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The Ethylene: From Senescence Hormone to Key Player in Plant Metabolism

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Senescence is a natural process that denotes completion of life cycle after the release of hormones responsible for the process. From evolutionary point of view, senescence was a phenomenon in the populations with the context of natural selection and persistence of plants. The available information from the plant demography and plant biology suggested that plants offer unique comparative studies on senescence. In the mid-1870, it was observed by Girardin [1] that certain trees and varieties of plants were defoliated when exposed to an illuminating gas [2]. Further, Neljubonv [3] suggested that the illuminating gas was ethylene responsible for fall of leaves, and that the olefin was identified as the biologically active component of the illuminating gas. It has been established that high ethylene concentration in plants causes senescence and loss of other plant's functions, such as chlorophyll degradation, decline in photosynthetic enzyme activity and leaf abscission [4-7]. The ability of ethylene to induce senescence and abscission was also considered merely as an interesting and remarkable curiosity. Ethylene-induced senescence was found to be age-related phenomenon that was induced only after the leaves reached at specific developmental stage [8,9]. At the first developmental leaf stage, ethylene production is high and subsequently declines when leaves reach the fully expanded stage, and finally increases again during senescence. It has been found that ethylene precursor; 1-aminocyclopropane-1-carboxylic acid (ACC) content and ethylene production increases in senescing leaves [10]. Later researches on ethylene suggested its contradictory reports on plant functions. The ethylene response is found variable and depends on the plant species because every plant or its part has different sensitivity to ethylene. Moreover, it has been now established that ethylene is an endogenous regulator not only for senescence but also of plant development under optimal and stressful environments. Therefore, it is appropriate to look into whether ethylene controls or influences plants developmental processes.

Recent developments in ethylene biology indicated that ethylene plays important role in the regulation of plant metabolism under both optimal and different stressful environments [11-16] (Table 1).

Ethylene influences many processes of plant growth and photosynthesis [6,14] and plays a crucial role in the adaptation to abiotic stress [12-14]. However, ethylene-regulated photosynthetic processes depend on the sensitivity of plants to ethylene [17]. Studies on ethylene suggested that it has potential to control sulfur metabolism [18], proline metabolism [13], nitrogen metabolism [19], antioxidant metabolism [15], osmolytes function [12,13,15], and photosynthetic attributes and growth [14] under both optimal and stressful environments.

Ethylene can control photosynthetic processes as a result of an altered stomatal conductance [15], allocation of nitrogen and sulfur to Rubisco protein [14,18] or by regulation of osmolytes production [12,13,15]. The effect of ethylene on photosynthesis seems to be concentration dependent [6] and sensitivity of plants [6,14]. Recent studies of Iqbal et al. [20] and Khan and Khan [14] have shown that photosynthesis in ethylene-insensitive *Brassica juncea* was less than ethylene-sensitive type [20]. The protection of photosynthetic inhibition by oxidative stress may also be due to the role of ethylene in controlling redox state of the cell by regulating reduced glutathione (GSH) level. A strong possibility of the involvement of ethylene in regulation of GSH in stress signal transduction concomitant with the regulation of photo-inhibition has been suggested by Yoshida et al. [21] in *Arabidopsis* under ozone stress and Asgher et al. [18] in *Brassica juncea* under Cd stress. Similarly, increased glycine betaine (GB) accumulation together with reduced ethylene under salt stress by SA application was associated with increased GSH content and lower oxidative stress. These results suggested that suppressed ethylene by SA under salt stress induces GB accumulation and enhances antioxidant system resulting in alleviation of adverse effects of salt stress on photosynthesis and growth [15]. Ethylene supply as ethephon application to heavy metals-treated plants lowered ethylene formation to optimal range responsible for maximal GSH synthesis and protection against heavy metals-induced oxidative stress [15,18]. In addition to these aspects ethylene may also influence at maturity stage of the plants. It influences fruit color development and firmness on the basis of concentration of ethylene supplied [22]. Thus, it may be said that ethylene has potential of regulating every aspect of development of plants not only under optimal conditions, but is also responsible for abating stress conditions, although the responses are dependent on its concentration and sensitivity. More studies are needed to unravel the network that controls upon ethylene responses. The classical association of ethylene with senescence phenomenon is unjustified in view of the multidimensional effects of ethylene. This hormone may be aptly called as a key player in development of plants under both optimal and stressful environments.

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Ethylene Concentration	Plant Name	Studied Metabolism	Response of Plant	Reference
0.75, 1.5 mM	*Brassica juncea*	Gas exchange and carbonic anhydrase activity	Up-regulated	[6]
3.0 mM	*Brassica juncea*	Gas exchange and carbonic anhydrase activity	Down-regulated	[6]
1 mM	*Ipomoea batatas*	Chlorophyll content index, Fv/Fm	Down-regulated	[7]
200 µL L^{-1}	*Brassica juncea*	Stomatal conductance, photosynthesis, nitrogen metabolism and growth	Up-regulated	[11]
200 µL L^{-1}	*Brassica juncea*	Antioxidant	Up-regulated	[14]
200 µL L^{-1}	*Brassica juncea*	Sulfur assimilation	Up-regulated	[18]
200 µL L^{-1}	*Brassica juncea*	Photosynthesis and growth	Up-regulated	[20]
500 ppm 1000 ppm 1500 ppm	*Pyrus pyrifolia*	Color development of fruit during ripening, physiological loss in fruit weight	Up-regulated	[22]
500 ppm 1000 ppm 1500 ppm	*Pyrus pyrifolia*	Fruit firmness	Down-regulated	[22]

Table 1: Recent advancement in ethylene-mediated responses in plants.

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