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Review Article

The corresponding relationship between roles of NADP-malic enzymes and abiotic stress in plants

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Abstract: Many proteins play important roles in production of metabolic energy and plant growth. NADP-malic enzyme is one of these proteins. It mainly locates on cell and organelle membrane. It not only takes part in the process of photosynthesis, but also joins the improving of plant stress tolerance. In this review, we stated the variation of the NADP-malic enzyme activity and the photosynthesis rate of plant under some main abiotic stresses (drought, salt and temperature stress). It is demonstrated that the activity of NADP-malic enzyme is increasing under different stresses, which was used to prevent the decline of plant photosynthesis to resist stresses. The expression of the NADP-malic enzyme gene, which is dissimilar under different stresses, is another point in this paper. At the same time, the enzyme in C4, CAM and C3 plant have different expression intensity under the same stress. We analyzed the mechanisms how NADP-malic enzyme to resist stresses by combined theory with experimental fact.

Keywords: NADP-malic enzyme, abiotic stresses, drought, salinity, temperature, mechanism.

دراسة استعراضية عن العلاقة بين الادوار المتماثلة من انزيمات NADP-malic والاجهاد الغير حيوي فى النباتات

ليو زينق – هي[1،2] ، زانق زينق- بن[2*]، جو لي- يي[1] و شاو هونك- بو[1،3*]

[1]معهد علوم الحياة في جامعة تشينغداو للعلوم والتكنولوجيا ، وتشينغداو 266042 ، الصين ،[2] مركز بحوث الموارد الزراعية ، ومعهد علم الوراثة والبيولوجيا التطورية ، الاكاديمية الصينية للعلوم ، شيجياتشوانغ 050021 ، الصين ، ومعهد للبحوث [3]يانتاى المنطقة الساحلية ، الاكاديمية الصينية للعلوم ويانتاى 264003 ، الصين

ملخص: هناك العديد من البروتينات تلعب دورا هاما في إنتاج الطاقة الإستقلابية لنمو النبات ويعتبر انزيم **NADP-malic** من اهم تلك البروتينات فهو يقع بشكل رئيسي في غشاء خلية النبات والعضيد، كما انه لا يستهلك جزء من عملية التمثيل الضوئي ولكنه ينظم ويحسن الإجهاد النباتي، وفى هذا الاستعراض نضع أيدينا على الاختلافات لنشاط انزيم **NADP-malic** ومعدل البناء الضوئي للنباتات التى تقع تحت الظروف الغير حيوية الرئيسية مثل الجفاف والملوحة وارتفاع درجات الحرارة، وقد تبين ان نشاط انزيم **NADP-malic** يزداد مع تنوع الظروف والضغوط للنبات، والذى يستخدم لحماية النبات من الانخفاض المفاجئ فى التمثيل الضوئي وبالتالي مقاومة الضغوط الخارجية، ويعتبر الجين لانزيم **NADP-malic** والذى يختلف باختلاف الظروف. فى جزء أخر من هذه الورقة العلمية وفى الوقت نفسه، يعتبر الانزيم **C4, CAM** في**C3** من هذه النباتات تمتلك مختلف ردات الفعل من نمو النبات تحت نفس الظروف وقد قمنا بتحليل آلية كيفية مقاومة الانزيم **NADP-malic** للظروف المختلفة من خلال جمع بين النظرية والتطبيق العملي.

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Introduction

There are many external adverse factors affecting the plant growth especially for crops, which include biotic factors and abiotic factors. Abiotic stresses would bring more significant influence compared with biotic factors for plant growth with the changing of environment. So focusing on the influence caused by abiotic stress is of great importance. Abiotic factors mainly include drought, salt and temperature. Plant can regulate the expression of anti-stresses genes to resist these different stresses. However, study on the functions of these genes and the gene expression regulation is very important for plant cultivation.

