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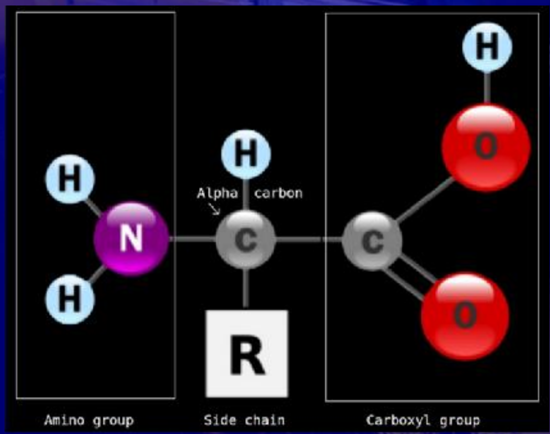
Plant Biochemistry
Lecture 10: AMINO ACIDS I



LEARNING OUTCOMES

Students, after mastering materials of the present lecture, should be able

1. to explain molecule structure, classification and biosynthetic pathway of amino acids (AA).
2. to explain the nitrate reduction as the initial reaction of AA biosynthesis.
3. to explain GS/GOGAT cycle and GS isoenzymes in the AA biosynthesis.
4. to explain Fd-GOGAT Role in Photorespiration in relation to AA biosynthesis.
5. to explain GDH Catabolic Role and N Assimilation-Controlling Isoenzymes in relation to AA biosynthesis.
6. to explain Light and Asparagine Biosynthesis in relation to AA biosynthesis.

LECTURE OUTLINE

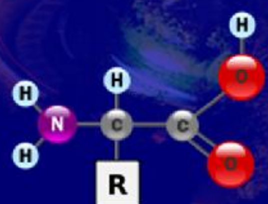
1. INRODUCTION
1. Definition
2. Functions
3. Classification
3. Biosynthesis Pathways

2. AMINO ACID BIOSYNTHESIS
1. Nitrate Reduction
2. Glutamate and Glutamine
3. GS/GOGAT Cycle
4. GS Isoenzymes
5. Fd-GOGAT Role in Photorespiration
6. GDH Catabolic Role
7. N Assimilation-Controlling Isoenzymes
8. Light and Asparagine Biosynthesis

1. INTRODUCTION

1. Definition

- Amino acids are compounds that contain amine (-NH_2) and carboxyl (-COOH) functional groups that are each attached to α carbon, along with a side-chain (R group) specific to each amino acid.



R : hydrocarbon alkyl groups (alkane branches) or aromatic (benzene rings) are non-polar.
R : various functional groups (acids, amides, alcohols, and amines) are polar.

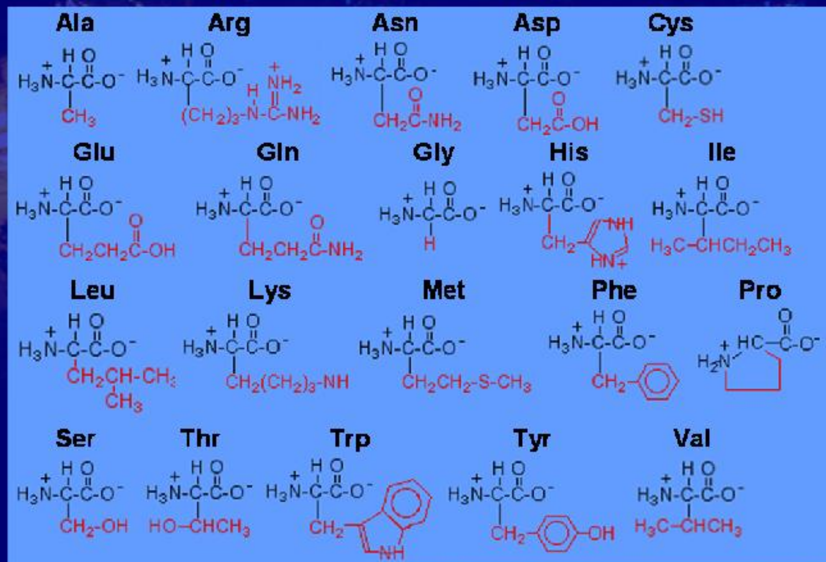
- Asparagine is the first amino acid isolated from asparagus by Louis-Nicolas Vauquelin and Pierre Jean Robiquet, French chemists, in 1806.

2. Amino Acid Functions

- In addition to their role in protein synthesis, amino acids perform essential functions in both primary and secondary plant metabolism. Some amino acids serve
  - to assimilate nitrogen (N) and transport it from sources to sinks
  - as precursors to phytohormones, such as indoleacetic acid and ethylene, or to an immense variety of secondary compounds involved in the interaction of plants with their abiotic and biotic environments.
- A growing body of literature leads to a new concept of functional AA, which are defined as those AA that regulate key metabolic pathways to improve health, survival, growth, development, lactation, and reproduction of organisms.

