In all cells, including plant cells, lipids must move from their main site of synthesis, the endoplasmic reticulum (ER), to subcellular membranes such as chloroplast and mitochondrial membranes. A set of cytoplasmic proteins called lipid transfer proteins, or LTPs, have been proposed to carry out the task of transferring lipids within the cell (Wirtz, 1991). Proteins with lipid transfer activity in vitro have been purified from bacteria, fungi, plants, and mammals. In mammals, several classes of lipid transfer proteins, including phosphatidylcholine transfer proteins, phosphatidylinositol transfer proteins (PI-TPs), and nonspecific lipid transfer proteins (nsLTPs), have been detected. However, only nsLTPs have been detected to date in plants (Arondel and Kader, 1990). Plant nsLTPs have been identified in both monocots and dicots, including barley, castor bean, maize, and spinach. The plant proteins share high sequence homology, but they are very different from mammalian nsLTPs. Plant and mammalian nsLTPs do share some general characteristics: nsLTPs from both sources are small (9 to 14 kD) and basic (pl of 9 or so).

The hypothesis that plant nsLTPs are located in the cytoplasm, where they shuttle lipids from organelle to organelle, was confounded by the discovery that they are synthesized as precursor proteins with amino-terminal signal sequences and are therefore likely to be secreted proteins (Tchang et al., 1988; Bernhard et al., 1991). The sequences also lack the consensus carboxy-terminal KDEL sequence that would allow the protein to be retained in the ER. If plant nsLTPs are secreted to an extracytoplasmic compartment within the cell or to the extracellular milieu, then despite their demonstrated ability to transfer lipids among vesicles in vitro, perhaps plant nsLTPs carry out some other function in vivo.

Plants are not the only organisms for which it has been difficult to assign a physiological function to LTPs. In fact, only in yeast has the in vitro function of an LTP been correlated with a function in vivo. This correlation came with the recent demonstration that the yeast SEC14 gene encodes PI-TP (Banksaitis et al., 1990). The SEC14 gene is required for the transport of secretory proteins through the Golgi complex, and the current hypothesis is that PI-TP maintains the proper ratio of phosphatidylinositol to phosphatidylcholine in the Golgi (Cleves et al., 1991b). If this ratio is disrupted, the Golgi cannot function. The discovery that the SEC14 protein and PI-TP are one and the same has led to the conclusion that yeast PI-TP activity is restricted to the Golgi. Contrary to expectation, PI-TP, in yeast at least, does not control bulk phosphatidylinositol flow in vivo (Cleves et al., 1991a).

Although functional analysis of plant LTPs is in its infancy, indications are that as with yeast PI-TP, plant nsLTPs will have more restricted functions in vivo than their in vitro properties had led people to believe. In this issue, two groups describe the distribution of plant nsLTP mRNAs and proteins. On pages 907-921, Sterk and coworkers report the cellular localization of carrot nsLTP, and on pages 923-933, Sossountzov and coworkers report the accumulation pattern of maize nsLTP. The bottom line from both studies is that in each of these plants, nsLTP mRNA and protein accumulate in a limited set of cells and tissues, principally epidermis.

The carrot nsLTP turned up in a screen for proteins secreted by embryogenic carrot cells in culture. Like cells from many plants, carrot cells can be readily induced to undergo somatic embryogenesis. The development of somatic embryos resembles that of their zygotic counterparts, and information obtained from the biochemically more accessible process of somatic embryogenesis should be useful in understanding zygotic embryogenesis. When somatic cells are induced to undergo embryogenesis, they secrete several proteins into the medium that are not found in the medium of non-embryogenic cells (De Vries et al., 1988). To isolate the genes for these proteins, Sterk and coworkers screened an expression library with antibodies against total proteins present in the medium of somatic embryogenic cells. Sequence similarity, biological activity, and immunoreactivity with an antibody to maize LTP indicates that one of the clones encodes carrot nsLTP.

Using antibodies to a purified carrot nsLTP fusion protein, Sterk and coworkers confirm that somatic embryos secrete this protein. Some protein is found in the outer cell walls of somatic embryos as well, but the cytosol is apparently devoid of nsLTP. In situ hybridization studies show that the nsLTP mRNA is localized to the protoderm cell layer of globular embryos of both somatic and zygotic origin, making it one of the earliest molecular markers for embryonic differentiation yet identified. The mRNA also accumulates in the suspensor of zygotic embryos, as well as in the integument, which will form the seed coat. In seed-
lings, nsLTP mRNA is restricted to the shoot apex, and in plantlets, it appears transiently in epidermal cells of leaf primordia and early floral organs.

Sossountzov and coworkers have found that the maize nsLTP gene is expressed in a pattern similar to that of the carrot gene. The mRNA is present in both embryos and endosperm, reaching maximal levels midway through seed maturation; it accumulates in the epidermis of both the coleoptile and the scutellum. After seeds have germinated, the mRNA continues to be present in the coleoptile epidermis. It is also detectable in the mesocotyl and the scutellum but is absent from roots. Immunolocalization studies in seedlings indicate that the protein is associated with cells in the outer epidermis of the coleoptile.

What function can be inferred from the restricted distribution of the nsLTP mRNAs, and why is the carrot protein secreted into the medium of somatic embryos? Because expression is largely limited to epidermal cells of developing aerial parts of the plant, Sterk and coworkers suggest that nsLTP may be involved in cuticle formation. They speculate that in somatic embryos nsLTP molecules facilitate the transport of cutin monomers to the outer side of the cell wall and are then released into the medium. Sossountzov and coworkers hypothesize that during maize seed maturation, LTP might be involved in the formation of triacylglycerol storage lipids in the scutellum. They also raise the possibility that high levels of LTP are required to cope with the heavy demand for new membrane synthesis during mid-embryogenesis.

Although much remains to be learned about the physiological functions of plant LTPs, the fact that they are synthesized as signal sequence-containing precursors, together with their absence from many plant tissues (in particular, roots, which lack nsLTP activity) implies that they do not play a general role in bulk lipid transfer within cells. However, although carrot nsLTP appears to be encoded by a single-copy gene, maize may contain several nsLTP genes (Tchang et al., 1988) and it is possible that in both plants additional nsLTP isozymes are expressed in other cells and tissues. In addition to establishing whether, and where, additional isozymes are expressed, it will be essential to determine the subcellular localization of the nsLTPs. Are they associated with particular compartments within cells, or are they secreted to extracellular spaces? The evidence of Sossountzov and coworkers suggests that in maize, at least, LTP may reside within cells.

To assess the true in vivo functions of nsLTPs, it may be necessary to prevent them from functioning in the cells that normally express them, possibly with antisense RNA. It may also be possible to screen for mutant plants that lack nsLTP activity, so long as the loss of nsLTP activity is not lethal to embryos. Similar screens in Arabidopsis (Somerville and Browse, 1991) have yielded mutants in several lipid biosynthetic pathways. Whatever method is used to eliminate nsLTPs in vivo, the resulting phenotype may, as it did so dramatically in the case of yeast PI-TP, give clues to the roles these proteins play in plants.

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REFERENCES


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