NADP-ME was widely distributed in plants, which mainly appeared in mitochondria, chloroplast and cytoplasm (Edwards and Andreo, 1992; Detarsio et al., 2003). It can catalyze the oxidative decarboxylation of malate to yield pyruvate, CO_2 and NADPH under metallic ion (Mg^{2+}, Mn^{2+} etc.) (Edwards and Andreo, 1992). So it is one of the critical enzymes in malate metabolism, which played an important role in plant development. It could keep osmotic potential of cell, stabilize pH of cytoplasm and keep balance of ion absorption (Detarsio et al., 2003; Martinoia and Rentsch, 1994; Drincovich et al., 2001). According to it different functions in plant, it could be classed to photosynthetic NADP-malic enzyme and non-photosynthetic NADP-malic enzyme. The photosynthetic NADP-ME was found in chloroplast, which mainly takes part in L-malate oxidative decarboxylation, and provides CO_2 to Ribulose bisphosphate carboxylase oxygenase for C fix (Edwards and Huber, 1981). This process can be regulated by light. So it has closed relationship with photosynthesis. The function of non-photosynthetic NADP-ME was not understood by people now. But it has higher *Km* value, lower specificity, narrower suitable pH and bigger molecular weight compared with photosynthetic NADP-ME (Pupillo and Bossi, 1979; Chi et al., 2004a). The expression of nonphotosynthetic NADP-ME genes was very particular, which is unlike in different developing stages, varying organs and changing environment (Martinoia and Rentsch, 1994 and Drincovich et al., 2001). The gene coding NADP-ME is not unique but rather a gene family. There are four genes in rice and *Arabidopsis thaliana* (Maurino et al., 2009). Through they shared a high degree of identify, they have different expression specificity in different plant tissues and have different structural and kinetic properties (Gerrard Wheeler et al., 2005; Maurino et al., 2009). The expressions of these gene are distinct under vary stresses. So it was deemed to have closely relation to environment stresses (Zhang, 2003). Meanwhile, Fu *etc*. clone NADP-ME gene ($TaNADP\text{-}ME_1$ and $TaNADP\text{-}ME_2$) from wheat at first in the world, and found that $TaNADP\text{-}ME_2$ belongs to the group of photochemical reaction. It may be the first cytoplasmic NADP-ME gene found in C_3 plant. It is proved that $TaNADP\text{-}ME_1$ and $TaNADP\text{-}ME_2$ may play important role in stress tolerance (Fu et al., 2009).

1. Drought and NADP-malic enzyme

Drought is a factor limiting the plant growth. It would cause osmotic stress. Drought stress could cause the accumulation of free radical and azotic acid and the membrane lipid peroxidation as well. The plant metabolism would be disordered. It will suppress the extension of leaf, cause the close of stoma, reduce the absorption of CO_2, raise the resistance of mesophyll cell and decrease the activity of some enzymes. They will affect the CO_2 fixed, destroy the structure of chloroplast and reduce the content of chlorophyll. The last result is suppressing the photosynthesis and lowing the photosynthetic rate in wheat under drought

stress (Ahmad et al., 2007; Sun et al., 2004; Fu et al., 2009).

Because of the function of NADP-ME in malate metabolism and photosynthesis, the NADP-ME plays an important role in anti-drought. The activity of NADP-ME in wheatear is higher than that in flag leaf. In mild-drought, the photosynthetic rate of all organism is declining. But the activity of NADP-ME is increasing obviously. It means that the expression of NADP-ME is induced by drought to resist drought (Wu et al., 2008). The leaf stoma was closed because of drought stress, which would decrease the content of malate in cell and raise the NADP-ME activity. It is proved that some malate entry the mitochondrion (Wei et al., 2003). ^{14}C marking experiment in wheat proved that some NADP-MEs were synthesized in mitochondrion, which may join the malate metabolism (Wei et al., 2003). While, *Outlaw* and *Laporte* reported that NADP-ME in wheat play a important role in controlling stoma open and close through regulating the degradation of malic in day (Outlaw et al., 1981).

