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Some Physiological Responses of *Nostoc* sp. JAH 109 to the Combination Effects of Limited Irradiance, pH and DIC Availability

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Abstract

Growth, pigment compositions, nitrogenase activity, photosynthesis and heterosyct frequency fluctuations of dominant species *Nostoc sp*. JAH 109, isolated from rice field, were evaluated in combination of limited irradiance (2 uE.m^{-2}.s^{-1}), different pHs (5,7,9) and inorganic carbon availability. *Nostoc* sp. JAH 109, can be considered as an alkalophilic organism. Optimal growth rate were observed at pH 9. Size of phycobilisomes and relationship between photosystem II and photosystem I increased in pH 9 and DIC available condition. This strain could not grow well in acidic condition, but neutral and alkaline condition cause active carbon dioxide concentration mechanism system. The pattern of nitrogenase activity seems more or less regular and linear at the first days after inoculation both in neutral and alkaline conditions. With respect to nitrogenase activity, the highest rate was in pH 9 and DIC availability. This seems true for heterocyst frequency fluctuations too. The higher photosynthetic capacity (P_{max}) per unit of chlorophyll was resulted in higher DIC concentration at alkaline condition.

Key words: Cyanobacteria, DIC, Nitrogenase, pH, Phycobiliproteins, Photosynthesis.

Abbreviations: APC allophycocyanin, Chla chlorophyll *a*, DIC dissolved inorganic carbon, PBP phycobiliproteins, PC phycocyanin, PE phycoerythrin

Introduction

Survival of cyanobacteria in natural environments depends upon their ability to acclimate to the variable conditions of environmental factors. Light is evidently one of the most important factors which determine the natural distribution of cyanobacteria. As other photosynthetic organisms, cyanobacteria are able to adapt to variations in light intensity; nevertheless, little work has been done in this area (Fernandez –Valiente and Leganes 1989; Soltani et al., 2006). In rice fields, light reaching the floodwater varies both daily and over the crop cycle. Because of the variation in light transmission caused by changes in rice canopy height. Underwater irradiance measured in Valencian rice fields (Spain) of full sunlight ranged from 700 umol photon.m^{-2}.s^{-1} early in growth of the crop to 5 umol photon.m^{-2}.s^{-1} when the crop was mature (Poza –Carrion et al., 2001).

In addition to light, pH is another factor, which clearly affects the distribution of cyanobacteria. Most cyanobacteria grow in environments that are neutral to alkaline and in laboratory cultures the optimal pH ranges from 7.5 to 10. Generally, a wide range of adaptation to pH has been observed not only among different genera but also between different isolates of the same species. In view of these precedents it seems clear that more work is needed to understand the physiological response of cyanobacteria to changes in pH and irradiances (Fernandez – Valiente and Leganes 1989).

In rice fields, the pH of flood water varies during the day and during the growth of the crop due to the photosynthetic activity of cyanobacteria, algae and other macrophytes. DIC concentration in the floodwater also varies on a daily and seasonal basis depending on

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photosynthetic and respiratory rate (Leganes and Fernandez-Valiente, 1991).

In the work presented here, we analyze the combined effect of three environmental factors, pH, low irradiance and DIC concentration, on growth, pigment composition and nitrogenase activity of the cyanobacterium *Nostoc* sp. JAH 109, a natural isolate from Golestan rice fields. We believe that this combination of environmental variables reflects nature more realistically.

In the economical point of view nostocalean cyanobacteria can possibly be used as biofertilizer in paddy fields. Due to importance of rice as main food in Iran, and also for the catastrophic damages of using large amount of chemical fertilizers it is necessary to survey using different sources of biofertilizers in paddy fields (Roger and Kulasooriya 1981). Reaching to this aim, evaluation the viability of heterocystous cyanobacteria especially nostocacales and stigonematales in response to environmental fluctuations seems basic (Boussiba 1988; Anand et al.,1990). In addition some potent bioactive compound that extracted from this genus, draw clear landscape for pharmacological industries (Olvera-Ramirez et al.,2000; Ghasemi et al., 2001; Tabatabii Yazdi et al., 2004; Soltani et al., 2005).

