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CHARACTERISTIC TEMPERATURE DEPENDENCES OF RESPIRATORY AND PHOTOSYNTHETIC ELECTRON-TRANSPORT ACTIVITIES IN MEMBRANE PREPARATIONS FROM *ANACYSTIS NIDULANS* GROWN AT DIFFERENT TEMPERATURES

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Electron-transport activities supported by seven different electron donor/acceptor couples in the light and in the dark, respectively, were measured in particle preparations of the cyanobacterium (blue-green alga) *Anacystis nidulans* after growth at 40, 30 and 25°C. The Arrhenius plots of the photosynthetic electron-transport reactions between ascorbate (plus 2,6-dichlorophenolindophenol (DCIP)) and $NADP^+$, diphenylcarbazide and DCIP, diaminodurene and benzyl viologen (O_2), and the plot of the photooxidation of reduced horse heart cytochrome *c* showed a single discontinuity at approx. 24–25, 15–17 and 10–13°C in membranes derived from cells grown at 40, 30 and 25°C, respectively. By contrast, the dark respiratory electron-transport reactions between NADPH, ascorbate (plus DCIP) or reduced horse heart cytochrome *c* and oxygen, and the reduction by horse heart cytochrome *c* of the aa_3-type terminal oxidase as followed directly by dual-wavelength spectrophotometry, all gave Arrhenius plots distinguished by two distinct breaks: The break at the higher temperature corresponded to the break also found in the Arrhenius plots of the photosynthetic reactions while an additional discontinuity was observed at 17–18, 8–9 and 5–6°C in membranes prepared from cells grown at 40, 30 and 25°C, respectively. The temperatures at which the discontinuities in the Arrhenius plots occurred depended on the temperature at which the cells had been grown; they were independent, however, of the specific electron donors and acceptors employed. The characteristic features in the Arrhenius plots of respiratory and photosynthetic electron-transport reactions are discussed in terms of lipid-phase transitions in the cytoplasmic and the intracytoplasmic (thylakoid) membranes of *A. nidulans*. Implications for possibly distinct sites of the respiratory and photosynthetic electron-transport systems in *A. nidulans* will be mentioned.

Introduction

It is well known that temperature plays a key role for determining the physical state of biological membranes. In particular, the lipid and fatty acid compositions of the membranes are governed by the growth temperature, lower temperatures favouring the synthesis of unsaturated fatty acids thus leading to increased fluidity of the membranes [1–6]. According to the fluid-mosaic model of biological membranes [7], the coordinate interaction of membrane-bound enzymes will depend on mobilities and relative positions of the individual enzyme proteins within the lipid matrix. This would be especially true of the electron-transport assemblies in photosynthesis and respiration.

Measurements based on spin labeling [8,9], X-ray diffraction [2,10], differential scanning calorimetry

Abbreviations: DAD, 2,3,5,6-tetramethyl-*p*-phenylenediamine (diaminodurene); DCIP, 2,6-dichlorophenolindophenol; TMPD, *N,N,N',N'*-tetramethyl-*p*-phenylenediamine.

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[11,12] and freeze-fracture electron microscopy [12–14] have all revealed transitions in the physical state of the membrane lipids from the liquid crystalline to the phase separation state below a certain threshold temperature. This phase transition might lead to disordered interaction of the membrane-bound enzymes, thus affecting the apparent thermodynamics of the respective physiological reactions which, in turn, would be reflected by discontinuities in the corresponding Arrhenius plots [9,15,16].

Lipid phase transitions in the thylakoid membranes of cyanobacteria, namely *Anacystis nidulans*, along with temperature dependences of various photosynthetic activities have been extensively studied by Murata and co-workers (Refs. 4,9,16–20; also cf. Ref. 21). Using X-ray diffraction [10] and spin labeling or chlorophyll *a* fluorescence [9,17], they found the phase transitions in thylakoid membranes of *A. nidulans* at 26°C (16°C) and 24–25°C (13°C), respectively, while the breaks in the Arrhenius plots of various photosynthetic reactions displayed by these membranes [20] were localized at 21–24°C (12–15°C) after growth of the cells at 38°C (28°C). Independent evidence from differential scanning calorimetry [12] and freeze-fracture electron microscopy [12,13] appears to confirm their findings.