In addition, there has C_4 plants photosynthesis enzyme system in C_3 plant. The activity of C_4 enzyme will be increasing to strengthen metabolism under drought stress, which goal is compensating the loss of photosynthesis rate in C_3 pathway caused by drought. Some studies indicate that the C_3 pathway would be suppressed in some plants by drought, but the C_4 pathway was reinforced (Laporte et al., 2002). Through increasing the activity of NADP-ME to compensate the decrease of other enzyme activity can prove that increasing the activity of NADP-ME is an ecological adaptation mechanism under drought stress (Li et al., 1999; Laporte et al., 2002; Wu et al., 2008).

There are many pathways to resist drought. The change found in one of them is a defensive system which is made up of some protein and enzyme induced by drought (Sharma and Rajwinder, 2007; Moyin-Jesu and Adeofun. 2008). NADP-ME is one of them. Now, many investigations found that the stress signal stimulate one signal system which can regulate the defensive genes expression in plant to resist drought (Shao et al., 2008; Shao et al., 2008a). It is reported that drought can induce the NADP-ME gene expression in ice grass in 1992(Ni et al., 2009). The ways of signal introduction were main classed ABA dependence and ABA independence. It is proved that the concentration of NADP-ME is increasing with the ascent of ABA in guard cell under drought stress (Cushman, 1992). It means the relation of ABA and the drought stress may closely. The function of reaction NADP-ME catalyzer is delivery CO_2 in photosynthesis (Zhang, 2003). In order to keep the reaction of photosynthesis, plant can increase the content of NADP-ME to reinforce the delivery and fix of CO_2 when the absorb of CO_2 is decreasing because of the shut of stoma under drought stress. The goal is compensating the deficiency of CO_2 in this situation. This theory can explain the reinforcement of C_4 enzyme system in C_3 plant under drought stress (Wu et al., 2008). At the same time, the protein of NADP-ME is hydrophilicity, which can protect cells through increasing the osmotic pressure of cell and decrease the water loss (Schroeder et al., 2001; Li et al., 2009).

There is a gene family to code the NADP-ME. So it is meaningful to investigate a gene family expression under stress. Four genes coding NADP-ME were found in rice. Three of them can increase expression under 10% PEG, only one was inclining. It means that not all NADP-ME genes have associate with drought stress.

2. Salt and NADP-Malic enzyme

Salt stress can bring harm for plant growth. The salinity in soil is 0.2%-0.5% can hamper the plant development (Sun et al., 2002). The harm is obvious, which mainly includes suppressing the growth and differentiation of unhalophytic plant tissues and organ and making plant enter

the development stage beforehand (Jiang et al., 2001; Malash and Khatab, 2008).

In order to limit the harm caused by salt, plant can produce some proteins and enzymes (For example, POD and SOD *etc*.) which defense gene expression were induced by salt (Jiang et al., 2001). Salt signal can induce NADP-ME gene expression, and increase the activity (Liao et al., 2007). Fu et al. (2010) found that the NADP-ME activity in leaf achieved its peak level after 6 hours at 200mM NaCl. It is two times higher than the normal. But the photosynthetic rate and transpiration rate are decreasing gradually. It proves that salt stress can induce NADP-ME gene expression (Fu et al., 2010). It is reported that the mRNA and the activity of NADP-ME in *Aloe vera* L. and *Aloe saponarea Haw* increased gradually after 12 hours under salt drought. It is continuing until 72 hours. It indicates that the expression of NADP-ME gene and the protein accumulation were induced by salt (Sun et al., 2003). While, Sun reported that the expression of NADP-ME gene induced by salt had close relation with its salt tolerance (Liao et al., 2007). CAM plant has a specific photosynthesis pathway. Its stomas open at night to absorb CO_2 which would be fixed by PEP and PEPC to produce IV carbonate (most of them are malate) (Zhang, 2003; Sun et al., 2003). Some facultative CAM plants can change their C_3 metabolism pathway to C_4 metabolism pathway under salt stress. At the same time, the activity of NADP-ME would increase 4-10 times (Lou et al., 2008; Holtum and Winter, 1982). That means NADP-ME is a critical enzyme in CAM pathway. It may play an important role in resisting salt stress in CAM plant and facultative CAM plants.

