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Dried field populations of *Nostoc flagelliforme* (Cyanophyceae) require exogenous nutrients for their photosynthetic recovery

Baosheng Qiu[1] & Kunshan Gao[1,2,*]
[1] *Institute of Hydrobiology, The Chinese Academy of Sciences, Wuhan, Hubei, 430072 China*
[2] *Marine Biology Institute, Science Center, Shantou University, Shantou, Guangdong, 515063 China*
([*,2] Author for correspondence; e-mail: ksgao@mailserv.stu.edu.cn)

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Abstract

The effects of nutrients on the photosynthetic recovery of *Nostoc flagelliforme* during re-hydration were investigated in order to see if their addition was necessary. Net photosynthesis was negligible in distilled water without nutrient-enrichment. Addition of K^+ resulted in significant enhancement of net photosynthesis, whereas other nutrients (Fe^{3+}, Mg^{2+}, Na^+, NO_3^-, PO_4^{3-}, Cl^-) and trace-metals (A_5) showed little effect. The recovered net photosynthetic activity increased with the increased K^+, and reached the maximum at concentrations above 230 μM. Desiccation and re-hydration did not affect the dependence of photosynthetic recovery on K^+. It was concluded that dried field populations of *N. flagelliforme* require exogenous addition of potassium for photosynthetic recovery and that growth may be potassium-limited in nature.

Introduction

Nostoc flagelliforme is a terrestrial cyanobacterium that has been known by the Chinese for hundreds of years owing to its edible and medicinal values (Jiang, 1981; Fang et al., 1984; Gao, 1998). Unfortunately its resources have become over-exploited due to the increasing market demands (Wang & Liang, 1989; Dai, 1992). A number of studies have been carried out in China on the ecology, physiology, morphology, reproduction, culture and resources of *N. flagelliforme*, which have been reviewed recently (Gao, 1998). Nevertheless, it has yet to be cultivated successfully (Zhu et al., 1982; Wang et al., 1992).

N. flagelliforme is distributed on bare lands or steppes in western and west-northern areas of China. Its habitat is extremely dry and the yearly precipitation is usually less than 300 mm (Qian et al., 1989). It can maintain about 50% of its maximal photosynthetic efficiency at 20–30% water content (Gao et al., 1998a) and it has been suggested that growth in nature might occur by absorbing dew (Qian et al., 1989; Gao, 1998). *N. flagelliforme* remains desiccated for months or years, but fully recovers its metabolic activity within hours to days after re-hydration (Dodds et al., 1995). After a prolonged drought period, the sequence of metabolic reactivation is in the order of respiration, photosynthesis and nitrogen fixation (Scherer et al., 1984). Respiratory electron transport is active immediately after re-hydration, while net photosynthetic oxygen evolution becomes fully active several hours later (Scherer et al., 1984). During re-hydration, the photosynthetic recovery of *N. flagelliforme* is correlated to the recovery of energy charge (Scherer et al., 1986) and is a light-dependent process (Gao et al., 1998b). ATP availability could influence the photosynthetic recovery of this alga (Scherer et al., 1986).

Although the photosynthetic activity of *N. flagelliforme* is comparable to that of other cyanobacteria (Scherer et al., 1984; Shi et al., 1992; Qiu & Gao, in preparation), its growth has been reported to be very slow. The daily photosynthetic production of *N. flagelliforme* estimated *in situ* was reduced to zero

by watering, while that without being watered was productive (Cui, 1985). On the basis of its C: N: P ratio, the growth of *N. flagelliforme* in nature has been suggested to be phosphorus-limited (Gao, 1998). On the other hand, photosynthesis and growth of *N. flagelliforme* may be limited by the availability of ions. However, this has not been investigated. Whether the photosynthetic recovery during re-hydration requires addition of nutrients or ions is of general concern in terms of artificial culture and experimental treatments for various studies. The present study aims to investigate the effects of various ions on the photosynthetic recovery during the re-hydration of *N. flagelliforme*.