No similar studies, however, have been performed on the respiratory electron transport in the cyanobacteria. A few aspects of the respiratory electron transport in *A. nidulans* have recently been studied [22–24], including characterization of the terminal oxidase as an aa_3-type cytochrome [25–27]. The present paper reports on investigations of the temperature dependence of various respiratory electron-transport reactions in membrane preparations of *A. nidulans* grown at different temperatures. The results are compared to simultaneous measurements of the photosynthetic activities in the same mebranes. It is concluded that part of the respiratory assembly of *A. nidulans* is located within a molecular environment different from that of the photosynthetic electron-flow chain.

Materials and Methods

Preparation of cells and membranes. Anacystis nidulans (strain 1402-1, Göttingen, F.R.G.) was grown axenically in modified medium D [27,28] at the desired temperature using a New Brunswick Bioflo fermenter, model C30, illuminated by a semicircular bank of warm white fluorescence tubes providing a light intensity of 100 W/m^2 at the surface of the vessel as measured with a YSI radiometer, model 65. An electronically operated pH-stat coupled to the valve of the CO_2 supply permitted the maintaining of the pH of growing suspensions at 8.2 throughout. During the late logarithmic growth phase the cells were continuously harvested while operating the fermenter as a turbidostat with a continued supply of fresh growth medium [27]. Cells were harvested by centrifugation [28]. Membranes were isolated either by brief sonication of lysozyme-pretreated cells [29] or by passing the cells through a precooled French pressure cell at 1400 kg/cm^2 as previously described [26]. All of the experiments reported in this paper were performed separately with membrane preparations obtained by both types of treatment; no significant differences were found in the catalytic behaviour of the membranes and, in particular, the shapes of the Arrhenius plots remained the same in both cases. Membranes prepared by either procedure were suspended in 25 mM potassium phosphate buffer, pH 7.5, containing 0.6 M mannitol. For the assays they were always used immediately after preparation. With the exception of the French pressure treatment cooling was avoided throughout the preparation procedures.

Assay of electron-transport reactions. Electron transport was assayed by use of the following donor and acceptor compounds (mM): sodium ascorbate (20), DCIP (0.1), NADP$^+$ (3), NADPH (5), diphenylcarbazide (10), DAD (5), menadion (0.05), benzyl viologen (5), cytochrome *c* (0.01) and O_2 (0.22). The reduction of the various acceptors in the presence of suitable donors (cf. Table I) was followed spectrophotometrically [29] or, in the case of O_2, polarographically [22] as described previously. Oxidation of reduced horse heart cytochrome *c* was measured with a Perkin Elmer dual-wavelength spectrophotometer, model 557, at 550 minus 540 nm [26,27]. Reduction of the membrane-bound aa_3-type cytochrome oxidase was followed anaerobically at 20°C with the same spectrophotometer at 600–590 and 605–590 nm in the presence and absence of 1 mM KCN, respectively, as described previously (Ref. 27; cf. Ref. 30). Other spectrophotometric measurements were performed with a Perkin Elmer double-beam recording spec-

trophotometer, model 200 [29]. In the case of illumination, the light was provided by an Oriel 1000 W xenon lamp and passed through interference filters (Scott AG, Jena; half-band width approx. 10–12 nm) of 630 nm for measurement of the Photosystem II reaction with diphenylcarbazide or of 700 nm for measurement of the other photosynthetic reactions.

Reactions were started by addition of the appropriate donor compounds to otherwise complete reaction mixtures which had previously been incubated at the desired temperature for 3–5 min before starting the experiments. Temperature was measured by a sensitive thermocouple connected to a pH meter with digital temperature display (Seibold, Vienna). The temperature was kept constant within ±0.1 K during each experiment using a rapidly circulating stream of thermostatically controlled water supplied by a thermomix, model 1441 (Braun AG, (Melsungen).

Determination of protein. This was performed by a modified biuret method as described previously [28].