Methods and Materials

Isolation of strain

The strain *Nostoc* sp. JAH 109 was isolated from soils of paddy fields of Golestan province (North of Iran). Isolation and purification was made by usual methods (Kaushik 1987). Following achievement of axenic culture, cyanobacteria were cultivated in liquid medium. Identification was done using Anagnostidis and Komarek (1988) and Castenholz (2001).

Culture conditions

Stock cultures were grown in the $BG11_0$. Temperature was maintained at 30 °C and cultures were incubated under a constant light intensity of 60 µmol photon.m^{-2}.s^{-1} supplied by three florescent lamps. Cells in logarithmic phase of growth were collected from stock cultures and used as inoculate for experiments. Cells from stock culture were inoculated in 300 ml of $BG11_0$ medium in 500 ml erlenmeyer flasks stoppered with cotton plugs. Culture media were buffered with 25mM Mes (for pH5), 2.5 mM HEPES (for pH7) or 10mM BTP (for pH9) and adjusted to the pH with HCl or KOH. Cultures were illuminated via different numbers of nets between light source and flasks. Illumination was supplied with 40 W cool white fluorescent tubes to obtain a desired of irradiance (2 µmol photon.m^{-2}.s^{-1}). Light measurements were made with Licor LI-1000 Datalogger equipped with quantum sensor. Aliquots were taken and used for determinations, when cells adapted to light regime and pH in logarithmic phase.

Finally we compared cultures without supplementary aeration or stirring (standing condition, DIC limitation) and aerated cultures (bubbled with air, DIC availability).

Analytical methods

Growth was estimated as the increase in dry matter, as described by Soltani (2006). The chlorophyll content was determined spectroscopically. Cells were extracted with pure methanol for 24 hours at 4°C according to Marker (1972). Absorption spectra of the cells were recorded against appropriate culture medium blanks. Phycobiliproteins were measured according to Wyman and Fay (1986). Peak heights for Chlorophyll and phycobiliproteins were 665 and 750, 652, 615, 562 respectively. Heterocyst frequency was determined via counting at least 1500 cell each time (Fernandez-Valiente and Leganes, 1989).

Nitrogenase activity

Nitrogenase activity was determinated by acetylene reduction in 15 ml aliquots of cell suspensions placed in stoppered 25 ml vials. First 10 % of the air was replaced with same volume of acetylene. In zero time and also sixty minutes after acetylene addition, 0.5 ml of samples were taken and ethylene concentration was determined in a Shimadzu GC-8 gas chromatograph. During this time the cells were incubated in same conditions as they were cultured (Soltani et al., 2006).

Photosynthesis

O_2 evolution was measured with a Clark-type O_2 electrode (Hach Chemical Company). Cells cultured in desired conditions (different light intensities and pHs) for 120 hours. Two ml aliquots of cell suspensions were placed in a temperature controlled cuvette (30?C) and illuminated with a quantum flux density of desired light intensities.

Results

We focused on three extreme representative pH values in rice fields (5,7 and 9), low irradiances (2 uE.m^{-2}.s^{-1}) and two conditions regarding DIC availability (use of standing cultures, DIC limitation; and air-bubbled cultures, more DIC available). The effect of DIC availability is reflected in a significant increase in growth (Figure 1). It seems obvious that aeration cause higher rate of growth both in neutral and alkaline conditions. It seems interesting that this strain have a powerful DIC concentration mechanism which possibly induced at alkaline and DIC available conditions (Figure 1).