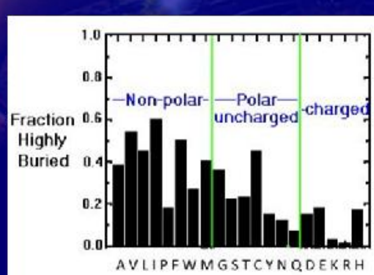
3. Classification

- Of over 700 types of amino acids (AA) found in nature and almost all of the AA are α-amino acids, plants produce several hundreds structurally diverse, nonproteinogenic amino acids with no obvious roles in protein synthesis.
- Only 20 amino acids appear in the genetic code, known as "proteinogenic" amino acids which are all L-α-amino acids of the general structure **R-CαH(NH_2)COOH**, with the exception of proline, which is a cyclic secondary amino acid.
- Amino acids are often classified as nonessential and essential AA (His, Ile, Leu, Lys, Met, Phe, Thr, Trp & Val) which are not synthesized (adequately) in animal and human body.



Proteinogenic amino acids:

- Other classification is based on the nature of side chains:
  - (1) Neutral and non-polar (Ala, Gly, Ile, Leu, Met, Phe, Pro, Val),
  - (2) Neutral and polar (Asn, Cys, Gln, Ser, Thr, Trp, Tyr),
  - (3) Acidic and polar (Asp, Glu), and
  - (4) Basic and polar (Arg, His, Lys)



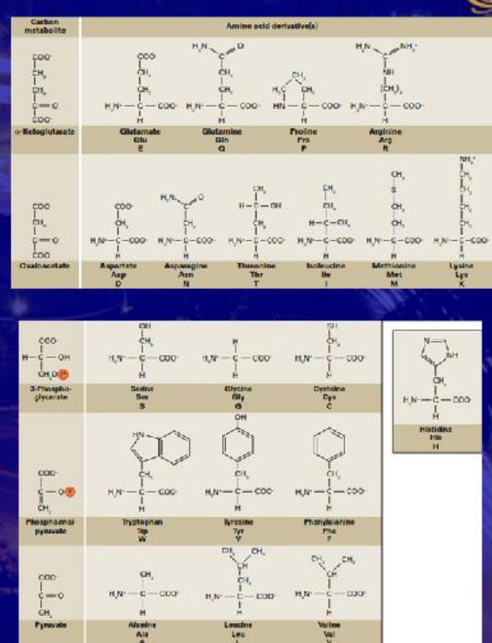
Ala (A), Arg (R), Asn (N), Asp (D), Cys (C), Glu (E), Gln (Q), Gly (G), His (H), Hyp (O), Ile (I), Leu (L), Lys (K), Met (M), Phe (F), Pro (P), Glp (U), Ser (S), Thr (T), Trp (W), Tyr (Y), and Val (V)

Hydrophobic amino acids are mostly buried within the core of the structure, and a smaller fraction of polar groups are found to be buried. Charged residues are exposed to solvent to a much higher degree.

4. Biosynthesis Pathways

- The carbon skeletons used by plants for amino acid biosynthesis are derived from intermediates of glycolysis, photosynthetic carbon reduction, the oxidative pentose phosphate pathway, and the citric acid cycle (Fig 7.1). This can be used also to classify amino acids as follows;
  - α-ketoglutarate (Citric Acid Cicle): Glutamate, Glutamine, Proline & Arginine
  - Oxaloacetate (Citric Acid Cicle): Aspartate , Asparagine, Threonine, Isoleusine, Methionine & Lysine,
  - 3-phosphoglyceraten (Glycolysis): Serine, Glycine & Cysteine,
  - Phosphoenolpyruvate (Glycolysis): Tryptophan, Tyrosine & Phenylanaline,
  - Pyruvate (Glycolysis): Alanine, Leucine & Valine.
  - Ribose 5-phiosphate (oxidative pentose phosphate cycle): Histidine

FIGURE 7.1 Organic acid products of glycolysis, the **citric acid cycle**, and the **Calvin-Benson cycle** provide the **carbon skeletons** from which 19 of the 20 standard amino acids are synthesized. Not shown is erythrose 4-phosphate, a substrate in the synthesis of all three aromatic amino acids, and ribose 5-phosphate, a substrate in both histidine and tryptophan synthesis (see Fig 7.2). Histidine is a special case, because formation of the carboxyl group is the last step in its biosynthesis. In this scheme, amino acids are arranged in relation to their respective common organic acid precursor. In textbooks of biochemistry, you usually find amino acids arranged with respect to side chain hydrophobicity. Both the one- and three-letter codes, respectively, are indicated



- The pathways generally accepted for amino acid biosynthesis in plants (Fig 7.2) have been inferred in large part from those defined for bacteria and fungi.
- The pathways were identified through the combined use of auxotrophic mutants, isotopically labeled precursors, enzyme studies, and the analysis of the corresponding genes.

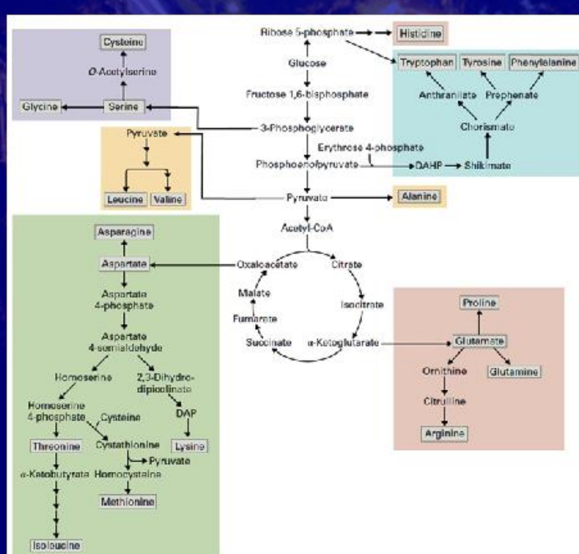


Fig 7.2 Overview of the biosynthesis of the 20 proteinogenic amino acids in plants.

