SULPHOQUINOVOSYL DIACYLGLYCEROL (SQDG) - THE SULPHOLIPID OF HIGHER PLANTS

Abstract: Plant sulpholipid, sulphoquinovosyl diacylglycerol (SQDG), has been found in all photosynthetic plants. It appears to be concentrated mainly in the chloroplasts of plants. Higher plant chloroplasts are completely autonomous for the SQDG synthesis. Concerning the pathway for the head group synthesis it was suggested that sulphoquinovose could be formed from a compound related to UDP-6-deoxy-4-ketoglucose which is an intermediate in L-rhamnose synthesis. The final intermediate in the pathway is UDP-sulphoquinovose which is used by the enzyme catalyzing the final stage of SQDG formation. The generally accepted view is that SQDG is hardly metabolized by higher plants apart from initial hydrolysis by acyl hydrolases and glycosidases, and it is considered widely that liberation of sulphate from sulphoquinovose is due to microbial activity. SQDG is associated with purified chloroplast CF0-CF1 ATPase and, like MGDG, plays a more specific and intimate role in the catalytic activity of proteins. Two SQDG molecules with predominant palmitic acid were found in the association of the LHC 11-apoproteins. Bound SQDG molecules are localized as prosthetic groups at the surface of native D1/D2 heterodimer, holding the dimmer together. But a SQDG-deficient mutants showed the same growth rates under optimal phototrophic growth conditions as the wild type, suggesting that SQDG was not essential for oxygenic photosynthesis. The results of studies, devoted to lipid involvement in adaptation processes, showed that both SQDG quantitative changes and fatty acid composition shifts take place. Besides, SQDG accumulation was observed in wheat plants infected by Puccinia graminis and kidney bean plants infected by tobacco mosaic and potato x viruses.

1. INTRODUCTION

Plants, algae, cyanobacteria and some photosynthetic bacteria contain a unique sulpholipid discovered and studied by Benson et al. (1963). Three products resulted from hydrolysis of this sulpholipid are glycerol, a sulphur-containing C6 compound and two fatty acids. The sulphosugar was identified as a sulphonic acid by its resistance to acid hydrolysis, and the hexose thought to be galactose with a β-linkage because the deacylated sulpholipid was hydrolysed by β-galactosidase. But it was found later, in fact, that all the major glycolipids occurring in plants (the sulpholipid and two β-D-galactosyl diacylglycerols) possess a linkage which may be cleaved by β-galactosidase and the hexose itself was identified as sulphoquinovose (Shibuya and Benson, 1961). Finally, the sulpholipid structure was defined as 1,2-di-O-acyl-3-O-(6-deoxy-6-sulpho-α-D-glucopyranosyl)-sn-glycerol (SQDG) (Fig. 1). The distinctive feature of this substance is carbon bonded directly to sulphur as C—SO3. Sulphonic acids of this type are chemically stable and strong acids over a wide pH range (Barber and Gounaris, 1986). The deacylation products of sulpholipid, sulphoquinovosyl glycerol, occur in plants at variable concentrations, but little or no sulphoquinovose has been found in plant extracts. SQDG is the most concentrated anionic sugar derivative in plants under most conditions.
Plant sulpholipid has been found in all plants, algae, cyanobacteria, purple sulphur and non-sulphur bacteria (Barber and Gounaris, 1986). Early studies suggested that it was a typical chloroplast constituent in eukaryotes e.g. green alga *Chlamydomonas reinhardtii* about 70% of SQDG localised in the thylakoids (Janero and Barrnett, 1981). Brown algae tend to have rather high levels of the compound, which represents 30% of the total lipids in *Hizikia fusiformis* (Fucales) (Harwood, 1998). The betaine lipid and the glycolipids – monogalactosyldiacylglycerol (MGDG), digalactosyldiacylglycerol (DGDG) and SQDG were major components in the marine brown alga *Dictyopteris membranacea*. MGDG, DGDG and SQDG are the major polar lipids in *Ectocarpus fasciculatus* (Ectocarpales, Phaeophyceae) also. The positional distribution of fatty acids in *Ectocarpus* showed that molecular species of “eukaryotic structure” accounted for 99% in MGDG, 98% in DGDG, 62% in PG but only 23% in SQDG. Thus, in the latter, labelled fatty acids were found in prokaryotic as well as in eukaryotic molecular species (Makewicz et al., 1997). This means, of course, that in the former species the diacylglycerol backbone of the SQDG originates predominately from acylation reactions within the chloroplast (Browse and Somerville, 1991). SQDG has also been reported in non-photosynthetic bacteria (e.g. *Rhizobium meliloti* (Cedergreen and Hollingsworth, 1994), in non-photosynthetic root nodule-forming bacteria (e.g. *Sinorhizobium meliloti*) (Weissenmayer et al., 2000) and in non-photosynthetic diatoms (e.g. *Navicula alba*) (Harwood and Jones, 1989).

In some lichens, the SQDG content is nearly one third of the total glycolipids, and sometimes surpasses the MGDG content (e.g. by two-fold in *Trebuoxia impressa*) and the DGDG (*Trebuoxia erici*) levels (Bychek-Gushchina, 1997). Two sulpholipids, SQDG and SQMG (sulphoquinovosyl monoacylglycerol) containing mainly palmitic (= 90%) and stearic (3-11%) acid residues with small amounts of heptadecanoic, oleic, arachidonic, unsocusanoic and lignoceric acyl residues have been isolated from the basidiolichen *Dictyonema glabratum* (Sassaki et al., 2001). In addition, a number of unusual sulphur-containing lipids have been detected in algae (Haines, 1973; Harwood and Jones, 1989; Kaya et al., 1993), but none of the other sulphur-containing lipids are quantitatively significant when compared to SQDG in mature (Heinz, 1993).