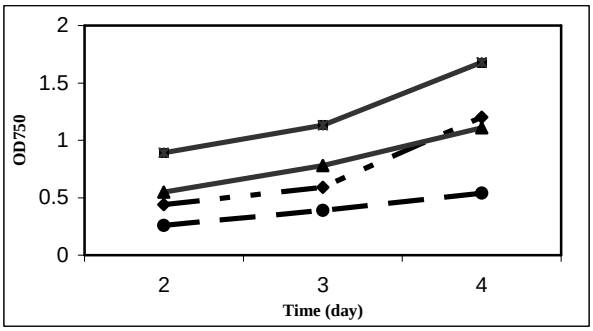

Fig 1. Growth curves of cyanobacterium *Nostoc* sp. JAH 109 at alkaline (pH9) and neutral (pH 7) conditions under DIC limitation and availability. ■ pH 9- DIC availability ▲ pH 7- DIC availability ♦ pH 9- DIC limitation ● pH 7- DIC limitation

Comparison of growth rates showed that the maximum growth rate (umax.) can be seen in pH9 and DIC available condition (data not shown). Figure 1. show that completely alkaline condition (pH9), although naturally inducing DIC, cause higher growth rate, the pattern of growth seems similar in both DIC available and limited conditions. In acidic condition (pH5), this strain can keep survival but growth rate decrease sharp comaring neutral and alkaline conditions. This seems considerably true at DIC limited condition (not shown).

It is well known that heterocysts are the sole sites of aerobic nitrogen fixation in heterocystous cyanobacteria and that a change in the number or quality of heterocysts clearly affects the rate of nitrogen fixation (Fernandez-Valiente and Leganes, 1989).

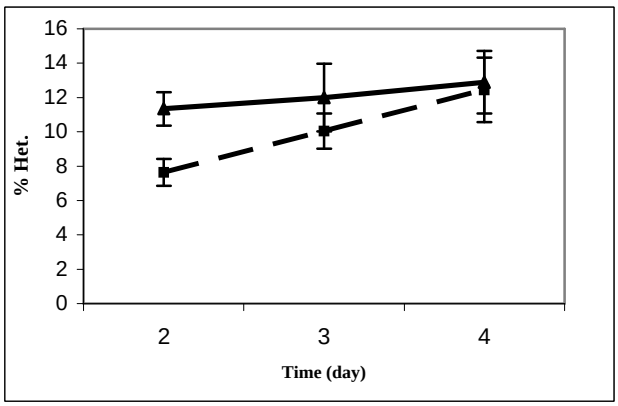

Fig 2. Heterocyst frequency changes (% Het.) of cyanobacterium *Nostoc* sp. JAH 109 at alkaline condition (pH9) under DIC limitation and availablity. ■ no aeration ▲ aeration

Figure 2 showed that the heterocyst frequency differences in cultures of *Nostoc* sp.JAH 109 grown at pH9 under limited and available DIC concentration, show insignificant difference in relatively older cultures (4 day after inoculation).

Effect of irradiance and pH on chlorophyll concentration can be seen in Table 1. As shown, chlorophyll content in pH 9 was higher than pH 7 and pH 5. The difference in chlorophyll content between pH 7 and pHs 5 and 9 was significant (ANOVA, $P<0.05$). Also there was higher chlorophyll. Content at available DIC in pH 7 and 9. This feature had not been seen in pH 5, as there was relatively weak growth of this cyanobacterium in acidic pH at variable carbon dioxide conditions.

Acidic condition (pH5) significantly decreased (ANOVA, $p<0.05$) the total phycobiliprotein content in standing as well as air bubbled cultures (not shown). However, the availability of DIC increased the PBP content under all pH conditions (ANOVA, $p<0.05$). The phycocyanin contents (PC) of standing and bubbled cultures were significantly higher in neutral (pH7) and alkaline (pH9) conditions. This is the same as bubbled cultures. Show that aeration cause outstanding increase in phycocyanin.

