Front. Agric. China 2010, 4(1): 84–90
DOI 10.1007/s11703-009-0089-8

REVIEW

Yingli LI, Yufang LIU, Jianguang ZHANG

Advances in the research on the AsA-GSH cycle in horticultural crops

Abstract The adaptation of plants to stressed environments depends greatly upon the metabolic level of antioxidant systems within their bodies. Among the enzymatic antioxidant systems, the AsA-GSH cycle occupies a vital place and has become a hot research field in recent years. The AsA-GSH cycle can directly scavenge H_2O_2 produced in plants on one hand, and the antioxidants AsA and GSH produced in the cycle can also scavenge other species of active oxygen by means of additional pathways on the other hand. Environmental conditions and exogenous formulations can alter the oxidative and reductive status in plants and mediate the metabolic level of the AsA-GSH cycle within a certain range, thus regulating the resistance of plants to stresses. The present paper reviews the advances in research on the AsA-GSH cycle with respect to horticultural crops, so as to provide some beneficial reference for further studies.

Keywords AsA-GSH cycle, horticultural crops, antioxidant system, antioxidant

1 Introduction

There are many antioxidant pathways that play important roles in plant adaptation to stressed environments. Among them, the AsA-GSH (ascorbate-glutathione) cycle has been regarded as the most important one (Smirnoff, 1995; Wang and Li, 2002). Research on the AsA-GSH cycle in horticultural crops began in 1990 s and has been done with limited types of fruit, vegetable and floral species so far (Dalton et al., 1991; Wang and Li, 2002; Larrigaudiere et al., 2003; Ding et al., 2005; Kenichi, 2005; Li et al., 2008). Bio-oxidation occurs at anytime within living organisms and the antioxidant systems are greatly responsible for stressed environments. In the present paper, the advances in research on the AsA-GSH cycle concerning horticultural crops in recent years will be reviewed so as to provide valuable reference for further studies.

2 AsA-GSH cycle

The details of the AsA-GSH cycle may vary with individual authors, but the basic framework is almost the same, which comprises a few relevant metabolic reactions (Fig. 1). In the AsA-GSH cycle, APX (ascorbate peroxidase) catalyzes the reduction of H_2O_2 (hydrogen peroxide) into water with AsA (ascorbic acid) serving as an electronic donor (Xiong et al., 1992; Tao et al., 1998; Zhang et al., 2008). DHAR (dehydroascorbate reductase) utilizes the electrons provided by GSH to reduce DHA (dehydroascorbic acid) into AsA, while DHA is previously produced from MDHA (monodehydroascorbate). Simultaneously, GSH is oxidized into GSSG (glutathione disulfide) by DHAR and GSSG is then reduced into GSH, catalyzed by GR (glutathione reductase). It is apparent that APX, MDAR, DHAR and GR are four key enzymes present in the AsA-GSH cycle (Ma and Chen, 2003, 2004). Van Montagu and Inze (1992) suggest that the AsA-GSH cycle in plants can scavenge H_2O_2 produced in plants, which exists extensively in many cellular organs. As an important antioxidant system, the AsA-GSH cycle can maintain an appropriate oxidative and reductive environment through regulating AsA/DHA, GSH/GSSG and NAD(P)H/NAD(P) interconversion (Kenichi, 2005).

3 ROS in relation to AsA-GSH cycle

During the process of plant growth, reactive oxygen species (ROS) are produced continuously due to

Received June 20, 2009; accepted October 14, 2009

Yingli LI, Yufang LIU, Jianguang ZHANG (✉)
College of Horticulture, Agricultural University of Hebei, Baoding 071001, China
E-mail: zhjg570315@sina.com

Jianguang ZHANG
Pear Engineering & Technology Research Center of Hebei Province, Baoding 071001, China

