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Nitrogen and sulfur assimilation in plants and algae

Mario Giordano [a,b,*], John A. Raven [c]

[a] Laboratorio di Fisiologia delle Alghe e delle Piante, Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, via Brecce Bianche, 60131 Ancona, Italy
[b] Institute of Microbiology ASCR, Algatech, Trebon 37981, Czech Republic
[c] Division of Plant Sciences, University of Dundee at TJHI, The James Hutton Institute, Invergowrie, Dundee DD2 5DA, UK

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ABSTRACT

Nitrogen and sulfur are abundant constituents of plant and algal cells that are assimilated at the lowest oxidation number, as NH_4^+ and S^{2-}, although they can (in the case of sulfur, usually must) be acquired with their highest oxidation number, as NO_3^- and SO_4^{2-}. Some occasional differences and variants exists for transport and assimilation systems; the greatest differences in the way vascular plants and algae use N and S, however, most probably resides in regulation. For instance, nitrate assimilation in plants is strongly regulated by phosphorylation. In algae, redox regulation appears to be more important. Similarly, sulfate reduction has its main control step at the level of APS reductase in higher plants, whereas in algae a redox regulation has been recently been hypothesized for ATP sulfurylase, the first step in sulfate assimilation. Unfortunately, the information on the regulation of N and S acquisition and assimilation is limited to very few species (e.g. *Chlamydomonas reinhardtii*, *Arabidopsis thaliana*) this is especially true in the case of sulfur. This review attempts to highlight the points of divergence in N and S utilization by plants and algae, leaving aside the biochemical details and the features that do not show any obvious difference.

1. Objectives

In this review we attempt to provide an overall assessment of N and S assimilation in algae and plants. The task is not a simple one, given the patchiness of the information and the fact that most studies refer to few model organisms. Numerous reviews exist for nitrogen and sulfur metabolism in higher plants. Much less was published for algae (possibly with the exception of nitrogen metabolism in *Chlamydomonas reinhardtii*, e.g. Fernandez et al., 2009). For this reason we decided to put somewhat more emphasis on algae, while however always comparing them with the embryophytes. We integrated the biochemical and molecular information with ecological and evolutionary concepts; the latter aspects have often been disregarded in previous reviews, yet they are inextricably intertwined with phylogeny, gene expression and metabolic regulation and decisively concur to similarities and differences in the way photosynthetic organisms deal with N and S.

2. Sulfur and Nitrogen in plants and algae

Average stoichiometries of plants and algae show that N and S are among the most abundant component of photosynthetic cells (Giordano, 2013). The cost of the assimilation of N (especially) and S estimated on these stoichiometries is not trivial (Table 1). Under energy limitation, competition may occur among the intricately interconnected C, N and S assimilation pathways (Ruan, 2013; Fig. 1) and the extent of such competition may depend on the flexibility of cell stoichiometry, on the availability of these elements in the environment and on the degree by which their acquisition and assimilation can be modulated. The cost of the assimilation process increases for assimilation in shoots of vascular land plants, where nitrate and – especially – sulfate are commonly assimilated. The assimilation of nitrate and sulfate generates OH^- (Raven and Smith, 1976; Raven, 1986; Andrews et al., 2013). Although the OH^- generated in the roots is mostly released into the soil, most of the OH^- that is produced as a consequence of shoot nitrate and sulfate assimilation is retained within the plants and must be neutralized by the production of organic acids (Raven and Smith, 1976; Andrews et al., 2009, 2013). The energy cost of producing the OH^--neutralizing organic acids outweighs energy saving from the more direct use of photosynthetically generated reductants with oxyanion reduction restricted to the photoperiod. Getting rid of excess acid produced as a consequence of ammonium and

* Corresponding author at: Corresponding author at: Università Politecnica delle Marche, Dipartimento di Scienze della Vita e dell'Ambiente, Laboratorio di Fisiologia delle Alghe e delle Piante, Via Brecce Bianche, 60131 Ancona, Italy.
Tel.: +39 071 220 4652; fax: +39 071 220 4650.
E-mail address: m.giordano@univpm.it (M. Giordano).

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Table 1
Estimate of costs for the assimilation of CO_2 into triose-P, nitrate into glutamate, sulfate into cysteine, for phytoplankton and for the shoot of herbaceous flowering terrestrial plants (herbaceous plants). The costs were estimated based on the ATP and electrons used in the most common assimilation pathway. The hydrolysis of 1 ATP was assumed to yield 55 kJ mol^{-1} and the transfer of $2e^-$ was assumed to correspond to 4 ATP equivalents. The average stoichiometries used for the calculations are those in Giordano (2013).

	Cost of the assimilation of 1 mole of CO_2, NO_3^- or SO_4^{2-}		Cost of CO_2, NO_3^- or SO_4^{2} assimilation in kJ according to average elemental stoichiometry, assuming $P=1$	
	ATP equivalents	kJ mol^{-1}	Marine phytoplankton	Herbaceous plants
$CO_2 \rightarrow CH_2OP$	11	605	75,020	87,120
$NO_3^- \rightarrow$ Glu	41	2255	36,080 (48% of C assimilation)	38,335 (44% of C assimilation)
$SO_4^{2-} \rightarrow$ Cys	33	1815	2360 (3% of C assimilation)	1561 (1.8% of C assimilation)

dinitrogen assimilation is much more difficult and it is restricted to roots, where ammonium or N_2 can be assimilated with excretion of protons to the rooting medium (Raven and Smith, 1976; Raven, 1986; Andrews et al., 2009, 2013).