Table 1. Chl. contents (µg.ml^{-1}) in *Nostoc* sp.JAH 109

Days	PH5 (NA)	PH 5 (A)	PH 7(NA)	PH 7 (A)	PH 9(NA)	PH 9 (A)
2	0.58± 0.09	0.78±0.11	0.89± 0.07	2.34±0.17	1.56±0.16	3.78±0.71
3	0.77±0.11	0.99±0.08	0.95±0.13	3.56±0.21	2.45±0.07	6.64±0.19
4	1.4±0.08	1.23±0.34	1.56±0.05	5.78±0.91	2.23±0.08	8.12±2.11

NA: no aeration; A: aeration

Size of phycobilisomes that usually can be represented with the ratio of (PE+PC)/APC (Wyman and Fay, 1986) showed that this parameter promoted by pH 9 and DIC availability (Table 2).

The ratio of APC/Chlorophyll which is used to show the quantify relationship between photosystem II and photosystem I (Yamaka and Glazer, 1981), increased in pH 9 and DIC available condition (Table 2).

Correlation between heterocyst production and nitrogenase activity was significant (r^2=0.92, stagnant and r^2= 0.88, bubbled air) until 3rd day after inoculation in both DIC limited and available conditions (Figures 3 and 4). Heterocyst production tends to outstanding higher quantity in DIC available condition (between 11-14%).

Table 2. Effect of combination of two pH values (5,7, 9) and two DIC conditions on (PC+PE)/APC and APC/Chlorophyll ratios, of *Nostoc sp.*JAH 109.

Culture conditions		(PC+PE)/APC	APC/Chla
PH	DIC		
5	NA	2.68± 0.46	0.79± 0.22
	A	2.89± 0.89	0.63± 0.08
7	NA	9.48 ± 1.44	0.79 ± 0.13
	A	7.45 ± .97	0.34 ± 0.17
9	NA	8.53 ± 1.72	0.88 ± 0.08
	A	11.73 ± 0.76	0.99 ± 0.03

NA: no aeration; A: aeration

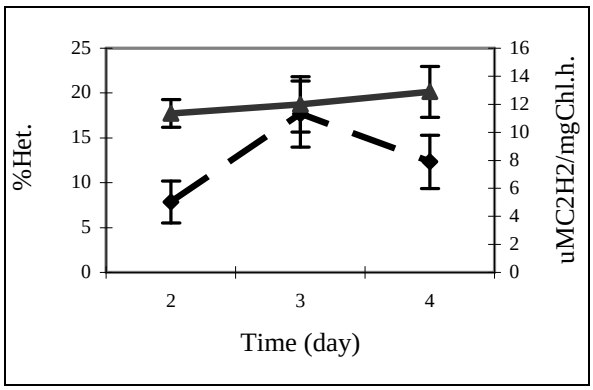

Fig 3. Nitrogenase activity and heterocyst frequency changes (%Het.) of cyanobacterium *Nostoc* sp. JAH 109 at alkaline condition (pH9) under DIC available condition. ♦ nitrogenase ▲ heterocyst

The pattern of nitrogenase activity seems more or less regular and linear at the first days after inoculation. This is interesting that this pattern is not in coincidence with growth of the strain (Figure 1). The pattern of ammonium liberation showed that the highest rate of overproduction of ammonium can be seen in the 3rd day after inoculation (data not shown). So it is logical to suppose that sharp decline in nitrogenase activity (in the opposite of increasing heterocyst frequency) may be due to overproduction of ammonium and liberation to the medium at the 3rd day after inoculation.

