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Cyanobacterial biodiversity and niche adaptation in lignocellulosic substrates

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Abstract
A study was undertaken to analyze the diversity and metabolic capabilities of cyanobacteria associated with wheat straw, paddy straw and the composts produced using these as substrates. Enrichment cultures raised in nitrogen depleted/supplemented BG-11 medium revealed the dominance of *Chrooococcus* sp., *Phormidium* sp. and *Nostoc* sp. Enrichment of rice straw in nitrogen supplemented medium recorded the highest values in term of FPase while wheat straw compost enriched with nitrogen supplemented medium recorded highest activity of xylanase. A reduction of 80-95% in total phenols was recorded in all the enrichment flasks, with the wheat straw enriched with nitrogen deficient medium exhibiting a 95.64% decrease over the raw substrate (wheat straw). This investigation is a first time report on the taxonomic diversity and metabolic versatility of native cyanobacteria associated with wheat/paddy straw and their composts, which are generally considered refractive substrates for most phototrophs. This study also highlights the potential of cyanobacteria in the breakdown of lignocellulosics and lowering phenol concentrations in these substrates per se or through synergistic interactions with the native bacterial/fungal flora. Such metabolic activities can improve the mobilization of nutrients and their availability to heterotrophs, when employed as mulches or organic supplements in agriculture.

Key words: composts; cyanobacteria; diversity; hydrolytic enzymes; metabolic activity; nutrient mobilization; paddy straw; wheat straw

Introduction

Cyanobacteria are a group of photosynthetic prokaryotes which show diversity in their morphological, biochemical and molecular characteristics, besides exhibiting a high level of adaptability to different environments. They represent an assemblage of versatile organisms which produce a diverse range of bioactive molecules exhibiting a broad spectrum of activity (Namikoshi and Rinehart, 1996; Prasanna *et al.,* 2010; Volk and Fulkert, 2006). These ubiquitous prokaryotes are currently being globally explored as valuable sources of pharmacologically active compounds useful in diagnostics, food/feed supplements and nutraceuticals, besides their well recognized roles as biofertilizers in agriculture (Gupta *et al.,* 2013; Prasanna *et al.,* 2008a, 2009a; Venkataraman, 1972).

The ability of cyanobacteria (blue-green algae), which are an ubiquitous distributed group of prokaryotic, photoautotrophic microorganisms, living in freshwater and marine environments, to metabolize aromatic substances, is a less investigated phenomenon (Prabha *et al.,* 2009; Shashirekha *et al.,* 1997; Wurster *et al.,* 2003). Because of their remarkable ability to adapt to unfavorable environmental conditions, they could contribute to bioremediation of polluted areas. The microbial diversity of several lignocellulosic substrates, especially rice straw degradation have been investigated by several researchers and novel genera such as *Kocuria*, *Microbacterium*, besides *Clostridium*, *Bacillus*, *Nitrospira* identified. In general, both Gram-positive and Gram-negative groups belonging to the order *Burkholderiales*, *Enterobacteriales*, *Actinobacteria*les and *Bacillales* have been recorded (Meghraj *et al.,* 1994; Chandna *et al.,* 2013). Tiwari and co-workers (2013) utilized the huydrolytic potential of a phytopathogenic fungus *Phoma* sp. for saccharification of lignocellulosic biomass. But photosynthetic microorganisms are a less explored area in lignocellulosic degradation.

Rice is a major crop grown worldwide which generates large amount of straw annually. Paddy straw contains 51.76% organic C, 0.65% nitrogen, 0.20% phosphorus, 0.30% potassium and has high C: N ratio. It is also rich in silica and lignin which makes it difficult to be degraded. A large amount of information is also available on the preparation of composts using composite inocula comprising fungi/ actinomycetes (Gaind and Nain, 2010; Kumar *et al.,* 2008; Pandey *et al.,* 2009). However, to date, no report exists on the cyanobacterial diversity in such lignocellulosic substrates and composts, although cyanobacteria are known to produce hydrolytic enzymes (Prasanna *et al.,* 2008; Viswajith and Malliga, 2008). These photosynthetic oxygen- evolving prokaryotes are considered ideal for the treatment of effluents containing aromatic compounds, since they can hasten the process of biodegradation as primary producers, through oxygenation and reduction of BOD, unlike heterotrophic microorganisms. In addition, they possess advantages over other bacteria and green algae due to their trophic independence for nitrogen besides carbon (Carr and Whitton 1982). The facultative mode of metabolism of certain cyanobacteria has also been investigated (Prasanna *et al.,* 2008a, 2009a; Rippka, 1972).