Biosyntheses of serine, glycine, and cysteine are referred to in Chapters 14 and 16, respectively. Alanine is derived from the glycolysis intermediate pyruvate in a single transamination step. Ribose-5-phosphate is produced in the oxidative pentose phosphate cycle.

2. AMINO ACID BIOSYNTHESIS

1. Nitrate Reduction

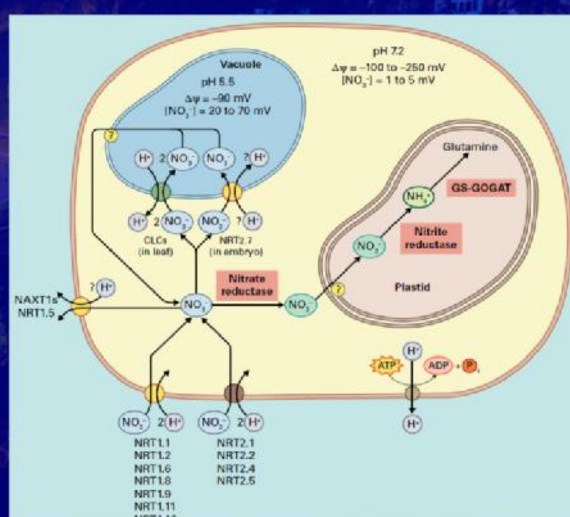
- The biosynthesis of amino acids is initiated by nitrate (NO_3^-) reduction followed by nitrite (NO_2^-) reduction to ammonium (NH_4^+) (Fig. 16.30).

NO_3^- + NAD(P)H + $8H^+$ ì NO_2^- + $NAD(P)^+$ + H_2O

NO_2^- + $6Fdx_{red}$ +$8H^+$ ì NH_4^+ + $6Fdx_{ox}$ + $2H_2O$

- The NO_3^- and NO_2^- reduction is catalyzed subsequently by nitrate reductase (NR) and nitrite reductase (NiR) in reactions involving reduced ferredoxin (Fdx_{red}). During this eight-electron transfer, the oxidation state of nitrogen drops from +5 to –3.
- Plants reduce nitrate and nitrite in both root and shoot tissues.

Fig 16.30 Nitrate assimilation by plant cells involves transport of nitrate across the plasma membrane and then reduction to ammonia in a two-step process. Nitrate can be stored in and remobilized from the vacuole. A H^+-ATPase maintains the electrochemical gradient that drives cellular uptake of nitrate.



The values shown for electrical potentials and intracellular nitrate concentrations are typical, but can vary significantly.

2. Glutamate and Glutamine

- Ammonium ($NH4^+$) is then assimilated into AA via reactions that consume organic carbon.
- In plants, NH_4^+ is partly released from organic compounds during several metabolic processes, including;
  - (i) the deamination of amino acids during either seed germination or the formation of phenylpropanoid compounds (e.g., lignins), and, in particular,
  - (ii) photorespiration in green tissues.
- Enzymes involved in the primary assimilation of inorganic nitrogen from the soil as well as in the reassimilation (secondary assimilation) of free ammonium (NH_4^+) within the plant are:
  1. Glutamine synthetase (GS)

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  2. Glutamate synthase (GOGAT)
  3. Glutamate dehydrogenase (GDH),
  4. Aspartate aminotransferase (AspAT), and
  5. Asparagine synthetase (AS) (Fig 7.4).
- The GS/GOGAT cycle is considered the principal route of NH_4^+ assimilation in plants (Fig 7.4).
  - GS catalyzes the ATP-dependent assimilation of **NH_4^+** into glutamine, using glutamate as a substrate, and
  - GOGAT (glutamine-2-oxoglutarate aminotransferase) catalyzes the reductive transfer of the amide group from glutamine to α-ketoglutarate (2- oxoglutarate), forming two molecules of glutamate (Fig 7.5).
- Thus glutamate (Glu) and glutamine (Gln) are the main products of initial NH_4^+ assimilation and function as substrates in protein biosynthesis and in **N-transport**. These AA readily donate nitrogen to the biosynthesis of other AAs, nucleobases, and a host of other N-containing compounds.

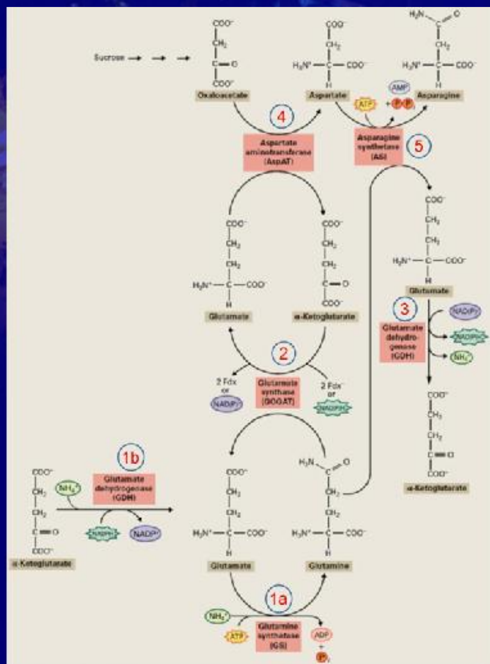


Fig 7.4 An overview of the enzymes that participate in ammonium ($NH4^+$) assimilation into the N-transport amino acids glutamate, glutamine, aspartate, and asparagine. Fdx, ferredoxin.

