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Minireview

The response of plant NAD$^+$ kinase to abiotic stresses

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NAD$^+$ kinase (ATP:NAD 2′-phosphotransferase, EC 2.7.1.23) is the only known enzyme which catalyses formation of NADP$^+$ from NAD$^+$ and ATP [1]. Thus NAD$^+$ kinase activity would be expected to have a profound influence on cell metabolism, since these two nucleotides have been shown to be not only cofactors of many dehydrogenases but also to play a role of positive and negative modulators of a variety of metabolic enzymes [2]. The maintenance of functional integrity in plants facing adverse environmental conditions requires physiological and biochemical adjustment. Regardless of the mechanisms of stress resistance, the adaptation process to stress conditions imposes an energetic cost to plants [3 - 7]. Following Atkinson's hypothesis [8, 9] on metabolism control by coordination of enzyme activities through general modifiers like adenylate energy charge AEC = (ATP + 0.5 ADP)/(ATP + + ADP + AMP), Quebedeaux [10] defined the redox charge [RC = NAD(P)H/NADP(H) + +NAD(H)] in a similar way. The values of these ratios are important measures of the cellular energy status: deviations from the standard values are considered to be sensitive indicators of the stress-induced metabolic disturbances [11 - 13]. High availability of reduced pyridine nucleotides [14, 15] and ATP [16] as "driving forces" for adaptation to unfavorable conditions has been postulated. This supposition points to involvement of NAD$^+$ kinase in plant response to different stress conditions.

Over the last few years, phosphorylation of NAD$^+$ to NADP$^+$ by NAD$^+$ kinase has received much attention mainly in relation to the control of metabolism by calcium ions and calmodulin (CaM)[1] [17 - 21]. Although an enormous amount of information is available on Ca^{2+}-calmodulin mediated processes in plant growth and development, including adverse environmental conditions [2, 22 - 27], according to our knowledge no attempts have been made to study the involvement of NAD$^+$ kinase and its dependence on calmodulin in the regulation of the metabolism under stress conditions.

The aim of the present review is to outline the changes in NAD$^+$ kinase activity occurring in different plant tissues subjected to stress conditions. We postulate that this enzyme is essential for plant defense against various stresses. The basic framework for understanding the role of NAD$^+$ kinase in regulation of plant metabolism under stress conditions consists in comparison of NAD$^+$ kinase response in plants of differing adaptive abilities, i.e. genetically determined physiological traits expressed under environmental constraints.

The comparative studies included:

–i. NAD$^+$ kinase response to aluminium ions in the root apical meristems of several cereal species (monocotyledons), differing in Al

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[1] Abbreviation: CaM - calmodulin

tolerance in the decreasing order: oat > rye > triticale > wheat > barley, as well as in two legume cultivars (dicotyledons): lupin (Al tolerant) and pea (Al sensitive) [28, 29];
- ii. NAD$^+$ kinase in leaf tissues of wheat subjected to water stress [30], and
- iii. NAD$^+$ kinase in winter rape leaf exposed to low temperature [31] – both these species are able to harden, i. e. to increase their resistance to specific stress factors (acclimation).

Plant NAD$^+$ kinase

NAD$^+$ kinase is ubiquitous in the plant kingdom. It occurs in photosynthetic tissues of higher plants: pea [25, 32 - 37], zucchini [38], spinach [39, 40], corn [41], wheat [21, 30], rape [31] as well as in photosynthetic tissues of *Lemna gibba* [42]. Its activity was also demonstrated in non-photosynthetic tissues of corn [43], pea [29, 44], lupin [29], wheat, rye, oat, barley and triticale [28, 29], fungi [17], and etiolated seedlings [21, 36, 45]. There are at least two isoforms of NAD$^+$ kinase: one of them, regulated by calmodulin, is a low molecular heat stable Ca^{2+}-dependent protein; the other is completely independent of either calmodulin or calcium [21, 25, 44].