Controls. Heat-denatured membranes (90°C, 5 min) were found to be incapable of catalyzing any one of the redox reactions assayed in the course of this study (cf. Table I). The preparation procedures employed apparently led to membranes devoid of water-splitting capacity (no detectable evolution of O_2 in the light; cf. Ref. 29); nevertheless, to obviate any possible interference by Photosystem II, 10 μM DCMU was included in the samples assayed for Photosystem I activity with DCIP, DAD or cytochrome *c* as electron donors. All values in the figures and tables are the means from at least three independent representative experiments; maximal deviations of single determinations from the corresponding mean were 10–15% of the mean for each given set of experiments. The significance of both the number and location of the intersections given in the Arrhenius plots (see Figs. 1–5) was established through mathematical treatment of the data according to Ref. 31.

Chemicals. All chemicals used were of the highest purity available. Substances poorly soluble in water were dissolved in freshly distilled dimethyl sulphoxide. Samples containing dimethyl sulphoxide alone (at most 1%, v/v) gave the same results as dimethyl sulphoxide-free controls.

Results

The rate of each of the reactions characterized in Table I was measured at a variety of different temperatures between 4 and 41°C and the results were used to construct the Arrhenius plots shown in Figs. 1–5. The Arrhenius plots of the temperature dependences of the photosynthetic activities displayed by the *Anacystis* membranes, viz., of NADP photoreduction by ascorbate plus DCIP (Fig. 1), of DCIP photoreduction by diphenylcarbazide (Fig. 2), and of the light-dependent O_2 uptake mediated by benzyl viologen which was photoreduced either with DAD (Fig. 3) or reduced horse heart cytochrome *c* (Fig. 4), all showed a single discontinuity at approx. 24–25, 15–17 and 10–13°C in membranes obtained from cells grown at 40, 30 and 25°C, respectively. Basi-

TABLE I

RATES OF RESPIRATORY AND PHOTOSYNTHETIC ELECTRON-TRANSPORT REACTIONS IN MEMBRANE PREPARATIONS OF *A. NIDULANS* GROWN AT 40°C

Unless otherwise stated, the assay temperature was 35°C and illumination was by 700 nm light (0.7 μE/cm² per min) at the surface of the vessels; see Materials and Methods). Samples contained between 0.8 and 5.3 mg protein/ml. Reaction components actually measured in the respective assays were the final electron acceptors throughout. Reactions were started by addition of the respective donor compound. Rates listed are initial rates.

Electron-transport reaction	Reaction rates (nmol/min per mg protein)
Light	
Ascorbate plus DCIP → NADP	36
Diphenylcarbazide → DCIP	270 [a]
DAD → benzyl viologen → O_2	950
Cytochrome *c* → benzyl viologen → O_2	180
Dark	
Ascorbate plus DCIP → O_2	71
NADPH → O_2	18
NADPH → menadion → O_2	27
Cytochrome *c* → O_2	40
Cytochrome *c* → cytochrome aa_3	240 [b]

[a] Samples illuminated with 620 nm light (0.9 μE/cm² per min).

[b] Determined at 20°C using $\Delta\epsilon$ (605 minus 590 nm) = 24 $mM^{-1} \cdot cm^{-1}$ [30].