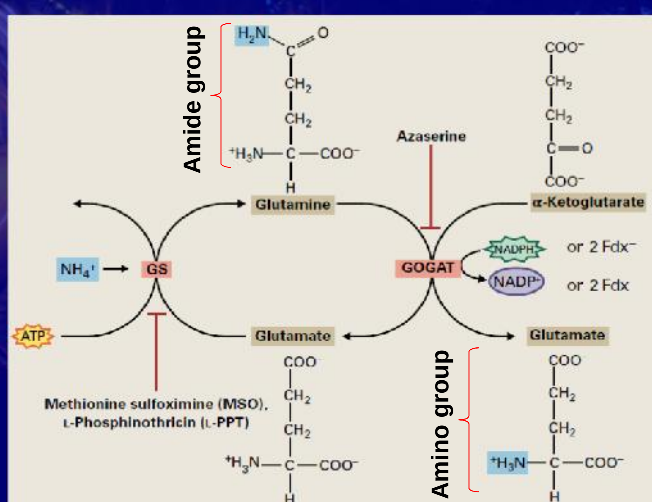


Fig 7.5 The glutamine synthetase–glutamate synthase (GS/GOGAT) pathway is thought to be the principal mechanism of primary and secondary ammonium assimilation. Sites of action are shown for several enzyme inhibitors. Fdx, ferredoxin.

- Alternatively, nitrogen assimilated into glutamate and glutamine may be incorporated into aspartate (Asp) and asparagine (Asn).
  - **Aspartate** is a metabolically reactive AA that serves as the nitrogen donor in numerous aminotransferase reactions and is the precursor of a large family of amino acids (see Fig 7.2).
  - **Asparagine**, on the other hand, is relatively inert and serves primarily as a **nitrogen transport** and **storage compound**.
- Glutamate, glutamine, aspartate, and asparagine are the major amino acids translocated in the phloem, but also in the xylem of most species including corn (Zea mays), pea (*Pisum sativum*), and Arabidopsis.
  - Total AA concentrations in the phloem are in the range of 100–200 mM and are about tenfold lower in the xylem.
- Tissue and phloem concentrations of these transported amino acids are not static; they are modulated by factors such as light (Fig 7.3) and nutritional or developmental stage.

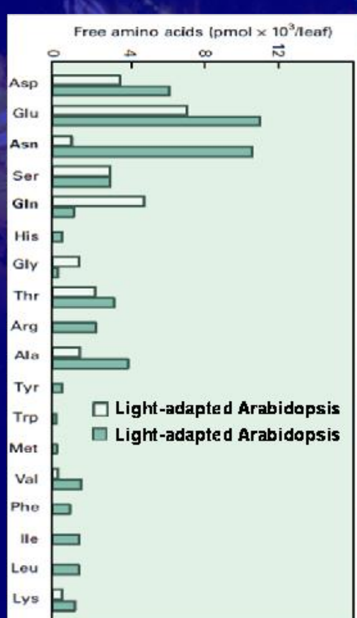


Fig 7.3 Concentrations of free AAs in light- and dark-adapted Arabidopsis, determined by HPLC. These light-induced reciprocal changes in concen-trations of asparagine and glutamine reflect the distinct natures of these amino acids. Glutamine, a metabolically very reactive amino acid, is preferentially synthesized in the light, whereas asparagine, which is relatively inert, is preferentially synthe-sized in the dark. Asparagine carries more nitrogen atoms per carbon atom than does glutamate and so is a more economical compound to transport nitrogen when carbon skeletons are limiting (in the dark).

- Aspartate, glutamate, asparagine, and glutamine constitute 70% of total free amino acids. Asparagine concentrations are induced dramatically in dark-adapted plants, whereas glutamine concentrations increase in the light.
- Increased concentrations of glycine in light-adapted plants result from photorespiration, which produces glycine as a byproduct.

3. GS/GOGAT Cycle

- The two major classes of plant GOGAT enzymes are a ferredoxin-dependent GOGAT (Fd-GOGAT, found also in cyanobacteria) and an NAD(P)H-dependent GOGAT [NAD(P)H-GOGAT].
- Fd-GOGAT and NADPH-GOGAT are plastid localized based on subcellular fractionation and identification of plastid-targeting sequences (Fig 7.6).

- Distinct isoenzymes of both GS and GOGAT have been identified in all plant species examined. The two GS isoenzymes, GS1 and GS2, have been localized to the cytosol and chloroplast, respectively (Fig 7.6), but GS2 has also been detected in mitochondria of Arabidopsis.

