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Review

Health effects and occurrence of dietary polyamines: A review for the period 2005–mid 2013

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ABSTRACT

This review continues a previous one (Kalač & Krausová, 2005). Dietary polyamines spermidine and spermine participate in an array of physiological roles with both favourable and injurious effects on human health. Dieticians thus need plausible information on their content in various foods. The data on the polyamine contents in raw food materials increased considerably during the reviewed period, while information on their changes during processing and storage have yet been fragmentary and inconsistent. Spermidine and spermine originate mainly from raw materials. Their high contents are typical particularly for inner organs and meat of warm-blooded animals, soybean and fermented soybean products and some mushroom species. Generally, polyamine contents range widely within the individual food items.

Contents

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1. Introduction

The category of biologically active, or physiological, polyamines (PAs) consists of putrescine (PUT; 1,4-diaminobutane), spermidine (SPD; *N*-(3-aminopropyl)-1,4-diaminobutane) and spermine (SPM; *N*,*N*′-bis-(3-aminopropyl)-1,4-diaminobutane) (Fig. 1). The polyamines were traditionally classified within the group of biogenic amines, however, they have been set apart as a peculiar group since the 1990s, particularly due to their different formation and specific roles in eukaryotic cells. Putrescine, being structurally a diamine, is classified in both groups. It is widely formed as a "true" biogenic amine by the decarboxylation of amino acid ornithine, but it is also an intermediate in SPD and SPM biosynthesis. Nevertheless, biogenic diamine cadaverine produced by enzymatic decarboxylation of lysine does not rank among physiological PAs, similar to agmatine, formed by enzymatic decarboxylation of arginine.

The polyamines are ubiquitous, widespread from bacteria to mammals. Their participation in cell growth and proliferation has been of primary interest. The knowledge of the main roles of PAs in health, disease and ageing was reviewed (Larqué, Sabater-Molina, & Zamora, 2007; Wallace, 2009), and various aspects of polyamine physiological effects in man were covered in a book by Dandrifosse (2009a). Body pool of the PAs is maintained by three sources: (i) endogenous (*de novo*) biosynthesis, (ii) production by intestinal bacteria or from constituents of epithelial cells shed into the gut lumen, and (iii) dietary intake. Diet provides a larger daily quantity of PAs than does endogenous biosynthesis. Dietary PAs are completely absorbed, so diet may be a useful source of these substances (Bardócz, 1995). Despite both polyamine daily cellular requirement and optimum levels of dietary intake being until now undetermined, plausible data on PAs content in foods and beverages are necessary for the estimation of their intake.

The aim of the review is to collect and evaluate data on dietary PAs published since 2005. The review follows a previous one (Kalač & Krausová, 2005).

2. Polyamines synthesis, homeostasis and catabolism

This chapter gives an overall characterisation, as it deals with biochemical and medical topics. Partial reviews will therefore be preferentially cited and the reader is directed to them and the references therein.

Polyamine homeostasis in mammalian cells is achieved by a complex network of regulatory mechanisms affecting both synthesis and degradation, as well as membrane transport of PAs. Depletion of cellular PAs rapidly induces an increased uptake of exogenous PAs, whereas an excess of PAs down-regulates the polyamine transporter(s).

Polyamine biosynthesis is an ancient metabolic pathway present in all living organisms. Their homeostasis is necessary for cell

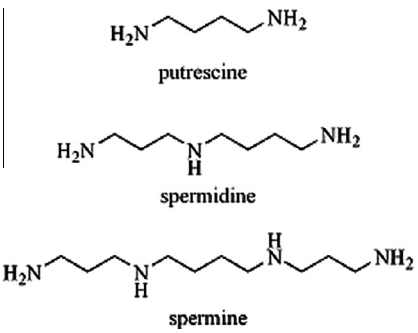

Fig. 1. Formulae of polyamines.

