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Predicting Light Acclimation in Cyanobacteria from Nonphotochemical Quenching of Photosystem II Fluorescence, Which Reflects State Transitions in These Organisms[1]

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An important factor in photosynthetic ecophysiology is the light regime that a photobiont is acclimated to exploit. In a wide range of cyanobacteria and cyano-lichens, the easily measured fluorescence parameters, coefficient of nonphotochemical quenching of photosystem II variable fluorescence (q_N) and nonphotochemical quenching, decline to a minimum near the acclimated growth light intensity. This characteristic pattern predicts the integrated light regime to which populations are acclimated, information that is particularly useful for cyanobacteria or cyano-lichens from habitats with highly variable light intensities. q_N reflects processes that compete with photosystem II photochemistry for absorbed excitation energy. In cyanobacteria, we find no evidence for energy-dependent quenching mechanisms, which are the predominant components of q_N in higher plants. Instead, in cyanobacteria, q_N correlates closely with the excitation flow from the phycobilisome to photosystem I, indicating that q_N reflects the state transition mechanism for equilibration of excitation from the phycobilisome to the two photosystems.

Chlorophyll fluorescence analysis is a useful monitor of photosynthesis, because it is noninvasive, sensitive, and scalable over large ranges of time, light, and distance. For natural samples, fluorescence signals are specific to photobionts and allow in situ measurements of small or dilute mixed natural populations. Chlorophyll fluorescence quenching analysis has been widely applied to characterize photosynthetic metabolism in cyanobacteria and cyanolichens (Lange et al., 1989; Miller et al., 1991; Badger and Schreiber, 1993; Büchel and Wilhem, 1993; Clarke et al., 1993, 1995; Campbell et al., 1995, 1996; Lüttge et al., 1995; Schreiber et al., 1995; Schubert et al., 1995a; Campbell, 1996; Sundberg et al., 1996). The characteristic fluorescence signals from cyanobacteria necessitate modifications of fluorescence measurement protocols and interpretations originally developed for higher plants (Büchel and Wilhem, 1993; Schreiber et al., 1995). On the other hand, cyanobacterial fluorescence can yield information not accessible from plant fluorescence signals.

An important feature of fluorescence signals from cyanobacteria are large changes in PSII fluorescence yield depending on illumination, termed state transitions (Murata, 1969). In contrast, in higher plants, state transitions have relatively minor influences on PSII fluorescence (Krause and Weis, 1991). In this article we present evidence that in cyanobacteria q_N primarily reflects state transitions rather than the q_E that predominates in plants. Furthermore, the pattern of q_N versus irradiance can be used to predict the light acclimation status of cyanobacteria.

MATERIALS AND METHODS

Cyanobacterial Cultures and Pigment Measurements

Cyanobacteria were grown in BG-11 inorganic medium (Rippka et al., 1979), supplementally buffered with 10 mM Mops, pH 7.5. For most experiments *Synechococcus* sp. PCC 7942 cultures of 300 mL were grown in flat flasks, bubbled with 5% CO_2 in air (about 1 mL s^{-1}) at 37°C with continuous, even illumination of 50 μmol photons m^{-2} s^{-1}. Chlorophyll and phycocyanin contents of *Synechococcus* were determined using whole-cell spectra according to the method of Myers et al. (1980), corrected for scattering by subtracting A_{750nm} from the chlorophyll and phycocyanin peaks. For other strains, chlorophyll was extracted in methanol and measured according to the method of Tandeau de Marsac and Houmard (1988). For *Synechococcus* sp. PCC 7942 and other strains used for q_N measurements shown in Figure 2, growth conditions were generally similar, but the temperature ranged from 18 to 37°C, the light ranged from 5 to 150 μmol photons m^{-2} s^{-1}, and CO_2 supply ranged from ambient to 5% in air. The other strains used were *Anabaena/Nostoc* sp. PCC 7120, *Calothrix* sp. PCC 7601, *Nostoc* sp. isolated from the lichen *Peltigera canina*, *Pseudan-*

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Abbreviations: DBMIB, 2,5-dibromo-3-methyl-6-iso-propyl-*p*-benzoquinone; FCCP, carbonyl cyanide *p*-(tri-fluoromethoxy)phenyl-hydrazone; *F*, fluorescence; F_m, maximal fluorescence; F_{mdark}, maximal fluorescence in the dark; F_m', maximal fluorescence in light-adapted cells; F_o, minimal fluorescence; F_o', minimal fluorescence in light-adapted cells; PAM, pulse amplitude modulated; q_E, energy-dependent quenching of PSII fluorescence; q_N, coefficient of nonphotochemical quenching of PSII variable fluorescence.

abaena sp. PCC 6901, *Synechococcus* sp. PCC 6301, and *Synechocystis* sp. PCC 6701.