N and S are both essential components of catalysts and intermediates of primary metabolism; both are found in amino-acids and hence proteins, in nucletotides (including ADP/ATP and $NAD(P)^+$/NAD(P)H) and hence in nucleic acids, in vitamins (N and S) and, in phototrophs, chlorophylls and phycobilin chromophores (N). Growth substances such as indoleacetic acid and cytokinins (N) are also essential to development in embryophytes and some algae. Both N and S are also involved in response mechanisms to changes in environmental conditions, both abiotic and biotic. These responses include qualitative and quantitative changes in the transcriptome (N) and proteome (N and S), in osmolites such us glycine betaine (N) and dimethylsulfoniopropionate (S), in growth substances such as auxin and cytokinins (N), in compounds like glutathione (N and S) involved in the defence against oxidative stress, in heavy metals chelators such as metallothioneins and phytochelatins (N and S), and in compounds defending

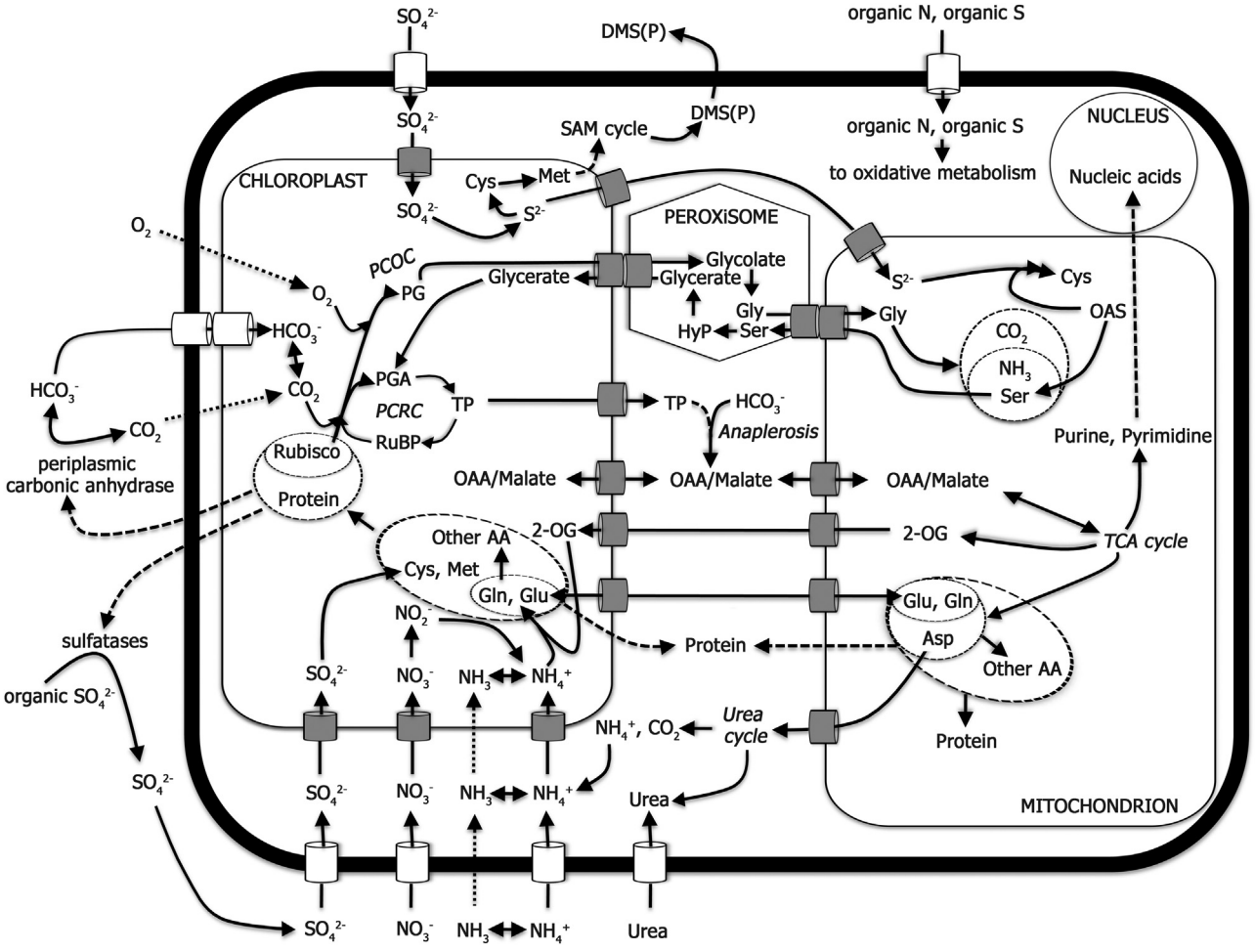

Fig. 1. Main interaction among C, N and S metabolism in algae and plants. Solid lines indicate known pathways. Dashed lines indicate pathways that are either not entirely known or are not shown in details in this figure. The dotted lines show the diffusive path of CO_2 and NH_3. Metabolic processes (e.g. anaplerosis, PCRC, PCOC) are in italics. Abbreviations: 2-OG, 2-oxoglutarate; AA, amino acids; Asp, aspartate; Cys, cysteine; DMS(P), dimethylsulfide (dimethylsufoniopropionate); Met, methionine; Gln, glutamine; Glu, glutamate; Gly, glycine; HyP, hydroxypyruvate; OAA, oxalacetate; OAS, *O*-acetylserine; PCOC, photosyntehic carbon oxidative cycle (photorespiration); PCRC, photosynthetic carbon reductive cycle (photosynthesis); PG, 2-phosphoglycolate; PGA, 3-phosphoglycerate; Rubisco, ribulose bisphosphate carboxylase/oxygenase; RuBP, Ribulose 1,5-bisphosphate; SAM. *S*-adenosilmethionine; Ser, serine; TP, triosephosphate.