Materials and methods

Nostoc flagelliforme (Berk. & Curtis) Bornet & Flah. was collected at Siziwangqi, Inner Mongolia, and stored dry for 2–3 years until used for experiments. Samples were rinsed 3–4 times in distilled water for 1–2 min each time before submerged in BG_{11} medium (Stanier et al., 1971), half BG_{11} medium (referring to BG_{11} diluted to half of the concentration) or distilled water under 40 μmol photon m^{-2} s^{-1} and 25 °C for 9–11 h, which was proved to result in full photosynthetic recovery (Scherer et al., 1984; Gao et al., 1998b). For the experiments of nutrient addition, various nutrients were added as stock solutions to distilled water in which the rinsed samples were then submerged for re-hydration. After addition, the final concentrations of nutrients were equal to those in BG_{11} medium. That is: NO_3^- ($NaNO_3$), 17,649 μM; PO_4^{3-} ($K_2HPO_4.3H_2O$ or $Na_2HPO_4.12H_2O$), 230 μM; K^+ ($K_2HPO_4.3H_2O$ or KCl), 460 μM; Mg^{2+} ($MgSO_4.7H_2O$), 304 μM; Fe^{3+} (FeEDTA), 11 mL L^{-1} (replacing ferric ammonium citrate); microelements (A_5), 1 ml L^{-1}. In order to test the effects of possible damage by rinsing in distilled water on the photosynthetic recovery, modified BG_{11} medium (replacing 230 μM $K_2HPO_4.3H_2O$ with 230 μM $Na_2HPO_4.12H_2O$) was used for comparative re-hydration. Samples for second re-hydration have been re-hydrated in KCl solutions at 40 μmol photon m^{-2} s^{-1} and 25 °C for 10 h, and then desiccated at 0.5 m s^{-1} wind and 20–25 °C for 20 h. Three weeks later, they were rinsed in distilled water 3–4 times and then re-hydrated as described above.

Photosynthetic CO_2 uptake was measured by infrared gas analysis (CGT-7000, Shimadzu). Both the open and closed systems were adopted. The algal mats used for photosynthetic measurements were about 8.6 cm in diameter, with the biomass per unit area less than 11 mg cm^{-2}. Higher density of the mats results in decreased photosynthesis due to self-shading (authors, unpublished data). A micro-incubator (Radnoti Glass Technology Inc.) with a water jacket for temperature control was used as an assimilation chamber. Algal mat on the net was maintained in the chamber. Temperature was controlled by a polystat refrigerated bath (Cole Parmer Instrument Co.) and illumination was provided above by a halogen lamp. Light intensity was measured with a quantum sensor (SKP 200, ELE International). Various light intensities were obtained by changing the distance of lamp from the assimilation chamber, and always elevated clockwise from zero to the maximum. Dry weight was determined after the samples had been dried at 80 °C for 20–24 h and cooled down in a desiccator. For those measurements conducted with the open system, photosynthetic activity [μmol CO_2 g (d.wt)$^{-1}$ h^{-1}] was determined as follows:

$$P_n \text{ or } R_d = (A - B)\cdot F\cdot 60\cdot 273/[(273 + T)\cdot 22.4\cdot W_d],$$

where A and B represent CO_2 concentrations (μL L^{-1}) in the inlet and outlet air from the chamber, respectively; F, the air flow rate (L min^{-1}); T, temperature in the assimilation chamber, W_d, the dry weight (g) of samples. For those measurements conducted with the closed system, photosynthetic activity was determined as follows:

$$P_n \text{ or } R_d = C/t\cdot V\cdot 273/(273 + T)1/22\cdot 4/W_d\cdot 60$$

where C/t is the negative slope of CO_2 concentration variation in the closed system in a time interval of data reading (about 1.5 min); V, the volume (0.579 L) of the closed system. Parameters for P-I curves were analyzed according to Jassby and Platt (1976) and Henley (1993).

Potassium content of *N. flagelliforme* was determined by wetting the samples (0.2 g d.wt) with deionized water (4 mL), oxidizing the wet samples with concentrated sulfuric acid (3 mL) and perchloric acid (1 mL), diluting the digested syrup, and then measuring the concentration of potassium with an atomic absorption spectrophotometer (WFX-1B, Beijing Second Optical Instrument Factory). Data were analyzed according to one-way ANOVA (analysis of variance), Tukey multiple comparison and T-test.

