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IN MEMORIAM

Dr. H.E. Dadswell

The death of Dr. H.E. Dadswell, Chief of the Division of Forest Products of C.S.I.R.O., occured suddenly in Melbourne on December 19th 1964. He is survived by Mrs. Dadswell and two sons. Dr. Dadswell was a former secretary-treasurer of the International Association of Wood Anatomists and was a member of its Council from 1935 until his death. In this capacity he was known to many members who appreciated his wide knowledge and warmth of personality.

Dr. Dadswell was a graduate in Science from Sydney University (1925) and was subsequently awarded the degree of Master of Science of that University from the School of Chemistry, and later for his botanical work was awarded the degree of Doctor of Science in the University of Melbourne. After graduation he spent two years at the Forest Products Research Laboratory of the United States Department of Agriculture in Madison. During this time although he was concerned primarily with work on the chemistry of wood he developed a keen critical interest in its anatomy and the fine structure of its elements. This dual interest in the chemistry and anatomy of wood was to dominate his subsequent outstanding contributions to forest products research. This can now be appreciated from his definitive studies on the anatomy of Australian timbers, his work on the distribution of chemical constituents in the cell wall, and his numerous studies relating the properties of wood to its anatomy, fine structure, and composition. The catholicity of his appreciation of forest products problems

ranging from those of fundamental chemistry and structure, to those involved with the everyday utilization of wood, coupled with his knowledge of wood structure and chemistry, brought considerable prestige to his laboratory.

In view of his many achievements, it appeared a natural step in his career that Dr. Dadswell was appointed Chief of the Division of Forest Products in 1960. It was pleasing to his friends that he was invited to be the Walker Ames visiting professor of forestry at the University of Washington, Seattle in 1955, and was guest lecturer at the special Field Institute in Forest Biology in Carolina State College in 1960.

Within Australia Dr. Dadswell was widely recognised for his work. He was a foundation member in the Australian Pulp and Paper Industry Technical Association and was its President from 1949-1950. He served on the Council of the Royal Australian Chemical Institute from 1943 and was its president in 1961-62, and in 1964 was President of the Botany Section of the Australian and New Zealand Association for Advancement of Science. He attended numerous international conferences where he made many friends and served on the committees of agencies such as F.A.O.

In his own laboratory Dr. Dadswell showed great administrative as well as scientific ability, his friendly and generous personality and his wide knowledge earned the affection and respect of his colleagues. He possessed a special capacity to encourage and gain the confidence and co-operation of young members of his staff. To all who knew him, the recognition of Dr. Dadswell's work during his lifetime is a matter of singular gratification.

A. B. Wardrop

EDITORIAL

Questions concerning the ultrastructure and the growth of the tylosis cell wall.

The interesting contribution of Korán, Z. and Côté, W.A. on the cell wall of tylosis in the last News Bulletin 1964/2 gives raise to the following remarks:

1. The plasmic bud which destroys the pit membrane when penetrating into the vessel seems to be a "naked" protoplast whose plasmalemma creates a cell wall de novo. This is a primary wall with dispersed texture which is continued inside the ray cell where the plasmalemma reverts to synthesizing a primary texture on the secondary wall*. In this respect the bud behaves like a cell plasmolised for a long time which occasionally may form a cell wall. Based on this evidence the formation of the cell wall of pollen tubes which is considered as the extended intine, ought to be reinvestigated.

2. A cluster of tyloses forms a kind of tissue, and it is shown that adjacent cells are separated by a normal set of wall layers i.e. middle lamella, primary wall and secondary wall. Yet this tissue is not the result of mitotic activity but merely a colony of cells which touch or are pressed against one another. Since it can be shown that in dividing cells the middle lamella is the product of Golgi activity, it would be of interest to establish, whether in tylosis wall formation the Golgi apparatus is involved as well or whether the plasmalemma produces the middle lamella by itself. This would be an additional indication of the homology of the Golgi membrane and the cell membrane or plasmalemma.

