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A dynamin-like protein FZL shapes thylakoid membranes and maintains their integrity against enhanced proton motive force

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A dynamin-like protein FZL is one of the few known thylakoid remodeling proteins and has been demonstrated to mediate thylakoid membrane fusion. However, its physiological functions have not been characterized well. First, to determine the sub-chloroplast localization of FZL, we sub-fractionated isolated chloroplasts/thylakoids and observed GFP-fused proteins, showing that FZL is enriched on curved grana edges. fzl knockout mutants displayed disorganized thylakoid morphologies; grana stacking was staggered, and the grana-stroma lamellae interconnection was scarce compared with that of wild type. Overall, we hypothesize that FZL fuses grana and stroma lamellae membranes at grana edges to shape the network-like thylakoids and that the lack of the FZL-mediated interconnections leads to the morphological disorder observed in the mutants. The thylakoid disturbance moderately altered the electron transfer but hardly affected the plant growth. However, in a series of double mutant analysis, we discovered that the fzl mutant plants were dwarfed when crossed with bfa1 and bfa3 mutants where chloroplast ATP synthase accumulation levels are reduced to 12.5 and 25 % of the WT levels, respectively. In particular, fzl bfa1 mutant exhibited swollen and damaged thylakoid membranes and dropped photosynthetic performance along with diminished photosystem accumulation. The declines in ATP synthase levels likely led to energy deficiency and incremented proton motive force (pmf) in thylakoid lumen; which factor so strongly enhanced the fzl phenotypes? To answer this question, we further crossed the fzl bfa1 double mutant with pgr1 and npq4 mutants and examined the effects of the additional mutations on the fzl bfa1 phenotypes. The former mutation is expected to restrict both energy production and pmf formation, and the latter vice versa. pgr1 suppressed the thylakoid collapse but enhanced the dwarfism, while npq4 recovered the plant growth without inhibiting the thylakoid swelling. This data suggests that the elevated pmf mainly led to the thylakoid explosion in the fzl mutant background, and we propose the novel function of FZL in protecting thylakoid membranes against high pmf. We discuss how one protein shapes and protects thylakoid membranes at the same time and also how membrane integrity is important to sustain the membrane proteins which are successfully translated.

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