Keeping in view the availability of composts in the Division of Microbiology, IARI, and their field level utilization as organic supplements, the present investigation aimed at analyzing the diversity of cyanobacterial genera associated with rice and wheat straw and their respective composts. Selected biochemical properties were also evaluated to understand their

metabolic activity in such refractive substrates and role of cyanobacteria in mobilizing nutrients for facilitating their effective utilization as integrated inputs in agriculture.

Materials and methods

Substrates and experimental set up

Paddy straw, wheat straw and composts (prepared using paddy straw/wheat by the method of Gaind and Nain (2010) were utilized to set up for enrichment in 250 ml Erlenmeyer flasks. Samples (1g) of the substrates were added to 100 ml of BG 11 medium, with / without supplementation with nitrogen (@1.5 g l^{-1} $NaNO_3$). The flasks were incubated under the light: dark cycles (16:8 h) under white light (50-55 µmol photons m^{-2} s^{-1}) and 28 ± 2° C. The physico-chemical characteristics of all the substrates used is given as Supplementary Table 1.

Microscopic observations

Microscopic examination of the growth observed in the flasks was undertaken periodically in order to identify the forms present. Identification was done following the keys of Desikachary Photographs were taken using the light microscope attached with Canon Power Shot S50 Digital Camera and Canon utilities Remote Capture Version 2.7.2.16 software. The specimens were observed at 40X magnification.

Total soluble proteins and phenols

The amount of proteins was determined with Bovine serum albumin as standard. The blue colour developed was recorded spectrophotometrically at 650 nm (Herbert *et al.*, 1971). Phenols were estimated in the cell free extracts by the method of Bray and Thorpe (1954).

Enzyme assays

Filter paperase /FPase activity (exo-β-1, 4 glucanase)

The cell free filtrates were assayed for the activity using filter paper strips as substrate and reducing sugars liberated were measured at 575 nm using standard curve of Glucose by DNSA method. One International Unit (IU) represents one umole of glucose liberated per ml of culture filtrate per min (Ghosh *et al.*, 1983).

Xylanase activity

The xylanase activity of the culture filtrate was analysed by the spectrophotometric method at 575 nm, using xylan as the assay substrate. One unit of xylanase activity was defined as µmoles of xylose released per mL per min under the assay conditions (Bailet *et al.*, 1992).

Statistical Analyses

The experimental data were tabulated and analyzed using Statistical package for Social Sciences (SPSS Version 10.0) and the ranking given as alphabets (superscripts in Table) are based on Duncan's Multiple Range Test.

Results and Discussion

Cyanobacteria, among the earth's oldest organisms, exhibit an array of sophisticated biosynthetic pathways to produce a rich source of bioactive natural products which have been an incredibly fruitful source of compounds in drug discovery efforts. In recent years, there has been a tremendous enhancement in our knowledge regarding the biological significance of these metabolites/hydrolytic or lytic enzymes produced by cyanobacteria (Castenholtz, 1969; Gupta *et al.*, 2013; Kulik, 1995; Prabha *et al.*, 2009; Prasanna *et al.*, 2008; Shashirekha *et al.*, 1997; Wurster *et al.*, 2003). Cyanobacteria have immense potential in wastewater and industrial effluent treatment, bioremediation of aquatic and terrestrial habitats, chemical industries and as biofertilizers, food, feed, fuel etc. (Cairns and Dickson, 1971). They are also highly effective as accumulators and degraders of different kind of environmental pollutants, including pesticides (Meghraj *et al.*, 1994), phenol and catechol (Ellis, 1977) and xenobiotics (Kuritz and Wolk, 1995).