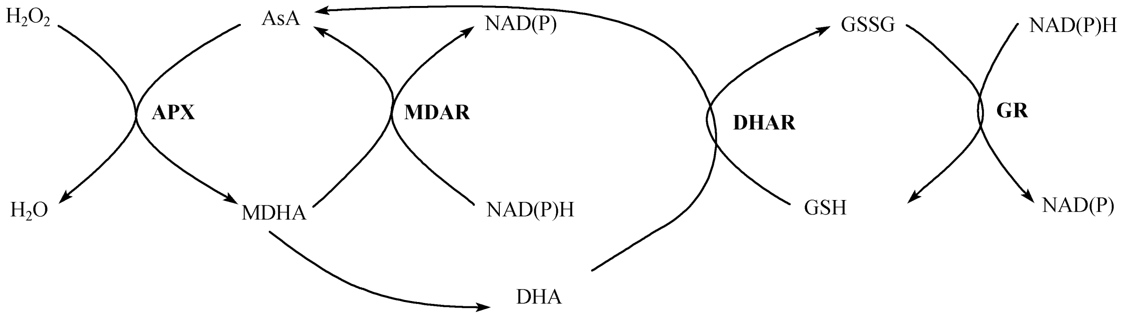

Fig. 1 Illustration of AsA-GSH cycle

Note: APX, MDAR, DHAR, GR, H_2O_2, AsA, MDHA, DHA, GSSG and GSH represent ascorbate peroxidase, monodehydroascorbate reductase, dehydroascorbate reductase, glutathione reductase, hydrogen peroxide, ascorbic acid, monodehydroascorbate, dehydroascorbic acid, glutathione disulfide and glutathione, respectively.

environmental or artificial stresses, and those free radicals include superoxidative anion (O_2^-), hydrogen peroxide (H_2O_2), singlet oxygen ($^1O_2$) and hydroxy radical (·OH). Among those ROSs, H_2O_2 occupies a vital place because many other ROSs could be converted into H_2O_2 via various pathways. Although H_2O_2 has very essential physiological functions, for example, it may participate in gene expression, cell metabolism, programmed cell death, sensitive response, senescence, etc. (Bowler and Fluhr, 2000; Dat et al., 2000; Jones, 2001; Abdel-Kader and Saleh, 2002; Scandalios, 2002), its abnormal accumulation can still harm the membrane systems of living organs. There are many ROS scavenging pathways in plants. Actually, it has been proven that H_2O_2 is mainly scavenged by the AsA-GSH cycle (May et al., 1998; Alscher et al., 2002; Jin et al., 2003). Song et al. (2008) have examined the responses of the photosynthetic and respiratory electron transport and antioxidant systems in cell organelles of cucumber (*Cucumis sativus* L.) and tomato (*Lycopersicon esculentum* Mill.) leaves infected by cucumber mosaic virus (CMV), finding that the changes in electron transport are accompanied by a general increase in the activities of SOD/AsA-GSH cycle enzymes, followed by an increased H_2O_2 accumulation in chloroplasts and mitochondria. Usually, a dynamic balance has to be maintained between AOS generation and scavenging in the subcellular area or within cellular organs in order to guarantee normal plant growth. Once plants are subjected to more severe environmental stresses resulting in an imbalance, a considerable amount of AOS will be accumulated in cells. Those AOSs can attack the unstable bonds in protein, sugar and nuclear acid molecules, which in turn causes a destruction of enzymes or proteins in the membrane, resulting in the superoxidation of membrane lipids and interference with normal physiological metabolism (Fridovich, 1998; Scandalios, 2002; Selote and Khanna, 2006). However, the antioxidant system, within a certain range, can scavenge active oxygen radicals to protect membrane structure and function. For this reason, it is taken for granted that plant resistance to stress is highly correlated with the metabolic intensity of antioxidant systems in the cells (Alscher, 1997; Jiao and Wang, 2000; Liu et al., 2004).