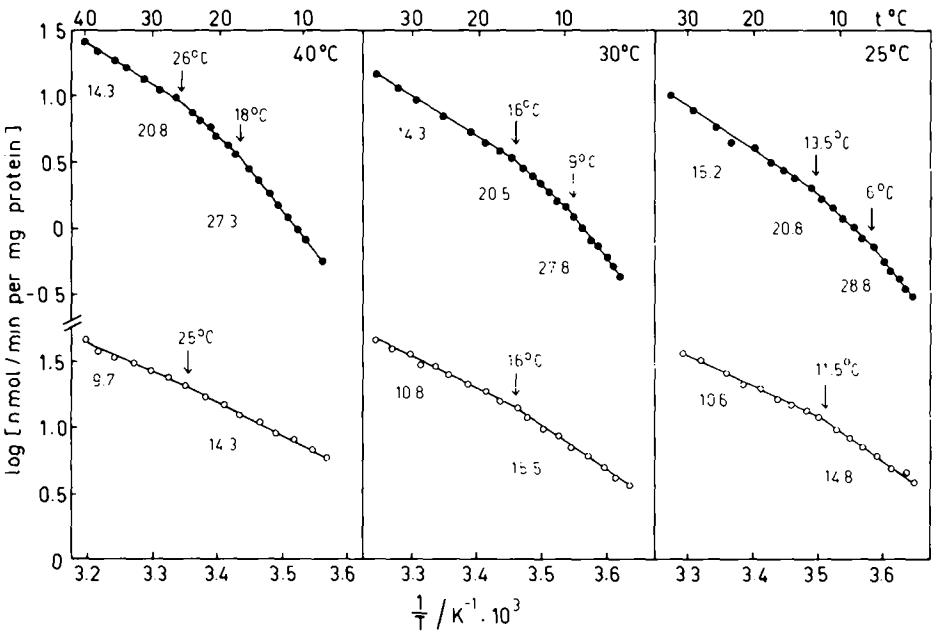

Fig. 1. Arrhenius plots of the temperature dependences of NADPH-supported O_2 uptake (•) in the dark and of NADP reduction by ascorbate plus DCIP (○) in the light (700 nm) in membranes prepared from *A. nidulans* grown at 40, 30 and 25°C. Discontinuity temperatures indicated by arrows. Numbers below the straight segments of the plots are the corresponding apparent activation energies (kcal/mol).

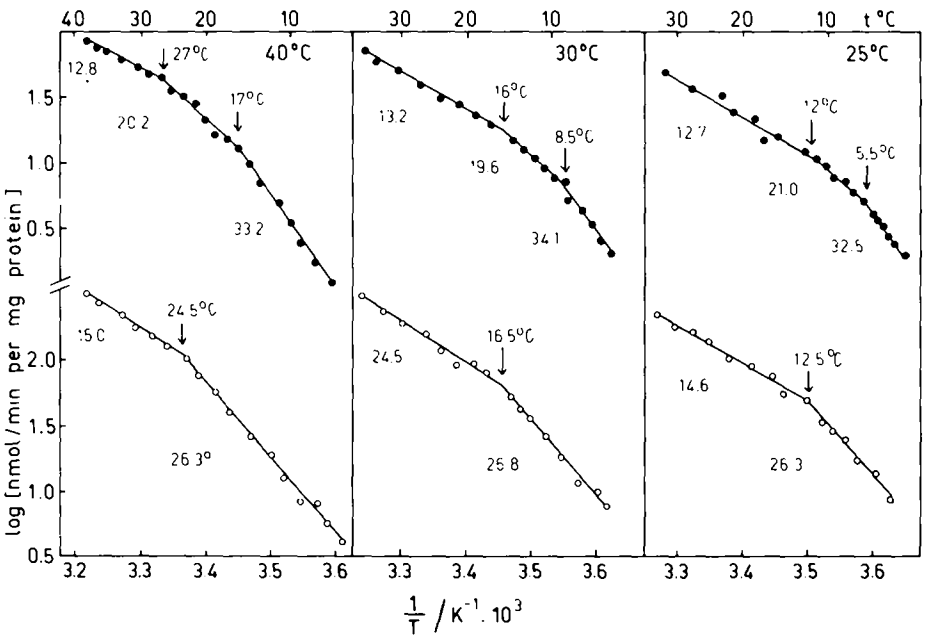

Fig 2. Arrhenius plot of the temperature dependences of O_2 uptake supported by ascorbate plus DCIP (•) in the dark and of diphenylcarbazide-dependent reduction of DCIP (○) mediated by 620 nm light in membranes prepared from *A. nidulans* grown at 40, 30 and 25°C. Discontinuity temperatures indicated by arrows. Numbers below the straight segments of the plots are the corresponding apparent activation energies (kcal/mol).