A. Frey-Wyssling

*Foster, R.C., Fine Structure of Tyloses, Nature 204 (494), 1964

SCIENTIFIC REVIEW

Formation and Development of the Cell Plate

by A. Frey-Wyssling, J.F. López-Sáez and K. Mühlethaler.

In a recent paper (1) the authors of this report show that the cell plate which separates dividing plant cells in the course of the mitosis and subsequently serves as a precursor of the cell wall, originates from Golgi vesicles. Such an origin of the cell plate has been suggested by Whaley and Mollenhauer (2) and demonstrated for the primary wall of root cap cells (3) and root hairs (4) by different authors. Since the electron micrographs obtained from the meristem in the root tips of Phalaris canariensis yield an especially convincing proof that the Golgi is an organelle which synthesizes wall substances, a complete ontogenetic series of the cell plate is reproduced here. Golgi bodies gather at the periphery and inside the phragmoplast. They yield vesicles that are uniformly dark when small (Fig. 1) but show only a black center when they are larger (Fig. 2a inset and 2b). These vesicles are arranged along the equatorial plane of the phragmoplast (Figs. 1 and 2a-c). This requires migration to the equator. Since Golgi vesicles are not capable of active movement, it must be assumed that they are transported by cytoplasmic currents. In fact, during anaphase, cytoplasmic streaming going from the poles to the cell equator has been observed by many workers. As Bajer (5) found by means of cinemicrographic studies, fragments of chromosomes move in the direction of the cell equator. The movement is caused by the

piston action of the half-spindles on the cytoplasm during the anaphasic stretching of the spindle. This movement of cytoplasm in most cases is clearly visible in all anaphasic cells and has been analyzed in detail (6).

The observations are in agreement with those indicated by Ris and Kleinfeld (7), who studied the elimination of chromatin during mitosis in certain insects. At anaphase, basophilic bodies shed by the chromosomes, move toward the equator where they form an "elimination plate". These currents can translocate the Golgi vesicles as well. Probably, the initiation of the cell plate in the central portion of the equatorial plane results from these cytoplasmic currents, which come to a standstill in the "zone of equilibrium" where the currents from both poles counterbalance each other.

The formation of the cell plate occurs by lateral coalescence of the Golgi vesicles along the equatorial plane (Fig. 2c). At certain points along the plane of coalescence, perpendicular strands of the endoplasmic reticulum (ER) prevent this fusion (Figs. 2b and 3a) and provide capillaries for future plasmodesmata (Figs. 4b and c).

The origin of the cell plate from Golgi vesicles can still be perceived after their coalescence. This is because the black centers of the vesicles remain visible even in the fused plate (Fig. 3c and inset). Only after a certain lapse of time is the dark material uniformly distributed in the middle of the cell plate (Fig. 4b).

The peripheral growth of the cell plate is achieved by marginal addition of laterformed vesicles (Fig. 3a). This process continues until the longitudinal wall of the mother cell is reached, where a rim has grown out of that wall (Fig. 3b below). As seen on the opposite wall, this rim originates also by fusion of Golgi vesicles.

There is not only growth in area, but also growth in width, of the cell plate. This occurs by incorporation of supplementary Golgi bodies at the surface of the cell plate. Their fusion with the cell plate is readily visible on the inset of Fig. 4a. The new wall substance added in this way is no longer dark, so that the contrasted central stratum of the plate does not increase in width whereas the adjacent gray strata do (Fig. 4b).