In green tissues the enzyme is located in the chloroplasts (64 - 97%), cytoplasm (2.7 - 35%) and mitochondria (0.4 - 3.1%) [21]. There are some discrepancies as to the location of these two isoforms of NAD$^+$ kinase within the cell, especially in the chloroplast. In pea, Simon *et al.* [37] found the CaM-dependent NAD$^+$ kinase activity in the chloroplast envelope and the CaM-independent form in the stroma, whereas Jarrett *et al.* [46] obtained opposite results. The finding of Kreimer *et al.* [25] that in pea the specific activity of either form changed differently with the plant age, and the observation of Muto & Miyachi [21] that cellular compartmentation of NAD$^+$ kinase varied depending on the species and plant growth conditions, seem to explain these discrepancies.

The functional role of both forms of NAD$^+$ kinase in different cellular compartments remains to be determined. According to the results of Kreimer *et al.* [25], stromal CaM-independent NAD$^+$ kinase catalyzes the light-induced conversion of NAD$^+$ to NADP$^+$ in the chloroplast. The CaM-dependent NAD$^+$ kinase located mainly in the cytoplasm and associated with outer organellar membranes is most likely a major regulator of NADP$^+$ formation, as pyridine nucleotides cannot cross the chloroplast envelope [47].

Total NAD$^+$ kinase activity under environmental stresses

Total NAD$^+$ kinase activity is consistent with the level of aluminium tolerance in roots of oat, rye, triticale, wheat and barley [29], the extent of frost tolerance in winter rape plants [31], and the level of the leaf dehydration tolerance in wheat [30]. Irrespective of the kind of the stress applied, total NAD$^+$ kinase activity increases or at least remains at the same level. In oats, the most aluminium tolerant cereal, total NAD$^+$ kinase activity increases three-fold, and in other cereals a two-fold increase was observed [29]. A rapid increase in total NAD$^+$ kinase activity was also observed in winter rape leaves beginning with the fourth day of cold acclimation [31]. The enzyme activity remains at practically the same level in wheat plants subjected to severe water deficit [30].

The increase in total NAD$^+$ kinase activity observed in the Al sensitive wheat may be recognized as induction of the enzyme synthesis since cycloheximide abolishes this activity to control level [28]. However, in the Al tolerant wheat, this inhibitor reduced the total activity only by half. In this wheat, the presence of aluminium may have lessened the cycloheximide inhibition of the enzyme synthesis by partial activation of NAD$^+$ kinase [29]. It is also unclear whether the increased total NAD$^+$ kinase activity in the cold-acclimated winter rape [31] or drought-acclimated wheat [30] is due to the effect on the synthesis of the enzyme and/or on the activation of the existing enzymatic protein. The increase in the enzyme activity paralleled by the increased content of soluble protein during plant acclimation to stress conditions [48, 49] is consistent with the appearance of a higher amount of the enzyme molecules. In this sense, the increased enzyme activity could be a part of the metabolic adjustment of the protein pattern to the constraints imposed by low temperature or water deficit. On the other hand, one cannot exclude the effect of metabolites on the maintenance of high NAD$^+$ kinase activity, e.g. of the NAD$^+$ level [50, 51]. This last supposition is in full agreement with the finding of Chung [52, 53] that NAD$^+$ kinase is remarkably stabilized by its substrate.

On reviewing the response of NAD$^+$ kinase activity to Al stress one should note that the reaction of NAD$^+$ kinase in two dicots: pea and lupin, is different from that in monocot cereals [29]. The total activity of the enzyme is twice as high in the Al sensitive pea than in the Al tolerant lupin, and moreover, the activity decreases under Al stress just opposite to the observed reaction in the monocot cereals [29].

Changes in the activities of CaM-dependent and CaM-independent NAD$^+$ kinases

CaM-dependent NAD$^+$ kinase constitutes 40 - 60% of the total enzyme activity in control leaves of wheat [30] and winter rape [31] not exposed to stress, and in roots of Al tolerant cultivars of oats, rye and lupin [29] but it amounts only to 20 - 30% of the total activity in roots of Al sensitive cultivars of wheat, barley and pea [29].

