isms [33]. They contain the CK2 regulatory subunit signature (C-P-X_3-C-X_{22}–CPXC), a cysteine-rich motif involved in the zinc-finger structure. The characteristic acidic stretch is also present in plants CK2β and, even though its amino acid sequence is not identical to the other CK2β subunits, the acidic residues that have been demonstrated as essentials by site-directed mutagenesis [34] are conserved. Adjacent to the acidic domain is located a region of 9 amino acids, previously reported in other CK2β regulatory subunits [35], that is described as a potential 'destruction box'; however, the functionality of this domain has been not demonstrated in plants.

It has been described that in animals, CK2 should be regulated by $p34^{cdc2}$ phosphorylation. However, the consensus site present in the C-terminal region in human CK2β, which is phosphorylated by $p34^{cdc2}$ [36] is not present in plant CK2β, suggesting a different regulation by phosphorylation of the plant enzyme. Moreover, in addition to the conserved autophosphorylation site described in other organisms, Arabidopsis and maize CK2β contain additional putative CK2 phosphorylation sites (according to the S/T-XX-D/E CK2 consensus), most of them also located in the NH_2-terminal region. The functional significance of autophosphorylation is not well understood but it is suspected to be involved in tuning of the kinase activity [37]. Due to this high number of autophosphorylation sites in plant CK2, it will be interesting to further investigate relevance of CK2β autophosphorylation.

To summarize, previous data in Arabidopsis [38] and our work in maize [13] indicate that plant CK2β subunits are able to interact with the other CK2α and CK2β subunits, allowing the formation of the typical heterotetrameric structure described in all the other organisms examined to date. However, in maize we have detected preferential interactions between α/β isoforms and β/β isoforms, suggesting that a high level of heterogeneity for the CK2β isoforms does exist in plants.

Discussion

Physiological role of CK2 in plants

The plant CK2 has a pleiotropic effect in the cells and is involved in many different processes most of them essentials for plant viability as summarized in Fig. 3. In animals, it has been reported that the protein kinase CK2 is able to phosphorylate more than 160 substrates [39], however a lower number of *in vitro* substrates of CK2 has been described in plants (see Table 1).

It has been clearly demonstrated that plant CK2 is involved in the regulation of the light-signal transduction pathway,

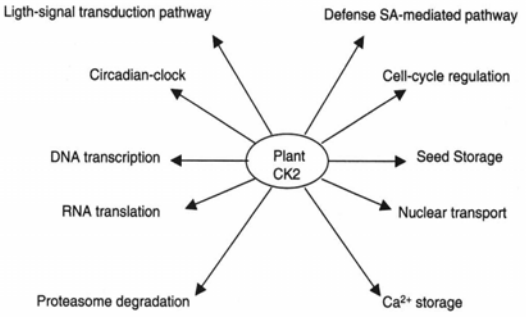

Fig. 3. Schematic representation of the physiological roles of protein kinase CK2 in plants.

through the phosphorylation of several transcription factors. Recently, studies on CK2α antisense Arabidopsis plants confirmed the role of CK2 is in the light-regulated gene expression and plant growth [14]. The CK2 enzyme phosphorylates and therefore affects the DNA binding activity of several transcription factors that bind to elements such as G-box or AT-rich regions which are located in the promoter regions of many light regulated genes. For instance, the GBF factor increases its DNA binding activity to G-box elements when it is phosphorylated by CK2 [6], on the contrary, phosphorylation by CK2 of transcription factors AT-1 [40] and ATBP-1 [41] seems to inhibit their binding to the AT rich regions. The circadian clock-associated (CCA1) and the late elongated hypocotyl (LHY) proteins are two Myb-related transcription factors essentials for the regulation of the circadian rhythms. CK2 is able to interact and phosphorylate both of them affecting their DNA binding activity [11, 42]. In animals, the myb proteins are also regulated by CK2 phosphorylation [43]. Moreover, transgenic plants overexpressing a CK2β subunit (CK2B3) display increased CK2 activity and shorter periods of rhythmic expression of CCA1 and LHY, demonstrating that CK2 is involved in the regulation of circadian rhythms in Arabidopsis [42]. It has been reported recently that the Arabidopsis bZIP transcription factor HY5, which has a role in the promotion of the photomorphogenesis or light-adapted development, is another target of CK2: unphosphorylated HY5 binds DNA of its target promoters, like the G-box in RBCS1a or CHS1 genes stronger than the phosphorylated form [44]. In this case the kinase activity is regulated by light, since a higher number of phosphorylated forms are present in dark conditions, and the CK2 phosphorylation prevents the protein degradation by the proteasome 26A. The authors postulate that this higher activity in darkness might reflect the effect of a specific CK2β regulatory subunit on HY5.

Also the maize bZIP transcription factor the Opaque 2 (O2) is likely to be regulated by CK2 phosphorylation, the phosphorylated forms, which are accumulated in the darkness,