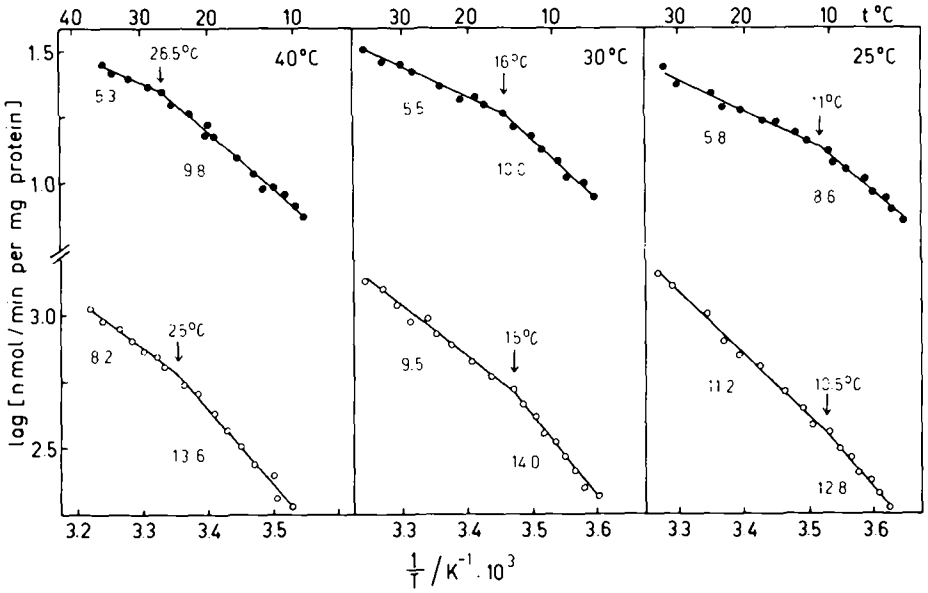

Fig. 3. Arrhenius plots of the temperature dependences of autoxidative O_2 uptake mediated by NADPH-reduced menadion (•) in the dark, and of autoxidative O_2 uptake mediated by DAD-reduced benzyl viologen (○) in the light (700 nm) in membranes isolated from *A. nidulans* grown at 40, 30 and 25°C. Discontinuity temperatures indicated by arrows. Numbers below the straight segments of the plots are the corresponding apparent activation energies (kcal/mol).

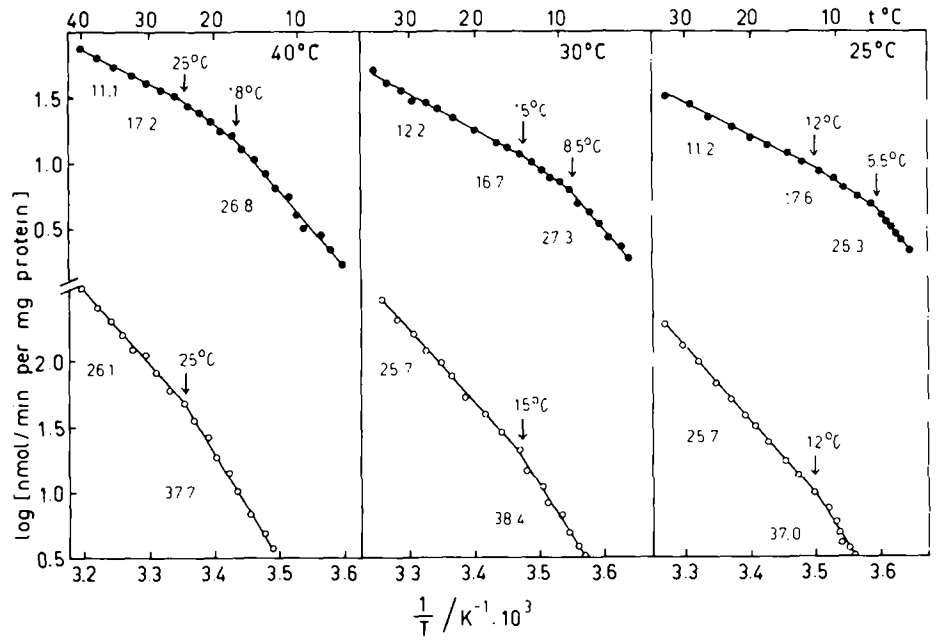

Fig. 4. Arrhenius plots of the temperature dependence of O_2 uptake supported by reduced horse heart cytochrome *c* in the dark (•) and in the light (700 nm; ○) in membranes prepared from *A. nidulans* grown at 40, 30 and 25°C. Discontinuity temperatures indicated by arrows. Numbers below the straight segments of the plots are the corresponding apparent activation energies (kcal/mol).

