross-striated muscle (Rome, 1967; April, 1975).

There have been several attempts at a quantitative comparison, based on theoretical calculations of electrostatic and van der Waals forces, several of which have been applied to the muscle filament lattice (Elliott, 1968; Miller and Woodhead-Galloway, 1971; Brenner and McQuarrie, 1973; Morel and Gingold, 1979). In the case of muscle, most of the comparisons showed a large discrepancy between the available experimental data and the calculated equilibrium spacing, a finding not altogether surprising since the actual muscle filament lattice is a poor approximation to the conditions used in calculating the interrod forces (cylindrical rods with uniformly distributed charge on their surface forming a single hexagonal lattice). Looking at the simpler TMV system, Parsegian and Brenner (1976) compared the limited data of Bernal and Fankuchen (1941) with theoretical electrostatic and van der Waals calculations and concluded that "The observed spacings are inconsistent with a force-balance model." They were, however, unable to identify the source of the discrepancy (i.e., in the calculation of electrostatic or van der Waals forces, or in additional factors) and urged further experimentation to clarify the situation.

It was this report (Parsegian and Brenner, 1976) that stimulated our interest in this problem, and over the last few years we have been collecting experimental data from TMV gels. All of these data have been compared with calculated curves for electrostatic and van der Waals forces. In particular, we designed experiments to test whether or not the relation between lattice spacing and external pressure agrees with that predicted from calculated electrostatic pressure, and whether a specific balance between electrostatic and van der Waals forces is responsible for the stability of the gels.

We used an osmotic stress technique to obtain curves relating the interaxial rod spacing to the externally applied osmotic pressure under a range of conditions of pH and ionic strength. The techniques used and some of the preliminary data are published in an earlier paper (Millman and Nickel, 1980). For convenience, our experimental data and the theoretical calculations are expressed in terms of pressure rather than force, since this is our experimental variable and pressure can be calculated more directly. If TMV gels are stabilized by an electrostatic-van der Waals force balance, we would expect our experimental data to correspond to the difference between electrostatic and van der Waals pressure. At very high pressures (>2,000 torr) other force systems (e.g., stereochemical and hydration forces) will contribute to the repulsive pressure, and will prevent the rods moving closer to one another. Over most of our experimental range (20–2,000 torr) van der Waals pressure is much smaller than electrostatic pressure (see Fig. 2), and we would thus expect the data to lie close to the electrostatic pressure curve. In general, we have found good agreement between theoretical calculations and experimental data in the mid-pressure range, but some anomalies appeared at the extremes of the range.

METHODS

The procedures used were those described by Millman and Nickel (1980). Small samples (2–3 mg) of purified TMV were removed from the final centrifuge pellet, placed in a small plastic chamber (of volume 5–10 μl) containing excess buffer solution, and allowed to equilibrate until an x-ray diffraction pattern showing the hexagonal phase was obtained (a few days to several weeks) (Fig. 1 *a*). The gels were then equilibrated with a larger volume (~5 ml) of buffer solution containing various concentrations of dextran, an uncharged, chemically inert molecule that is too large (200,000 or 2,000,000 mol wt) to penetrate the gel phase. Thus, the dextran exerts an osmotic pressure on the gel. The externally applied osmotic pressure is a function of the dextran concentration and was determined from previously obtained calibration curves (Millman et al., 1983). The lattice spacing (or interaxial spacing between the virus rods, designated by *C*) was obtained from low-angle x-ray diffraction photographs of the gels. Only gels that gave clear x-ray diffraction patterns were used, and all of these showed sharp patterns characteristic of an hexagonally ordered system (Fig. 1). The ionic strength of the buffer solution was varied from 0.9 to 0.001 M and the pH from 5 to 7.2. Spacing measurements were also made under conditions of zero applied pressure (i.e., in buffer solutions without any dextran). To check that polymer molecules were not entering the spaces between the TMV particles, in some experiments the dextran solution was separated from the gel by a sheet of dialysis membrane (similar to that used for the pressure calibration). No significant difference was detected between results with and without the dialysis membrane (Fig. 2). We conclude that no significant amount of dextran entered the gel spaces in the experiments without the dialysis membrane.

RESULTS AND DISCUSSION

Electrostatic Interactions

TMV gels, prepared and equilibrated in dextran solutions using 0.1 M sodium phosphate buffer at pH 6, were used as a standard to which results obtained under other conditions could be compared. The standard conditions of pH and ionic strength approximate those found in physiological solutions and are also conditions where the charge on the TMV rods has been determined (Caspar, 1963). A considerable amount of data and the most accurate curve of interrod spacing as a function of pressure were obtained under these conditions (Fig. 2).