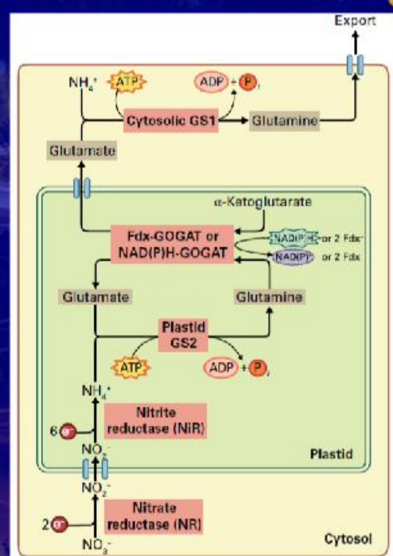


Fig 7.6 Isoenzymes of glutamine synthetase (GS) are present in both the plastids (GS2) and the cytoplasm (GS1). Fdx, ferredoxin.

- Some proteins in the latter class are more active in the presence of NADH than NADPH and are, therefore, termed NADH-GOGAT, which are expressed prefe-rentially in nonphotosynthetic tissues, such as roots.

- GS has a high affinity for ammonium and so can operate at the low ammonium concentrations present in living cells (Km 3–5 µM).
- Labeling studies to trace the fate of $^{15}NH_4^+$ confirm that the label is incorporated primarily into the amide group of glutamine and then appears in the amino group of glutamate (Fig 7.5) and other amino compounds, including glutamine.
- The addition of GS inhibitors, for example, the glutamate analogs methionine sulfoximine (MSO) or L-phosphinothricin (L-PPT) (Fig 7.7), inhibit, but do not completely block labeling of the amido group of glutamine and the amino group of glutamate.

- Another GS inhibitor is tabtoxinine-β-lactam (Fig 7.7) which is produced by plant pathogenic Pseudomonas syringae as a phytotoxin.
- The GOGAT inhibitor azaserine (a glutamine analog) blocks incorporation of the radiolabel into glutamate.
- The results of the studies, among others, support the hypothesis that the majority of inorganic nitrogen is assimilated through the GS/GOGAT pathway in plants.

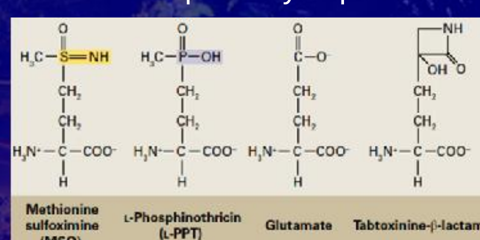


Fig 7.7 Methionine sulfoximine, phosphinothricin, and tabtoxinine-β-lactam are inhibitors of gluta-mine synthetase. Phosphinothri-cine is part of the tripeptide bialo-phos, an antibiotic produced by certain streptomycetes, and tabtoxinine-β-lactam is part of the dipeptide tabtoxin produced by the plant pathogen Pseudomonas syringae.

4. GS Isoenzymes

- GS1 and GS2 can be separated by ion-exchange chromatography and so can be assayed and studied individually from plant extracts.
- Although the biochemical properties of these enzymes do not differ significantly when assayed in vitro, GS1 and GS2 have distinct physiological functions in vivo.
  - GS2 is the predominant isoenzyme in leaves, where it may function both in primary ammonia assimilation and the reassimilation of photorespiratory ammonia.
  - Cytosolic GS1 isoenzymes are present at low concentrations in leaves and at higher concentrations in roots, suggesting this isoenzyme has a role in primary assimilation in roots.
- In some nitrogen-fixing legumes, nodule-specific cytosolic GS isoenzymes (termed GSn) assimilate nitrogen fixed by rhizobia.

5. Fd-GOGAT Role in Photorespiration

- GOGAT enzymes are flavoproteins containing iron–sulfur (Fe–S) clusters.
- Eukaryotic GOGAT enzymes consist of a single polypeptide chain, which in case of NADH-GOGAT seems to have evolved through a fusion of the α and β subunits, while Fd-GOGAT shares similarity only with the α subunit.
- The ammonia is then channeled through a tunnel within the α subunit to the oxoglutarate-binding site, where an iminoglutarate is formed.
- The iminoglutarate is then reduced to the second glutamate; electrons from NADPH arrive from the β subunit via Fe–S clusters and flavin mononucleotide (FMN).

- In Arabidopsis, Fd-GOGAT is encoded by two genes (GLU1 and GLU2), and NADH-GOGAT by a single gene (GLT).
- All GOGAT isoforms are located exclusively in plastids different from the situation with GS.
  - Fd-GOGAT is the predominant GOGAT isoenzyme in leaves and has 95–97% of total leaf GOGAT activity.
  - In contrast, the NADH-GOGAT isoenzyme is low in leaves, but constitutes the predominant isoenzyme in nonphotosynthetic tissues such as roots, where it has the same expression pattern as GS1.
- Eubacterial NADPH-GOGAT has a basic (αβ) subunit structure, in which the glutamine amidotransferase activity releases the first glutamate and ammonia.
- These organ-specific distribution patterns suggest a major role for Fd-GOGAT in primary nitrogen assimilation and photorespiration in leaves, whereas NADH-GOGAT may function predominantly in primary assimilation in the roots (Fig 7.8).

- Light (mediated in part by phytochrome), carbon (in particular sucrose), and nitrogen signals (e.g. NO_3^- and NH_4^+) interact in the complex regulation of both Fd- and NADH-GOGAT (Fig 7.8).

