Intracellular Transport Apparatus of Phloem Fibers

Abstract. *Rotational streaming of cytoplasm occurs in the form of longicellular currents in immature and relatively mature fibers of bean stems. Plastids carried by these currents move continuously on their rotational course from one end of the cell to the other in relatively straight lines. A distance of approximately 2 millimeters, the average length of the fibers, is covered in about 3 minutes (3.6 cm per hour). The same type of streaming occurs in immature phloem fibers that develop within 24 hours after bean seeds are planted and before the plants appear above the soil surface. Rotational streaming also occurs in xylem fibers of bean stems and in cells which appear to be fibers in stems of young cucumber, tomato, sunflower, and flax.*

The role ascribed to plant fibers, with their thickened cell walls, has long been that of affording mechanical support (*1, 2*) and this viewpoint was recently reemphasized (*3*). Little attention has been given to the cytoplasmic behavior of phloem fibers during various stages in their development.

We have observed rotational cytoplasmic streaming in immature phloem fibers of several kinds of plants (*4*). This type of streaming in cells other than fibers has been reported and it is thought that some of the protoplasm of all living cells is in motion (*5*). The presence of rotational streaming in fibers, however, is of particular interest since substances are apparently carried by this type of cytoplasmic movement over an intracellular course for a relatively long distance in these elongated cells. This intracellular transport mechanism is described here as it occurs in the phloem fibers of bean plants. Rotational streaming observed in phloem fibers was only rarely seen in other types of cells in the bean stems.

The long, narrow cells in which rotational streaming was observed in bean plants (*6*) were identified as phloem fibers (*1, 4, 7*), also referred to previously as pericyclic fibers (*2, 8*), since they were inside of and adjacent to the endodermis and were pointed at the ends. The more mature cells of this kind possessed pits and exhibited secondary thickening of the walls, which are characteristics of fibers.

The streaming observed in the fibers occurred as longicellular currents (streams of cytoplasm moving in a longitudinal direction). These currents were distinguishable from, and appeared to be slightly more dense than, the clear cytoplasm surrounding them. It should be emphasized that the term "current" is used here with the understanding that the basic molecular substance of the current may or may not be the same as that of the remainder of the cytoplasm. The longicellular currents extended from one end of the fiber to the other and, although they continuously changed in shape, their general courses were parallel and the currents were easily distinguishable from diffraction lines, especially when observed near the end of a fiber. Usually two, and sometimes three, such currents were observed at one time within one of these fibers. However, each fiber may have contained additional currents. The thickness of the moving cytoplasm often changed; as the current moved past one point close to a seemingly vertical fiber wall (edge view), it was sometimes relatively thin and then expanded to 2 or 3 times this thickness when a portion of the current carrying one or more plastids moved past the point of observation. When observed against a horizontal wall of a fiber (face view), a current was often wider than the plastids carried in it (*4*).

Cytoplasmic currents within a fiber usually appeared to move in opposite directions past a point of observation because of the rotational course of the currents. In immature phloem fibers, the currents carried numerous plastids which moved in relatively straight lines, as evidenced by their remaining in focus for some distance as they were carried along. These currents in the immature fibers appeared to be located against the wall surface. It was not possible either with bright-field or phase microscopy to detect the plasma membrane which, no doubt, existed between the currents and the cell walls.

As a plastid being carried in a longicellular current approached the end of a fiber, its direction of movement changed. The plastid was turned so that it faced in the opposite direction and was carried in the same or sometimes in another current toward the other end of the fiber. This process often occurred with little change in speed of forward movement of the plastid. Plastids seldom accumulated more than momentarily at any point on their rotational course. The currents converging at the ends of fibers often formed a mass of cytoplasm which was similar in appearance to that in the currents themselves.

Plastids were carried in the currents of phloem fibers at an average rate of 3.6 cm/hr, the rates observed varying from 2.5 to 6.5 cm/hr. Such rates are relatively slow compared with the translocation rates that are generally attributed to sieve tubes (*9*). No difference was apparent in the average rate of movement of an occasional cluster of plastids and that of individual plastids carried in the same or in other currents. Also, no difference in the rate of rotational streaming was noted in phloem fibers of stem sections cut from a different intact bean plant every 4th hour during a 24-hour period; neither did any apparent variation result from changes in light intensity that occurred under greenhouse conditions.

Phloem fibers in different stages of development were studied. Rotational streaming was observed repeatedly in the thin-walled phloem fibers in stem sections from relatively immature bean plants. Rotational streaming of living protoplasts was also observed in the relatively thick-walled phloem fibers of the stems (above the cotyledons) and in hypocotyls before and after the plants had produced flowers.

