

the fluid environment bathing the receptor can be precisely controlled experimentally and is not complicated by the presence of the many "antagonistic" cations found in Ringer's solution, sea water, or extracellular body fluids. Furthermore, since this fluid environment is of very low ionic strength, cations in the concentrations present are without osmotic effect (4); therefore, the amount of calcium added to elicit the feeding response experimentally perhaps closely approximates the actual amount of calcium necessary for the natural functioning of GSH-receptors.

*Note added in proof:* In addition to the specific cation requirement reported here, anions also were found to influence the feeding reflex. The order of effectiveness of the anions in increasing the duration of the feeding reflex was: Cl > Br > I = NO<sub>3</sub>. This order seemed to be the reverse of the lyotropic series.

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### Molting of Preadult Nematodes of the Genus *Paratylenchus* Stimulated by Root Diffusates

**Abstract.** The nonfeeding preadult larvae of the plant-parasitic nematodes, *Paratylenchus projectus* and *P. dianthus*, survive in moist soil during long periods in the absence of host plants. In water, only small percentages molt to the adult stage. In root diffusates from some but not all plants, nearly all of them molt.

The last larval or preadult stage of certain species of the genus *Paratylenchus* Micoletzky often constitutes a high percentage of the total population in Illinois field soils and in old pot cultures; even in the presence of suitable

Table 1. Efficacy of carnation-root diffusate in inducing molting of *P. projectus* and *P. dianthus* preadults.

Treatment	No. of molts among 125 nematodes				
	3 days	6 days	9 days	12 days	15 days
	<i>P. dianthus</i>				
Control* Root	1	1	2	2	2
diffusate	28	73	96	99	104
	<i>P. projectus</i>				
Control* Root	0	1	8	16	20
diffusate	0	87	123	124	125

\*Distilled water to which activated carbon (Darco G-60) was added and which was then decanted and filtered. Indistinguishable results were obtained with nontreated distilled water.

host plants. Results of recent studies (1) indicate that the preadults of *P. projectus* and *P. dianthus* do not feed and that they are capable of long survival in moist soil without feeding; also, that those of *P. projectus*, at least, are more tolerant of desiccation and sudden freezing than are younger stages or adults. The preadult stage of these two species and also of *P. hamatus* and two apparently undescribed species is readily distinguishable from other stages by the greatly reduced stylet and esophagus and by an accumulation of opaque granules in the region of the esophagus, yet this stage seems to have attracted little attention. Reuver (2) described it for *P. amblycephalus* after the study reported here was far advanced. Thorne and Allen (3) evidently recognized but did not describe it in *P. hamatus*, and Ferris and Bernard (4) commented on its abundance in *Paratylenchus* spp. in some samples from Illinois soybean and corn fields.

In Petri-dish cultures of host plants in agar, preadults of *P. projectus* begin the final molt within 4 or 5 days after emerging from the preceding one and at no time constitute any large percentage of the total population. In pot cultures of this same species with red clover, after 100 days the preadults constituted only 7.7 percent of the total population but increased progressively to 66 percent during the following 85 days. In many older pot cultures and field samples, the proportion of preadults has exceeded 80 percent of the population of a species. The cause of this accumulation is not known, but evidently it operates either by preventing the final molt or by failing to provide the stimulus necessary to initiate it.

Working with preadults of *P. projectus* from field collections and old pot cultures and of *P. dianthus* chiefly from a jar of soil that had been stored moist for over 2 years until all other nematodes were dead, we found that preadults do not molt readily in water

but that they are stimulated to molt by some substance or substances that diffuse from roots immersed in water. Leachate from actively growing pot cultures frequently, but not consistently, induces molting.

Consistently effective root diffusate was obtained by immersing the roots of heavily rooted White Sims carnation cuttings in 50 ml of distilled water for 72 hours, with 12 hours of artificial illumination each day. Table 1 presents results of a representative experiment in which preadults, in five lots of 25 each, were placed into small Syracuse dishes containing about 1 ml of carnation-root diffusate, or of water for the controls, and were held at 23° to 26°C in the dark. Fluids were changed at 3-day intervals, diffusate that had been stored at about 7°C being used. Nematodes in which the adult form and size of stylet had developed were counted as having molted.

