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Review

Current understanding on ethylene signaling in plants: The influence of nutrient availability

Noushina Iqbal [a], *, Alice Trivellini [b], **, Asim Masood [a], Antonio Ferrante [c],
Nafees A. Khan [a]

[a] *Department of Botany, Aligarh Muslim University, Aligarh 202002, India*
[b] *Department of Agriculture, Food and Environment, University of Pisa, Viale delle Piagge 23, 56124 Pisa, Italy*
[c] *Department of Agricultural and Environmental Sciences, Università degli Studi di Milano, Via Celoria 2, 1-20133, Italy*

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ABSTRACT

The plant hormone ethylene is involved in many physiological processes, including plant growth, development and senescence. Ethylene also plays a pivotal role in plant response or adaptation under biotic and abiotic stress conditions. In plants, ethylene production often enhances the tolerance to sub-optimal environmental conditions. This role is particularly important from both ecological and agricultural point of views. Among the abiotic stresses, the role of ethylene in plants under nutrient stress conditions has not been completely investigated. In literature few reports are available on the interaction among ethylene and macro- or micro-nutrients. However, the published works clearly demonstrated that several mineral nutrients largely affect ethylene biosynthesis and perception with a strong influence on plant physiology. The aim of this review is to revisit the old findings and recent advances of knowledge regarding the sub-optimal nutrient conditions on the effect of ethylene biosynthesis and perception in plants. The effect of deficiency or excess of the single macronutrient or micronutrient on the ethylene pathway and plant responses are reviewed and discussed. The synergistic and antagonist effect of the different mineral nutrients on ethylene plant responses is critically analyzed. Moreover, this review highlights the status of information between nutritional stresses and plant response, emphasizing the topics that should be further investigated.

1. Introduction

Ethylene is a simple gaseous plant hormone that regulates several aspects of plant growth and development under optimal and stressful environment. It regulates germination, leaf, stem, and root growth, carbon assimilation, sex determination; fruit ripening, organ abscission, leaf and flower senescence [1]. In addition to its functions in plant growth and development ethylene is also involved in regulating plant responses to both biotic and abiotic stresses.

Ethylene interacts with nutrients uptake and controls plant responses under growth-limiting conditions or stress [2–7]. The interaction between ethylene and nutrients availability has been a concern of many physiologists, but till date a collective study is lacking to discuss the importance of ethylene in relation to different nutrients. The published papers having as subject ethylene and plants in the database of ISI web of knowledge are more than 34,561 from 1950 to 2013. The search of literature performed including the different macro and micronutrients reported few thousands papers. The most part of studies is limited to nitrogen

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Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; ACO, 1-aminocyclopropane-1-carboxylic acid oxidase; ACS, 1-aminocyclopropane-1-carboxylic acid synthase; Al, aluminum; AVG, aminoethoxyvinylglycine; Ca, calcium; CTR1, constitutive triple response 1; Cu, copper; EIN3, ethylene insensitive 3; EIN4, ethylene insensitive 4; EBF1, EIN3 binding F-box 1; EBF2, EIN3 binding F-box 2; ER, endoplasmic reticulum; EGTA, ethylene glycol tetraacetic acid; ERS1, ethylene response sensor 1; ERS2, ethylene response sensor 2; ETP1, EIN2 targeting F-box protein 1; ETP2, EIN2 targeting F-box protein 1; ETR1, ethylene receptor 1; ETR2, ethylene receptor 2; Fe, iron; K, potassium; JA, jasmonic acid; HCN, hydrogen cyanide; IAA, indole acetic acid; MAPK, mitogen-activated protein kinases; (MAPKKK), mitogen-activated protein kinase kinase kinase; Mg, magnesium; Mn, manganese; MTA, 5′-deoxy-5′-methylthioadenosine; N, nitrogen; NH_4, ammonium; P, phosphorus; RAN1, responsive to antagonist 1; ROS, reactive oxygen species; RTE1, reversion to ethylene sensitivity 1; S, sulfur; SAM, S-adenosyl L-methionine; Se, selenium; SOD, superoxide dismutase; Zn, zinc.

* Corresponding author. Tel.: +91 571 2702016.
** Corresponding author. Tel.: +39 050 2216506; fax: +39 050 2216524.
E-mail addresses: naushina.iqbal@gmail.com (N. Iqbal), alice.trivellini@gmail.com (A. Trivellini).

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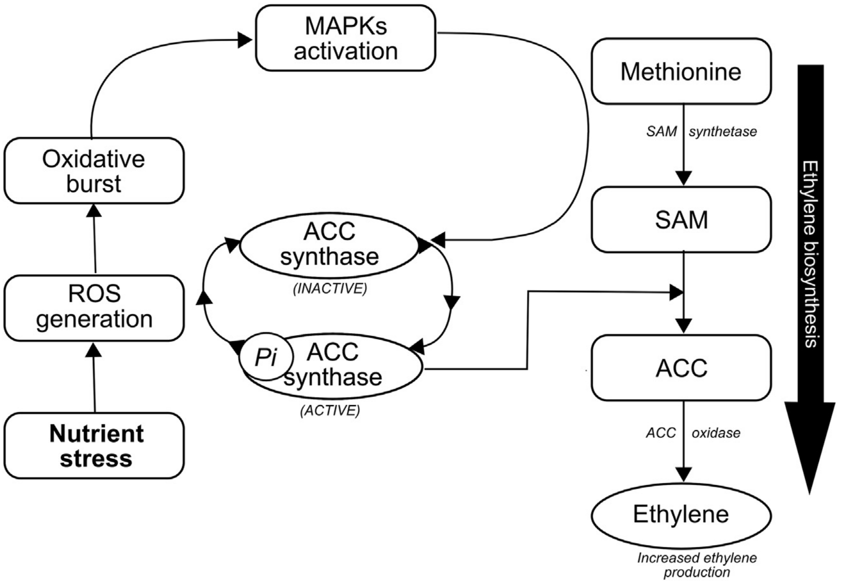