Fluorometer Measurements and Treatments

Chlorophyll *a* fluorescence induction was measured as described elsewhere (Clarke et al., 1995; Campbell, 1996; Campbell et al., 1996) using a PAM fluorometer (Walz, Effeltrich, Germany; Schreiber et al., 1986) with the PAM 103 accessory and a Schott KL1500 lamp (Schott, Mainz, Germany) to provide saturating flashes. A PAM-compatible system consisting of a cuvette, magnetic stirrer, oxygen electrode, and Björkman-type actinic lamp were used for the simultaneous measurement of fluorescence and oxygen evolution (Hansatech, King's Lynn, UK; Walker, 1987).

The parameters F, F_{mdark}, F_o', F_m', and F_m were used for calculation of q_N (van Kooten and Snel, 1990); $q_N = 1 - ([F_m' - F_o']/[F_m - F_o])$, as described elsewhere (Campbell et al., 1996). F_m was measured by adding DCMU to illuminated cells. See Figure 5 for an illustration of a fluorescence trace.

The inhibitors DCMU and DBMIB (Trebst, 1980) were used to artificially control electron transport. FCCP is an ionophore uncoupler that collapses the transthylakoid pH gradient (Good, 1977). Inhibitor titrations were determined at 37°C and 50 μmol photons m^{-2} s^{-1} for the DCMU and DBMIB treatments and under a range of light intensities for FCCP. ATP and ADP concentrations were measured according to the method of Gardeström and Wigge (1988) using a luciferin-based luminescence protocol.

77 K Fluorescence Emission Spectra

A clear, acrylic rod sample holder for 77 K fluorescence was dipped briefly into the Hansatech PAM cuvette to collect about 100 μL of culture sample and then plunged directly into liquid nitrogen. The sample holder was attached to a fiberoptic-based fluorometer, and 77 K fluorescence emission spectra were collected as described previously (Ögren and Öquist, 1984). Excitation was at 574 and 430 nm, to preferentially excite phycocyanin and chlorophyll, respectively. With this procedure, the 77 K spectra are from cells that were preincubated under the same conditions as those used for room temperature fluorescence quenching and oxygen measurements.

RESULTS

Figure 1 shows a typical light-response curve of the q_N for the cyanobacterium *Synechococcus* sp. PCC 7942. The growth light intensity for the cultures was 50 μmol photons m^{-2} s^{-1}. In cyanobacteria, the in vivo PSII fluorescence yield is low in dark-adapted cells (Fig. 5; Mullineaux and Allen, 1986; Miller et al., 1991; Clarke et al., 1993, 1995; Campbell, 1996; Campbell et al., 1996), and this is reflected in a high q_N, which is typically 0.6 to 0.8 for healthy cultures. Upon illumination q_N decreases to a minimum near the growth light intensity. As the light exceeds the growth level, q_N increases somewhat, but never to the high levels observed in dark-adapted cells. A similar pattern is observed with a Stern-Volmer formulation, the nonphotochemical quenching parameter (Krause et al., 1982; Krause and Weis, 1991), to estimate nonphotochemical quenching (data not presented).