Hypocotyls were also examined at a very early stage in the growth of bean plants so that the development of rotational streaming in phloem fibers could be studied. Well-defined and continuous rotational streaming was observed in a limited number of immature phloem fibers found in sections of hypocotyls made within 24 hours after bean seeds were planted and before the plants emerged from the soil. The cells in which this early streaming occurred were located adjacent to the endodermis and were arranged longitudinally as a column one or two cells wide. Although greatly elongated in comparison with surrounding cells, they were at this stage of development only about one-fourth the length of mature fibers in older plants. As the plants emerged from the soil and the hypocotyls became erect, many immature phloem fibers were apparent in longitudinal sections. Rotational streaming developed in the

fibers during this period, but at first the movement was intermittent. Within 2 or 3 days, however, cytoplasm in all of the elongated cells streamed at an even rate characteristic of more mature phloem fibers.

The stems of bean plants also developed immature phloem fibers with rotational cytoplasmic streaming at a very early stage in their growth. For example, cells adjacent to the endodermis had elongated and became relatively free of reserve materials by the time the first internode was approximately 1 mm long. Within 2 days of the plants' appearance above the soil surface, elongated immature phloem fibers with pointed ends had developed in the first internodes which were then approximately 2 mm long. At this stage of stem development, the cytoplasm in the elongated cells had assumed a steady rate of rotational streaming typical of that observed in more mature fibers.

The average phloem fiber in the hypocotyl of a relatively mature plant was approximately 2 mm in length—about 200 times the width of the fiber and approximately 25 times the length of the average phloem parenchyma cell in the same plants. An individual plastid was observed continuously for several minutes as it was carried by a longicellular current within a phloem fiber. This plastid traveled 1.84 mm before reaching the pointed end of the cell where it turned and the direction of movement was reversed.

Although emphasis was placed on the study of phloem fibers in stems of bean, rotational streaming was also observed in xylem fibers of this plant. In addition, rotational streaming was observed in cells which appeared to be fibers in stems of young cucumber, tomato, sunflower, and flax. The rate of streaming in all of these cells appeared to be similar to that observed in the phloem fibers of bean plants.

Cross sections through stems of relatively mature bean plants showed an average of about 1400 phloem fibers when counts were made by observing the cut surfaces of these sections. Secondary thickening in the walls of mature phloem fibers might be expected to reduce the volume of cytoplasmic streaming in this type of cell. At flowering, approximately half of these fibers in the lower third of bean stems appeared to be closed sufficiently, due to secondary thickening, to greatly reduce the volume of streaming cytoplasm compared with that which could be found in them at an earlier stage. The remaining fibers did not show enough thickening for the volume of streaming cytoplasm to be appreciably reduced.

Since molecules must enter living phloem fibers, and this is thought to take place partly through pits, counts were made which showed that there were about 280 of these pits in the average mature fiber. The width of the pit canals leading from the inner wall surfaces to the primary walls was approximately 0.7 to 1.0 μ. Pits of this type leading from fiber cells to parenchyma cells, as well as from fiber to fiber, were noted in the stems of bean plants.

In view of the rotational streaming in the form of longicellular currents of cytoplasm described here, it appears that, upon entering a fiber, molecules or other particles would be moved mainly in an upward and downward direction to other points within the fiber where some would be expected to leave the cell. The rate of transport within a cell would depend mainly upon the rate of rotational streaming in the fiber. It should be emphasized that the speed of movement of plastids observed in the longicellular cytoplasmic currents described here was not necessarily indicative of the speed of movement of the molecular or submicroscopic units that composed the longicellular currents themselves.

Evidently, an intracellular transport system develops in immature phloem fibers very early in the growth of the plants. The system appears to be capable of moving substances from one end of the cell to the other at a relatively slow but essentially constant rate. The fact that these elongated fiber cells are generally arranged as closely-packed columns, the cells being interconnected by many pits, suggests the possibility that substances may also move to some extent from cell to cell through these columns.

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References and Notes

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9 June 1964

Reinforcement as Input: Cyclic Variable-Interval Schedule

Abstract. *Daily exposure of pigeons to four cycles of a reinforcement schedule in which the density of reinforcements varied cyclically as a function of time induced a periodicity in their responding matching that of the schedule, but out of phase with it. The technique used of presenting the same sequence of interreinforcement intervals in every session may have useful application in determining animals' adjustment to more complex temporal patterns of reinforcement. Investigation of animals' response to cyclic schedules of different frequencies suggests links with engineering methods of frequency analysis.*

A hungry animal will learn to peck a key or press a lever in order to receive food. Animals will do this even if food (the reinforcer) does not follow every response, but is only made available intermittently. When the rule specifying which response is reinforced depends in some way on time, the procedure is termed a temporal schedule of reinforcement. Such schedules make the reinforcer available at intervals determined solely by the time elapsed since the preceding reinforcement; the simplest temporal schedule is the fixed-interval schedule (FI)—minimum (*I*) interreinforcement interval is fixed from reinforcement to reinforcement. All other temporal schedules—in which time between reinforcements is not fixed but varies in some specified way—are termed variable-interval (VI) schedules. Historically, such schedules (with the interval between reinforcements varying irregularly or randomly) were devised