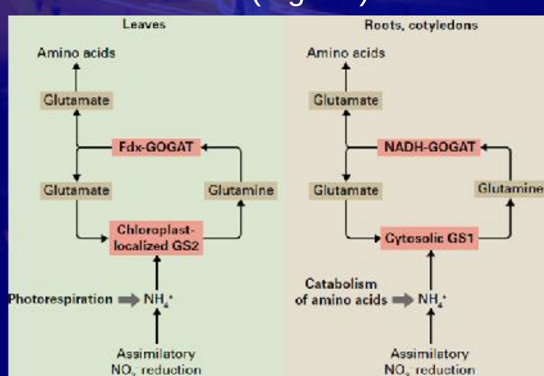


FIGURE 7.8 NADH-dependent and ferredoxin-dependent isoenzymes (NADHGOGAT and Fd-GOGAT, respectively) of GS play different physiological roles in plant metabolism.

- The importance of Fd-GOGAT in photorespiration can be seen in the *Arabidopsis gluS* mutants of GLU1, in which leaf Fd-GOGAT activity is reduced to less than 5% of wild-type levels (the low amounts of NADH-GOGAT activity in wild-type plants remain unaffected).
- All Fd-GOGAT-deficient mutants have a conditional lethal phenotype: they are chlorotic when grown in atmospheric conditions and are rescued when photorespiration is suppressed (1% CO_2) (Fig 7.9).
- On the other hand, NADH-GOGAT deficiency in the Arabidopsis mutant (*glt1*-T) has only a weak phenotype (in particular, reduction in glutamate levels), and this is not related to impaired photorespiration because the phenotype persists in the presence of 1% CO_2.

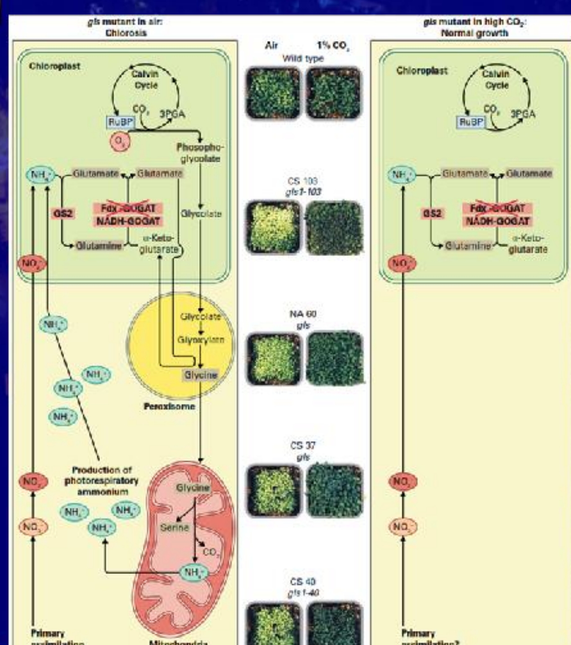


Fig 7.9 Proposed role of Fd-GOGAT in primary N assimilation and in assimilation of **NH_4^+** produced as a byproduct of photorespiration. gls (Fd-GOGAT) mutants of Arabidopsis demonstrate a chlorotic phenotype when grown in air (0.03–0.04% CO_2), but can tolerate growth in a 1% CO_2 atmosphere that suppresses photorespiration. Source: Photographs: Coschigano *et al*. (1998). Plant Cell 10:741–752.

6. GDH Catabolic Role

- GDH, an enzyme present in nearly all organisms, can catalyze both the synthesis and catabolism of glutamate.
  1. GDH catalyzes the reductive amination of α-ketoglutarate using NAD(P)H In the forward direction;
  2. GDH catalyzes the oxidative deamination of glutamate in the reverse reaction, with $NAD(P)^+$ as oxidant, to yield α-ketoglutarate and ammonium (Fig 7.10).

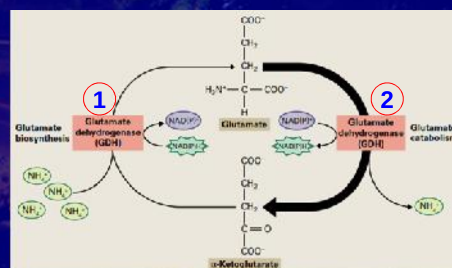


FIGURE 7.10 GDH is thought to function primarily in glutamate catabolism (deamination), but may produce glutamate when ammonium concentrations are high, primarily as a detoxification mechanism.

- Plants contain two classes of GDH enzymes: an NADH-dependent GDH found in the mitochondria, and an NADPH-dependent GDH in the chloroplast.
- GDH has a high Km for ammonium (10–80 mM), whereas tissue concentrations of ammonia typically range 0.2–1.0 mM. Furthermore, experiments in which $^{15}NH_4^+$ is fed to plants indicate a precursor–product relationship between glutamine and glutamate, consistent with primary nitrogen assimilation by GS/GOGAT.
- It is generally accepted that the primary role for GDH in vivo is in **glutamate catabolism**, for example, in darkness to provide carbon skeletons to fuel the citric acid cycle, or in germinating seeds and senescing leaves, when rates of amino acid catabolism are high.