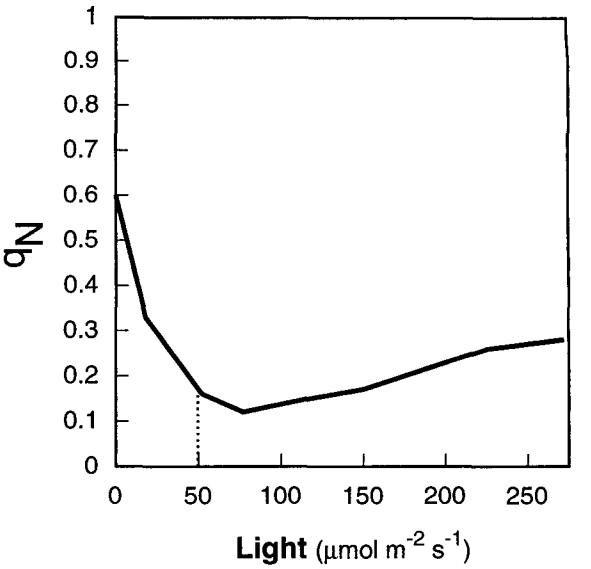


Figure 1. Nonphotochemical quenching of fluorescence versus light. A typical light-response curve of nonphotochemical quenching in the cyanobacterium *Synechococcus* sp. PCC 7942. The growth light intensity was 50 μmol photons m^{-2} s^{-1}.

The experiment presented in Figure 1 was repeated with seven different strains of cyanobacteria grown under a wide range of conditions. The growth light intensities ranged from 5 to 150 μmol photons m^{-2} s^{-1}, with temperatures from 18 to 37°C, and CO_2 supplies ranged from ambient air to bubbling with 5% CO_2. The absolute levels and changes of q_N varied between experiments, but the characteristic pattern presented in Figure 1 was very consistent. From each light-response curve of q_N, we determined the light intensity at which q_N reached minimum. In Figure 2, we plot this light intensity for minimum q_N, versus the growth light intensity. q_N reaches minimum near the growth light regime for this wide range of cyanobacterial strains and culture conditions. The pattern of q_N versus light did not correlate with the other factors tested, including CO_2 supply, cyanobacterial strain, and growth temperature (data not presented).

To examine the origin of the changes in cyanobacterial fluorescence yield measured by q_N, we titrated electron transport in *Synechococcus* sp. PCC 7942 using the inhibitors DCMU and DBMIB. Figure 3 follows q_N and oxygen evolution in the presence of DCMU (Fig. 3A) or DBMIB (Fig. 3B) at 50 μmol photons m^{-2} s^{-1}. Each inhibitor caused a progressive decrease in electron transport, measured by oxygen evolution. With DCMU inhibition, q_N decreased from the low control level to 0. In contrast, under similar inhibition by DBMIB, q_N increased progressively to a high level, similar to that seen in dark-adapted cells.

This differential regulation of q_N by specific electron transport inhibitors suggests that q_N in cyanobacteria originates from the state-transition mechanism for equilibra-

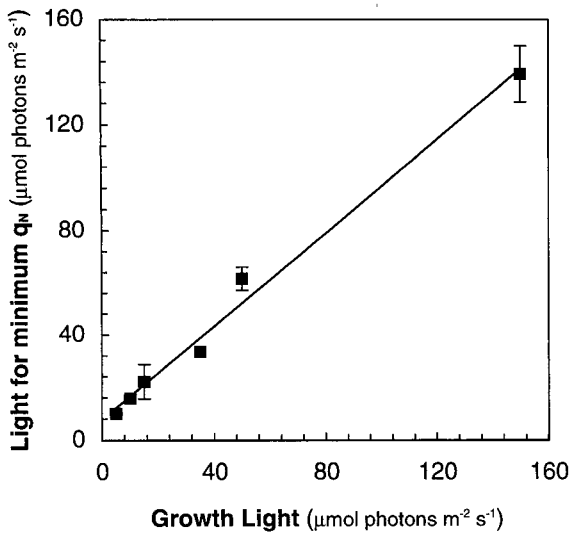


Figure 2. Near the growth light intensity q_N reaches minimum for a wide range of cyanobacterial strains and culture conditions. Average values were plotted for strains grown at 5 (n = 3), 10 (n = 5), 15 (n = 6), 35 (n = 1), 50 (n = 20), and 150 (n = 3) μmol photons m^{-2} s^{-1}. The strains were *Anabaena/Nostoc* sp. 7120, *Calothrix* sp. PCC 7601, *Nostoc* sp., *Pseudanabaena* sp. PCC 6901, *Synechococcus* sp. PCC 7942, *Synechococcus* sp. PCC 6301, and *Synechocystis* sp. PCC 6701.

tion of excitation energy between the photosystems. In cyanobacteria, state transitions are regulated by the redox status of the electron transport chain (Mullineaux and Allen, 1986; Dominy and Williams, 1987; Vernotte et al., 1990).