cally, this agrees with the findings of Ono and Murata [20] who have studied the temperature dependence of photosynthetic activities in *Anacystis* membranes isolated from cells grown at 38 and 28°C, taking into account the slightly different growth temperatures (cf. Fig. 6). The discontinuity temperatures did not depend on the nature of electron donors and acceptors used in the peculiar reaction. This would be expected if the discontinuities indeed reflected lipid phase transitions in the photosynthetic membrane as a whole and not some intrinsic changes in the reactivities of the enzymes specifically involved in each reaction. On the other hand, the apparent activation energies calculated for corresponding segments of the plots (see Figs. 1–4) were significantly different for the different reactions studied; the order was E_A(cytochrome c → benzyl viologen → O_2) > E_A(diphenylcarbazide → DCIP) > E_A(ascorbate plus DCIP → NADP) > E_A(DAD → benzyl viologen → O_2), thus reflecting different rate-limiting steps involved in the reactions listed. However, the activation energies did not vary with the growth temperature of the cells indicating that the rate-limiting steps remained the same for each reaction (see Figs. 1–4).

In marked contast to the photosynthetic activities, the Arrhenius plots of the temperature dependences of respiratory O_2 uptake in the dark mediated by NADPH (Fig. 1), ascorbate plus DCIP (Fig. 2) and reduced horse heart cytochrome c (Fig. 4) consistently showed two distinct breaks at approx. 25–27 and 17–18°C, 15–16 and 8–9°C, and at 12–14 and 5–6°C in membranes from cells grown at 40, 30 and 25°C, respectively. The higher discontinuity temperatures were practically the same as found for the pho-

