Available online at
http://currentagriculturetrends.vitalbiotech.org/

ISSN (E): 2583 – 1933

Curr. Agri.Tren.:e- Newsletter, (2026) *5*(11), 01-05

Current Agriculture Trends: e-Newsletter

Article ID: 773

Ascorbic Acid and Its Multifaceted Role in Plants: A Natural Ally for Healthy Growth and Stress Tolerance

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Article History
Received: 01.11.2026
Revised: 05.11.2026
Accepted: 10.11.2026

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INTRODUCTION

Over-production of reactive oxygen species (ROS) in plants under stress conditions is a common phenomenon. Plants tend to counter this problem through their ability to synthesize ROS neutralizing substances including non-enzymatic and enzymatic antioxidants. In this context, ascorbic acid (AsA) is one of the universal non-enzymatic antioxidants having substantial potential of not only scavenging ROS, but also modulating a number of fundamental functions in plants both under stress and non-stress conditions (Akram *et al.,* 2017). Ascorbic acid (vitamin C) is an abundant component of plants. It reaches a concentration of over 20 m*M* in chloroplasts and occurs in all cell compartments, including the cell wall. It has proposed functions in photosynthesis as an enzyme cofactor (including synthesis of ethylene, gibberellins and anthocyanins) and in control of cell growth (Smirnoff N & Wheeler, G.,2000). To understand how ascorbic acid performs these diverse physiological functions in plants, it is essential to examine its biosynthesis and the metabolic pathways responsible for its production and accumulation in plant tissues.

Biosynthesis of l-Ascorbic Acid in Plants

Some fungi can synthesize erythroascorbic acid, a vitamin C analogue with similar metabolic functions, but among prokaryotes, only blue green algae have been reported to have a small amount of AA (Arrigoni and De Tullio 2002). It also acts directly to neutralize superoxide radicals ($O_2^{\bullet -}$), singlet oxygen ($^1O_2$) or hydroxyl radical (•OH) simply by acting as a secondary antioxidant during the reductive recycling of the oxidized form of α-tocopherol (Noctor and Foyer 1998). In mammals, d-glucuronic acid is generated from d-glucose via the intermediates: d-glucose-1-P, UDP-glucose, UDP-d-glucuronic acid, UDP-d-glucuronic acid-1-P, and d-glucuronic acid. d-Glucuronic acid is then converted to l-gulonic acid by glucuronate reductase which is then converted to gulono-1,4-lactone by aldono-lactonase (gluconolactonase).

l-Ascorbic acid is generated from gulono-1,4-lactone through the action of gulono-1,4-lactone oxidase which produces 2-keto-gulono-*γ*-lactone which spontaneously converts to l-ascorbic acid (Burns., 1967). Although the biosynthetic pathway described above explains ascorbic acid production in mammals, plants possess distinct biosynthetic pathways that enable them to produce this compound, which subsequently plays a vital role in protecting plant cells against oxidative stress

Ascorbic Acid: The Plant's Natural Antioxidant Shield

Ascorbic acid (AsA), or vitamin C, is one of the most abundant, versatile, and effective molecules in plants. Ascorbic acid plays multiple roles: it directly scavenges ROS, regenerates other antioxidants, regulates redox signaling, and participates in hormone biosynthesis and stress signaling cascades. Its biosynthesis primarily occurs through the L-galactose (Smirnoff–Wheeler) pathway, though alternative pathways also contribute under specific conditions. The ascorbate–glutathione cycle further enhances the efficiency of AsA by recycling it in reduced form. Through these mechanisms, AsA protects photosynthetic machinery, stabilizes membranes, and supports cellular homeostasis under diverse stress conditions (Pramanick *et al.,* 2026). Beyond its general antioxidant functions, ascorbic acid also plays a specific role in photosynthesis by donating electrons in key biochemical reactions, thereby contributing to the protection and efficient functioning of the photosynthetic machinery.

AsA Act as an Electron Donor for Photosynthetic Systems

Photosynthesis in plants starts at the thylakoid membrane with two light reactions taking place simultaneously at photosystem I (PSI) and photosystem II (PSII) (Njus *et al.,* 2020, Valero *et al.,* 2016). PSI is a chromoprotein complex composed of multiple protein subunits on the photosynthetic membrane which catalyzes the transfer of electrons from the inside to the outside of the thylakoid membrane (Morgan *et al.,*2006). The photosynthetic electrons are transferred from plastocyanin (PC) to reduced ferredoxin (Fd) (Valero *et al*., 2016). PSII is a photosynthetic unit exerting a water/plastoquinone (PQ) oxidoreductase function in the thylakoid membrane, including the peripheral light-harvesting chromophore protein complex (LHCII), the reaction center (RC) P680, and the manganese complex [Mn_4O_5Ca] (Stirbet *et al.,* 2020).