To detect a possible relation between q_N and state transitions, we incubated cells of *Synechococcus* sp. PCC 7942 in the in vivo fluorescence cuvette under a range of light intensities (0, 12.5, and 50 μmol photons m^{-2} s^{-1} and 50 μmol photons m^{-2} s^{-1} plus DCMU). Under each light treatment we measured q_N, and snap-froze a small sample for 77 K fluorescence emission spectra. Emission spectra were measured under excitation at 574 nm, absorbed by the phycobilisome. Figure 4A presents a comparison between the 77 K emission spectra and q_N values for one sample, preincubated in darkness, or at the growth light intensity, or after the addition of DCMU. The dashed lines on the 77 K emission spectra emphasize that PSII fluorescence increases, while PSI fluorescence decreases slightly, in parallel with a decline in q_N. Emission spectra were also measured under excitation at 430 nm, absorbed by chlorophyll, and PSI fluorescence at 727 nm was determined for every sample under the two excitation wavelengths. In Figure 4B the ratio: PSI fluorescence under phycobilisome excitation to PSI fluorescence under chlorophyll excitation is plotted versus q_N for each treatment. It shows that q_N correlates closely with increasing phycobilisome excitation of PSI fluorescence. For treatments causing high q_N (darkness or low light), excitation flow from the phycobilisome to PSI was high. As q_N decreased, phycobilisome excitation of PSI fluorescence declined.

Figures 3 and 4 indicate that in cyanobacteria q_N reflects the redox-regulated state transition, which equilibrates excitation between the photosystems. In plants, a large body of literature shows that the predominant component of q_N is q_E, which is driven by the accumulation of the transthylakoid pH gradient (Krause et al., 1982; reviewed by Krause and Weis, 1991). We therefore investigated possible influences of the transthylakoid pH gradient on q_N in *Synechococcus* sp. PCC 7942. We incubated the cells in the in vivo fluorescence cuvette in darkness and then under the growth light intensity (50 μmol photons m^{-2} s^{-1}) without or with FCCP (2.5 μmol l^{-1}), an ionophore uncoupler of the transthylakoid pH gradient (Good, 1977). The resulting fluorescence trace (Fig. 5) shows that the uncoupler did not collapse nonphotochemical quenching. Indeed, F_m' actually decreased upon addition of FCCP, because of an increase in q_N upon the collapse of the pH gradient. The pattern in higher plants is the opposite; collapse of the pH

