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Review

Higher polyamines restore and enhance metabolic memory in ripening fruit

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Abstract

Polyamines are ubiquitous, biogenic amines that have been implicated in diverse cellular functions in most living organisms. Ever since spermine phosphate crystals were isolated over three centuries ago, scientists have kept busy in unraveling the mystery behind biological roles of spermine and other known polyamines, viz., putrescine and spermidine. Although the pathway of polyamine biosynthesis has been elucidated, the molecular basis of their *in vivo* function is far from being understood. Molecular biology tools have provided a promising avenue in this direction, with success achieved in altering endogenous polyamines in plants by over-expression and knock-out of the genes responsible for polyamine biosynthesis. Such transgenic material has become a good genetic resource to learn about the biological effects of polyamines and their interaction with other signaling molecules. Interestingly, engineered accumulation of higher polyamines, spermidine and spermine, in tomato in a fruit-specific manner restored metabolic activity even at late developmental stages of fruit ripening, reviving cellular programs underlying N:C signaling, energy and glucose metabolism. Along with these, a wide array of genes regulating transcription, translation, signal transduction, chaperone activity, stress proteins, amino acid biosynthesis, ethylene biosynthesis and action, polyamine biosynthesis, isoprenoid pathway and flavonoid biosynthesis was activated. Based on various reports and our results, we suggest that polyamines act as 'surrogate messengers' and nudge other signaling molecules, such as plant hormones and NO, to activate a vast genetic network to regulate growth, development and senescence.

Keywords: Spermidine; Spermine; Transcriptome; Metabolome; Fruit ripening; Nitrogen:carbon signaling

Contents

1. Introduction

Polyamines are ubiquitous, aliphatic polycation class of biogenic amines with essential functions in living organisms. The most common plant polyamines are the diamine putrescine and the higher polyamines spermidine and spermine. Anton Leeuwenhoek was the first to observe crystals of spermine phosphate in human semen as early as 1678, predating the discoveries of the defense signaling molecule nitric oxide (1772) and plant hormone ethylene (1794) (see [1] for historical time line). Putrescine was identified more than two centuries later while spermidine was discovered only in 1927. Spermine and spermidine were early examples of trimethylenediamine

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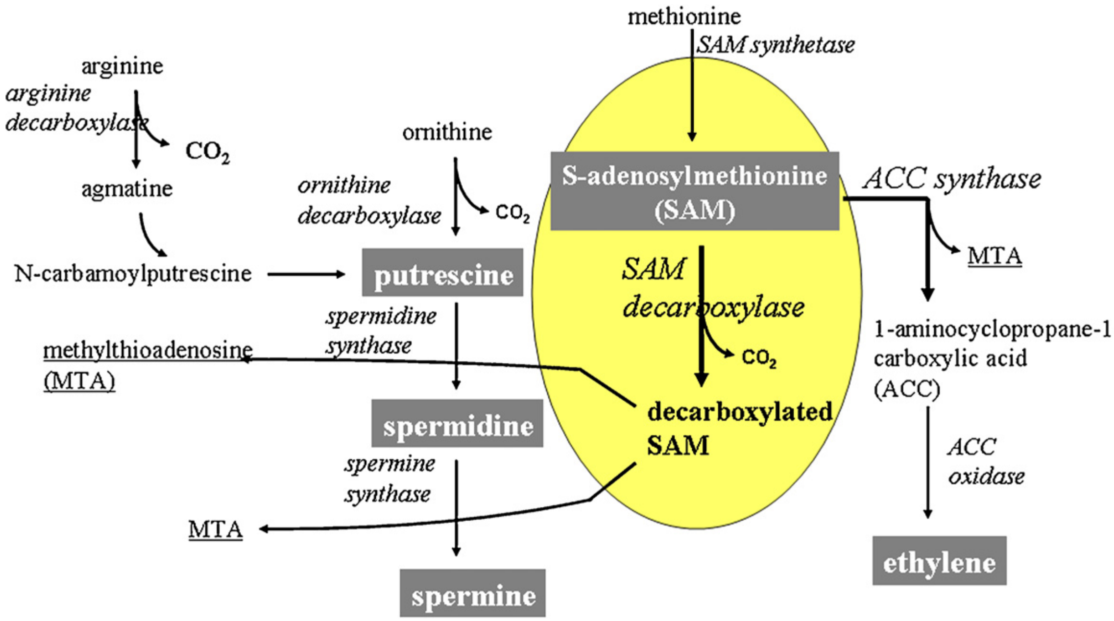

