Topic: N_2 Fixation by Cyanobacteria
B.Sc. Botany (Hons.) I
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Cyanobacteria can fix N_2 and these organisms make a major contribution to the global nitrogen cycle. Cyanobacteria generate all of their cellular carbon and nitrogen from atmospheric sources: they literally live on fresh air. Cyanobacteria possess unique mechanisms for the protection of nitrogenase, the nitrogen fixing enzyme, against O_2 and for nitrogen control of the expression of the N_2-fixing machinery and form symbioses with widely different organisms.

N_2-fixing cyanobacteria-

N_2 -fixing cyanobacteria can be subdivided into three groups:

I. filamentous cyanobacteria with heterocysts;

II. non-heterocystous filamentous or unicellular cyanobacteria, capable of N_2 fixation under fully aerobic conditions; and

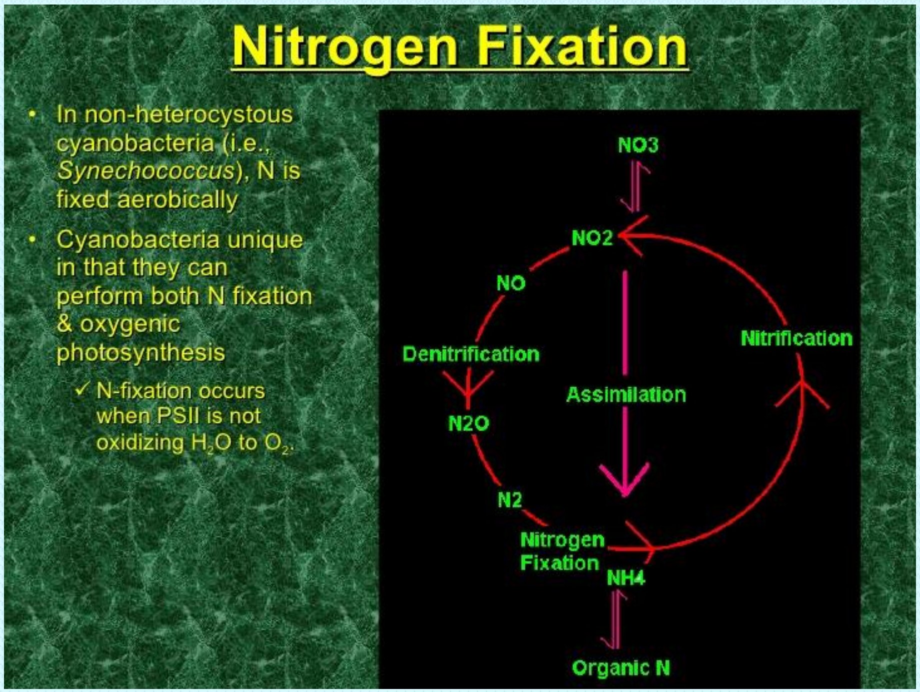
III. non-heterocystous filamentous or unicellular cyanobacteria that induce nitrogenase activity only anaerobically.

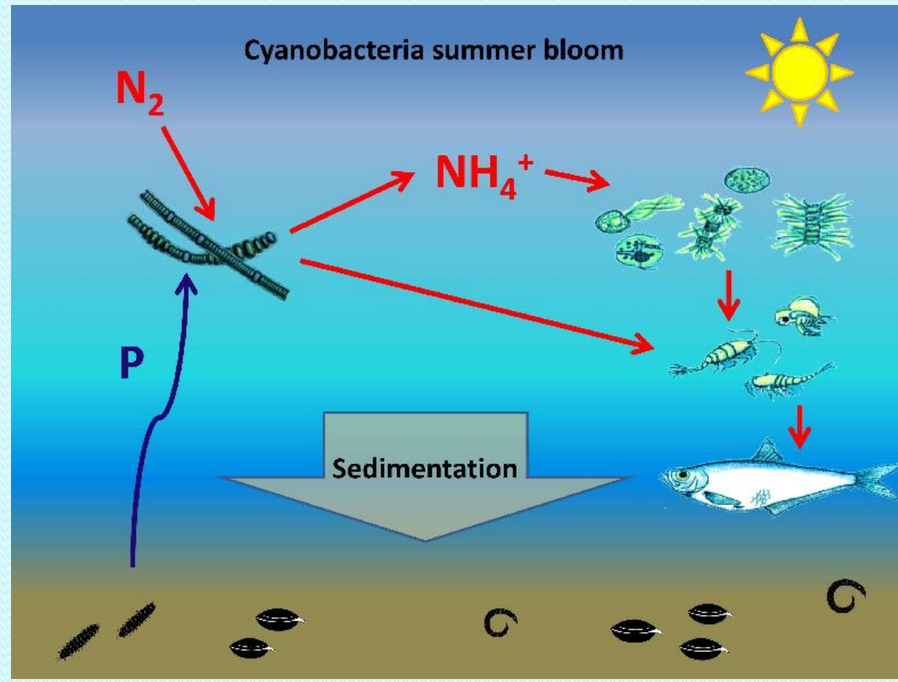
- These groups (free-living and symbiotic) are found in a wide range of environments ranging from terrestrial to aquatic environments, the latter including limnic (lakes and streams), brackish (e.g. the Baltic Sea) and fully marine habitats (oceans), and cyanobacteria may be found from cold polar regions (e.g. Svalbard) to the warmer Mediterranean and tropical areas.
- Heterocystous cyanobacteria are clearly best adapted for diazotrophic growth, but cyanobacteria also manage well without heterocysts. However, cyanobacteria constituting 30-40% of all non-heterocystous cyanobacteria, lack one or more O_2 protective mechanisms.
- Sulfur in environments characterized by high concentrations of sulphide and extended periods of anoxia. Some anaerobic N2-fixing cyanobacteria occur in such environments. Sulphide is an inhibitor of oxygenic photosynthesis and, at high concentrations, cannot co-exist with O2 .