The management of rice residues through direct incorporation of straw in soil is known to be associated with several problems, including immobilization of plant nutrients particularly nitrogen and reduced germination of subsequent crops. Moreover, paddy straw wastes have high C: N ratio, about 80:1, and are rich in silica and lignin which make it difficult to be degraded. Although few reports are published on the potential of cyanobacteria in degrading lignocellulosic substrates through the production of hydrolytic enzymes (Prasanna *et al.*, 2008; Viswajith and Malliga, 2008), there is a dearth of information on the biodiversity of cyanobacteria associated with wheat/rice straw and their composts. Our study focused towards analyzing the taxonomic and metabolic diversity of cyanobacteria associated with paddy/wheat straw and their composts using enrichment studies undertaken in both nitrogen supplemented /depleted media.

Microscopic observations of samples from the enrichment flasks revealed that the non- heterocystous cyanobacteria were the dominant members in all the treatments (Table 1; Fig. 1).

Table: 1. Microscopic observations of enrichment cultures of rice straw / wheat straw and the respective composts in BG 11 medium (+N/-N) observed over a period of 60 d

Treatments	Cyanobacterial genera recorded
Wheat Straw (+N)	*Chroococcus* sp., *Lyngbya* sp., *Phormidium* sp.
Wheat Straw (-N)	*Nostoc* sp. , *Phormidium* sp.
Wheat Straw Compost (+N)	*Phormidium* sp.
Wheat Straw Compost(- N)	*Chroococcus* sp. ,*Phormidium* sp.
Rice Straw (+N)	*Oscillatoria* sp., *Lyngbya* sp., *Phormidium* sp.
Rice Straw (-N)	*Gloeocapsa* sp, *Chroococcus* sp., *Oscillatoria* sp.
Rice Straw Compost (+N)	*Chroococcus* sp.
Rice Straw Compost (-N)	*Chroococcus* sp., *Nostoc* sp., *Cylindrospermum* sp.; *Anabaena* sp., *Phormidium* sp.