Fig. 1. The biosynthetic pathways of polyamines and ethylene in plants. Shown are precursors, intermediates and enzymes (in italics) involved. S-adenosylmethionine (SAM), formed from methionine by SAM synthetase, is decarboxylated by SAM decarboxylase. Decarboxylated SAM provides aminopropyl groups that are used by spermidine synthase and spermine synthase to synthesize, respectively, spermidine from putrescine and spermine from spermidine, and a common product methylthioadenosine (MTA; underlined). Putrescine is formed from arginine and/or ornithine by arginine decarboxylase and ornithine decarboxylase, respectively. SAM is also a substrate for 1-aminocyclopropane-1-carboxylic acid (ACC) synthase, forming ACC and MTA. ACC is then converted to ethylene by ACC oxidase. Both these pathways, therefore, use SAM as a substrate and MTA as a product. MTA is readily metabolized and recycled to methionine.

derivatives among natural products. We are only now beginning to understand their role in growth, development and senescence through molecular genetics and modern biochemical approaches. Polyamines have been implicated in a myriad of biological processes including cell proliferation, cell division and differentiation, apoptosis, homeostasis, gene expression, protein and DNA synthesis [1–5]. The list gets longer when processes implicated in plants are considered: cell division, cell elongation, embryogenesis, root formation, floral initiation and development, fruit development and ripening, pollen tube growth and senescence, and in response to biotic and abiotic stress [1–4]. Interest in polyamine research has further intensified because of their (and polyamine analogs') potential involvement and implications in such diverse disciplines as oncology [6], obesity [7], gastroenterology [8], cerebral stroke and other disorders [9], parasitology [10], oxidative stress [9,11,12], apoptosis (programmed cell death) [8,13], and plant developmental processes [2–4,12,14]. Applications in pharmacology and medicine, including cancer therapy and as anticancer agents [6,11,15] are exciting new avenues for polyamine research. Likewise, the elucidation of the roles polyamines play in modulating pre- and postharvest biology will contribute to the development of functional foods using modern biotechnology [16,17].

The biosynthesis pathway and genes encoding the enzymes catalyzing these pathway reactions have been elucidated and identified in both prokaryotes and eukaryotes, as reviewed in [1–4,10,18]. In addition to putrescine, spermidine and spermine, flowering plants also synthesize cadaverine, 1,3-diaminopropane, and other modified forms [1]. An isomer of spermine, thermospermine, has been found widespread in bacteria and higher plants [19]. In plants, putrescine is formed from either arginine via an intermediate agmatine, a reaction catalyzed by arginine decarboxylase, or from ornithine by ornithine decarboxylase. Spermidine is synthesized from putrescine and the aminopropyl group donated by decarboxylated S-adenosylmethionine (SAM), which is a product of SAM decarboxylation (Fig. 1). In turn, spermidine incorporates another aminopropyl group (from decarboxylated SAM) to form spermine. SAM is a key intermediate for another plant growth regulator that controls ripening of fruits, ethylene [20–22]. Ethylene is synthesized from SAM by a sequential action of two ethylene-biosynthesis enzymes, 1-aminocyclopropane-1-carboxylate (ACC) synthase and ACC oxidase (Fig. 1). It would appear that a living cell has the potential to commit the flux of SAM either into polyamine biosynthesis, ethylene biosynthesis, or both. Our foray into polyamine research was catalyzed by studies, first published in early 1980s, which showed that polyamines inhibit ethylene biosynthesis in a variety of fruit and vegetative tissues [23–26]. These studies brought to light a possible temporal relationship between polyamines and ethylene during plant development, which led to suggestions that changes in the levels of polyamines and ethylene may influence specific physiological processes in plants [1–4]. One of these papers, published in Plant Science Letters in 1982 [24], reported that Ca^{2+} and spermine inhibited ethylene biosynthesis in a temperature-dependent manner which was related to the prevention of decreased membrane microviscosity associated with ripening and senescence. A quarter century later, down regulation of spermine in a mutant of *Arabidopsis* was found to cause hypersensitivity to NaCl possibly via Ca^{2+}-homeostasis impairment [27]. Salt tolerance