The role of guard cell photosynthesis in biotic stress-induced stomatal closure

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Guard cells (GCs) control gas exchange and transpirational water loss of leaves by turgor-driven volume changes. Environmental and hormonal signals regulate opening and closure by activating diverse signalling networks and membrane transporters. GCs also respond to the presence of microbes following perception of microbe-associated molecular patterns, such as a fungal elicitor chitosan (CHT). It has been shown that CHT inhibits the blue light-induced stomatal opening and can trigger stomatal closure through distinct signaling pathways and transporters. Stomatal opening and closure is related to the H⁺-ATPase activity in the GC plasma membrane, as it affects the transport of osmotically active solutes. ATP for proton pumping is partly supplied from photophosphorylation in Vicia faba GCs (Mawson 1993). In order to investigate whether CHT affects the photosynthetic ATP production, the light-dependence of the photosynthetic electron transport rate of individual GCs was assayed. We found that when CHT was applied before sunrise, the apparent relative linear electron transport rate (ETR) remained low contrary to control. However, when CHT was sprayed on leaves by day, it only induced slight stomatal closure without a significant change of these photosynthetic parameters. CHT was shown to induce the generation of both reactive oxygen and nitrogen species in pea GCs (Srivastava et al. 2009). Using fluorescent probes we found that one hour of CHT treatment led to a significant increase in both hydrogen peroxide (H₂O₂) and nitric oxide (NO) levels of Vicia GC chloroplasts. H₂O₂ accumulated mainly in chloroplast stroma and nucleus, while NO was found in the cytosol and chloroplasts. We also found that the inhibitory effect of CHT on the morning photosynthesis can be mimicked by exogenously applied NO, therefore it can be hypothesized that CHT acts through the NO signaling pathway.

NO triggers the release of Ca²⁺ from intracellular stores in GCs, which leads to stomatal closure. NO may also have an indirect effect through the decrease of intracellular ATP level generated by GC chloroplasts. Earlier we showed that NO slows down electron transfer between Q₁ and Q₀, and inhibits charge recombination reactions of Q₁ with the S₁ state of the water-oxidizing complex in pea leaves (Wodala et al. 2008). The microcopy version of a pulse-amplitude-modulated chlorophyll fluorometer (PAM) combined with a rapid solution exchanger allowed us to monitor the photosynthetic activity of a GC before and after the addition and also rapid removal of NO. The concentration of NO released from GSNO under light was measured in a solution entering the recording chamber using a NO-electrode. We found that NO decreases the electron transport rate resulting in a modest acidification of the thylakoid lumen and conceivably a reduced ATP synthesis. Variable fluorescence yield (Fv) was increased immediately in a biphasic manner after the inflow of the NO-containing solution, in line with the kinetic differences in the changes of photochemical and non-photochemical quenching. The wash-out of NO resulted in a sudden decrease of Fv, which was further accelerated by bicarbonate, a competitor of NO to the binding side of the non-heme iron between Q₁ and Q₀.


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