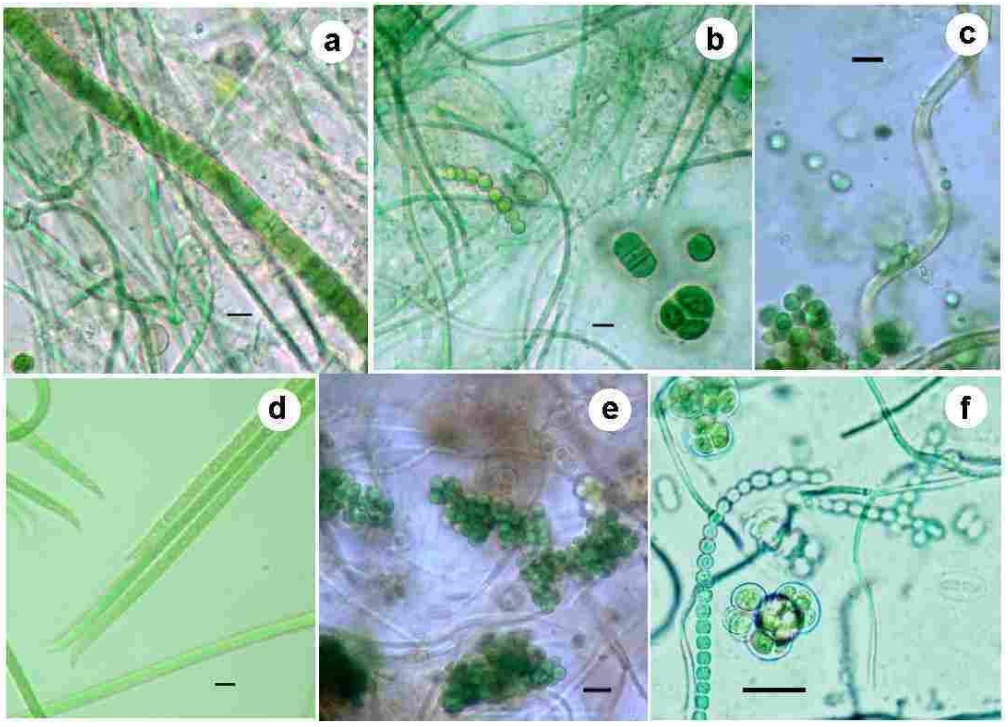

Fig. 1: Dominant cyanobacterial genera in the samples (a-j)-10. a. *Chroococcus* sp. (WS +N), b. *Gloeocapsa* sp. (RSC -N), c. *Chroococcus* sp. (RS +N), d. *Phormidium* sp. (RS +N), e. *Phormidium* sp. (WS), f. *Oscillatoria* sp. (RS +N), g. *Lyngbya* sp. (WS +N), h. *Nostoc* sp. (RSC -N), i. *Nostoc* sp. (WS), j. *Cylindrospermum* sp. (RSC -N). Scale bar indicates 20 µm.

The cyanobacterial growth in wheat straw compost flasks was less dense, when observed visually; this can be attributed to the lower pH of wheat straw compost (i.e. 6.5 as compared >7.0 in the other treatments).This may represent a less conducive environment for cyanobacteria, which exhibit a preference for alkaline environments. Unicellular forms such as *Chroococcus* and other coccid forms were present in greater numbers (Fig.2 a-d) *Oscillatoria* was also present in rice straw enrichment cultures. An interesting form was *Cylindrospermum* sp., as also two types of *Nostoc* sp. and *Anabaena* sp. present in rice straw compost enrichment flask (Fig.2 a-d). In general, a greater abundance and diversity of cyanobacteria was recorded in rice straw and rice straw compost. This can be attributed to the greater prevalence of cyanobacteria in rice fields (vis a vis wheat fields) which may have survived as epiphytes or as resting spores/ akinetes on the straw. Several cyanobacteria are known to exhibit tolerance to high temperature (Castenholz, 1969) and therefore, may have been able to survive the thermophilic phase of composting, leading to their growth even in the enrichment flasks with the compost(s).Wheat and paddy straw have been earlier evaluated as carriers for cyanobacterial inoculants, and the former proved more promising in terms of shelf life and other attributes (Prasanna and Kaushik, 1998; Prasanna *et al.*, 1998; 2013). In the present study, both these raw substrates exhibited similar cyanobacterial genera, but in terms of composts, paddy straw compost exhibited greater diversity.