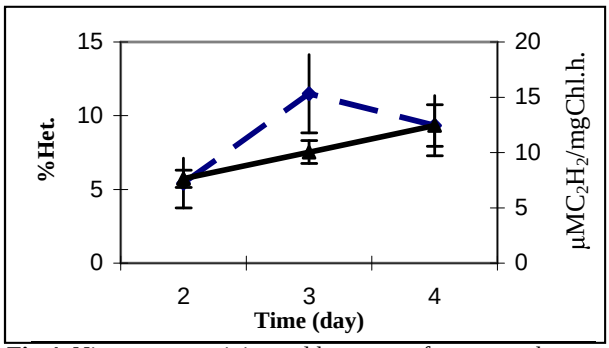

Fig 4. Nitrogenase activity and heterocyst frequency changes of cyanobacterium *Nostoc* sp. JAH 109 at alkaline condition (pH9) under DIC limitation. ♦ nitrogenase ▲ heterocyst

The combined effect of pH and DIC availability on the photosynthetic activity of the cells was also examined to analyze the functional significance of the altered pigment pattern, saturation curves of the photosynthetic net oxygen evolution were measured (Table 3). Results indicated that at pH 5 there was no clear response to variation in irradiance. The light saturated photosynthetic rate (P_{max}) and the irradiance at which photosynthesis reaches saturation (I_k), was affected by irradiance irrespective to pH in such a way that both of them increased with enhancing DIC availability, the feature was more pronounced at pH 9. As shown in table 3, α was higher in pH 9. P_{max} of cells grown at pH 9 aeration conditions were approximately four fold to the cells grown at air limited condition and same pH.

Table 3. Effect of combination of two pH values (7, 9) and two DIC condition on photosynthetic parameters of *Nostoc* sp. GAH 109. Data are means of three experiments ± SD.

pH	DIC	Pmax µmol O_2.mg chl^{-1}.h^{-1}	α	I_k
7	NA	265.9±10.4	1.4±0.1	189.9
	A	475.3±12.8	1.7±0.1	279.6
9	NA	159.5±10.2	2.9±0.8	55
	A	709.1±28.4	4.4±0.5	161.2

Discussion

With respect to the effect of of pH on dinitrogen fixation, no detailed work has been reported to our knowledge. We have weak

quantity of papers about cyanobacteria of paddy-fields of Iran (Shokravi et al., 2002). Logically the amount of researches with physiological and ecophysiological theme tend to zero (Shokravi et al., 2002; Soltani et al., 2006).

Nostoc sp. JAH 109, can be considered as an alkalophilic organism. Optimal growth rate were observed at pH 9, which seems in agreement with another strain of nostocalean cyanobacteria (*Nostoc* sp., possibly *N.ellipsosporum*) which has been isolated and characterised from rice fields of Golestan province (Khavarinejad et al., 2001). In addition Soltani (2006) reported that *Fischerella* sp. FS18, an estigonematalean cyanobacteria isolated from rice-fields of Guillan province, showed the maximum growth rate at pH 9. In Khavarinejad (2002), the strain which has been studied were not able to acclimate with acidic conditions and this seems the same for *Fischerella* sp. FS18 in Soltani (2006). *Nostoc sp*.JAH 109 in the opposite way can survive at pH 5, but of course hard metabolic problems that may be reflected on it's behavior such as very weak growth, large time dour reproduction, and very weak chlorophyll and phycoboliprotein producing ability. This is in agree with results of Amirlatifi (unpublished) data about a –possibly- same speciescollected from Gorgan (near Caspian sea).

DIC concentration in the flood water was almost depleted before noon early in the crop cycle, whereas substancial amounts of DIC could be measured at noon at the end of the crop cycle (Poza –Carrion et al., 2001). The amount of bicarbonate ions rises up to 98% in pH 9 (Shokravi et al., 2002). So having a bicarbonate DIC concentration mechanism seems essential in strains that survive in rice-fields. Growth patterns of *Nostoc* sp. JAH 109, showed that this strain must activate bicarbonate DIC concentrating pump that enable accumulation of bicarbonate and change to carbon dioxide which is the suitable form of inorganic carbon source for photosynthetic systems (Whitton and Paul 1988; Yu et al., 1994).

An increase in irradiance and pH resulted in a concomitant increase in the photosynthetic activity, both in standing and air bubbled cultures. These results agree with those reported in other cyanobacteria where, under saturating conditions of irradiance and DIC, cells grown at lower irradiance showed lower values of Pmax. Than cells grown at high irradiance (Poza-Carrion et al., 2001).