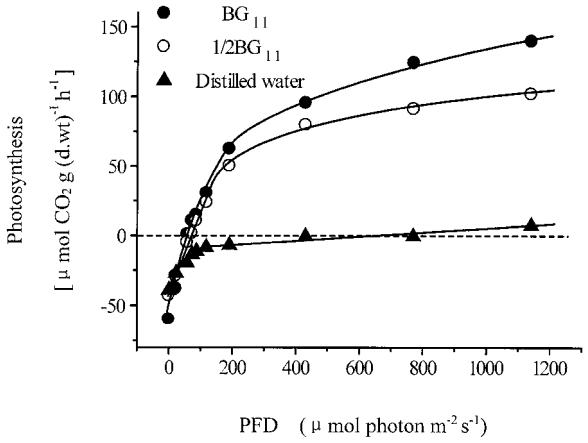

Figure 1. P–I curves of *N*ostoc *flagelliforme* determined after re-hydrated in distilled water, half and full BG_{11} medium, respectively, at 40 μmol photon m^{-2} s^{-1} and 25 °C for 9–11 h. The samples had been rinsed in distilled water for 3–4 times before re-hydration. Photosynthetic measurement was conducted at 25 °C and 360 μL L^{-1} CO_2 with the open system. Each datum indicates the mean of two measurements.

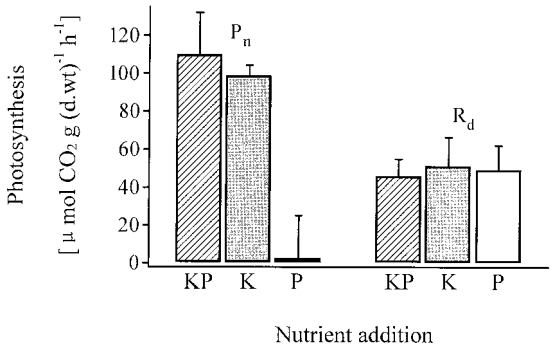

Figure 2. Responses of recovered photosynthetic activity of *N*ostoc *flagelliforme* to additions of KP ($K_2HPO_4.3H_2O$, 230 μM), K (KCl, 460 μM) and P ($Na_2HPO_4.12H_2O$, 230 μM). The samples had been rinsed in distilled water for 3–4 times before being re-hydrated at 40 μmol photon m^{-2} s^{-1} and 25 °C for 9–11 h. Photosynthesis was measured at 770 μmol photon m^{-2} s^{-1}, 25 °C and 360 μL L^{-1} CO_2 with the open system. Mean of 3 mats ± SD.

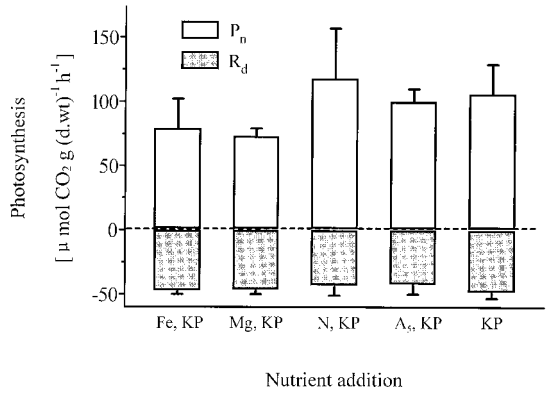

Figure 3. Combined effects of various nutrients with $K_2HPO_4.3H_2O$ on the photosynthetic recovery of *N*ostoc *flagelliforme*. Nutrients were added as stocking solutions to distilled water before the rinsed samples were submerged at 40 μmol photon m^{-2} s^{-1} and 25 °C for 9–11 h. Concentrations of the nutrients were as follows: Fe (FeEDTA), 11 ml L^{-1}; KP ($K_2HPO_4.3H_2O$), 230 μM; Mg ($MgSO_4.7H_2O$), 304 μM; N ($NaNO_3$), 17,649 μM; A_5, 1 ml L^{-1}. Photosynthesis was measured at 770 μmol photon m^{-2} s^{-1}, 25 °C and 360 μL L^{-1} CO_2 with the open system. Mean of 3 mats ± SD.