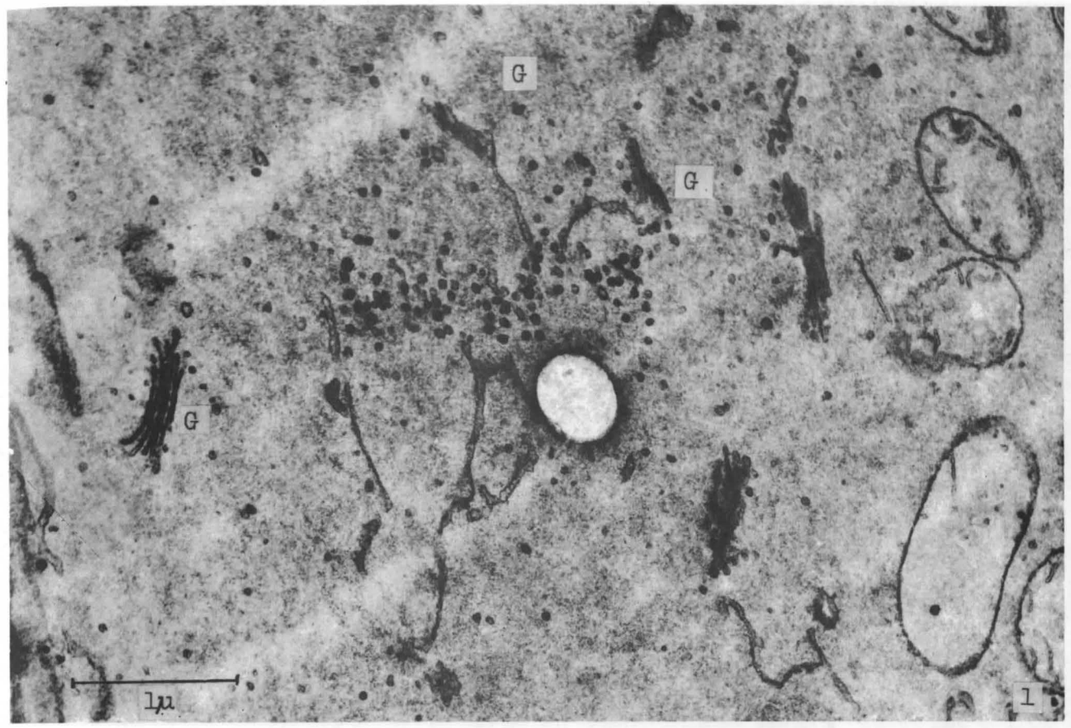
According to classical statements, the cell plate is identical with the middle lamella of the future cell wall (8). However, after the apposition of the primary wall (Fig. 4c) a well-defined middle lamella cannot be delineated in the young cell wall, because the laying down of the material for the primary wall continues by Golgi activity in the same way as the growth in width of the cell plate.

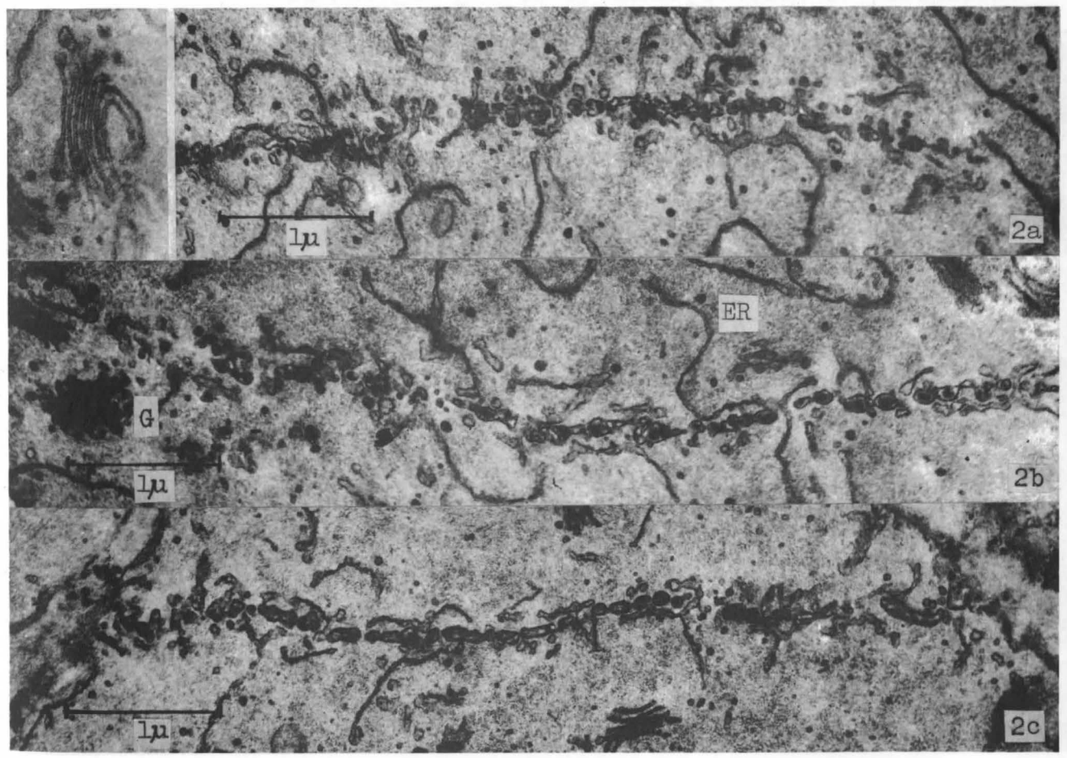
Thus the Golgi vesicles are involved not only in cell plate formation, but in growth of the cell wall as well.