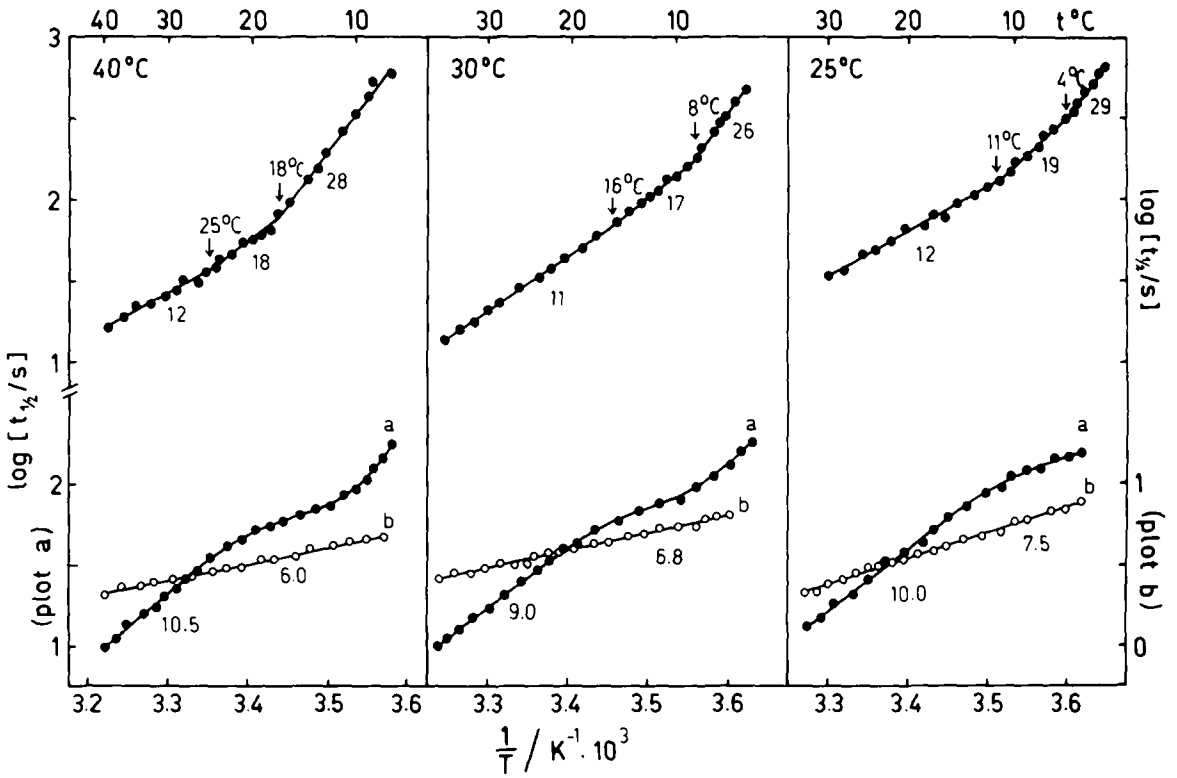

Fig. 5. Arrhenius plots of the temperature dependence of the reduction of the membrane-bound cytochrome aa_3 of *A. nidulans* by 75 μM reduced horse heart cytochrome c under nitrogen (upper part) and in the presence of 1 mM KCN (lower part, curve a), and of the anaerobic cytochrome aa_3 reduction by 10 mM ascorbate plus 0.1 mM TMPD (lower part, curve b). Reaction rates characterized by the half-rise time of maximal absorbance at 605 (600) minus 590 nm. Experiments were performed with membranes derived from cells grown at 40, 35 and 25°C. Discontinuity temperatures indicated by arrows. The numbers below the straight segments of the plots are the corresponding apparent activation energies (kcal/mol).

tosynthetic activities; the additional break appeared at temperatures 6–10 K lower than the first break. No additional break, however, was detected in the Arrhenius plots of the O_2 uptake mediated by NADPH-reduced menadion in the dark. Menadion ($E'_0 = -0.01$ V) is supposed to be reduced by the flavoprotein NAD(P)H dehydrogenases, thus withdrawing electrons from the early dehydrogenating segment of the respiratory chain [23,24].

Also, with the respiratory electron-transport reactions, the discontinuity temperatures were higher in membranes obtained from cells grown at higher temperatures and approximately independent of the particular electron donor employed. The apparent activation energies in turn did not vary with the growth temperature of the cells but were different for the particular donors used, although variations were not as large as with the photosynthetic reactions (cf. Figs. 1–4). The same two discontinuities were found also in Arrhenius plots of the temperature dependence of the rate of reduction of the membraneous cytochrome aa_3 by reduced horse heart cytochrome *c* as characterized by the half-rise time of maximal absorbance at 605 minus 590 nm (Fig. 5, above). However, when the temperature dependence of the reduction with ascorbate plus TMPD was studied (Fig. 5, curve b), or when the reduced horse heart cytochrome *c* was allowed to reduce only the cytochrome *a* moiety of the oxidase (as measured at 600 minus 590 nm in the presence of KCN; see Fig. 5, curve a), no distinct Arrhenius discontinuities could be localized.

Discussion

The present investigation attempts to relate the observed breaks in Arrhenius plots of the temperature dependences of various respiratory and photosynthetic activities in membrane preparations of the cyanobacterium *A. nidulans* to the lipid phase transitions described for these membranes [9,10,12,20]. Some correlation between the physical state of biological membranes and the Arrhenius discontinuities exhibited by membrane-bound enzymatic reactions certainly would be expected on thermodynamical grounds; general agreement, however, has not been obtained so far (cf. Refs. 12 and 32). Unfortunately, the membranes of most (mesophilic) organisms show phase transitions at temperatures far below zero [32], i.e., at temperatures where enzymatic reactions would no longer be relevant to the organisms. Certain Arrhenius discontinuities are known to occur independently of any lipid phase transitions, e.g., in the case of the cytochrome oxidase of eukaryotes [33].

After all, with certain thermophilic organisms [4] and also with *A. nidulans* which grows optimally at 41°C showing lipid phase transitions in its membranes well within the physiological temperature range, the correlation between the physical state of the thykaloid membranes and the Arrhenius discontinuities of a variety of photosynthetic activities appears to be well established through the extensive studies of Fork, Murata and co-workers [4,9,16–20]; our own findings basically support their conclusions (Fig. 6). Moreover, since no similar data are so far available for respiratory activities in *A. nidulans*, we extended our studies to selected partial reactions of the respiratory electron transport [23,24]. Our results indicate a major difference in the apparent thermodynamics of both types re reaction: Each of the photosynthetic reactions investigated displayed a single break in the corresponding Arrhenius plot while respiratory reactions usually showed two distinct breaks. One of these breaks occurred at the same temperature as found also with photosynthetic activities while the second