Fig. 1. Nutrient stress causes the accumulation of ROS and results in oxidative burst inside the plant cells. MAPK cascade respond to the resulting oxidative burst and induce the activation/phosphorylation of ACC synthase. The phosphorylated ACC synthase become stabilized and subsequently enhance the production of ethylene.

(N) with 1222 and calcium (Ca) with 1049 published papers. Studies regarding ethylene and selenium (Se) are only 26. These results indicate that there is the interaction between ethylene and nutrients in plants. In the following pages the effect of the availability of nutrients on ethylene pathway and plants' responses is reviewed with emphasis on ethylene signaling under optimal and different nutrient availability.

2. Ethylene biosynthesis and signaling in plants under optimal and stressful environments

Ethylene is a simple hydrocarbon with gaseous nature and because of the simple structure of ethylene, a number of compounds are proposed as its precursors, including linolenic acid, propanal, β-alanine, and methionine. However, later it was discovered that methionine was the precursor of ethylene in a chemical model system and showed that ethylene was derived from C_3 and C_4 of methionine [8]. Yang and Hoffman [8] brought about the major discovery in ethylene biosynthesis by reporting the role of S-adenosyl L-methionine (SAM) and 1-aminocyclopropane-1-carboxylic acid (ACC) as the precursors of ethylene in plants.

Under optimum conditions the biosynthesis of ethylene occurs through a relatively simple metabolic pathway that has been extensively studied and well documented in plants [8,9]. Ethylene is derived from the amino acid methionine. The methionine is converted to SAM by the enzyme SAM synthetase. The SAM is then converted to ACC and 5′-deoxy-5′-methylthioadenosine (MTA) by ACC-synthase (ACS). The conversion of SAM to ACC is the rate-limiting step in the biosynthetic pathway. The ACC-oxidase (ACO) catalyzes the conversion of ACC to ethylene. Thus, these two enzymes (ACS and ACO) are the most important in the formation and oxidation of the immediate precursor of ethylene i.e. ACC. The final conversion of ACC to ethylene is oxygen dependent [9] and yields CO_2 and cyanide as by-products. The conversion of ACC to ethylene catalyzed by ACO is oxygen dependent, and, under anaerobic conditions, ethylene formation is completely suppressed. In this reaction, Fe^{2+} and ascorbate are required as a cofactor and a co-substrate, respectively. The other reaction product, MTA must be recycled back into the methionine pathway to provide an adequate supply of methionine as substrate for the continual production of ethylene. The poisonous gas hydrogen cyanide (HCN) formed from the decomposition of ACC to ethylene is detoxified by β-cyanoalanine synthase.

Plants exposed to environmental stresses speed up their ethylene production rate. Various types of stresses enhance production of ethylene from plant tissues [1]. However, the mechanism of ethylene biosynthesis is the same under stress such as under optimum conditions. Under nutrient stress conditions plant accumulates ROS (reactive oxygen species) and results in oxidative burst inside the plant cells. This leads to activation of mitogen-activated protein kinases cascade (MAPK) in response to the oxidative burst, and induces the activation/phosphorylation of ACC synthase the enzyme involved conversion of SAM to ACC [10]. The phosphorylated ACC synthase becomes stabilized and subsequently enhances the production of ethylene (Fig. 1).

Stearns and Glick [11] through a model explained the seemingly paradoxical effects of ethylene-stress induced on plants emphasizing the fact that in stressed plant tissues there is an initial small peak of ethylene close to the onset of stress and then a second much larger peak later. The first small peak is thought to initiate a protective response by the plant, such as transcription of pathogen-related genes [12]. It is thought to consume the existing pool of ACC in plant tissues, in the meantime the transcription of ACS genes is activated and more ACC begins to accumulate as fuel for the second wave of ethylene production [13]. This occurs due to the regulation of ACS genes by environmental and developmental cues and the enhancement of its enzymatic action during stress conditions [8]. Therefore, if the ethylene production might be modulated also the stress related injuries might be reduced.

The ACS and ACO enzymes are encoded by multigene families in response to external and internal stimuli. Their activities are controlled at the transcriptional and posttranscriptional level. In plants, ethylene biosynthesis is controlled by two systems: the ethylene auto-inhibitory system 1, which generally operates during normal vegetative growth of plant; and system 2, regulated by a positive feedback mechanism, usually responsible for the rapid increase in ethylene production in senescing ethylene-sensitive plant organs, and in ripening climacteric fruits [14–16].