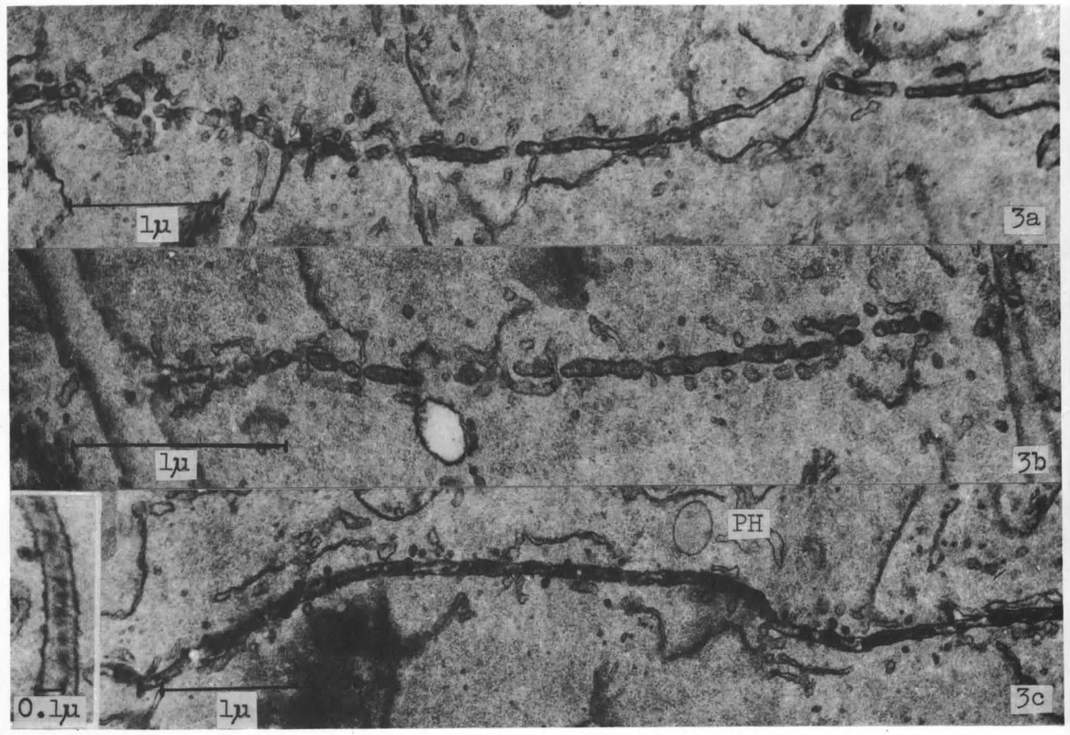
Since the cell plate and the bulk of the primary wall consist of the matrix (9), which is an amorphous mixture of highly hydrated hemicelluloses and uronides (including pectic material), it seems likely that the Golgi vesicles involved