4 Main components in the AsA-GSH cycle

4.1 Antioxidants

4.1.1 AsA

AsA and GSH are the most abundant low molecular weight non-enzymatic antioxidants in plant cells participating in ROS scavenging through the AsA-GSH cycle. AsA is widely distributed in plant tissues and its oxidative and reductive system consists of AsA, MDHA and DHA (Noctor and Foyer, 1998). In this process, AsA is oxidized by APX into MDHA first, further converting into DHA. MDHA can be reduced by MDAR into AsA, with NAD(P) H providing electrons, and AsA can be also regenerated from DHA by DHAR, with GSH supplying electrons (Asada, 1994). Therefore, the oxidative and reductive status of AsA can represent the oxidative and reductive conditions in the cellular environment, and when stresses happen the concentrations of AsA and GSH can change accordingly (Davey et al., 2000). Many experiments have proven that environmental stresses can induce an increase of endogenous AsA. For instance, the AsA contents during the process of drought stress increase in slightly stressed apple leaves and azalea seedlings (Ke and Yang, 2007; Xu et al., 2008). Wang et al. (2004) reported that the AsA content increases in grape leaves acclimated at high or low temperatures but MDA (Malondialdehyde) content decreases, implying that resistance was raised to high or low temperatures. In an experiment conducted by Wang et al. (2009) in which a high voltage electric field was applied to mediate fruit maturing senescence, the results indicated that the consistent electric field could maintain a higher content of GSH and AsA in fruit tissues, and both components could reduce the accumulation of H_2O_2, O_2^-

and other reactive oxygen radicals, and as a consequence a lower level of active oxygen radicals was achieved in tomato fruit treated with a high voltage electric field. Ishikawa and Shigeoka (2008) reviewed the recent advances in AsA biosynthesis and the physiological significance of APX in photosynthesizing organisms and concluded that AsA plays important roles in antioxidant defense, particularly via the AsA-GHS cycle. Pallanca and Smirnoff (2000) studied the rate of AsA synthesis and turnover in pea seedling embryonic axes in relation to its pool size, finding that AsA loading could affect the APX, MDAR, DHAR and GR activity, and the APX activity decreased after AsA loading.

4.1.2 GHS

Glutathione is a crucial antioxidant associated with regenerating AsA in the AsA-GSH cycle, and thus GSH is also involved in the regulation of H_2O_2 (Hung et al., 2005). A reduced form of glutathione (GSH) is considered to protect the cell from oxidative damage, based on its redox buffering action and abundance in cells. GSH is an effective regulator for enzymatic activity and plays an essential role in maintaining antioxidant capacity and signal transduction. GSH is also an effective scavenging agent of peroxides produced when plants are subjected to oxidative stresses. In plants, GSSG can convert into GSH, thus enhancing the resistant ability of plants to environmental stresses (May et al., 1998). GSH can participate not only in scavenging H_2O_2 through the AsA-GSH cycle but also in a direct reaction with other active oxygen species (May et al., 1998). Many experiments have showed that the size of the GSH pool in plants and the status of oxidation and reduction are associated highly with plant resistance to stressed environments (Chen et al., 2004). Moreover, the GSH content and GSH/GSSG ratio are the decisive factors affecting the performance of the AsA-GSH cycle (Jiménez et al., 1998). Zhang et al. (2008) found that the GSH content in apple peels was negatively correlated to the extent of stress exerted by high temperature and excessive solar radiation within a certain range. When apple fruit was slightly stressed by high temperature and excessive light, the GSH content increased but it declined as the stress was accented. In addition, it has been reported that at chilling acclimation at 0°C for 72 h, the GSH content in strawberry leaves reached the maximal values and it then decreased, but it was significantly higher than the control (Zhang et al., 2008). de Paula et al. (1996) revealed that GSH could inhibit the senescence of sunflower seeds and the AsA-GSH cycle is the major detoxifying mechanism in both dry and imbibed sunflower seeds. However, Devarshi et al. (2006) thought that there were no significant changes in the GSH content during drought acclimation, but the GSH/GSSG ratio decreased significantly. Under more severe stress thereafter, both reduced GSH and total GSH contents rose substantially with no marked changes in the GSH/GSSG ratio (Selote and Khanna-Chopra, 2006). Therefore, it is concluded that the oxidative and reductive status of AsA and GSH are closely related to the adaptation of plants to stressed environments, and the accomplishment of AsA function depends largely on the available GSH supply and the conditions of oxidation and reduction in cells (Pastori and Foyer, 2006).

