RUBISCO ACTIVITY MAINTENACE IN ENVIRONMENTAL STRESS CONDITIONS – HOW MANY STRATEGIES ?

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Rubisco (ribulose-*1,5*-bisphosphate carboxylase-oxygenase) is a crucial enzyme of the Calvin cycle. In one catalytic site it catalyses two different reactions – carboxylation of ribulose bisphosphate or its oxygenation. Moreover, Rubisco has different affinity for the CO_2 and O_2, but it results in competition between Calvin cycle and photorespiration among C_3 plants. In physiological conditions, Rubisco is supported by two accompanying enzymes – Rubisco activase (RCA) and carbonic anhydrase (CA). RCA is acting as Rubisco molecular chaperone, controlling the correct assembly of subunits into active complex and proper conformation of the active center, as well as removing blocking sugars and binding the correct substrate. RCA is an ATP-dependent enzyme. CA is a Zn-containing enzyme catalyzing reversible CO_2 hydration and HCO_3^- dehydration and does not require ATP. In chloroplasts, CA is donating gaseous CO_2, necessary both for activation of Rubisco active centers, as well as for carboxylation of RuBP. CA activity promotes carboxylation process, whilst RCA – responsible for activation of Rubisco active sites – seems to be necessary both in carboxylation, as well as in oxygenation of RuBP. Under physiological conditions only about 60-70% of Rubisco active centers are active. This value is called Rubisco activation state (RAS) and can be modified in stress conditions.
Relationships between these three enzymes have not been fully elucidated yet. However, it is worth to pay attention to roles of RCA and CA in regulation of Rubisco activity in environmental stress conditions.
Rubisco seems to be a main target of many stresses. At high light, high CO_2, ozone, drought, high temperature or heavy metal influence decrease in Rubisco activity was one of their main effects, but the mechanisms of Rubisco inactivation were different, depending on individual stress:

- at high CO_2 a down regulation of Rubisco results from decrease in RAS since RCA is not able to cope with faster catalysis, thus faster deactivation of active centers;
- at high light a feedback inhibition from carbohydrates is the main limiting factor of Rubisco activity;
- at ozone stress decrease in Rubisco content due to accelerated senescence was reported
- at high temperature RCA is a limiting factor in regulation of Rubisco activity due to decreased ATP synthesis in chloroplasts and increase in RCA-inhibitory ADP;
- at drought stress CO_2 limitation due to stomatal closure and blocking of Rubisco active centers by 5C sugars was observed;

- at heavy metal stress substitution by heavy metal ion the Mg^{2+} in the active center or Rubisco subunits release were reported.

Inhibition of Rubisco activity has great impact on the whole photosynthesis. Decrease in carboxylation results in depleted functioning of the Calvin cycle. This can cause accumulation of ATP and reduced NADP, thus a feedback inhibition of photosynthetic electron transport, increase in thylakoidal proton gradient and damage to photosystem II.

To maintain or restore Rubisco activity C_3 plants have developed complicated mechanisms, involving activity of RCA and CA. According to the present knowledge four different mechanism could be proposed:

- increase in CA activity, resulting in more efficient supply of gaseous CO_2 for Rubisco activation and for carboxylation. This mechanism does not need any additional energy consumption and was shown to operate at drought stress, high light, high temperature and moderate Cd stresses;
- shift of Rubisco activity from carboxylation to oxygenation. This mechanism results in higher utilization of ATP and reduced NADP and was observed for ozone stress and heavy metals such as: Mn, Co and Cu;
- increase in RAS resulting from activity of RCA. This mechanism is consuming high amounts of ATP and was reported for high temperature, moderate Cu and severe Cd stresses;
- increase in Rubisco synthesis. This mechanism is consuming ATP and has low efficiency in terms of Rubisco activity maintenance or restoring. It was reported for ozone stress in a young leaves and for severe Cu stress.

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