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Review

Biological functions of asparagine synthetase in plants

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ABSTRACT

Ammonium is a form of inorganic nitrogen derived from several metabolic pathways, and is assimilated into glutamine, glutamate, asparagine and carbamoylphosphate. These molecules play important roles in nitrogen assimilation, recycling, transport and storage in plants. Ammonium assimilation into asparagine is catalyzed by ammonia-dependent asparagine synthetase encoded by *asnA* (EC 6.3.1.1) or glutamine-dependent asparagine synthetase encoded by *asnB* (EC 6.3.5.4) in prokaryotes and eukaryotes. These organisms display a distinct distribution of these two forms of asparagine synthetase. Gene and primary protein structure for asparagine synthetase-A and -B from prokaryotes and eukaryotes is examined. Using nucleotide sequences, we constructed a phylogenetic tree that distinguished two major classes (classes I and II) for *ASN* genes from a range of organisms. Only the glutamine-dependent asparagine synthetases-B have been identified, and are encoded by a small multigene family in plants. The isoenzyme encoded by each member of the gene family provides asparagine at specific phases of development. These include the nitrogen mobilization in germinating seeds, nitrogen recycling in vegetative organs in response to stress, and nitrogen remobilization during seed embryogenesis. The expression of genes for asparagine synthetase is regulated by light and metabolites. Genetic and molecular data using mutants and transgenic plants have provided insights into the light perception by the photoreceptors, carbon and nitrogen sensing and signal transduction mechanism in the *asn* regulation. Global analysis of carbon and nitrogen metabolites supports the impact of *asn* regulation in the synthesis and transport of asparagine in plants.

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1. Introduction

Plants take up inorganic nitrogen in the form of nitrate and ammonium in the soil and dinitrogen in the atmosphere. Ammonium is the final form of inorganic nitrogen derived from primary nitrate reduction mediated by nitrate reductase (NAD[P]H-NR, EC 1.6.6.1; EC 1.6.6.2; EC 1.6.6.3) and ferredoxin (Fd)-nitrite reductase (Fd-NiR, EC 1.6.6.4) (Fig. 1). Ammonium derives also from absorption from the soil and symbiotic dinitrogen fixation in root nodules of leguminous plants. Irrespective of the metabolic pathways, ammonium is mainly assimilated into glutamine and glutamate *via* glutamine synthetase (cytosolic GS1 and plastidial GS2, EC 6.3.1.2) and glutamate synthase (Fd-GOGAT, EC 1.4.7.1; NADH-GOGAT, EC 1.4.1.14), known as the GS/GOGAT cycle (Fig. 1). Asparagine synthetase (EC 6.3.1.1 and EC 6.3.5.4) needs energy producing hydrolysis of ATP and catalyzes the asparagine synthesis by amidation of aspartate using either glutamine or ammonium as an amino donor [1] (Fig. 1). Plants can also incorporate ammonium into carbamoylphosphate by carbamoylphosphate synthetase (CPSase, EC 6.3.5.5) which utilizes either glutamine or ammonium as an amino donor [2,3] (Fig. 1). Alternatively, glutamate dehydrogenase (NADH-GDH, EC 1.4.1.2) might assimilate ammonium into glutamate, while several lines of evidence indicate that the enzyme catabolizes glutamate into 2-oxoglutarate and ammonium [4–6] (Fig. 1). Asparagine and glutamine serve as the major nitrogen transport and storage compounds from source to sink organs of most non-leguminous plants [7] (Fig. 1). Asparagine is an optimal nitrogen transport and reserve compound due to its high nitrogen/carbon ratio and stability. In particular, asparagine is the major amino acid translocated in the xylem from roots to leaves of legumes such as alfalfa, pea, clovers and trefoil [8–10].

In this review, we first describe the current information on the asparagine synthesis and its distribution in different organisms. Then the structure and reaction mechanism of asparagine synthetase are examined on the basis of molecular and biochemical data. Finally, we discuss their physiological roles in the nitrogen mobilization in germinating seeds, ammonium (re)assimilation in leaves, and nitrogen remobilization from senescent leaves to developing seeds.