Under all conditions studied, the interaxial spacing (*C*) decreased with increasing applied pressure (Fig. 1). The pressure-spacing curve showed a relationship between *C* and the logarithm of pressure, which was approximately linear (Figs. 2–4). About half of the experimental data were obtained with a sheet of dialysis membrane separating the TMV gel from the external (dextran) solution; the rest of the data were obtained without such a membrane. While there appeared to be a slight tendency for the experiments without dialysis membrane to give smaller spacings than those where the dialysis membrane was used, the difference was not significant. It is possible that the larger spacings occurred because some samples with dialysis membrane had not fully equilibrated with the external solution when the x-ray diffraction patterns were obtained, since in other systems equilibration is slower with dialysis membrane (Millman et al., 1983). Only under conditions approaching zero applied pressure (i.e., when no dextran was used) did the experimental data depart significantly

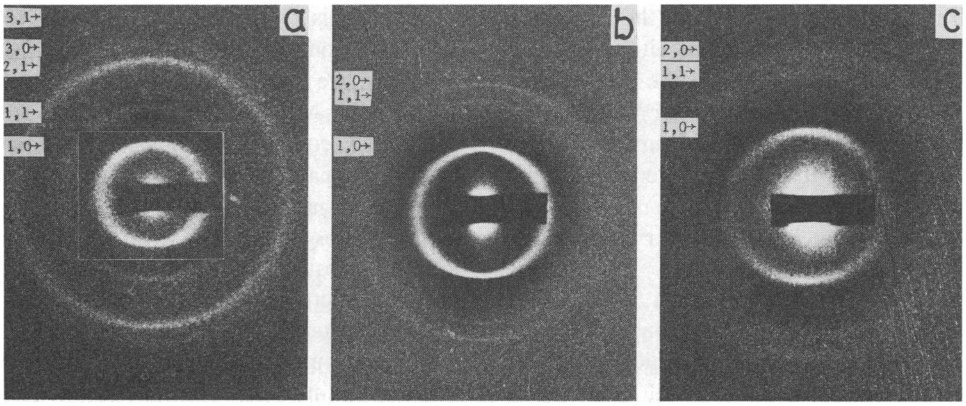

FIGURE 1 Low-angle x-ray diffraction patterns from TMV gels taken at a specimen to film distance of 23.7 cm. (*a*) gel in 0.01 M phosphate buffer, pH = 6. (An insert is overlayed from the back x-ray film to show the central part of the pattern, which was heavily overexposed.) (*b*) and (*c*) show the same gel in similar buffer but with 10.4 and 28.5% dextran, respectively. Reflections are indexed on the hexagonal lattice as noted.

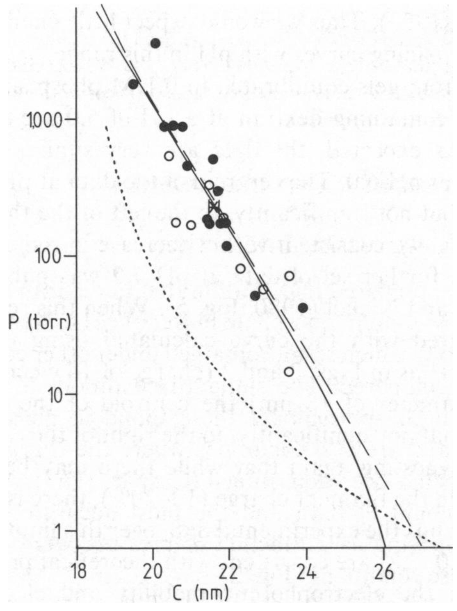

FIGURE 2 Interaxial spacing (*C*) as a function of applied osmotic pressure (*P*) for TMV gels in sodium phosphate buffer of ionic strength 0.096 M and pH 6.0. Circles are experimental observations with (●) and without (○) dialysis membrane, the cross is the centroid of the data with standard error bars. Lines are theoretical curves for electrostatic pressure (dashed line), van der Waals pressure (dotted line), and the difference between electrostatic and van der Waals pressure (solid line).

from a linear relationship between *C* and the logarithm of pressure (Fig. 2), and this condition will be discussed later.