In response to Al stress, the activity of CaM-dependent isoenzyme decreases both in the Al tolerant mono- and dicots examined, whereas it increases in the sensitive ones. So, in spite of the differences observed in total NAD$^+$ kinase between mono- and dicots under Al stress, the response of the CaM-dependent isoenzyme was the same. Thus, in all Al tolerant species, Al stress caused a withdrawal of the CaM-dependent NAD$^+$ kinase in favor of the CaM-independent one [28, 29]. To evaluate properly the physiological meaning of the altering share of the two NAD$^+$ kinase isoforms under stress conditions one should know whether they differ in the affinity towards ATP and NAD$^+$. Neither this information is available nor these isoforms have been separated.

Contrary to the effect of Al stress, acclimation of plants to unfavorable water and temperature conditions leads to the increase of CaM-dependent NAD$^+$ kinase activity in the leaves both of wheat hardened to water deficit [30] and of winter rape hardened to cold [31]. The difference between the response of the CaM-dependent NAD$^+$ kinase to Al stress and other stresses can be readily explained by the fact that Al competes with calcium for calmodulin [54], eliminating calmodulin from cellular metabolism. In wheat leaves acclimated to drought, the difference is expressed in kinetics of the changes caused by water deficit; the activity of CaM-dependent isoenzyme decreases only gradually with the increasing water deficit, albeit its share still remains high (75%) at high water deficit (60% WSD). On the other hand, in non-hardened plants, CaM-dependent activity declines rapidly in response to low water deficit (20% WSD), but reappears with severe water deficit (40 - 60% WSD) constituting then only about one-third of the total enzyme activity [30]. This surprising and reproducible derepression of the CaM-dependent activity is consistent with the same phenomenon observed with sublethal Al doses [28]. The mechanism of this derepression is not known; it might be ascribed either to formation of a new CaM-dependent isoform or to depression of the enzyme repressor [28].

In cold tolerant rape plants, low temperature slightly induced (by about 10%) the share of CaM-dependent isoenzyme in the total NAD$^+$ kinase activity [31]. The mechanism of this stimulation is not clear.

It should be mentioned that at low temperatures the level of free Ca^{2+} is increased in cytosol [55, 56], therefore a possible effect on the Ca^{2+}-CaM complex may also be responsible for the observed increase of the CaM-dependent NAD$^+$ kinase activity in the cold. In drought the level of free Ca^{2+} does not vary in water stressed leaves and in the chloroplasts isolated from these leaves [57, 58]. Moreover, reduction of Ca^{2+} concentration in the incubation medium increased both the CaM-dependent and CaM-independent activity of NAD$^+$ kinase [29]. It is known that the requirements for Ca^{2+} may be met either by direct activation of NAD$^+$ kinase or through increased participation of calmodulin [2]. Thus, the extent to which Ca^{2+} concentration affects the ratio of the two NAD$^+$ kinase isoforms is uncertain. However, the results obtained in our experimental systems indicate that stress conditions do change the share of CaM-dependent and CaM-independent isoenzymes in the total NAD$^+$ kinase activity [28 - 31]. The mechanism of these changes remains unknown.

Possible implications of the role of NAD$^+$ kinase under stress conditions

Due to polygenic control of plant response to abiotic stresses [59], the mechanisms of tolerance must consist of several supplementary strategies which assure a high final resistance of the whole plant to stress factors. During the last few years, among the many postulated targets of aluminium toxicity, calmodulin has been considered the most important [54], although Al chelating properties of several compounds such as dicarboxylic acids, polyuronic acids, cell wall constituents and other factors have been postulated the mechanism of Al tolerance [60, 61]. In relation to cold stress, attention has been focused mainly on the membrane-associated processes [62]. Under water stress, shrinkage of cell volume leads to increased ion concentrations which are thought to be responsible for the inhibition of many enzymes [63].