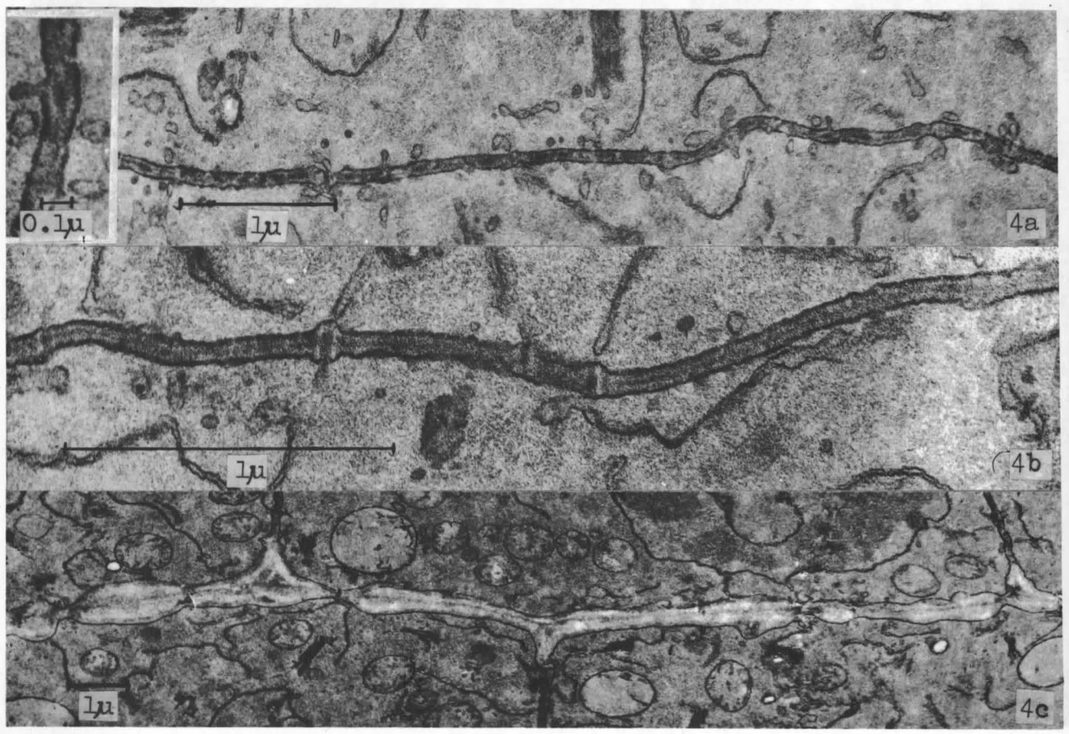
Fig. 1 : Accumulation of Golgi vesicles in the equatorial region. Location of Golgi bodies and mitochondria around Golgi bodies (G) within the phragmoplast x 27,500.

Fig. 2 : (a) Arrangement of Golgi vesicles along the equatorial plane. Inset: Golgi vesicles display an electron dense center. (b) Golgi vesicles with a dark center. The strand of the ER perpendicular to the equatorial plane (arrow) anticipates a future plasmodesma. G Golgi apparatus sectioned tangentially. (c) Beginning fusion of Golgi vesicles x 25,000.









in wall formation may contain soluble oligomeric carbohydrates and uronides as well. After their incorporation into the cell wall, such materials may become high-polymeric, and consequently insoluble in water.

The anionic character of the vesicular content was demonstrated by Becker (10), who performed vital staining with basic dyes, especially cresyl blue. On the basis of the anionic character of the vesicular content, Becker concluded that the vacuoles he had discovered as precursors of the cell plate contained pectic material. Although there seems to be no doubt concerning the identity of Golgi vesicles and the vacuoles described by Becker, some difficulties concerning their size do arise. Vitally stained vacuoles, to be ob-

Fig. 3 : (a) Formation of the cell plate with plasmodesmata in the central part of the equatorial plane (above). Centrifugal growth by incorporation of peripheral Golgi vesicles (below) x 25,000. (b) Contact of the cell plate with the longitudinal walls of the mother cell. Additional Golgi vesicles along the cell plate. x 35,000. (c) The middle lamella of the new cell wall. Its origin by fusion of individual vesicles with an electron dense centre is still visible. PH, phragmosome x 25,000. Inset: Higher magnification (x 40,000) showing the electron dense central stratum of the cell plate.