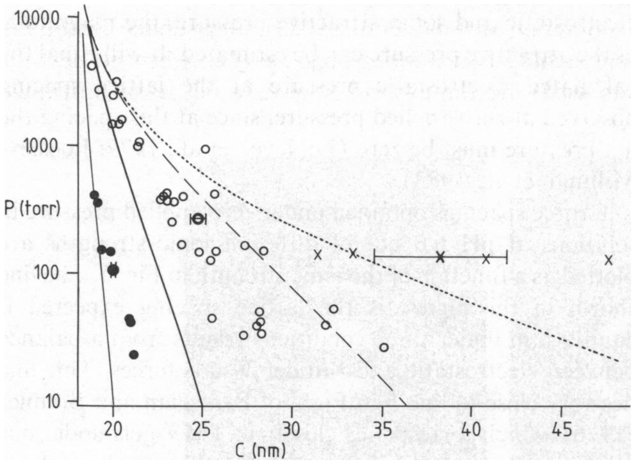

FIGURE 3 Interaxial spacing (*C*) as a function of applied osmotic pressure (*P*) for TMV gels in sodium phosphate buffer at pH 6.0 compared with theoretical electrostatic pressure curves at ionic strengths of 0.9 M (● and thin solid line), 0.01 M (○ and dashed line), and 0.001 M (X and dotted line). The thick solid line is the theoretical electrostatic pressure curve for an ionic strength of 0.096 M from Fig. 2. Symbols with error bars are the centroids of the data with the bars indicating one standard error.

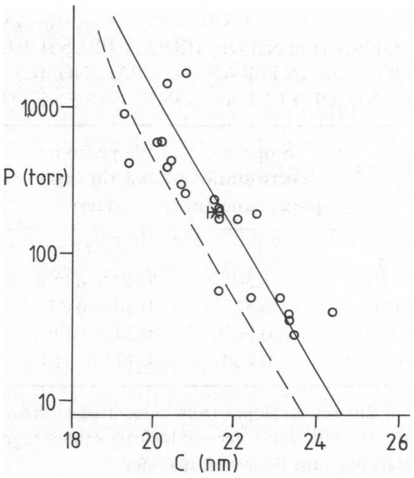

FIGURE 4 Interaxial spacing (*C*) as a function of applied osmotic pressure (*P*) for TMV gels in sodium phosphate buffer at pH 5.0 and ionic strength of 0.096 M as in Fig. 3. The lines are the theoretical curves for electrostatic pressure with rod charges of 14 electrons/nm (solid line) and 7 electrons/nm (dashed line). The cross indicates the data centroid with standard error bars.

Under the standard conditions (I = 0.1 M, pH = 6), isolated subunits of TMV have a net negative charge of two electrons (Caspar, 1963). There are 49 subunits in each axial repeat of 6.9 nm, so that if no charge is bound or lost when the virus assembles, the intact virus should have a net charge of 14 electrons/nm. Electrostatic pressure curves were calculated from nonlinearized solutions to the Poisson-Boltzmann equation as described by Millman and Nickel (1980) using a rod charge of 14 electrons/nm, a charge diameter of 18 nm (approximately the outside surface of the intact virus), and ionic concentrations appropriate to each experimental condition as calculated by the method of Perrin and Sayce (1967). The curve for the standard conditions is shown as the dashed line in Fig. 2. Calculations using the Alamov/Wooding method of Parsegian and Brenner (1976, Eq. 1) gave pressures ~35% higher for the same conditions, whereas the planar-linearized solution used by Millman and Nickel (1980) (in particular for the muscle filament lattice) gave pressures ~20% lower. Thus, theoretical curves calculated by these different methods differed by less than the scatter in the experimental points. Van der Waals pressure was calculated from the equations of Brenner and McQuarrie (1973), using a rod diameter of 18 nm and a Hamaker coefficient of 7×10^{-14} erg (Parsegian and Brenner [1976] give a range from 5–9×10^{-14} erg), and is shown as the dotted line in Fig. 2. The solid line represents the difference between the curves (electrostatic − van der Waals) and clearly is in good agreement with the experimental data. This agreement confirms our assumption that most of the pressure observed under these conditions is electrostatic. As predicted, the effects of van der Waals forces are significant only at very low pressures; elsewhere the curve is dominated by the electrostatic pressure. Least-squares fits were made to each set of data (excluding points at zero applied pressure) assuming that the logarithm of pressure is linearly related to *C* (a good assumption over the

TABLE I
SLOPE OF CURVES FOR (LOG_{10}) PRESSURE AS A FUNCTION OF INTERAXIAL SPACING (C) AT pH 6.0 AND DIFFERENT IONIC STRENGTHS*