AsA could supply electrons to PSII in the natural state (Toth *et al.,* 2011). The half-time of electron donation ($t_{1/2}$) to PSII in *Arabidopsis thaliana* AsA-deficient mutant *(vtc2*) leaves is significantly prolonged, reaching 55 ms, while the wild-type is only 25 ms (Toth *et al.,*2009). Furthermore, exogenous supplementation of AsA can restore the $t_{1/2}$ to PSII in *vtc2* mutants to normal levels (Toth *et al.,*2009). Under acidic pH or UV-B conditions, AsA is protoxidized in PSII to replace water as the electron donor (Mano *et al.,* 2004). Additionally, AsA has the ability to donate electrons to PSI in maize bundle sheath cells (Ivanov., 2014). The electron contribution rate from AsA to PSI reaches approximately 50–100 μ equivalents (mg Chl)$^{-1}$ at the AsA concentration of 70–80 mM (Ivanov *et al.,* 2001). Under saturated light conditions, leaf CO_2 uptake is reduced by approximately 50% in two ethyl methane sulfonate-induced AsA synthesis defective mutants (*GGP-5261* and *GGP-49C12*), suggesting that AsA is the main limitation for photosynthesis (Alegre et al., 2020). As photosynthesis proceeds, ATP generation on the inner membrane of the thylakoid is accompanied by the production of harmful reactive oxygen species (ROS, e.g., hydroxyl radical •OH, hydrogen peroxide H_2O_2, superoxide radical $O_2^{\bullet-}$) (Edgar, J.A., 2019). In relation to plant growth, development,

and stress responses, AsA has the action of scavenging ROS by donating electrons (Holler *et al.,* 2015). For example, the growth of axillary buds is in a quiescent state under high H_2O_2 levels in rosebush; in turn, with the rise in AsA content, H_2O_2 scavenging is induced, which finally allows axillary buds to outgrow (Porcher *et al.,* 2020). AsA also contributes to seed development by regulating cellular processes and protecting developing seeds against oxidative stress

Ascorbic acid for healthy seed development

Ascorbate (AsA) is one of the main antioxidants in the cell, but its functions go beyond this in the cell metabolism, acting as a key regulator in plant growth and development. The presence of AsA in plants seems to be indispensable for survival and indeed, plants without ascorbate are inviable (Dowdle *et al.* 2007).