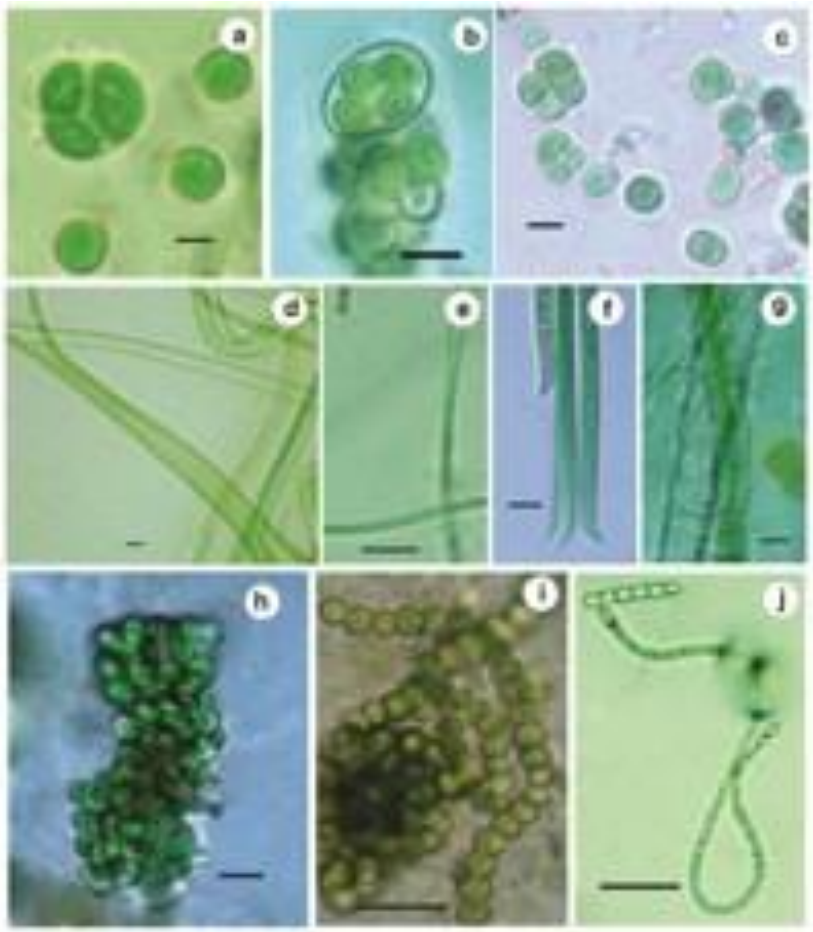

Fig. 2: Cyanobacterial diversity in the samples (a-f). a. *Phormidium* sp., and *Lyngbya* sp. (WS +N), b. *Phormidium* sp., *Lyngbya* sp., and *Chroococcus* sp. (WS), c. *Phormidium* sp., *Chroococcus* sp. (RS +N), d. *Oscillatoria* sp. (RS +N), e. *Nostoc* sp., *Phormidium* sp. (RSC -N), f. *Chroococcus* sp., *Phormidium* sp., *Anabaena* sp. (RSC -N). Scale bar indicates 20 µm.

In terms of total soluble proteins (Table 2), rice straw compost (+N) followed by rice straw (+N, -N) exhibited the highest value which can be a quantifiable indicator of the microbiota / enzymes. Higher FPase activity was also recorded in rice straw, indicator of the flora possessing this ability. Earlier studies (Prabha *et al.,* 2009; Prasanna *et al.,* 2008; 2009b) have revealed that cyanobacterial strains may exhibit hydrolytic enzyme activity. In terms of xylanase activity, the highest value was recorded in wheat straw compost (+N).The activity of hydrolytic enzymes, especially in wheat straw compost revealed that cyanobacterial enrichment may help in improving the utility of compost, through breakdown into simple substances which can be utilized by microflora /fauna in soil. The possibility of wheat straw compost as a suitable carrier for maintaining the metabolic activity of cyanobacteria can also be envisaged. Paddy straw, as against paddy straw compost showed greater hydrolytic enzyme activity, reflective of the stabilized nature and maturity of compost. The significant role of cyanobacteria in carbon sequestration also needs to be highlighted as the enrichment of such substrates by cyanobacterial growth can indirectly enhance microbial load and subsequent activity in soil when applied in fields. Interestingly, wheat straw compost enrichment samples were among the top three ranks for both enzymes and total phenols.

Table: 2. Evaluation of biochemical parameters of rice straw / wheat straw and the respective composts after enrichment in BG 11 medium (+N/-N) after 60 d incubation

Treatment	Xylanase (IU ml^{-1})	Fpase $(IU\ ml)^{-1}$	Total proteins (µg ml^{-1})	Total phenol (µg ml^{-1})	Percent reduction in phenol*
Wheat Straw #(+N)	0.227^{E}	0.179^{F}	431.80^{E}	98.60^{C}	90.95
Wheat Straw (-N)	0.270^{D}	0.196^{D}	596.60^{D}	47.42^{E}	95.64
Rice Straw #(+N)	0.351^{C}	0.280^{A}	1052.30^{B}	155.43^{A}	79.90
Rice Straw (-N)	0.392^{B}	0.189^{E}	710.20^{C}	84.38^{D}	89.10
Rice Straw Compost #(+N)	0.089^{E}	0.194^{DE}	1162.10^{A}	89.22^{D}	15.00
Rice Straw Compost (-N)	0.163^{F}	0.183^{F}	581.00^{D}	103.03^{C}	1.90
Wheat Straw Compost #(+N)	0.695^{A}	0.209^{C}	589.30^{D}	157.70^{A}	75.70
Wheat Straw Compost(+N)	0.360^{C}	0.228^{B}	370.26^{F}	119.7^{B}	81.58
CD@5%	0.005	0.002	6.87	2.51	-

Paddy straw is recalcitrant and contains high amount of silica, besides lignin which is decomposed into fulvic acid and humic acids which in turn become the stable fraction of soil organic matter (Crawford and Crawford, 1980; Huang *et al.,* 2008). These humic substances act as permanent source of energy for the growth of microorganisms and regulate the carbon cycle (Kimura and Tun, 1999; Veekan *et al.,* 2000). The humification process is generally associated with lignocellulolytic fungi and actinomycetes (Chandna *et al.,* 2013; Kumar *et al.,* 2008; Tiwari *et al.,* 2013; Weber *et al.,* 2001); however, phototrophs are less investigated (Viswajith and Malliga, 2008).