In the long evolution history, plant form some specific physiology and biochemistry paths itself to resist or limit the harm caused by salt stress. Salt tolerance and salt avoidance are the main strategies for plants when they exposed to salinity. The details of these courses mainly include the synthesis and accumulation of organic substances, the increasing activity of Na^+/K^+ pump and H^+-ATP, the enhancing of the aquaporins genes expression and the changing of the metabolism way (Figure 1) (Winter et al., 1982; Dajic, 2006; Zhang et al., 2009). The study about NADP-ME gene expression regulation under salt stress is rare now. Different regulation mechanism may cooperate with each other under salt stress to keep plant vital signs. The mechanism of Na^+ crossing cell membrane is not certain. There are two imaginable pathways that are crossing: K^+ channel and nonselective channel. So as to balance these input positive ions, many negative ions were accumulated. Malate and Cl^- are the main members (Li et al., 1999; Shao et al., 2008b; Zhang et al., 2009). Malate is synthesized through the reaction catalyzed by Phosphoenolpyruvate carboxylase, which was stored in vacuole. The destiny of malate is not clear. But there are some studies proving that NADP-ME was synthesized in this stage, which may be taking part in the malate metabolism (Wu et al., 2008; Shao et al., 2009).

3. Temperature and NADP-Malic Enzyme

Plants have to experience temperature change in one year. High temperature may cause enzyme deactivation. Its result is that enzyme system would be destroyed and the water in body would be lost. The root vitality, the liquidity of protoplasm and the activity of NADP-ME are inclining when the temperature is very low. At the same time, the chlorophyll would be decomposed. The result of all above can cause metabolic disorders (Zhang et al., 2000; Xu and Yan, 2003).