- At least two genes encode GDH in plants, *GDH1* and *GDH2*.
  - As GDH has a hexameric structure, a total of seven isoforms of the holoenzyme can be formed, and these can be separated electrophoretically: the two homohexamers of *GDH1* and *GDH2*, and a total of five GDH1/2 heterohexamers, provided *GDH1* and *GDH2* are coexpressed in the same cells.
- The *gdh1* mutant of Arabidopsis displays an impaired growth phenotype under conditions of excess inorganic nitrogen (nitrate + ammonium; Fig 7.11).

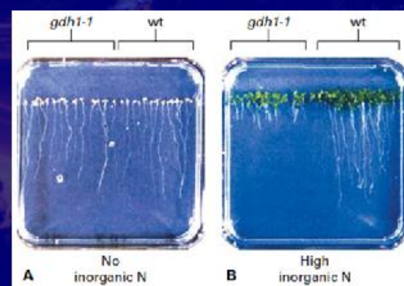


Fig 7.11 *gdh1-1* mutant seedlings can grow in the absence of inorganic N (B), but their growth is inhibited (A) by high N concentrations (20 mM NH_4^+ + 40 mM NO_3^-). Source: Melo-Oliveira *et al*. (1996). Proc. Natl. Acad. Sci. USA 93:4718–4723.

- The *gdh1/gdh2* double mutant is particularly sensitive to prolonged dark periods, during which plants suffer carbon starvation.
- Thus, the main function of GDH appears to provide the C5 carbon skeleton (α-ketoglutarate) of glutamate.

7. N Assimilation-Controlling Isoenzymes

- Nitrogen, after its initial assimilation into glutamine and glutamate, can be distributed to many other compounds by transaminases or aminotransferases (AT).
- Because glutamate-utilizing transaminations regenerate α-ketoglutarate, these reactions permit primary assimilation to continue in the absence of de novo α-ketoglutarate synthesis.

- In particular, synthesis of aspartate regenerates the carbon skeletons required for further nitrogen assimilation by transferring an amino group from glutamate to oxaloacetate.
- AspAT, the best characterized aminotransferase in plants, plays a central role in both aspartate synthesis and catabolism (Fig 7.12).
- AspAT, also known as glutamate:oxaloacetate aminotransferase (GOT), is a pyridoxal phosphate-dependent enzyme, like all transaminases (Fig 7.13).

Fig 7.12 Aspartate aminotransferase catalyzes the reversible transamination of oxaloacetate by glutamate to yield α-ketoglutarate and aspartate.

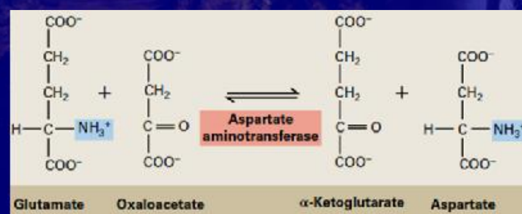
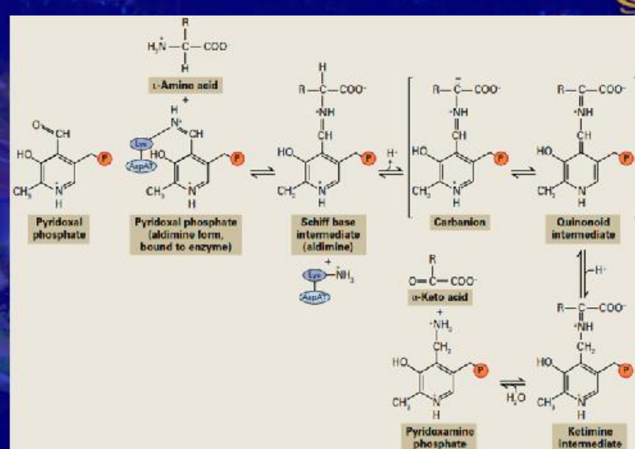


Fig 7.13 Pyridoxal phosphate mechanism/Schiff base formation. The deamination half-reaction catalyzed by a transaminase is diagrammed from left to right.



In the case of AspAT, the l-amino acid substrate at left is glutamate, and the α-keto acid product at right is α-ketoglutarate. Note the carbanion (in the brackets) is formed by deprotonation of the α-C of the bound amino acid, and the pyridinium N serves as an electron sink driving the formation of the quinonoid intermediate.

- AspAT, also known as glutamate:oxaloacetate aminotransferase (GOT), is a pyridoxal phosphate-dependent enzyme, like all transaminases (Fig 7.13).
- The ability of AspAT to interconvert these important carbon and nitrogen compounds places it in a key position to regulate plant metabolism.
- In line with the fact that aspartate is used to transfer carbon, nitrogen, and reducing equivalents between intracellular compartments, isoenzymes of AspAT have been localized to four cellular compartments: the cytosol, mitochondria, chloroplasts, and peroxisomes.
- In Arabidopsis, the entire gene family of AspAT isoenzymes has been characterized, and mutants of the two major AspAT isoenzymes (cytosolic AAT2 and plastid AAT3) have been identified.

8. Light and Asparagine Biosynthesis

- In prokaryotes, separate genes, asnA and asnB, encode structurally distinct ammonium- and glutamine-dependent asparagine synthetases (ASs), respectively, whereas in plants, only genes encoding glutamine-dependent AS have been identified.
- The plant AS catalyzes the ATP-dependent transfer of the amido group from glutamine to aspartate, generating glutamate and asparagine (Fig 7.14A).
- Although glutamine is the preferred substrate for nearly all of the AS enzymes studied in plants, some evidence indicates that ammonium-dependent asparagine synthesis may also occur (Fig 7.14B).
- K_m values for NH_4^+, however, are more than 10-fold higher than in the case of glutamine synthesis.