Ionic strength	Debye constant	Slope of electrostatic pressure curve	Slope from experimental data	Number of observations
M	*nm*$^{-1}$	*nm*$^{-1}$	*nm*$^{-1}$	
0.87	3.04	−1.56	−0.58 ± 0.05‡	7
0.096	1.01	−0.52	−0.50 ± 0.05	24
0.048	0.73	−0.36	−0.24 ± 0.09	11
0.010	0.33	−0.169	−0.171 ± 0.016	32

*Comparison of theoretical slopes from calculated electrostatic pressure curves with experimental slopes derived by least-square regression of data for $\log_{10}$ (pressure) against interaxial spacing.
‡Standard error.

observable range). The centroids and slopes are compared with theoretical electrostatic pressure curves in Figs. 2–4 and in Table I.

Changing the ionic strength would be expected to cause a considerable change in the electrostatic pressure (because of ionic shielding) but to have little effect on van der Waals pressure. Experimental data at ionic strengths of 0.001, 0.01, and 0.9 M are shown in Fig. 3, along with calculated electrostatic pressure curves. The changes in the experimental curves are similar to those predicted and the data lie close to the appropriate theoretical curves. It is particularly significant that the experimental slopes (obtained from least-squares reduction of the experimental data) change with the ionic strength almost exactly as predicted from the calculated curves (Table I). The exception here is for the data at $I = 0.9$ M where the slope of the experimental curve is lower than predicted. Such a result is hardly surprising given that the Poisson-Boltzmann equation is not expected to apply at ionic strengths above ~0.1 M (see Millman and Nickel, 1980). But even at an ionic strength of 0.9 M, the positions of the data and the centroid calculated by least squares do not depart dramatically from the theoretical curve (Fig. 3). The data at lower ionic strengths (0.01 and 0.001 M) show greater scatter than the data at the higher ionic strengths, reflecting a decreased gel stability at the greater rod separations.

Changing the pH while holding the ionic strength constant would be expected to give pressure-spacing curves of similar shape, but shifted parallel to the horizontal axis according to the change in rod charge (Millman and Nickel, 1980). The isoelectric point for intact TMV particles is between 3.0 and 3.5 (Bernal and Fankuchen, 1941; Caspar, 1963). Above the isoelectric point, an increase in pH would be expected to increase the rod charge and thus increase the interaxial spacing, whereas a decrease in pH would do the opposite. Electrophoretic mobility studies, however, suggest that the change in charge above pH 5 is small: shifts of one pH unit change the charge by <10% (Kramer, 1957). Thus we would expect little change in the pressure-spacing curves with pH in this range.

Data from gels equilibrated in 0.1 M phosphate buffer solutions containing dextran at a pH of 5.0 are shown in Fig. 4. As expected, the data are very similar to those obtained at pH 6.0. The centroid of the data at pH 5.0 lies slightly, but not significantly, to the left of the theoretical curve (Fig. 4), consistent with a decrease in rod charge of ~10%. A further set of data at pH 7.2 was published in Millman and Nickel (1980, Fig. 5). When this set of data is compared with the curve calculated using the same parameters as in Figs. 2 and 3 (charge of 14 electrons/nm and a diameter of 18 nm) the centroid of the data lies slightly, but not significantly, to the right of the calculated curve, suggesting again that while there may be a small increase in the filament charge (10–20%), there is no large change. Thus the experimental data over this limited range of pH (5.0–7.2) are consistent with theoretical predictions based on the electrophoretic mobility and electrostatic pressure calculations.

Van der Waals Interactions

TMV gels will generally form stable lattices in ionic solutions where no external pressure is being applied (i.e., no polymer in the external solution) (Bernal and Fankuchen, 1941; Caspar, 1963; Gregory and Holmes, 1965). The fact that a stable equilibrium can be obtained under such conditions implies that there must be an attractive pressure counteracting the repulsive electrostatic pressure and that both of these must be greater than the thermal (kT) disruptive pressure, which will tend to destroy any lattice regularity (Millman and Nickel, 1980; Fig. 10). If one assumes that the interaxial spacing under zero applied pressure is largely the result of a force balance between electrostatic and some attractive pressure, the magnitude of the attractive pressure can be estimated. It will equal the calculated electrostatic pressure at the lattice spacing observed at zero applied pressure, since at this spacing the net pressure must be zero (LeNeveu et al., 1977; Loosley-Millman et al., 1982).