Results

The light-saturated rates of net photosynthesis of *Nostoc flagelliforme* were much lower when re-hydrated in distilled water than in BG_{11} (Figure 1). They were higher in full BG_{11} than in half BG_{11} medium. The maximal net photosynthetic rate recovered in BG_{11} was about 16 times that in distilled water and 1.4 times that in half BG_{11}. Dark respiration was also enhanced in BG_{11} medium. The photosynthetic efficiency (α) at limiting PFDs was lower in distilled water than in half and full BG_{11} media. The value of α in BG_{11} was about 3 times that in distilled water. Net photosynthesis was saturated at 236, 228 and 113 μmol photon m^{-2} s^{-1} in BG_{11}, half BG_{11} and distilled water, respectively. Less light for saturation of photosynthesis was needed in distilled water without nutrient enrichment.

The effects of nutrients on the photosynthetic recovery of *N. flagelliforme* are shown in Table 1. Net photosynthesis of rewetted *N. flagelliforme* was significantly enhanced by the addition of $K_2HPO_4.3H_2O$ ($P < 0.05$, Tukey multiple comparison). The enhancement was quantitatively similar to that with BG_{11}. Little effect on net photosynthesis was found among the treatments by FeEDTA, $MgSO_4.7H_2O$, $NaNO_3$, A_5 microelements or distilled water ($P > 0.05$, Tukey multiple comparison). The value of dark respiration was least with addition of FeEDTA and most with addition of $NaNO_3$. Thus, it seems that dried field populations of *N. flagelliforme* require exogenous K_2HPO_4 for their photosynthetic recovery.

Potassium had more effect on net photosynthetic recovery of *N. flagelliforme* than phosphorus (Figure 2). The difference of recovered net photosynthetic activity between two different sources of potassium (K_2HPO_4 and KCl) was not significant ($P > 0.05$, T-test). Phosphorus (Na_2HPO_4) had little effect on the net photosynthetic recovery. Addition of K^+ and/or PO_4^{3-} had little effect on dark respiration ($P > 0.05$,

Table 1. Effects of various nutrients on the photosynthetic recovery of *Nostoc flagelliforme*. The samples had been rinsed in distilled water 3–4 times before being submerged in the solutions at 40 μmol photon m^{-2} s^{-1} and 25 °C for 9–11 h. Photosynthetic measurements were conducted at 770 μmol photon m^{-2} s^{-1}, 25 °C and 360 μL L^{-1} CO_2 with the open system. Mean ± SD ($n = 3$)

Nutrient solution	Net photosynthesis μmol CO_2 g (d.wt)$^{-1}$ h^{-1}	Dark respiration μmol CO_2 g (d.wt)$^{-1}$ h^{-1}
Control (distilled water)	-3 ± 16^{a}	-34 ± 9^{a}
Fe.EDTA (11 ml L^{-1})	-13 ± 9^{a}	-29 ± 7^{a}
$MgSO_4.7H_2O$ (304 μM)	-7 ± 6^{a}	$-37 \pm 2^{a,b}$
$NaNO_3$ (17.65 mM)	0 ± 13^{a}	-54 ± 8^{c}
A_5 microelements (1 ml L^{-1})	7 ± 7^{a}	$-42 \pm 5^{a,c}$
$K_2HPO_4.3H_2O$ (230 μM)	106 ± 2^{b}	$-49 \pm 4^{b,c}$

[a,b,c] Those with different superscripts are significantly different ($P < 0.05$, Tukey multiple comparison)

ANOVA). Thus, it was K^+ rather than PO_4^{3-} or Cl^- that affected the net photosynthetic recovery. Meanwhile, combinations of K^+ ($K_2HPO_4.3H_2O$) with FeEDTA, $MgSO_4.7H_2O$, $NaNO_3$ or A_5, respectively, did not result in any interactive effects on the photosynthetic recovery (Figure 3). Both net photosynthesis and dark respiration showed little difference under these five treatments ($P > 0.10$, ANOVA).