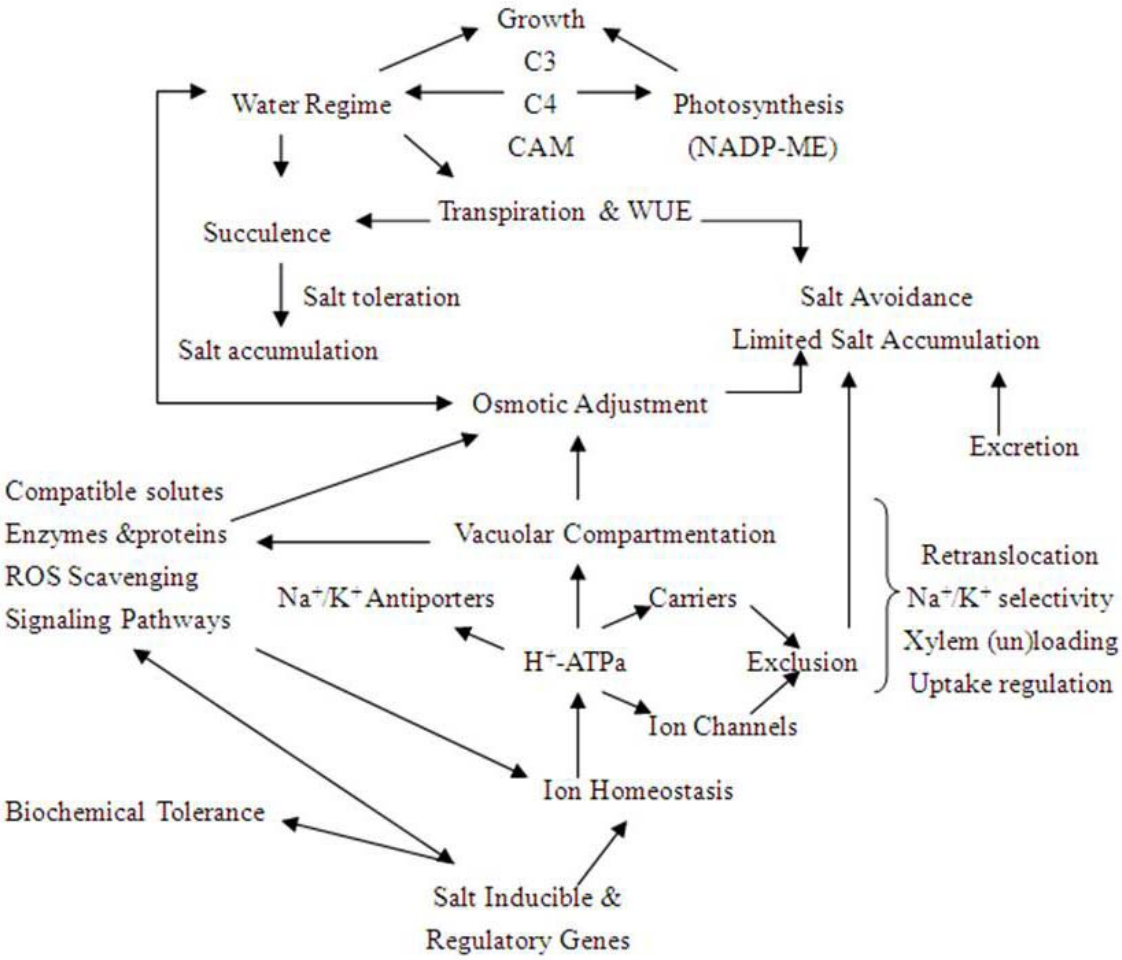

Figure 1. Determinants of salt tolerance relate to the main adaptive strategies (to salt tolerance and salt avoidance) of plants under salt stress.

Low temperature can affect plant growth significantly. It could be classified chilling injury and frozen injury. Frozen injury can destroy plant fate. But chilling injury can slow the growth rate and change the leaf color, which cannot freeze the cellular fluid. And the injury could be restorable under certain conditions (Xu and Yan, 2003). It is known that the activity of NADP-ME in wheat leaf is increasing gradually under 4 in 24 hours. But the index of photosynthesis is not having the same trend. It means that the activity of NADP-ME was affected seriously by low temperature. The enzyme has responded to the stress at protein level. Through RT-PCR study, the gene TaNADP-ME_1 and TaNADP-ME_2 have the same variation trend, which was increasing after 3 hours declining under low temperature stress (Sun et al., 2003). These evidences indicate that cold stress can induce the expression of NADP-ME gene, which have closely relationship with resisting cold of plant.

The content of NADP-ME would be increasing when the absorbility of CO_2 is decreasing under cold stress. It proved that NADP-ME may play resist cold stress beside catalyze the reaction. The membrane system in cell is the most sensitive part under cold stress. Its

liquidity and stability is the basis of the cell and the plant. The phase transition temperature is lower, the ability of cold tolerance is better (Lin et al., 1995; Gareth, 1998; Yamaguchi-Shinozaki and Shinozaki, 2004). In order to decrease the phase transition temperature and strengthen the cold tolerance, the cold signal would induce some stress responsive genes express, which can produce some protein to keep the liquidity of the membrane (Lin et al., 1995; Wang et al., 1997; Yamaguchi-Shinozaki, and Shinozaki, 2004; Chinnusamy et al., 2006; Floris et al., 2009). The aim is to stop the membrane phase change. NADP-ME is one of these proteins, which mainly locate in membrane (cytomembrane, mitochondrial membrane, chloroplast membrane and thylakoids) (Wang et al., 1994; Jiang et al., 2001; Floris et al., 2009). Cold signal can induce NADP-ME gene expression, which produce the NADP-ME protein to keep the liquidity of membrane and keep the metabolism as usual. Moreover, NADP-ME is a kind of hydrophilicity protein (Jiang et al., 2001; Salamon et al., 2010). It can absorb more free water and change them to bound water. That course could decrease ice in cell under cold stress to raise the cold tolerance. This may one of the pathways to resist cold in plants.