In air-bubbled cultures of *Nostoc* sp. JAH 109, although we observed that cells grown at acidic condition showed slightly higher values of chlorophyll than cells grown at low DIC, the differences were not statistically significant. The effect was more pronounced in neutral (pH 7) and alkaline (pH9) conditions. In these case, especially phycocyanin contents were statistically significant comparing acidic condition (ANOVA $p<0.05$). These results were in the opposite of *Nostoc* sp. UAM 206 which has been isolated and studied from the rice-fields of Spain (Poza – Carrion et al., 2001). In Soltani (2006), phycoerythrins were the most prominent phycobilliproteins

The availability of DIC increased the total phycobiliprotein content in in *Fischerella* sp.FS18 which seems in disagreement with our results. standing as well as air-bubbled cultures. However the availability of DIC increased the PBP contents specially at alkaline condition. There was a close parallel between the observed behavior of PC contents, with respect to external pH and availability of DIC. As the phycobilisome is mainly componed of these components, the effects of these experimental conditions were more pronounced on PC content than in PE content. With respect to DIC availability, air-bubbled cultures showed higher values of PC and PE than cells under standing condition (ANOVA $p<0.05$). Similar results have been reported for PC in *Anacystis nidulans* (Muller et al., 1993). It seems that DIC availability cause positive effect on phycobilliproteins and especially phycocyanin production and naturally may have indirect role in irradiance adaptation (Soltani et al., 2006).

Light energy absorbed by phycobilisomes is known to be efficiently transferred to photosystem II. Transfer of energy within the phycobilisome follows the path from phycoerythrin (when present) to phycocyanin to allophycocyanin to the long-wavelength pigment (Mimuro et al., 1986). These additional pigments function as light-harvesting antennae, can exhibit a high sensivity to variation of light quality/intensity (Reuter and Müller, 1993). In this respect the variability of phycobilisomes size and structure was examined. In *Nostoc sp*. JAH 109, PC is the main component of phycobilisomes. On the other hand total PBP, PC and APC were promoted in neutral pH. Latter feature was disagree with result of *Nostoc sp*. strain UAM206 (Poza-Carri?n et al., 2001). Taking consideration to light intensity affect, data

showed all pigments lower in lower DIC condition (not shown). In *Microcystis aeruginosa*, the chlorophyll a and phycocyanin contents decreased by increasing light intensity for growth (Raps et al., 1983). Müller et al., (1993) indicated that regardless of the CO_2 concentration during growth, adaptation to 2 W/m^2 induces a parallel increase of the chlorophyll and phycocyanin content. The results of Poza-Carri?n et al., 2001 were the same. The amounts and change of PE was relatively uncertain.

As is known, upon transfer of cells from high to low light, the size of the antenna first increases (by elongation of the phycobilisome rods), followed by an increase in the number of phycobilisomes per unit area of thylakoid membrane (Marsac and Houmard, 1993). This feature can be seen in *Microcystis aeruginosa* (Raps et al., 1983). Also this statement can explain the improvement in APC in this irradiance, because the core of phycobilisomes remains constant, and APC is a component of core.

Results of size of phycobilisomes and relation between PS II and PS I in *Nostoc sp*.JAH 109 are in disagreements of the results were reported in relation to irradiance in *Anacystis nidulans* and *Nostoc sp.* UAM206 (Poza-Carri?n et al., 2001; Müller et al., 1993; Vierling and Alberte, 1980). Size of phycobilisomes are higher in pH 9 than in pH 7 and increased with DIC concentration enhancing. The relation of PSII/PSI decreased not significantly with decreasing pH. the phenomenon which was not seen in pH 7. According to different strategies of adaptation of photosynthetic apparatus by irradiance (Reuter and Müller, 1993) it seems that *Nostoc sp*. JAH 109 modulate size of he phycobilisomes, not number of them, while transfer to different pHs and inorganic carbon concentration. Anyway, it seems that the ratios of the alternations within the distinct pigments are organism-specific.