Despite the differences in the proposed general mechanisms of negative effects exerted by abiotic stresses, it seems that the dependence of NAD^+ kinase on stress conditions is not accidental. The occurrence of differentially regulated NAD^+ kinase isoenzymes may permit final and more flexible control over pyridine nucleotide levels. It is unlikely that all the partial processes involved in plant metabolism respond in the same way to changing temperatures or ionic conditions.

Little is known about the NAD^+ kinase gene but the same chromosomal location of the Al tolerance genes and the gene(s) coding for NAD^+ kinase in Chinese Spring wheat seems worth mentioning. Genes controlling this enzyme activity and also Al tolerance are located on the long arms of chromosomes 2D and 4D; on the short arm of chromosome 5A, genes controlling other mechanisms of Al tolerance, not related to NAD^+ kinase, are located [29].

Despite the differences in total NAD^+ kinase activity, the response of the CaM-dependent isoenzyme to Al stress is the same in monocots and dicots, suggesting that the mechanism of Al tolerance is manifested in the ability to withdraw from cellular metabolism that enzyme form which is a target of Al toxicity.

The opposite response of the total NAD^+ kinase activity in monocots and dicots may suggest that this enzyme is involved in the regulation of different metabolic pathways. In cereals, the consequential increase in total NAD^+ kinase activity might, because of the increased $NADP^+$ supply, promote the pentose phosphate pathway and thus cause an increase in the availability of intermediates of this pathway for biosynthesis of amino acids, nucleic acids, pentoses and phenols, some of which may be important in Al defense strategy [64, 65]. In legumes, one can assume that the decrease of the total NAD^+ kinase activity might stimulate the glycolytic pathway because of the increase in NAD^+ availability. NAD^+ participates in the oxidation of glyceraldehyde-3-phosphate and thus, *via* pyruvate, to increase the pool of the Krebs cycle intermediates i.e. citric acid, and malic acid, the known efficient Al chelators [59, 60, 66].

It has been found that, at low temperature, the increase in the total enzyme activity is associated with the increase in anabolic redox charges reflecting the cell enhanced ability for reductive synthesis [50]. Moreover, in winter rape leaves, cold treatment stimulates the activity of the oxidative pentose phosphate pathway (Maciejewska and Bogatek, personal communication) by increasing availability of $NADP^+$ [2]. This may also speak in favor of NAD^+ kinase involvement in the cold acclimation process in winter rape.

The significant increase of the $NADP^+$ $NADPH/NAD^+$ NADH ratio in wheat acclimated to soil drought [51] clearly demonstrated the effect of NAD^+ kinase activity on the acclimation process. One can pose the question whether this change in the nicotinamide nucleotide pool is connected with the observed shift of NAD^+ kinase towards the CaM-dependent form within the total unchanged NAD^+ kinase activity. This supposition could be confirmed by information about possible differences in kinetic properties of the two NAD^+ kinase forms and the data on the distribution of nicotinamide nucleotides in the individual compartments of the cell exposed to drought.

We have presented the evidence that NAD^+ kinase may play an important regulatory role in plants subjected to various environmental stresses by the modulation of cellular metabolic activity, both directly by maintaining the $NADP^+$ supply in the cytosol and chloroplasts and indirectly by affecting the oxidation processes *via* the Krebs cycle and/or the pentose phosphate pathway and the transport of reducing equivalents from chloroplasts. It seems that, in plants exposed to abiotic stresses, NAD^+ kinase might be of great importance in diverse control mechanisms since it appears to participate in reversibly switching cell metabolism from anabolic, NADP$^+$-dependent, to catabolic NAD$^+$-dependent processes.

We are aware that the role of NAD$^+$ kinase in the regulation of metabolic processes which are fundamental for the mechanisms of plant adaptation to abiotic stresses is still far from being understood. The hypotheses which have been discussed in this review need further verification.

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