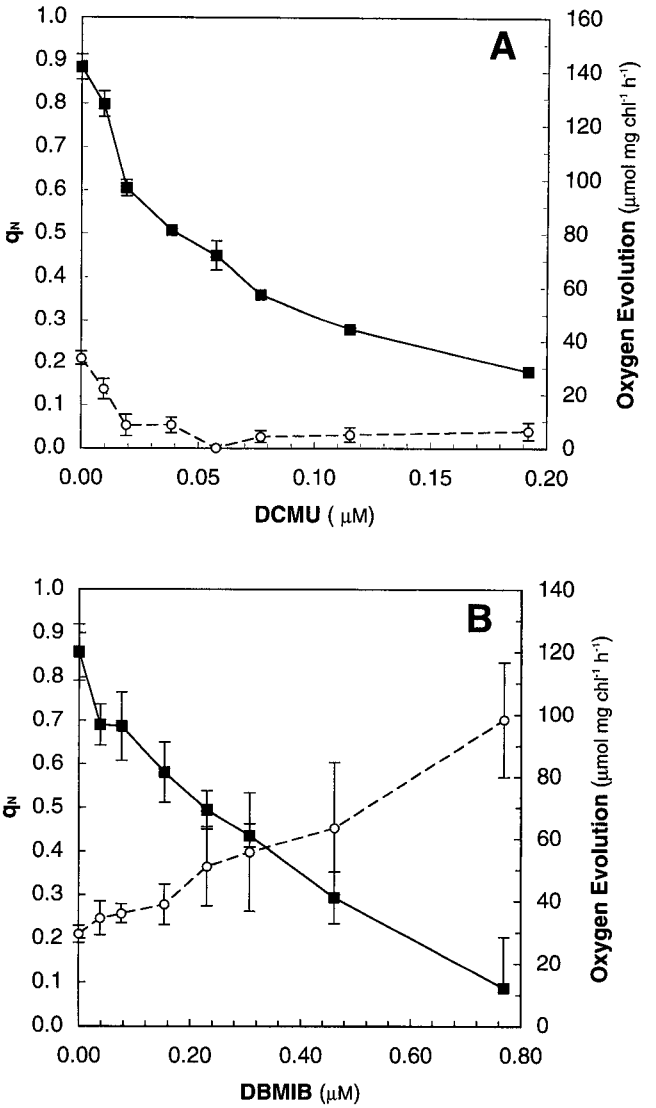


Figure 3. Nonphotochemical quenching of fluorescence and electron transport under DCMU (A) and DBMIB (B) treatments. ○, q_N; ■, oxygen evolution. Results are averages ± SE of measures on the same culture at 37°C, n = 3. chl, Chlorophyll.

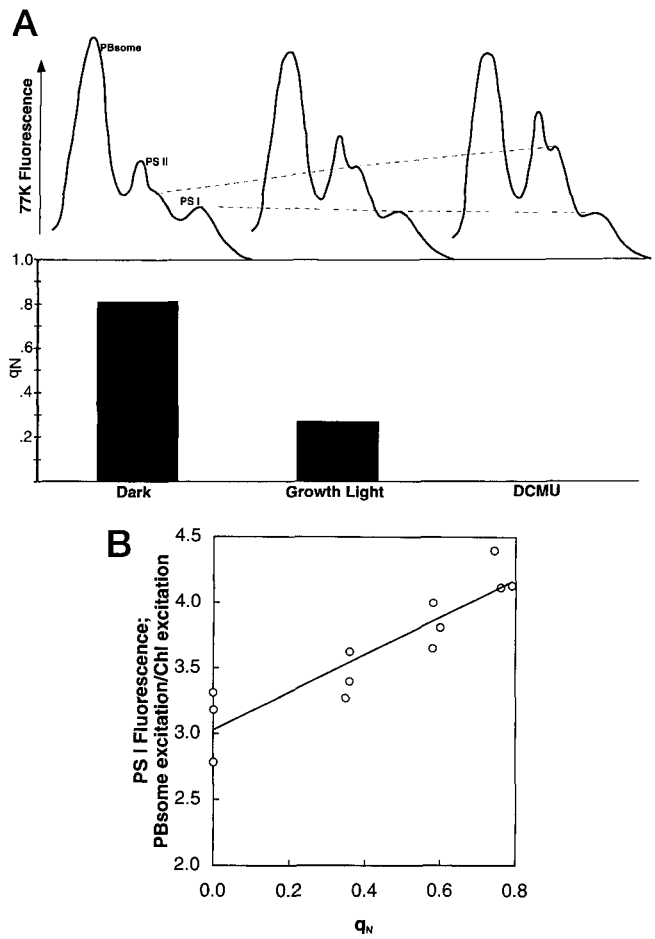


Figure 4. Nonphotochemical quenching correlates with phycobilisome excitation of PSI fluorescence emission at 77 K. *Synechococcus* culture samples were incubated in darkness under the growth light intensity of 50 μmol photons m^{-2} s^{-1} and after the addition of DCMU under continuing illumination. q_N was measured, and a small sample was taken for 77 K fluorescence emission spectra. A, Dashed lines on the 77 K emission spectra emphasize increasing PSII fluorescence and decreasing PSI fluorescence, in parallel with a decrease in q_N. Excitation of 77 K fluorescence was with 574 nm light, absorbed by the phycobilisome. The spectra were not normalized. B, The ratio: PSI fluorescence excited by phycobilisome absorbance to PSI fluorescence excited by chlorophyll (Chl) absorbance was plotted versus q_N. r^2 = 0.83 for the linear regression line.

gradient leads to an increase in PSII fluorescence and loss of most of the q_N (Krause et al., 1982). CO_2-dependent oxygen evolution progressively decreased upon addition of FCCP (data not shown), verifying that the uncoupler entered the cells and acted on the thylakoids.