In a temperature experiment with *P. projectus* no molting occurred at 5°, 10°, or 35°C in carnation-root diffusate or in water during 16 days. The numbers of those that molted among 125 nematodes in diffusate and 125 in water, respectively, were as follows, at four intermediate temperatures: at 15°C, 43 and 0; at 19°C, 124 and 9; at 26°C, 124 and 23; and at 30°C, 125 and 8. Molting occurred at a much more rapid rate at 26° and 30°C than at 15° and 19°C, and more rapidly in diffusate than in water at the two higher temperatures.

Seedlings of nine species of dicotyledonous plants, representing seven families, grown in sand and fertilized with an N-P-K fertilizer (Hyponex), produced root diffusates that markedly increased molting of one or both nematode species. Nine other plant species, six of them monocots, produced diffusates that were without effect on either nematode in a single test, and six additional plant species produced diffusates that were no more than slightly active. There was an imperfect agreement between suitability of plants as hosts and their production of active root diffusate. For example, *Trifolium pratense* L. (Kenland red clover) is a suitable host for both nematodes, yet in repeated tests it has yielded root diffusates that induce molting in *P. projectus* but not in *P. dianthus*.

The activity of certain root diffusates in stimulating hatching or emergence of larvae from cysts of *Heterodera* spp. is a well-known phenomenon, but we are not aware of any prior demonstration that root diffusates may stimulate the molting of plant-parasitic nematodes.

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## Growth of Tobacco Mosaic Virus Particles

**Abstract.** Past studies have characterized the structure of tobacco mosaic virus particles by a variety of methods. In the present report the screw dislocation theory of crystal growth is applied to the formation of tobacco mosaic virus particles. The growth mechanism is shown to account for the rodlike morphology. It is also deduced that the biosynthetic process occurs at the growth step at the end of a particle.

The screw dislocation mechanism of crystal growth (1) has been proposed to account for gross discrepancies between observed and theoretically estimated growth rates. Since the inception of the dislocation theory of crystal growth, much activity has been stimulated in studies of growth phenomena, and understanding of these phenomena has been advanced markedly.

It is of interest to indicate the main features of the dislocation growth mechanism and to relate these to an important problem, the growth of tobacco mosaic virus particles. A crystal which is bounded by close-packed crystallographic planes can only grow by the addition of new atoms or molecules to steps at the edge of crystal layers partially covering the face. When a particle layer totally covers the surface, the bounding step grows out of existence and growth ceases. Growth can only continue through nucleation of a new patch of crystal plane. Nucleation will occur at an appreciable rate when the supersaturation exceeds a critical value. Thus, a close-packed face will not advance in slightly supersaturated solutions but will only grow above a critical supersaturation.

It has been pointed out that a permanent step exists (1) on a close-packed surface at which a screw dislocation terminates. The step extends from the dislocation to an edge or to a dislocation of opposite hand intersecting the same surface and may advance at low supersaturations. Unlike the edge of a partial layer, the step associated with a screw dislocation never grows out of existence, and the dislocated surface will grow at very low supersaturations.

If a crystal is formed which bears a

screw dislocation or dislocations in a single direction, growth at low supersaturations (2) can only proceed in the direction of the screw axis. Such crystals have been grown of a variety of materials. They are thin rods of constant cross section and are called crystalline whiskers. The relevance of the preceding discussion to the growth of tobacco mosaic virus is immediate, because tobacco mosaic virus particles grow as crystalline whiskers.

Tobacco mosaic virus particles have a rodlike structure consisting of a thick-walled tube of protein surrounding a core of nucleic acid. The present discussion is concerned with the growth mechanism of the outer protein tube. Experiments on solution and reprecipitation of tobacco mosaic virus protein (3) demonstrate that the tubular habit is independent of the presence or absence of the nucleic acid core. X-ray diffraction (4) studies reveal that the tube walls are made up of structurally equivalent elements arranged on a helix having a pitch of 23 Å. It has been estimated that there are  $3n + 1$  elements in three helical turns where  $n \sim 12$ . The outer cylinder diameter is 150 Å, and the inner diameter is 51 Å.

The protein cylinder can be dissolved in water in the sense that native tobacco mosaic virus protein or elementary structural units are the solute molecules. The protein may be recrystallized at a pH of about 5 to form hollow cylinders, of varying length but arranged in a helical structure. At a pH of 6, cylinders do not form, but tiny washers do.