Lattice spacings obtained under zero applied pressure in solutions at pH 6.0 but of different ionic strengths are plotted as a function of the ionic strength in Fig. 5. The line shown in this figure is the lattice spacing expected if equilibrium under these conditions results from a balance between electrostatic and van der Waals forces. This line lies very close to line *b* in Fig. 1 of Parsegian and Brenner (1976), which corresponds closely to TMV gels under our conditions (where $C = 7.0\ \mathrm{nm}^{-2}$). On this graph, we have also plotted comparable data from Bernal and Fankuchen (1941) that were obtained in ammonium sulphate solutions at high ionic strengths. We find good agreement between theory and experiment at ionic strengths near 0.1 M, whereas at lower ionic strengths the observed spacings are less than predicted. It is unlikely that we have underesti-

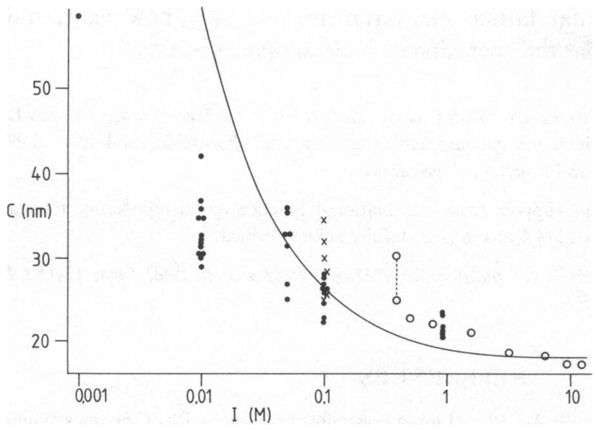

FIGURE 5 Interaxial spacing (C) under zero applied pressure as a function of ionic strength. ●, data from gels in sodium phosphate buffer; X, data in sodium or potassium chloride solutions; O, data of Bernal and Fankuchen (1941) in ammonium sulphate solutions. The line represents the spacings at which electrostatic and van der Waals pressures are equal.

mated the van der Waals pressure, and thus at low ionic strengths other attractive forces must be contributing to the gel stability. Such additional force(s) may be related to additional entropic free energy associated with the ordering of the gel as suggested by Onsager (1949; see also Straley, 1973). We would expect that such entropic forces would be important only at low ionic strengths, the regime where additional forces seem to be required. At higher ionic strengths (0.2–2 M) the observed spacings are greater than predicted, probably because the electrostatic pressure departs from Poisson-Boltzmann statistics at such high ionic strengths (e.g., Fig. 3 and Parsegian and Brenner, 1976). At very high ionic strengths (>2 M) the lattice appears to be fully collapsed and its spacing reflects only the diameter of the virus rods (i.e., stereochemical and hydration forces).

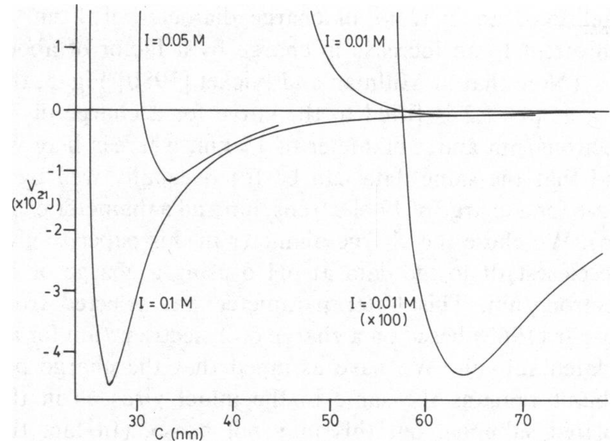

FIGURE 6 Interaction energy per virus particle calculated using Eq. 1 for ionic strengths of 0.1 M, 0.05 M, and 0.01 M. For details see text.

In the data at zero applied pressure we observed a large scatter, especially at the lower ionic strengths. It has been suggested (Brenner and McQuarrie, 1973; Parsegian and Brenner, 1976) that the depth of the energy well (i.e., the interaction energy at equilibrium spacing) may be $\leq kT$. If so, this could account for the large scatter observed. We have calculated the interaction potential for our gels by numerical integration of our calculated curves for electrostatic and van der Waals pressure (e.g., Fig. 2). The potential energy per virus particle (V) in a hexagonal gel is given by

$$V = \sqrt{3}\,\ell \int_C^\infty [P(\mathrm{es}) - P(\mathrm{vdW})]\, C\, dC, \qquad (1)$$

