This Week's Citation Classic

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Park R B & Sane P V. Distribution of function and structure in chloroplast lamellae. *Annu. Rev. Plant Physiol.* **22**:395-430, 1971. [Dept. Botany, Univ. California, Berkeley, CA]

The model for chloroplast membrane structure proposed by Sane, Goodchild, and Park is reviewed. One large membrane is folded into stacked and unstacked interconnecting regions. While photosystem I and small freeze fracture particles exist in both regions, photosystem II and large particles are restricted to the stacked regions. [The *SCI*® indicates that this paper has been cited over 115 times since 1971.]

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"This work was the outgrowth of the experiments performed by P.V. Sane, D.J. Goodchild, and myself in 1969 and 1970.[1] I was on a Miller research professorship at the time and had my first opportunity in 10 years to devote full time to photosynthetic experiments. Berkeley in 1969-70 was something of a battleground and we retreated to the basement of the Life Sciences Building, aware of the outside world primarily through traces of tear gas that entered the ventilation system and occasional student marches down the halls.

"Despite these outside disturbances, we discovered some unique facts about the organization of the internal membranes of higher plant chloroplasts. We found that the shear gradient technique developed at the Carnegie Laboratory at Palo Alto for separating the membranes of fractions with different chlorophyll a/b ratios was actually separating stroma (unstacked) lamellae from grana (stacked) lamellae. This conclusion first became tenable when we noted that the rapidly sedimentary membrane fraction contained grana stacks of low chlorophyll a/b ratios, no longer connected by stroma lamellae, and the slowly sedimentary membrane fraction contained vesicles of high chlorophyll a/b ratio and was thus a candidate for the missing interconnecting stroma lamellae.

"The key observation which convinced us that the small vesicles were actually derived from stroma lamellae came from freeze-fracture observations. We noted for the first time in intact chloroplasts that the fracture planes of grana contained two sizes of fracture particles whereas the stroma lamellae contained only small particles. When we discovered that the slowly sedimenting vesicles also only contained small particles we knew we were on the right track. Ultimately we demonstrated that the grana lamellae were enriched in chlorophyll b, contained photosystem I and II, and both large and small freeze fractured particles, while the stroma lamellae were enriched in chlorophyll a and demonstrated primarily photosystem I activity.

"The review cited here related this work and its implications to other physiological and structural observations and proposed a model which could be tested. The form of the review was inspired by the lessons I had learned as an associate editor of the *Annual Review of Plant Physiology* at the knee of then Editor Leonard Machlis. Reviews only summarizing bibliographies were always boring and never very useful. It was reviews which brought about a synthesis of existing ideas and pointed the way toward future research that pleased us as editors. In retrospect, I believe this review is among the most cited items in its field because it did exactly that: synthesized from existing knowledge a path toward future research in the field."

1. Sane P V, Goodchild D J & Park R B. Characterization of chloroplast photosystems I and II separated by a non-detergent method. *Biochim. Biophys. Acta* **216**:162-78, 1970.