Rinsing in distilled water had little effect on the photosynthetic recovery of this organism (Figure 4). There was no difference between distilled water and BG_{11} ($P > 0.05$, Tukey multiple comparison) in both net photosynthetic and dark respiratory activities of the samples re-hydrated in the same media, modified BG_{11} (Figure 4a, b) or BG_{11} (Figure 4c, d). However, absence of K^+ in the modified BG_{11} medium (Figure 4a, b) significantly depressed the photosynthetic recovery of *N. flagelliforme* ($P < 0.05$, Tukey multiple comparison) compared to BG_{11} medium with K^+ (Figure 4c & d). The recovered dark respiration displayed significantly difference ($P < 0.05$, Tukey multiple comparison) 5 h later between the modified BG_{11} and BG_{11} media. This further demonstrated that the photosynthetic recovery of dried field populations of *N. flagelliforme* was potassium-dependent, and was not influenced by the experimental treatment (being rinsed in distilled water).

The recovered net photosynthetic activity of *N. flagelliforme* depended on the amount of added K^+ in the medium used for soaking the colonies (Figure 5). About 17% net photosynthesis was recovered in 57.5 μM KCl. The half-concentration of K^+ for full recovery (K_m) was about 125 μM. As the concentration of K^+ increased to 345 M, about 90% of the net photosynthetic activity was recovered. Further increase in the amount of K^+ resulted in the net photosynthesis leveling off. No significant difference in the net photosynthesis was found between treatments in the range 345–920 μM K^+ treatments ($P > 0.05$, Tukey multiple comparison). The difference in dark respiration over all K^+ concentrations (57.5 to 920 μM) was insignificant ($P > 0.05$, ANOVA). Samples of *N. flagelliforme*, that had been soaked in solutions of various K^+ concentrations in the laboratory, wind-dried and stored for 3 weeks, were re-hydrated in distilled water. The recovered net photosynthetic activity increased with increasing K^+ concentration in the solution. The values of P_n and R_d were extremely close to those of dried field populations firstly re-hydrated in corresponding K^+ solutions ($P > 0.05$, T-test), indicating that desiccation and subsequent rehydration did not affect the dependence of *N. flagelliforme* on K^+ for its photosynthetic recovery. This implies that the dried field populations of *N. flagelliforme* required exogenous potassium for their photosynthetic recovery.

The potassium content in *N. flagelliforme* affected the extent of its photosynthetic recovery (Figure 6). The recovered P_n increased with the increase of K^+ content from 0.16 to 0.34% dry weight. The content of K^+ for half of the maximal net photosynthetic recovery was 2.7 mg g (d.wt)$^{-1}$. When it reached 0.42% dry weight, more than 95% of the photosynthetic activity was recovered.