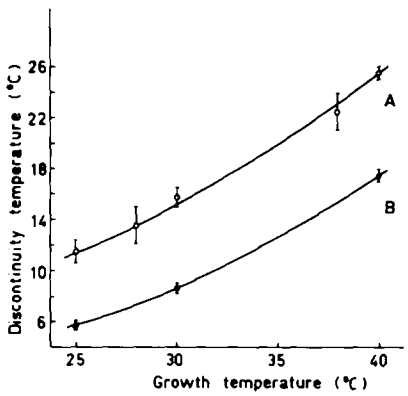

Fig. 6. Relationship between growth temperature of *A. nidulans* and Arrhenius discontinuities observed for photosynthetic (A) and respiratory (B) electron-transport reactions catalyzed by membranes isolated from cells grown at the respective temperatures (see Figs. 1–5). The values at 28 and 38°C (growth temperature) are those of Ono and Murata [20].

break appeared at lower temperatures. These findings were interpreted as follows:

Both the photosynthetic and part of the respiratory electron-transport assemblies of *A. nidulans* are located on the thylakoid membranes [25,34] which are known to display changes in their physical state at temperatures approximately identical to those at which the Arrhenius discontinuities are observed. This statement would not necessarily prove, but does not conflict with, the view that part of the respiratory and the photosynthetic electron transport in cyanobacteria may share common components [35,36] as is firmly established for the photosynthetic bacteria sensu stricto [37].

However, the second Arrhenius discontinuity observed by us with respiratory electron-transport reactions in the *Anacystis* membranes deserves special attention. The additional discontinuity consistently occurred at temperatures 6–10 K lower than the break common to both respiratory and photosynthetic activities. Its position remained at the same temperature irrespective of whether the respiratory O_2 uptake was supported by NADPH, ascorbate plus DCIP or reduced horse heart cytochrome *c* (cf. Figs. 1, 2, 4, 5). The three reactions obviously involve the terminal oxidase which was recently suggested to be an aa_3-type cytochrome in *A. nidulans* studied by spectrophotometry [26,27]. Direct measurements of the temperature dependence of cytochrome aa_3 reduction by cytochrome *c* as followed by dual-wavelength spectrophotometry [27] gave results fully consistent with the O_2 uptake measurements in the presence of NADPH, ascorbate plus DCIP or cytochrome *c*. However, when the reduction of only the cytochrome *a* moiety (of the cyanide-complexed oxidase) was studied, or when ascorbate plus TMPD (instead of cytochrome *c*) was used to reduce the uninhibited oxidase, no clear-cut breaks were observed in the corresponding Arrhenius plots. This might indicate that the cytochrome *a* of the oxidase is situated near the surface of the membrane, thus not involving steps intrinsically dependent on the physical state of the membrane lipids when being reduced by cytochrome *c*. Similarly, the artificial redox couple ascorbate plus TMPD might simultaneously reduce cytochromes $a + a_3$ without being affected by the physical state of the bulk lipids in the membrane.

Our findings are taken to indicate that part of the respiratory assembly including, in particular, the terminal oxidase, might be situated either in a particular molecular environment of the same thylakoid membranes, or (either alternatively or in addition) in the plasma membrane. The former possibility which has recently been envisaged for the ATPases in *Rhodospirillum rubrum* [38] clearly would imply that part of the respiratory electron transport in *A. nidulans* takes place topographically separated from the mainstream of the photosynthetic electron flow, yet within the same (thykaloid) membranes. On the other hand, using ultracytochemical techniques, we were recently able to localize respiratory functions in the plasma membrane of *A. nidulans*, in addition to respiratory sites clearly detectable in the thylakoid membranes [25,34]. Moreover, respiratory studies performed on membranes isolated from photobleached *A. nidulans*, the thylakoids of which had been selectively and reversibly disintegrated by controlled photooxidative treatment [39,40], pointed in the same direction [24]. Finally, it may be recalled that freeze-fracture electron microscopy indeed has revealed the plasma membrane and the thylakoid membranes of *A. nidulans* to possess lipid compositions different from each other [13,41]. Quite recently, Murata and Ono [41], using both freeze-fracture electron microscopy and measurements of the temperature dependence of passive K^+ release by whole cells of *A. nidulans* suggested the lipid phase transitions of the plasma membrane to occur at 15 and 5°C in cells grown at 38 and 28°C, respectively; these figures would not be too different from the temperatures at which the second break in our Arrhenius plots was localized for the respiratory activities catalyzed by the membrane preparations used which are known to comprise both plasma and thylakoid membranes [22,28]; unfortunately, satisfying preparative separation of the two types of membrane has not been accomplished so far with any cyanobacterium (cf. Ref. 42).

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