where ℓ is the length of the virus particle (equaling 300 nm), and P(es) and P(vdW) are the electrostatic and van der Waals pressures, respectively. The results at three ionic strengths are shown in Fig. 6, and are qualitatively similar to the curves shown in Fig. 7 of Brenner and McQuarrie (1973). At an ionic strength of 0.1 M, there is a well-defined potential well, but its depth (4.6×10^{-21} J) is only slightly $> kT$ (4.0×10^{-21} J). At this ionic strength we observe gels of reasonable stability at spacings that correspond to the spacing predicted from an electrostatic-van der Waals force balance. The fact that the depth of the well is about the same magnitude as kT indicates that the gel must be stabilized by co-operative effects involving several virus particles. At ionic strengths of 0.01 M and lower, the interaction energy per particle is tiny (~1% of kT) and this is much too small to produce a stable gel. Thus, as noted above, such low ionic strength gels must be formed by and rely for stability on attractive forces additional to van der Waals forces. That gels are observed at all under such conditions is surprising to us. Some of the additional force may result from ionic impurities in the solutions used, contamination with small amounts of polymer, or from containment of the gel within a small space. Variability in lattice spacing seems to be characteristic of TMV gels, however. Even crystalline gels of TMV that have been kept under stable conditions for many years show comparably large variations in equatorial spacing (D. Caspar, personal communication). But although the equilibrium spacing varies greatly from one gel to another, the x-ray reflections from a single gel are very sharp (Fig. 1), indicating a uniform spacing within any one gel.

CONCLUSIONS

Some comments should be made here about our choice of parameters for the calculated curves and the effects of changes in these parameters. The slopes of the electrostatic pressure curves are determined primarily by the ionic strength, through the Debye constant. We have found good agreement between experiment and theory for this parameter (Table I). The effects of changing charge and charge diameter are similar to each other; i.e., a shift in the curve parallel to the horizontal axis. For the TMV case under our conditions, an increase in charge diameter of 1 nm is equivalent to an increase in charge by a factor of about two. (Note that in Millman and Nickel [1980] Fig. 5, the data at pH 7.2 is fitted to the curve for a charge of 35 electrons/nm and a diameter of 17 nm, whereas here we find that the same data can be fitted equally well by a curve for a charge of 17 electrons/nm and a diameter of 18 nm). We chose the charge diameter in this paper to give the closest fit to the data at pH 6 using a charge of 14 electrons/nm. This latter parameter was selected from Caspar (1963) based on a charge of 2 electrons/nm for an isolated subunit. We have assumed that the charge per subunit remains the same in the intact virus as in the isolated subunits, but this may not be so. (In fact the isoelectric point drops from 4.5 in the isolated subunits to ~3.2 in the intact virus [Caspar, 1963]). If the intact virus does have a larger (or smaller) charge, then to fit the data, the charge diameter would have to be decreased (or increased) accordingly, though any change here would likely be <1 nm. The diameter we have used is close to the interaxial spacing found by Bernal and Fankuchen (1941) at the isoelectric point (18.5 nm), but is a little larger than the smallest spacing they observed (17.3 nm) in 6 N salt (where it is possible that the rods could be slightly compressed). In any case, these results indicate that the charge diameter determined here is close to the outside diameter of the virus and thus there cannot be a substantial layer of bound water on the outside of the virus particles; any such bound water must form a layer less than one molecule thick (see e.g., Morel and Gingold, 1979).

From the above results we conclude that the major long-range force system in aqueous gels of TMV is electrostatic, and that the electrostatic pressure (or force) can be calculated from solutions to the Poisson-Boltzmann equation (Parsegian and Brenner, 1976; Millman and Nickel, 1980). At ionic strengths of 0.05 M and above, such gels seem to be formed and stabilized by a balance between electrostatic and van der Waals forces as suggested originally by Bernal and Fankuchen (1941). At lower ionic strengths, however, van der Waals forces alone are insufficient to balance the electrostatic pressure, and other attractive forces are necessary to explain the observed balance.

It now becomes possible to use calculations of electrostatic and van der Waals forces to study other gel-like systems such as the filament lattice of striated muscle (Millman and Nickel, 1980; Millman, 1981; Millman et al., 1983). The muscle system is considerably more complex than the TMV system. It contains thick filaments with prominent projections, forming a double hexagonal lattice with a second set of thinner filaments. From comparisons between calculated pressure-spacing curves and experimental lattice measurements we may now learn more about the operation of such complex systems.

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