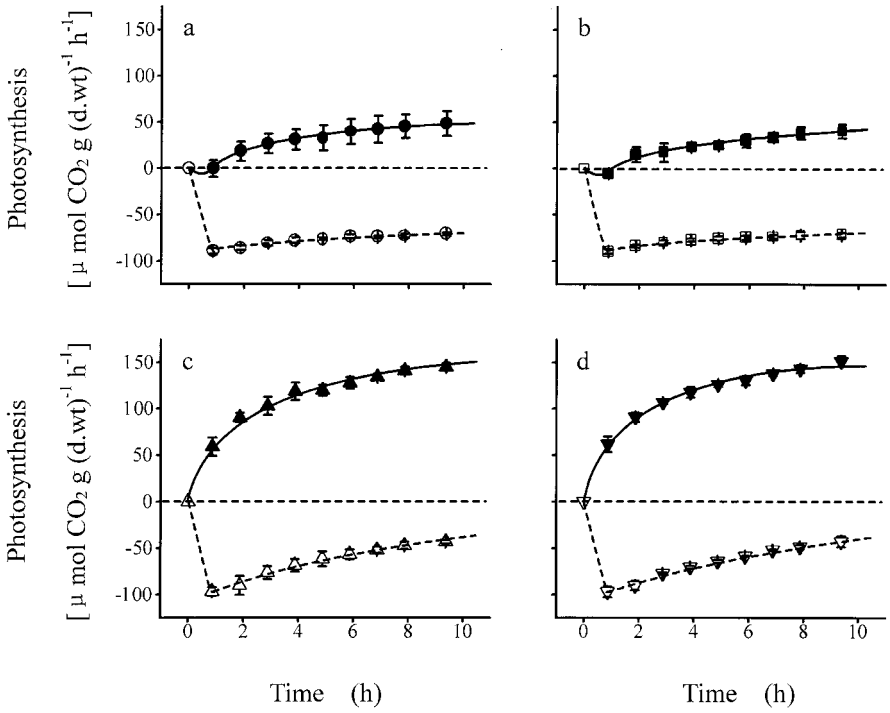

Figure 4. Time course of the photosynthetic recovery of *Nostoc flagelliforme* treated in different ways: a) rinsed in distilled water and re-hydrated in the modified BG_{11} medium; b) rinsed in BG_{11} medium and re-hydrated in the modified BG_{11} medium; c) rinsed in distilled water and re-hydrated in BG_{11} medium; d) rinsed in BG_{11} medium and re-hydrated in BG_{11} medium. Samples were re-hydrated at 40 μmol photon m^{-2} s^{-1} and 25 °C. The measurement of photosynthesis was conducted at 770 μmol photon m^{-2} s^{-1}, 25°C and 360 μL L^{-1} CO_2 with the closed system. Solid, net photosynthesis; open, dark respiration. Means of 4 mats ± SD.

Discussion

This study has made it clear that the photosynthetic recovery of *N. flagelliforme* during re-hydration requires exogenous potassium, implying that the dried field populations of this organism do not possess enough intracellular potassium to reactivate its photosynthesis. A concentration of 2.7 mg K g $(d.wt)^{-1}$ *N. flagelliforme* results in more than half of the net photosynthetic activity being recovered (Figure 6). This value is higher than the K content in dried field populations of *N. flagelliforme*, which usually contain < 2.0 mg K g $(d.wt)^{-1}$ (Ma et al., 1989; Dai et al., 1991). It is far lower than in seaweeds (30.0–82.0 mg g $(d.wt)^{-1}$: Deboer, 1981) and higher plants (20.0 mg g $(d.wt)^{-1}$: Ni, 1998).

The soil in the habitats where *N. flagelliforme* occurs is extremely low in nutrients, with less than 2% organic matter and less than 0.1% total N or P (Qian et al., 1989; Liu et al., 1995). However, its habitats are not deficient in potassium. The surface soil of the habitats in Alashanzuoqi (Inner Mongolia), Hexi (Gansu), Ningxia and Yongden (Gansu) contain 1.73–2.85% K_2O (Dai et al., 1989; Qian et al., 1989; Liu et al., 1995). When the soil is soaked with rain, K^+ would be available for *N. flagelliforme*. However, the amount of K^+ that the alga can take up depends on how long it is submerged. The habitats of *N. flagelliforme* are located 1000 ~ 2800 m above sea level, and are dry with the annual rainfall between 50–300 mm. The annual evaporation is 10 ~ 20 times the rainfall (Qian et al., 1989). Therefore, there are few chances for *N. flagelliforme* to be exposed to ionic potassium due to the dry environment and fast evaporation. Dew may supply some of the water for *N. flagelliforme* to grow, but hardly dissolve the potassium salts to release K^+ for the alga to absorb. Consequently, photosynthesis and growth of *N. flagelliforme* can be K^+-limited in nature.