4.1.3 AsA/DHA

Many experiments have indicated that AsA/DHA ratio is a valuable indicator for weighing the available AsA level (Li et al., 2006; Ma et al., 2008; Zeng et al., 2008). Generally, a higher ratio of AsA/DHA represents a higher content of AsA. Under low oxygen stresses, the total AsA and reduced AsA contents in the apple rootstocks show an initial increase, accompanied by a succeeding decrease. During the process, the DHA content is slightly higher than the control and the ratio of AsA/DHA increases initially and then decreases, indicating that lower oxygen stresses could slightly increase AsA level in apple rootstocks and alter the status of oxidation and reduction. As a result, the antioxidant capacity increases within a certain range but after that the function decreases gradually (Li et al., 2008).

4.2 Main enzymes

Four enzymes are included in the AsA-GSH cycle, namely APX (EC 1.11.1.7), DHAR (EC 1.8.5.1), MDAR (EC 1.6.5.4) and GR (EC 1.6.4.2). APX plays a central role in the cycle and is emerging as a key enzyme in cellular H_2O_2 metabolism (Chaitanya et al., 2002; Dash and Mohanty, 2002; Panchuk et al., 2002; Geehev et al., 2003; Larkindale and Huang, 2004; Xu et al., 2004; Sun et al., 2005; Ishikawa and Shigeoka, 2008). Within a certain range, the stressed conditions can induce a rise in APX activity (Ma et al., 2006). Wang et al. (2008) reported that APX activity increased as fruit sunburn was accented within a certain range, thus raising the resistance to high temperature stress. However, the activity decreased significantly when the temperature surpassed a fixed threshold, because APX may also be damaged under extremely high temperature and excessive light conditions. Jin et al. (2003) found that slight loss of water in detached leaves of several conifers may cause a rise in APX and MDAR activity, but severe loss of water may result in a decrease in the activity. Under high salt stress, the activity of APX and GR in the leaves of a halophytic plant (*Suaeda salsa* L.) and soybeans increases, while the MDA content decreases (Pang et al., 2005; Cicek and Cakirlar, 2008). Under 40°C stress conditions, the DHAR, APX and GR in leaves of potted apple trees show an initial rise and then declines, implying that the AsA-GSH cycle exerts positive regulation within a certain range in response to the high temperature stress. After the mediating ability of AsA-GSH achieves the maximum, it would decrease as the stress time is prolonged, which would lead to injury to plants (Ma et al., 2008). Liu et al. (2003) reported that at low temperatures, the APX and DHAR activities in grafted watermelon seedlings were significantly higher than those in self-rooted seedlings and there was a great difference in cold tolerance among different seedlings on various types of rootstocks. Cold-tolerant grafted seedlings had a higher APX and DHAR activity than the grafted seedlings with poor cold resistance. Under heat stress, the activity of APX, GR and MDAR may decrease in a heat-sensitive plant (*Eupatorium adenophorum*), and a more severe membrane overoxidation would be caused (Lu et al., 2008).

5 Regulation of AsA-GSH cycle

5.1 AsA or GSH

The metabolic patterns and intensities of the AsA-GSH cycle could be mediated by environmental and artificial factors (Song et al., 2006; Wang et al., 2006; Zhao et al., 2006; Huang et al., 2008). Many experiments have proven that the application of exogenous formulations could raise the activity of antioxidant enzymes, thus enhancing plant resistance to different stresses (Luo et al., 1999; Zhang et al., 1999). Wang et al. (2006) concluded that treatment with exogenous AsA or GSH could improve the tolerance to water loss in 'Samantha' China rose cut flowers by inducing a higher activity of APX or GR in petals (Jin et al., 2006). Exogenous application of AsA can alleviate the unfavorable impact on plant growth and development by stressed environments. Ma et al. (2006) indicated that the MDA contents decreased significantly, compared to the control, in detached apple leaves cultured on a medium containing 5 $\mathrm{mmol \cdot L^{-1}}$ AsA, implying that the increase in AsA could partly inhibit the process of superoxidation of membrane lipids and alleviate leaf senescence. Application of exogenous AsA can also raise the antioxidant ability of fruit (Zhang and Fu, 2006). As Zhao et al. (2006) have reported that exogenous GSH application could effectively increase the endogenous GSH content in *Hydrocharis dubia* leaves and alleviate toxic injury due to zinc.