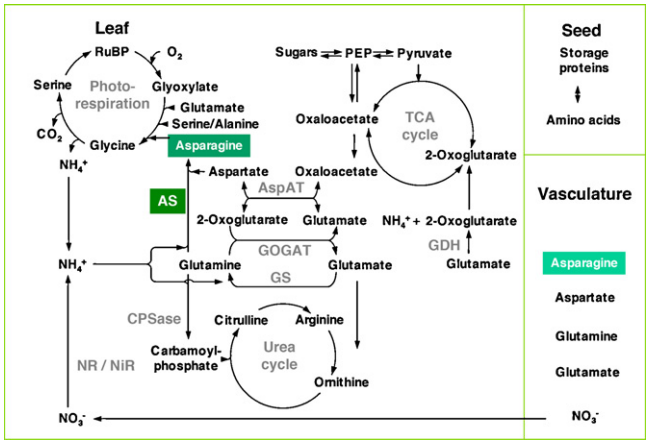

Fig. 1. Interaction of asparagine and asparagine synthetase in the nitrogen assimilation, photorespiratory nitrogen cycle and nitrogen translocation. The stoichiometry of the interconnected enzymatic reactions and organelle localization are not included. AS: asparagine synthetase (EC 6.3.5.4), AspAT: aspartate aminotransferase (EC 2.6.1.1), CPSase: carbamoylphosphate synthetase (EC 6.3.5.5), GDH: glutamate dehydrogenase (EC 1.4.1.2), GOGAT: glutamate synthase (EC 1.4.7.1, EC 1.4.1.14), GS: glutamine synthetase (EC 6.3.1.2), NiR: nitrite reductase (EC 1.6.6.4), NR: nitrate reductase (EC 1.6.6.1), PEP: phospho*enol*pyruvate, RuBP: ribulose 1,5-bisphosphate. Adapted from Potel et al. [3].

2. Asparagine synthesis pathways

Asparagine synthetase catalyzes an ATP-dependent transfer of ammonia to aspartate yielding asparagine in the presence of magnesium ion. The amide group of glutamine or ammonium serves as the amide nitrogen donor. Aspartate derives from transamination of oxaloacetate (Fig. 1) and is a precursor of the essential amino acids: lysine, threonine, methionine and isoleucine. There is also evidence that cyanide (HCN) could be a nitrogen donor for asparagine synthesis by another pathway. Cyanide is formed as a byproduct of the ethylene synthesis [11,12] and also of the conversion of glyoxylate and hydroxylamine to cyanide [13]. Cyanide and cysteine are converted to β-cyano-L-alanine and sulfide (H_2S) by β-cyanoalanine synthase (EC 4.4.1.9), which has been detected in plants [14]. β-Cyanoalanine is hydrolyzed to asparagine by β-cyanoalanine hydratase (EC 4.2.1.65) [15]. This alternative asparagine synthetic pathway may be limited by the availability of cyanide and cysteine in plant cells [16]. Asparagine may also be formed by a third pathway *via* the transamination of 2-oxosuccinamic acid in a reverse reaction by asparagine:oxoacid transaminase (EC 2.6.1.14). However, the asparagine synthesis through this reaction appears to be of a low magnitude in plants [17].

3. Occurrence in prokaryotes and eukaryotes

Asparagine synthetases have been identified and characterized from prokaryotes and eukaryotes. In prokaryotes such as *Escherichia coli* and *Klebsiella pneumoniae* [18], asparagine is formed by two structurally distinct asparagine synthetases (National Center for Biotechnology Information: http://www.ncbi.nlm.nih.gov/). One is ammonium-dependent asparagine synthetase-A (AS-A, EC 6.3.1.1) encoded by *asnA* [19] (reaction 1). The other is glutamine-dependent asparagine synthetase-B (EC 6.3.5.4) encoded by *asnB* [20]. Asparagine synthetase-B can use either glutamine or ammonium, while glutamine is a preferred amide donor (reaction 2):

1. Asparagine synthetase-A (*asnA*):

$$\text{Reaction1} \qquad NH_4^+ + \text{L-Asp} + ATP \rightarrow \text{L-Asn} + AMP + PPi$$

2. Asparagine synthetase-B (*asnB*):

$$\text{Reaction2} \qquad \text{L-Gln}[\text{or}NH_4^+] + \text{L-Asp} + ATP \rightarrow \text{L-Asn} + \text{L-Glu} + AMP + PPi$$

The *asnA* gene is found only in prokaryotes such as *E. coli* [21,22]. *asnB* is present in both prokaryotes and eukaryotes including mammals [23,24], *Saccharomyces cerevisiae* [25,26], *Chlamydomonas reinhardtii* [27] (National Center for Biotechnology Information: http://www.ncbi.nlm.nih.gov/) and a wide variety of higher plants [28].

4. Gene and primary protein structure

A search of the complete genomic sequence of *E. coli* identified two asparagine synthetase genes, *asnA* and *asnB*, which are located on the chromosome at 84 and 16 min, respectively [18,29]. The *E. coli asnA* gene consists of 990 nucleotides, which encode a polypeptide of 330 amino acids with a molecular mass of 36.7 kDa [19]. *asnB* is composed of 1662 nucleotides, and the deduced 554 amino acid-polypeptide has a molecular mass of 62.7 kDa [20]. Genome analysis of another bacterium, *Bacillus subtilis*, predicted three asparagine synthetase genes, *asnB*, *asnH* and *asnO*, but no *asnA* gene was identified [30,31]. *asnB*, *asnH* and *asnO* encode polypeptide of 72.5 kDa, 85.7 kDa and 70.6 kDa, respectively. AsnB, AsnH and AsnO proteins are orthologous to asparagine synthetase-B of *E.*

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