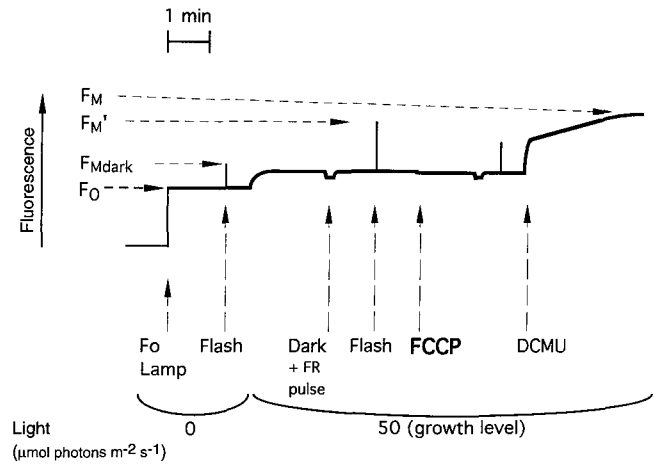
Figure 6 shows further evidence suggesting that nonphotochemical quenching does not reflect membrane energization in cyanobacteria. Samples for ATP/ADP determinations were taken from treatments such as that presented in Figure 5, under a range of light intensities (0, 10, 50, and 200 μmol photons m^{-2} s^{-1}) in the absence or presence of FCCP (2.5 or 10 μmol l^{-1}). For each treatment q_N was measured and plotted versus the ATP/ADP ratio of the cells, as an approximate index of membrane energization. There was no correlation between q_N and the cellular ATP/ADP ratio.

DISCUSSION

In cyanobacteria, nonphotochemical quenching decreases from high dark levels to a minimum near the growth light intensity. This characteristic pattern holds in a wide range of cyanobacterial strains of different origins, morphologies, physiological properties, and pigmentations. The position of the q_N minimum does not appear to correlate with other factors, such as CO_2 supply, growth temperature, or strain.

This empirical finding can thus be used to predict the light intensity to which a cyanobacterial population is acclimated. The nonphotochemical quenching parameter, an alternate quantification of nonphotochemical quenching (Krause et al., 1982), shows a similar pattern and can also be used to predict the acclimated light level. Even more simply, F_m' can be measured with a saturating flash under any light regime. A plot of this fluorescence level versus actinic irradiance reaches maximum near the acclimated light intensity.

This prediction method should prove useful for natural samples, giving a simple means to determine the integrated light regime that the cyanobacteria actually exploit. In variable light environments (Schubert et al., 1995a, 1995b), cyanobacteria experience large and rapid change in irradiance, and the light level to which they acclimate may prove to be a complex function of several environmental and physiological factors. The generality of the pattern suggests that mixed populations will prove amenable to the prediction. The relation holds for a *Nostoc* strain isolated from a cyano-lichen, *P. canina*, and appears to be valid for intact cyano-lichens as well (Sundberg et al., 1995). For models of cyanobacterial photosynthesis based on fluorescence parameters, it is important to use the acclimated light inten-



$$q_N = 1 - ((F_M' - Fo')/(F_M - Fo))$$

Figure 5. An uncoupler of the transthylakoid pH gradient does not collapse nonphotochemical quenching in cyanobacteria. Note that F_m' decreases upon addition of FCCP because of an increase in q_N. The fluorescence trace was redrawn from a chart recorder output.

sity to avoid serious estimation errors under excess light (Sundberg et al., 1995). A further application is to track changes in light acclimation in natural or laboratory samples.