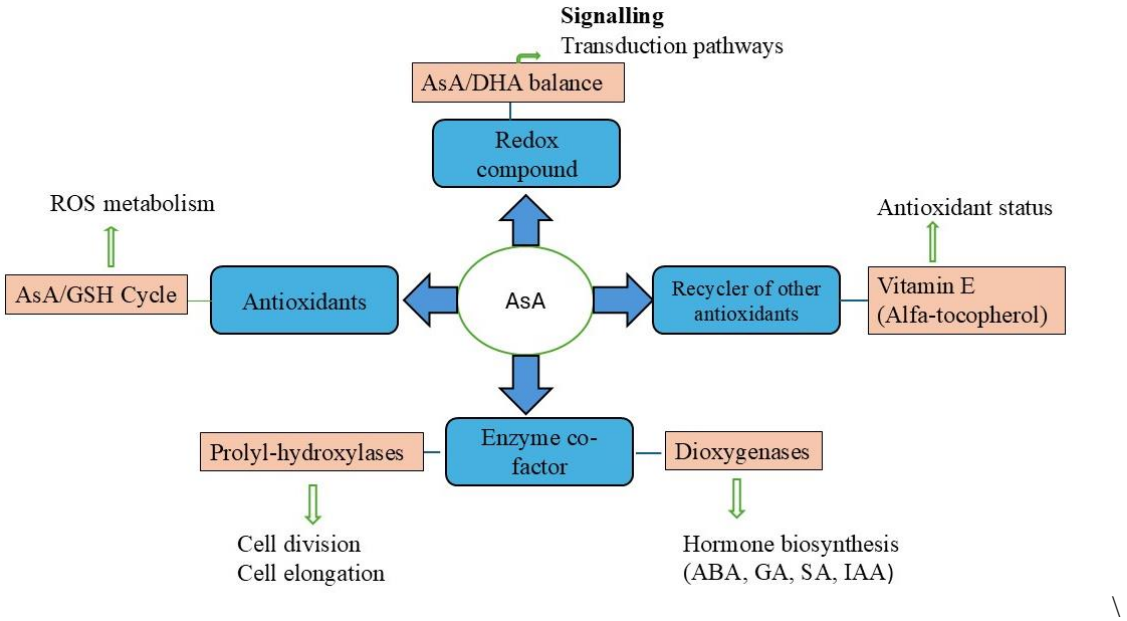


Fig. 1: Ascorbic acid metabolism in plants

The isolation of mutants in the biosynthetic AsA pathway containing less AsA or the application of a biosynthesis inhibitor like lycorine are useful tools for the study of plant development in a low AsA content environment. AsA acts as a cofactor of dioxygenases in the biosynthesis of several phytohormones such as ethylene, gibberellins (GA), auxins (IAA), and abscisic acid (ABA).

Role of AsA in stress conditions

AsA, a powerful non-enzymatic antioxidant, plays a key role in helping plants cope with drought stress by alleviating oxidative damage (Akram *et al.,* 2017). It works by neutralizing ROS, which protects cell membranes and the photosynthetic machinery from harmful effects such as lipid peroxidation and protein breakdown (Rudenko *et al.,* 2023). Additionally, AsA facilitates osmotic adjustment by promoting the accumulation of compatible solutes, such as proline and soluble sugars, which help plants retain water during drought conditions (Khazaei *et al.,* 2020). Furthermore, AsA enhances the activity of vital antioxidant enzymes such as POX and CAT, thereby bolstering the plant's defense mechanism against oxidative stress induced by drought.

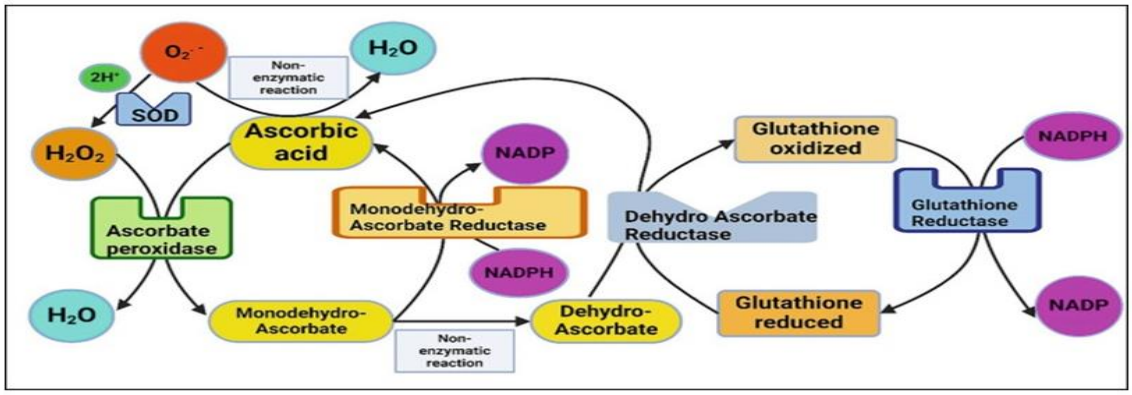


Fig. 2: Role of ascorbic acid in detoxifying ROS

Agricultural Applications

The physiological importance of ascorbic acid has attracted considerable interest among plant physiologists, seed scientists and agricultural researchers. Its potential applications include seed priming, seed coating, foliar application and research aimed at increasing the natural vitamin C content of crops.

Important Precautions and Future Research

Despite its promising functions, ascorbic acid should not be regarded as a universal solution for every agricultural problem. Its effects depend on the crop species, genotype, developmental stage, concentration, application method and prevailing environmental conditions. Excessive or unsuitable treatments may fail to improve plant performance and can sometimes produce adverse effects.

CONCLUSION

Ascorbic acid is a remarkable example of how a single naturally occurring molecule can participate in numerous biological processes. In plants, it functions as an antioxidant, supports photosynthesis, contributes to cell division and expansion, participates in hormone-related pathways and helps regulate responses to environmental stress. At a time when crop production faces increasing pressure from drought, heat, salinity and other environmental challenges, understanding the functions of ascorbic acid may help researchers develop improved approaches to crop establishment and plant stress management.

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