- In some systems, cyanobacteria therefore perform an oxygenic photosynthesis whilst, in others, photosynthesis is temporarily switched off by sulphide, thereby allowing N_2 fixation to flourish.
- Evidence has also been obtained for a spatial separation of oxygenic photosynthesis and N_2 fixation within lamined benthic mats. Either fixed nitrogen is transported or organisms move through the system, changing from N_2 fixation to photosynthesis.
- Microbial mats are typically built by non-heterocystous cyanobacteria (e.g. *Oscillatoria*) though heterocystous species may occasionally dominate.
- Many mats are strongly diffusion limited and accumulate photosynthetic O_2 during the day, while at night the system turns anaerobic, probably permitting N_2 fixation by some non-heterocystous strains.
- Planktonic cyanobacteria are common in lakes as well as in open oceans and in the Baltic Sea. The major N_2-fixing cyanobacterium in oceans is an aerobic, non-heterocystous species, Trichodesmium. In contrast, freshwater blooms of diazotrophic

Cyanobacteria consist of heterocystous species (e.g. *Anabaena*), and these are also dominant in brackish systems such as the Baltic Sea with blooms of Nodularia and Aphanizomenon.

- Heterocystous species are also found as symbionts in marine plankton (diatoms), so the absence of free-living representatives in the open ocean remains a mystery. There is a great need to fully understand the behaviour of these bloom forming cyanobacteria in their natural environment.
- In combination with classical measurements of N_2 fixation there is also a need to study nif gene expression and the occurrence of nitrogenase in natural systems.
- The regulation of nitrogenase activity by environmental factors (e.g. N, P, Fe) and the transport of fixed nitrogen within the ecosystem, are other important areas to be addressed.
- Cyanobacteria growing in terrestrial locations and in streams and rivers need to be studied. The latter are particularly interesting because they differ from their


Nitrogen Fixation
In non-heterocystous cyanobacteria (i.e., Synechococcus), N is fixed aerobically
Cyanobacteria unique in that they can perform both N fixation & oxygenic photosynthesis
N-fixation occurs when PSII is not oxidizing H_2O to O_2.
NO3
NO2
NO
Denitrification
N2O
N2
Nitrogen Fixation
NH4
Organic N
Assimilation
Nitrification


Cyanobacteria summer bloom
N_2
NH_4^+
P
Sedimentation

counterparts in lakes by being perennials.

- There is also an urgent need to identify the ecological niches that are occupied by the different N_2- fixing cyanobacteria.
- Cyanobacterial systematics using various genetic techniques will in addition be an extremely valuable complement to studies on N_2 fixation. A precise taxonomic position of cyanobacteria living in different environments will allow comparisons of data collected in different ecological niches and cultivated in different laboratories. This is also required in order to evaluate the diversity of the N_2-fixing machinery in cyanobacteria.
- A knowledge of the biodiversity of symbiotic cyanobacteria in relation to host species, habitat and geographical location will contribute to an understanding of the specificity of cyanobacterial symbioses and will form a valuable basis for the future elaboration of artificial symbioses.