- Tracer studies with $^{15}NH_4^+$ have shown that glutamine is labeled efficiently, so the direct amidation of aspartate does not appear to occur at significant rates in vivo unless plants may encounter toxic concentrations of NH_4^+.

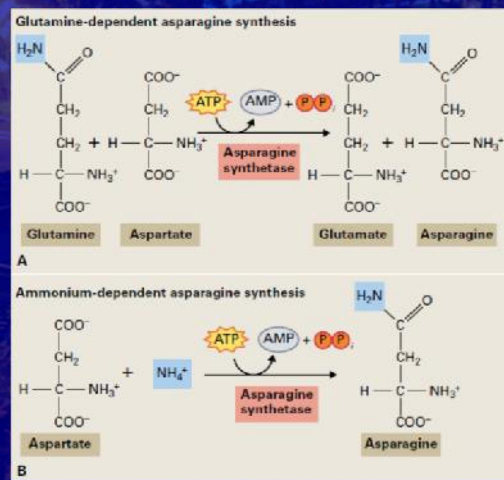
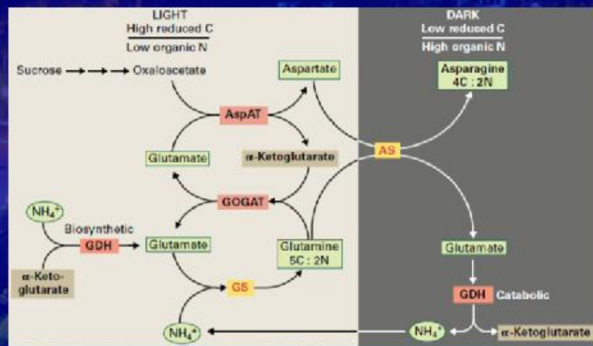


Fig 7.14 Asparagine synthetases from plants preferentially use glutamine as a nitrogen donor (A), but can catalyze the assimilation of inorganic nitrogen when ammonium is plentiful (B).

8. Effect of Light and Carbon Metabolism

- Based on the reciprocal effects of carbon and organic N on the expression of GS2 and ASN1, a metabolic control model has been proposed (Fig 7.15).
  - In this model, GS2 expression is induced by light or when carbon skeletons required for ammonia assimilation are abundant.
  - Thus, in the light, nitrogen is assimilated and transported as metabolically reactive **glutamine**, a substrate in numerous anabolic reactions.
- In contrast, ASN1 expression is induced when darkness prevents photosynthetic carbon reduction, or when concentrations of organic nitrogen are high relative to those of carbon.
  - Thus, under conditions of low carbon availability or high organic nitrogen, plants direct assimilated nitrogen into inert asparagine, which has a higher N:C ratio than glutamine and, therefore, can transport and store nitrogen more efficiently when carbon skeletons are limiting.

Fig 7.15 Synthesis of glutamine and asparagine is sensitive to light and to the availability of reduced carbon. Expression of plastid-localized GS is upregulated by light or sucrose, promoting formation of the metabolically reactive nitrogen donor, glutamine.



AS is inhibited by light or sucrose, and this inhibition can be released by increasing the concentration of amino acids in plant tissues. Darkness promotes AS expression and enhances synthesis of the inert nitrogen storage compound, asparagine. Note that asparagine represents a more efficient use of reduced carbon than glutamine does: Both amino acids bind two nitrogen atoms, but glutamine contains five carbon atoms, asparagine four.

SUMMARY

1. Amino acids, the building blocks of proteins in all organisms, play additional roles in plants.
2. In plants, amino acids serve as precursors to a plethora of natural products that provide defense against pathogens and herbivores and tolerance to abiotic stress.
3. They also store or transport nitrogen from sources to sinks. The control of amino acid synthesis in plants, therefore, affects many aspects of growth, development, and survival.
4. The synthesis of essential amino acids in plants and the amino acid composition of seeds relate indirectly to animal and human nutrition.
5. Thus, understanding the pathways that allow and control amino acid synthesis in plants has significance with regard to basic research on the control of metabolic pathways as well as practical implications.
6. Although amino acid biosynthetic pathways have been well defined in microbes, the situation in plants is still less defined, in part because of additional unique complexities.

7. For example, in many instances, plants have multiple isoenzymes that catalyze the same biosynthetic reactions. These isoenzymes may be localized in distinct organelles or distinct cell types, or may be present at different developmental stages.
8. Defining each step in an amino acid biosynthetic pathway and determining how each step is regulated, not only within the context of the respective pathway but rather in the context of the general metabolic network, are some of the key aspects of current research in amino acid biosynthesis in plants.
9. Molecular, genetic, and biochemical approaches have been combined to elucidate the steps of these pathways in plants and to understand the regulation of these pathways at the level of gene regulation and beyond.
10. Plant mutants in amino acid biosynthetic enzymes, which can now readily be identified in T-DNA insertion lines, have shown that the synthesis of amino acids in vivo affects numerous diverse processes, including photorespiration, hormone biosynthesis, and plant development.
11. Thus, while being products of primary metabolism, amino acids also control many diverse aspects of plant growth and development.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