In cyanobacteria, nonphotochemical quenching of PSII fluorescence correlates closely with the extent of excitation flow from the phycobilisome/PSII supra-complex to PSI, which changes during state transitions. The redox balance of the electron transport chain between the photosystems regulates this state-transition mechanism (Mullineaux and Allen, 1986; Dominy and Williams, 1987; Vernotte et al., 1990). In state II, a reduced electron transport chain drives low PSII fluorescence, high excitation transfer to PSI, and high q_N. When the electron transport chain becomes oxidized, the cells shift to state I, resulting in higher PSII fluorescence, less excitation transfer to PSI, and low q_N. The high q_N in the dark results when respiratory electron flow poises the transport chain toward a reduced condition (Mullineaux and Allen, 1986). The underlying mechanism(s) for this state-transition excitation equilibration remains controversial, with evidence for both changes in coupling of phycobiliproteins to PSI (Allen et al., 1985) and also variable energy spill-over from PSII to PSI (Salehian and Bruce, 1992). Recent interpretations indicate that neither simple model can fully account for all of the experimental evidence (Lazenby et al., 1994; Bruce et al., 1995). In any case, it is reasonable that, under the acclimated light intensity, the requirement for energy equilibration between the photosystems is minimal, reflected by a low q_N.

An interesting exception to the general pattern of a low q_N under the growth light intensity occurs in *Calothrix* sp. PCC 7601 (Campbell, 1996) growing under green light. The only photosynthetic pigment absorbing the green light is phycoerythrin in the phycobilisomes. In this case q_N remains high across a wide range of green light intensities, as does phycobilisome excitation of PSI fluorescence.

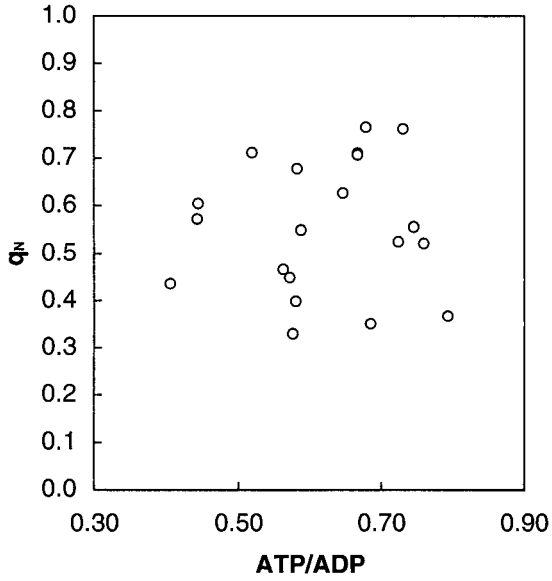


Figure 6. Nonphotochemical quenching does not reflect membrane energization in cyanobacteria. *Synechococcus* sp. PCC 7942 grown under 50 μmol photons m^{-2} s^{-1} was incubated under a range of light intensities (0, 10, 50, and 200 μmol photons m^{-2} s^{-1}) in the absence or presence of FCCP (2.5 or 10 μmol l^{-1}), an uncoupler that collapses the proton gradient across thylakoid membranes. Nonphotochemical quenching was measured, and samples were taken for ATP/ADP determination.

We find that in cyanobacteria q_N can be fully explained through the state transition. There is therefore no need to invoke a contribution from energy-dependent quenching. In plants some forms of energy-dependent quenching may involve protonations of light-harvesting chlorophyll-proteins (Crofts and Yerkes, 1994; Horton and Ruban, 1994), which are absent from cyanobacteria. Upon collapse of the thylakoid proton gradient, q_N actually increased in *Synechococcus*. This may reflect a partial state transition driven by reduction of the electron transport chain when CO_2 fixation was inhibited by the lack of ATP.

In plants energy-dependent quenching is generally interpreted as thermal dissipation, which down-regulates overall photosynthetic activity, and this q_E is considered to be the primary component of q_N (Krause and Weis, 1991; but see Hurry, 1995). It is therefore very important to note that in cyanobacteria q_N does not necessarily reflect energy dissipation but rather excitation equilibration to maintain balanced electron transport. The cyanobacterial electron transport chain functions in both respiration and photosynthesis and is thus closely connected to all aspects of metabolism. Therefore, excitation equilibration is required in the face of unbalanced or changing excitation (Schubert et al., 1995a, 1995b; Campbell, 1996) but also to meet changing metabolic demands for ATP and NADPH (Romero et al., 1992). In some circumstances, excitation flow to PSI might result in energy dissipation through heat, in an alternate strategy for down-regulation of photosynthesis under excess excitation, as in desiccated intertidal red algae (Öquist and Fork, 1982a, 1982b).

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