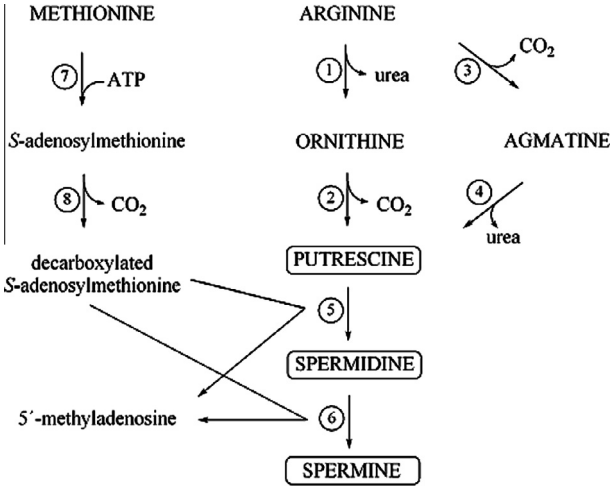

Fig. 2. A simplified scheme of polyamine biosynthesis pathways (Kalač, 2010). The pathway via agmatin, known in bacteria and plants, was proposed also for mammals. Methionine is a donor of aminopropyl unit for spermidine and spermine formation. Putrescine is an intermediate of spermidine and spermine biosynthesis. Participating enzymes: (1) arginase (EC 3.5.3.1); (2) ornithine decarboxylase (EC 4.1.1.17); (3) arginine decarboxylase (EC 4.1.1.19); (4) agmatinase (EC 3.5.3.11); (5) spermidine synthase (EC 2.5.1.16); (6) spermine synthase (EC 2.5.1.22); (7) adenosyltransferase (EC 2.5.1.6); (8) S-adenosyl-L-methionine decarboxylase (EC 4.1.1.50).

survival. Its deregulation is involved in illnesses, such as cancer or neurodegenerative disorders. In healthy cells, PAs level are intricately controlled by biosynthesis and catabolic enzymes (Pegg, 2009). The biosynthesis uses the amino acids arginine, ornithine and methionine. A simplified scheme is given in Fig. 2. The pathway starts with the production of ornithine from arginine by the mitochondrial enzyme arginase. Ornithine is then decarboxylated by one of the key enzymes, ornithine decarboxylase, to produce PUT. In parallel to PUT formation, L-methionine is converted into S-adenosyl-L-methionine (AdoMet). It is then decarboxylated by another key enzyme, S-adenosyl-L-methionine decarboxylase, to produce decarboxylated AdoMet. This compound is then used as a donor of aminopropyl group to either PUT (by spermidine synthase) to produce SPD, or to SPD to produce SPM (by spermine synthase).

SPD and SPM can be converted back to PUT. The rate-limiting catabolic enzyme is cytosolic N^1-acetyltransferase (SSAT), which acetylates both SPM and SPD. The acetylated polyamines then move into the peroxisome where they are oxidised by polyamine oxidase. SSAT is necessary for the formation of PUT from SPD. SPM can also be back-converted into SPD by spermine oxidase in the cytoplasm (Minois, Carmona-Gutierrez, & Madeo, 2011). Polyamine transport plays an essential role in PA regulation. Despite substantial research, no polyamine transporter has been identified in mammals until now. Alternatively, it is thought that PAs uptake in mammals could be performed by endocytosis (Minois et al., 2011).

3. Biological roles in man

PUT, SPD and SPM, under physiological conditions, are strong flexible polycations exhibiting 2, 3 or 4 positive charges, respectively (see Fig. 1). They are able to interact with negatively charged macromolecules such as nucleic acids, phospholipids and proteins. These ionic interactions, which are reversible, lead to the stabilisation of DNA, RNA, membranes and some proteins (Sánchez-Jiménez, Ruiz-Pérez, Urdiales, & Medina, 2013). This determines PAs as the essential factors for the growth, maintenance and function of normal cells.