5.2 SA

Salicylic acid (SA) is an important regulating and signal transducing substance in response to environmental stresses (Larkindale and Huang, 2006). Huang et al. (2008) concluded that exogenous SA application could reduce lipid peroxidation in the pulp of 'Cara cara' navel orange (*Citrus sinensis* L.) fruit stored at 6°C and 20°C by regulating the antioxidant system, suggesting that pretreatment with SA combined with lower storage temperature might provide a useful means of maintaining beneficial antioxidant activity during storage of navel orange.

5.3 NO, Cd, Mo or MV

Many elements or compounds can affect the AsA-GSH cycle. Fan et al. (2008) reported that exogenous NO treatment could significantly raise APX and GR activity of cucumber leaves stressed by salt. For cabbage seedlings treated with 1 $\mathrm{mg \cdot L^{-1}}$ Cd, the GR activity as well as GSH and AsA contents continuously increase with GSH/GSSG ratio rise and DAsA/AsA ratio decrease during the whole process of treatment, which apparently guarantees that the cycle performs smoothly and effectively to provide sufficient amounts of available AsA (Sun et al., 2004). However, a higher concentration of Cd (10 $\mathrm{mg \cdot L^{-1}}$) causes a significant decrease in APX activity, implying that APX is sensitive to environmental changes. Song et al. (2006) investigated the activities of enzymes of the AsA-GSH cycle in chloroplasts, mitochondria and cytosol of cucumber leaves subjected to methyl viologen (MV) treatment and found that there were significant increases in DHA, GSH, and GSSG, except for the content of AsA in chloroplasts and cytosol, which was slightly decreased. However, GSSG in mitochondria and GSH in cytosol were minimally influenced by the MV treatment. The results by Nie et al. (2007) showed that total AsA and reduced AsA concentrations in the Chinese cabbage increased with Mo application rates, and simultaneously, Mo application may lead to an increase of the activities of APX, MDAR, DHAR and GR.

5.4 Environmental acclimation

It has been proven that appropriate drought or chilling acclimation can raise the activity of APX, MDAR, DHAR and GR, thus conferring oxidative stress tolerance by inducing a coordinated antioxidant defense (Su, 2000; Selote and Khanna, 2006; Ke and Yang, 2007; Luo et al., 2007; Xu et al., 2008). Therefore, the regulation and improvement of external environments should be an important pathway in enhancing plant resistance to oxidative stress.

6 Conclusions

As far as the studies on AsA-GSH cycle in horticultural crops is concerned, it has been preliminarily shown that the AsA-GSH cycle is highly related to plant antioxidant defense, and the metabolic intensity of the cycle is directly associated with the capacity of plant resistance to stress. In general, studies on this field have been very limited so far, with less species of horticultural crops being covered and superficial investigations being dealt with, and many key links still need to be clarified. Moreover, it has been known that environmental conditions and exogenous formulations can change the status of oxidation and reduction in plants so that the metabolic intensity of the AsA-GSH cycle can be mediated within a certain range, which will provide a possibility for altering the antioxidant ability in plants. Future studies should focus on the physiological place and characteristics of the AsA-GSH cycle in antioxidant metabolism among individual horticultural crops, the clarification of the bottleneck factors affecting the performance of the AsA-GSH cycle as well as a further probe into an effective pathway to mediate the cycle.

Acknowledgements This research was supported by Ministry of Agriculture, P. R. of China. Project title: Study on top-working and high-efficient production of pears (Pear 3–38) and by Ministry of Science and Technology, P. R. of China. Project title: Study on high-efficient standardized growing techniques for main fruit crops (No. 2008BAD92B08).

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