In air-bubbled cultures, DIC concentration at pH 9 is higher than pH 7 (Poza –Carrion *et al.*, 2001). Thus at pH9 under light limitation, cells probably have enough DIC to maintain the activity of the of the carboxylating activity of Rubisco and do not fully induce the carbon dioxide concentrating mechanism as has been reported in several strains of *Synechococcus* (Yu et al., 1994). This may be possibly the reason of increasing heterocyst frequency despite of decline in nitrogenase activity, which has been shown in bubbled and DIC limited conditions.

The higher photosynthetic capacity (P_{max}) per unit of chlorophyll of *Nostoc* sp. JAH109 was resulted in higher DIC concentration and it is clearly observed in pH 9 (Table 3). These results agreed with those reported in other cyanobacteria (Vierling and Alberte, 1980). External pH also had an increasing effect on P_{max}. Cells grown in pH 9 had higher value of photosynthesis than cells grown in pH 7. Also the effect of pH 9 on I_k was clearly visible. Irrespectively to irradiance, photosynthesis could saturate at lower light intensity in cells grown in pH 9 than cells grown in pH 7. The slope of photosynthetic rate in pH 9 was higher indicating the capacity of carbon assimilation in limited irradiance. At pH 5 there was not a clear response to variation in irradiance. Different pH effects have been reported in other strains of cyanobacteria as no observed difference in P_{max} between pH7.5 and pH8.5 in *Synechococcus* PCC7942 (Yu et al., 1994). Our observation was agreed with *Nostoc* sp.UAM 205 (Fern?ndez-Valiente and Leganés, 1989).

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بررسی برخی واکنش‌های فیزیولوژیک سیانوباکتریوم *Nostoc* sp. JAH 109 به شرایط توام نور محدود، تغییر pH و DIC

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چکیده

رشد، وضعیت رنگیزه‌ای، فعالیت تیتروژنازی، تغییرات هتروسیست و فتوسنتز سیانوباکتریوم غالب شالیزار *Nostoc* sp. JAH 109 در شرایط توام نور محدود (۲ میکرومول کوانتا در متر مربع در ثانیه)، تغییرات اسیدیته (pHs ۵،۷،۹) و تفاوت در شرایط محدودیت کربن معدنی محلول مورد بررسی قرار گرفته است. نتایج نشان می‌دهد که *Nostoc* sp. JAH 109 سویه‌ای قلیا دوست می‌باشد. بیشینه نرخ رشد ویژه در شرایط pH معادل ۹ بدست می‌آید. اندازه فیکوبیلی زوم‌ها و نسبت PSII به PSI در شرایط pH ۹ و عدم محدودیت DIC مشاهده می‌گردد. سویه در شرایط اسیدی قادر به رشد مطلوب نیست، اما شرایط خنثی همانند شرایط قلیایی احتمالاً سبب فعال شدن سیستم مربوط به مکانیسم تراکمی دی اکسید کربن می‌گردد. الگوی فعالیت نیتروژنازی کمابیش در روزهای نخست پس از تلقیح منظم و خطی است. بیشترین میزان تثبیت نیتروژن در شرایط pH ۹ و عدم محدودیت DIC مشاهده می گردد. این امر در مورد الگوی نوسان فرکانس هتروسیست نیز صدق می‌نماید. بیشینه ظرفیت فتوسنتزی (Pmax) در واحد کلروفیل در شرایط DIC بدون محدودیت و به طور مشخص در شرایط قلیایی مشاهد گردیده است.

واژه‌های کلیدی: سیانوباکتریوم، غلظت کربن معدنی، فتوسنتز، فیکوبیلی پروتیین، نیتروژناز، اسیدیته