As an algal macronutrient, the physiological functions of potassium mainly lie in acting as an activator of certain enzyme systems and taking part in osmotic regulation (O'Kelley, 1974; Deboer, 1981). It has been proposed that potassium is an activator

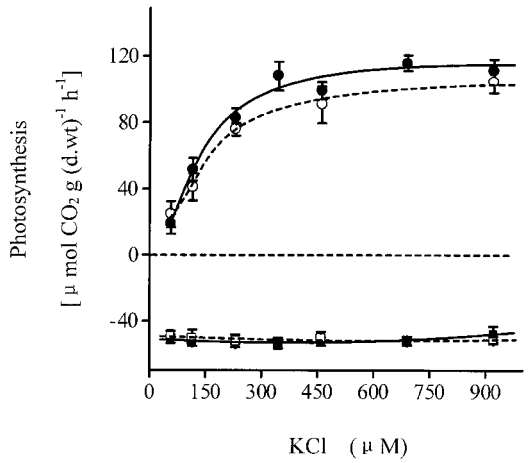

Figure 5. Recovered photosynthetic activity of *Nostoc flagelliforme* as a function of the concentrations of KCl. Solid line indicates the recovered activity in the first re-hydration in KCl solutions ($n = 3$); dotted line, that of the samples firstly re-hydrated in KCl solutions, then wind dried (0.5 m s^{-1} and 20–25 °C for 20 h) and secondly re-hydrated in distilled water 3 weeks later ($n = 5$). The samples had been rinsed in distilled water for 3–4 times before the first and second re-hydration at 40 μmol photon m^{-2} s^{-1} and 25 °C for 9–11 h. Photosynthesis was measured at 770 μmol photon m^{-2} s^{-1}, 25 °C and 360 μL L^{-1} CO_2 with the closed system.

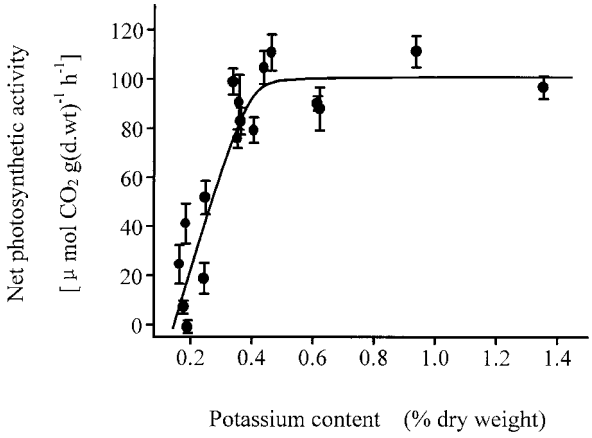

Figure 6. Net photosynthetic activity of *Nostoc flagelliforme* as a function of potassium content (%) of the dry alga. Photosynthesis was measured at 770 μmol photon m^{-2} s^{-1}, 25 °C and 360 μL L^{-1} CO_2 with the closed system. Mean of 5 mats ± SD.

for certain enzyme systems in which it maintains an ionic environment suitable for preserving the three dimensional structures necessary for optimal enzyme activity (Evans & Sorger, 1966). Our results showed that the photosynthetic recovery in *N. flagelliforme* is sensitively affected by the availability of K^+. Whether this is also true for other terrestrial algae needs further investigations. A few studies have shown that photosynthetic CO_2 uptake was diminished by potassium deficiency in several species of higher plant (e.g. Cooper et al., 1967; Terry & Ulrich, 1973; Peoples & Koch, 1979; Longstreth & Nobel, 1980). K^+ stimulated photosynthetic oxygen evolution in the marine cyanobacterium *Synechococcus* UTEX 2380 (Spiller et al., 1994). Net photosynthetic recovery in dried field populations of *N. flagelliforme* is highly sensitive to the availability of K^+, so it would be a useful material to provide insight into the relationships between photosynthesis and potassium in other phototrophs. The photosynthetic recovery of *N. flagelliforme* is related to the recovery of energy charge, and ATP availability influences the photosynthesis in colonies of prolonged drought (Scherer et al., 1986). Thus, potassium might affect the synthesis of ATP by influencing the establishment of a pH gradient. In addition, K^+ is an important regulatory cation for intracellular pH (Kroll & Booth, 1981). Photosynthetic recovery of *N. flagelliforme* may be indirectly affected by the availability of K^+ via pH adjustment.

Acknowledgements

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