In the tubular form,  $12\frac{1}{3}$  structural elements are arranged on each turn of a spiral. Twelve elements enclose  $350^\circ$  of a circle, as shown in Fig. 1 (top). Either of two configurations might occur: The ring might deform in its own plane and form a bond (Fig. 1, middle) between elements A and B, or the ring might be elastically deformed into a lock washer (Fig. 1, bottom) so that addition of new structural elements could occur at either end of the lock washer, as shown in Fig. 2. As each element was added, its edge could serve as a further add-on site. The configuration of Fig. 2 corresponds to a crystal with a screw dislocation in which the unit cells are the structural elements. This growth behavior corresponds to that of a crystalline whisker.

A necessary condition for the operation of the growth mechanism is that the screw-dislocated configuration must be accessible to thermal fluctuations. The preceding condition may be written

$$E_s \leq 20 kT \quad (1)$$

The strain energy  $E_s$  of an elastically deformed lock washer displaced by a distance  $\tau$  is given (5) by

$$E_s = \frac{\mu \tau^2 b}{4\pi} \left[ \ln \frac{r_1}{r_0} - 1 \right] \quad (2)$$

where  $\mu$  is the elastic modulus,  $b$  is the thickness of the washer, and  $r_1$  and  $r_0$  are the inner and outer radii, respectively. Substituting the numerical values  $b = 2.3 \times 10^{-7}$  cm,  $\tau = 2.3 \times 10^{-7}$  cm,  $r_1 = 7.5 \times 10^{-7}$  cm, and  $r_0 = 2.5 \times 10^{-7}$  cm, the pertinent elastic modulus

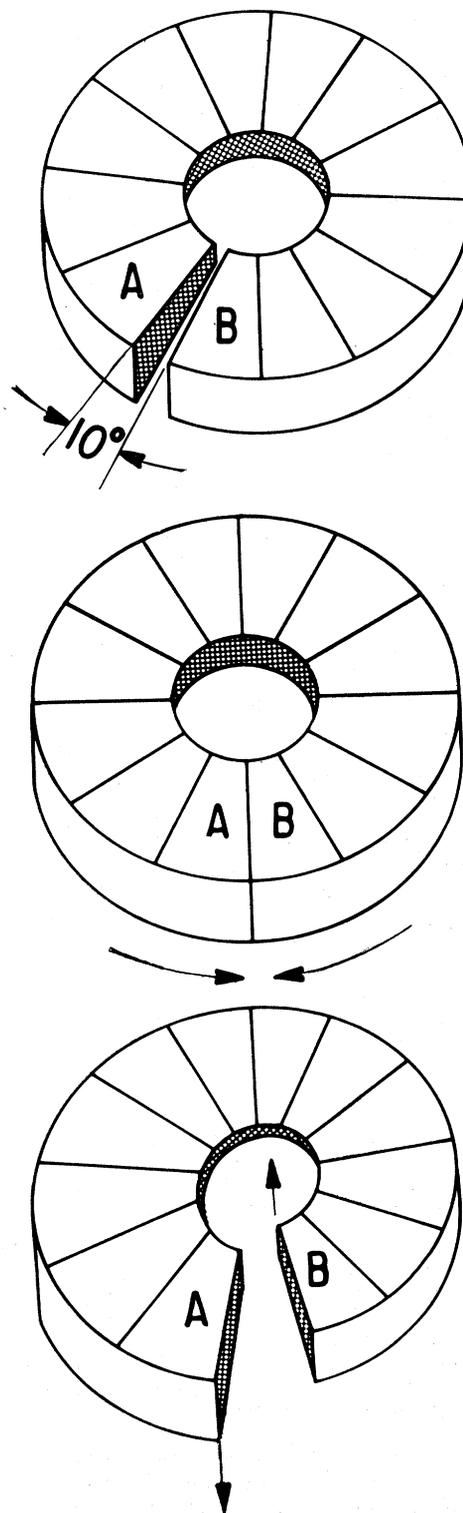


Fig. 1. (Top) Unstrained washer. (Middle) Ring with edge dislocation. (Bottom) Ring with screw dislocation.