Fig. 4 : (a) Fusion of lateral Golgi vesicles with the cell wall causing growth in width x 25,000. Inset: Higher magnification (x 50,000) showing surface incorporation of vesicles. (b) The middle lamella of the new cell wall covered by the plasmalemma with the ultrastructure of a unit membrane. Plasmodesmata correlated to the ER x 40,000. (c) The new cell wall with the electron dense middle lamella and clear primary walls deposited on either side by rather irregular apposition x 10,000.

servable in the light microscope, must have a diameter of the order of 0.3 µ. Our Golgi vesicles, however, are only 0.1 µ in diameter, i.e. they are below the resolution of the light microscope. Thus, the vesicles investigated by Becker (staminal hairs of Tradescantia) must have been either larger Golgi vesicles or the first stages of coalescence and fusion as shown in Fig. 3b.

Another puzzling question is why in many cases only the center of the Golgi vesicles stains with manganese. It could be that only the central part of the vesicles has anionic properties, while the periphery contains neutral carbohydrates.

The most important cytological consequence resulting from the described ontogeny of the cell plate is the fate of the vesicular membrane. This membrane is part of the Golgi system and constitutes a unit membrane. When neighbouring vesicles coalesce, their membranes fuse as well. In this way the growing cell plate is coated by a Golgi membrane. This is also true for the capillaries of the plasmodesmata. Later, this Golgi membrane forms the surface film of the adjacent cytoplasm; therefore, it represents the cell membrane, or plasmalemma, with its three narrow strata, satisfies the requirements of a unit membrane. On the basis of our results, we conclude that Golgi membranes and plasmalemma are ontogenetically interrelated.

Further addition of wall material to the full-grown cell plate leads to the deposition of the primary wall. This deposition occurs in an irregular manner, so that the entire surface of the growing wall is sinuous (Fig. 4c) in addition to local constrictions caused by the formation of plasmodesmata. The fast incorporation of wall substances may cause an astonishingly irregular boundary between cytoplasm and cell wall (11). We believe that the observed mechanism of

local addition of semifluid viscous material stored in vesicles to the wall produces only the amorphous ground mass that is called the matrix. A more complicated process underlies mechanical strengthening of the wall (12). Formation of cellulosic elementary fibrils is involved in this strengthening process (13). As shown by Moor and Mühlethaler (12) the elementary fibrils of the primary wall are produced by special surface areas of the plasmalemma. Thus the plastic matrix of the cell wall and its strengthening fibrillar system are of different origin. But since the Golgi membranes and the plasmalemma seem to be homologous surface films, this difference is more of a morphological than of a fundamental kind.

Conclusion

The Golgi vesicles is shown to be an organelle capable of synthesizing alloplasmatic substances that can serve as precursors for cell wall matrix and plant mucilages. The Golgi vesicles which hold these substances possess a euplasmatic unit membrane capable of differentiating into a plasmalemma with its manifold physiological functions. The Golgi bodies do not produce their vesicles at the equatorial plane nor in direct contact with the emerging cell plate. Instead, the vesicles are translocated a certain distance from the emerging cell plate and aligned in a position suitable for growth in harmony. Such positioning occurs by as yet unknown morphogenetic forces harbored in the dense ground plasm of the phragmoplast.

The elementary fibrils which coalesce laterally to forming the microfibrils of the strengthening system in the cell wall, are synthesized by special surface areas of the plasmalemma.

As a consequence the two components of a meristematic cell wall, the matrix and the microfibrils are of different origine. But, as the plasmalemma and the Golgi-membranes are homologous, both components are derived from ontogenetically related organelles.

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