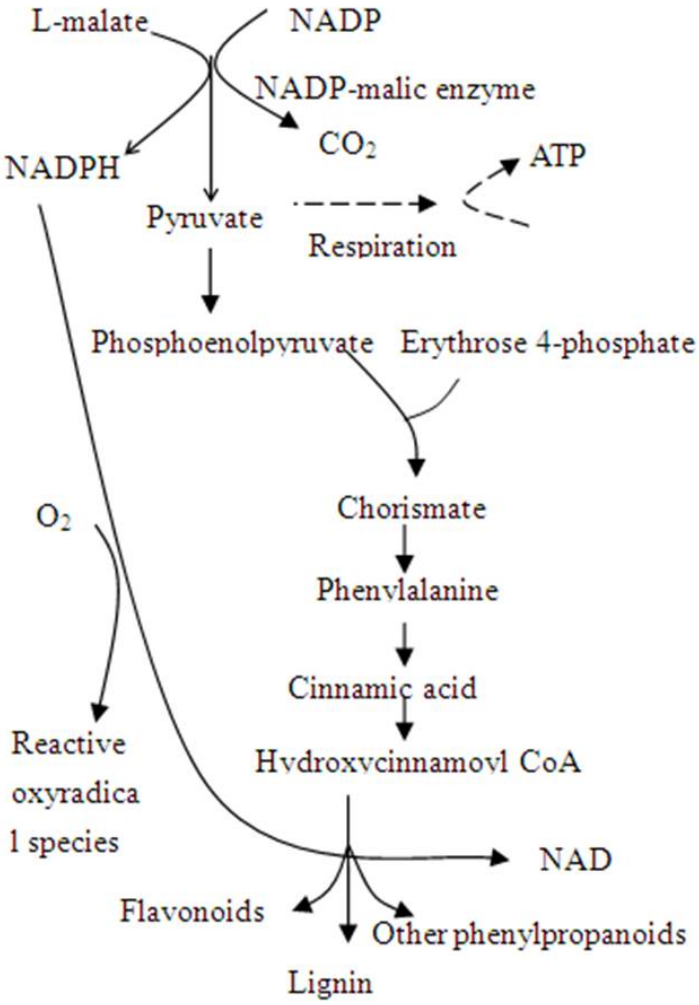

Figure 2. Scheme showing the possible role of NADP-ME in plant defense. Arrows do not indicate single enzymatic reaction.

Summary

The mechanisms to resist various stresses are cooperating with each other. The changing environment factors make plant form itself defensive quality. There are many factors which affect plant growth beside drought, salt and temperature (Ding et al., 2003; Tsuchida et al., 2001). NADP-ME is a critical enzyme in photosynthesis pathway. There are many substances related with it. Its change can lead to other substance change, which would arouse anti-stress response (Figure 2) (Casati et al., 1999; Shao et al., 2009). The activity of NADP-ME is changing under drought, salt and temperature stress. It means that the NADP-ME gene is non-specific induced gene, which may have closely relation with these stresses.

With the development of biomolecular technology, more and more resistance genes were found. It can help people to improve the plant stress resistance. But now, the study about the regulation of NADP-ME gene expression under different stresses is rare, particularly in transgenic research. The relation between NADP-ME gene expression and metabolism system of transgenic plant has not sufficiently studied, which limited it applied in breeding. For example, one of directions of crop breeding is raising the photosynthetic rate of C_3 through transgenic C_4 genes technology. In C_4 plant, the expression quantity of NADP-ME gene is more than that in others. So it has high photosynthetic rate (Sun et al., 2003; Dajic, 2006). It is proved that NADP-ME in transfer NADP-ME gene rice is seven times than that in ordinary rice. But the exchange of CO_2 and photosynthetic rate are not altered. Meanwhile, it can lead to leaf bleaching, slow growth and intense photo-inhibition (Sun et al., 2003; Ding et al., 2003; Shao et al., 2008 ; Casati et al., 1999). There are some research proved that the expression of NADP-ME gene from C_4 plant in C_3 plant may bring harm for chloroplast (Ding et al., 2003; Ngele et al., 2009). So, it can include that transfer NADP-ME gene from C_4 plant is not helpful for improving C_3 plant photosynthetic rate (Casati et al., 1999; Sun et al., 2003; Ding et al., 2003 and Chi et al., 2004b). The reason for above phenomenon is that the study about the regulation of NADP-ME gene expression in transgenic plant under different stresses is rare. This is an important point for future research.

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