Phenols, which are an integral component of the lignocellulosics substrates, are known to denature proteins or disrupt membrane; however, they are not known to be sporicidal. It can therefore be surmised that only the spore forming microalgae forms were able to survive the high concentration (100-155 ug ml^{-1}) of phenols, and degrade them substantially. The first report on phenol degradation by the freshwater cyanobacteria *Anabaena cylindrica* and *Phormidium foveolarum* was given by

Ellis (1977), but no metabolites or cleavage of the aromatic ring was recorded. Ten *et al.* (2004) found that the addition of photosynthetic bacteria led to enhanced biodegradation of petroleum products. The phenol concentration in the raw substrates before enrichment in media (Supplementary Table 1) of the composts was 40-50% lower as compared to the substrates. However, the phenol concentration in the enrichment flasks with wheat/rice straw vis a vis control samples (not enriched with BG 11 medium) revealed an 79-95% reduction as a result of cyanobacterial growth (Table 2). Lowest values of phenols were recorded in wheat straw enrichment set up in nitrogen deplete medium, which was 95.64% lower than the un-enriched counterpart (wheat straw; 1090 ug ml^{-1}). Paddy straw compost samples set up for enrichment showed only a marginal reduction in phenol composts (1.9 -1 5%); however, the enrichment se up with wheat straw compost samples exhibited a significant reduction, ranging from 75 to 81.58%. Earlier reports on phenol degradation by cyanobacteria (Prabha *et al.*, 2009; Wurster *et al.*, 2003; Viswajith and Malliga, 2008), had revealed the role of laccase and polyphenol oxidase and our further efforts are now in focused in this direction.

The minimum inhibitory concentration (MIC) of phenols and their derivatives range from 20-5000 ug ml^{-1}, and in our study, the cyanobacteria were able to grow at concentrations ranging from 775-1090 ug ml^{-1} and bring about a drastic 7-10 folds reduction in flasks. Values are much higher than those reported by Shashirekha *et al.* (1997) who reported that a marine cyanobacterium *Phormidium valderianum* was able to tolerate a phenol concentration of 50mg/L and remove 38 mg l^{-1} Additionally, it needs to be emphasized that such epiphytic cyanobacteria can sequester CO_2 from the environment, or that evolves during the degradation process, which in turn, may help to sustain heterotrophic flora, especially aerobic flora. Additionally, such multitrophic interactions and associations can have implications in reducing CO_2 related global warming problems.

Conclusions

The study provides an interesting insight into the unusual niche occupied by cyanobacteria, especially plant materials such as paddy/wheat straw and composts. The presence of such photosynthetic microorganisms in these refractive substrates highlights their adaptive traits and ubiquity in nature. Studies need to be initiated towards understanding the carbon sequestering potential of cyanobacteria in such substrates, which can improve the agronomic value of these organic supplements widely employed in field grown crops. To our knowledge, our study represents a first time report on the cyanobacterial diversity and their metabolic capabilities in paddy/wheat straw and their composts.

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Supplementary Table: 1. Physico-chemical properties of the substrates used for enrichment

Properties	Paddy straw	Paddy straw compost	Wheat straw	Wheat straw compost
pH	7.2	7.34	7.63	6.5
EC	1.0	1.2	0.9	1.1
Organic C (%)	39.2	14.15	53.01	14.2
Nitrogen (%)	0.5	1.48	0.48	1.665
Phosphorus (%)	0.18	0.39	0.16	0.83
C/N	78.4	16.22	110.0	10.1
Humus	-	12.0	-	13.84
Phenols (ug ml^{-1})	775.01	105.02	1090.03	650.01