Charges of Nicotinamide Adenine Nucleotides and Adenylate Energy Charge as Regulatory Parameters of the Metabolism in *Escherichia coli*

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**Klaus B. Andersen** and **Kasper von Meyenburg**

*From the University Institute of Microbiology, Øster Farimagsgade 2A, Copenhagen K, DK-1353 Denmark*

Methods for measurements of catabolic reduction charge (defined as NADH/(NADH + NAD⁺)) and anabolic reduction charge (defined as NADPH/(NADPH + NADP⁺)) are described using [14C]nicotinamide labeling of *Escherichia coli* cultures. Together with these parameters the adenylate energy charge (ATP + ½ADP)/(ATP + ADP + AMP) was measured using labeling with [3-3H]adenine. These three charges were found under different exponential growth conditions to have values independent of the growth conditions: catabolic reduction charge, 0.05; anabolic reduction charge, 0.45; and adenylate energy charge, 0.9. The charges were examined during interruption of growth primarily affecting catabolism, respiration, or anabolism, leading to changes of the charges. The changes of charges are evaluated as a possible regulation of the metabolic rates utilizing or producing the nucleotides by their respective charges.

Regulation of cellular metabolism and growth takes place on different levels and on different time scales: regulation of enzyme production, feedback inhibition of enzyme activities, and general metabolic regulation of enzymatic activities by substrate and product levels; the latter is examined in this study. The components of the three important energy transfer systems in the cell, which connect major parts of cellular metabolism, are: adenosine phosphates, nicotinamide adenine dinucleotides, and nicotinamide adenine dinucleotide phosphates. Adenosine phosphates bring energy from substrate degradation and the oxidative phosphorylation system to anabolism, NADH brings reduction equivalents from substrates to the oxidative phosphorylation system or to precursors of fermentation products during fermentation, and NADPH brings reduction equivalents from substrates in the pentose-phosphate shunt (1), or via NADP-dependent isocitrate dehydrogenase (2), or from the energy-dependent transhydrogenase (3) to anabolism. The turnover rates of the three nucleotide systems are all very rapid; 1 to 10 s⁻¹ (4, 5). The internal concentrations of these different compounds are in the order of millimolar; thus, it is possible that they are saturating their respective enzyme systems (6). An absolute change in the concentrations of these compounds would, therefore, only have a minor influence on the rate of enzymic reactions compared to the influence of a change in the charge of the compounds.

The charges measured in this study are catabolic reduction charge, defined as NADH/(NADH + NAD⁺), anabolic reduction charge, defined as NADPH/(NADPH + NADP⁺), and the adenylate energy charge, defined as (ATP + ½ADP)/(ATP + ADP + AMP) (7).

These three charges were examined during steady state growth and during alterations of the growth from the steady state condition. The charges are here evaluated as possible regulatory parameters on the cell metabolism.

This mode of metabolic regulation has been discussed extensively for the adenylate energy charge (8, 9). This generalized theory involves (a) a negative control on the rates of metabolic reactions charging a nucleotide by the respective charge, and (b) a positive control on the rates of metabolic reactions discharging the nucleotide by the charge. Since the turnover of the nucleotides is very rapid, the rate of charging and discharging reactions must always be well balanced.

The charge regulation during steady state growth and transitions can be described in terms of regulatory curves of the rates of charging and discharging reactions as function of the charge (8, 9). The steady state charge can be interpreted as the charge of the meeting point for (a) the curve of the rate of charging reactions (decreasing with increasing charge), and (b) the curve for the rate of discharging reactions (increasing with increasing charge). If only one of these regulation curves is changed by a rapid change of growth conditions, the rate of the other reaction would change with the charge until a new balance is established; this latter balance would be determined by the meeting point of the changed curve and of the unchanged curve. According to this hypothesis, the response by the charge on the rate of the unchanged reaction can then be studied.

*Escherichia coli* is here being viewed as a metabolic network. The important parameters in an electrical analogue are the current and the voltage. To design an electric network information about the ability of the components to regulate between voltage and current is necessary. In this study the relation between metabolic rates and charges was examined.

**MATERIALS AND METHODS**

*Organism —* *Escherichia coli* B/r strain NF 196, a ton A (phage T1 resistant) derivative of wild type CP 14. All cultures were grown in...
that almost all radioactive material in the cell had been incor-
mide was estimated to 0.2
molar in the cells was acid soluble, indicating that it consisted of
small molecules. The sum of the four nicotinamide nucleotides
rial in the cell was during conversion of adenine nucleo-
tides to guanine nucleotides in the cell. [2-3H]Adenine (Amersham,
England) is added to a volume of the main culture (A,,, = 0.1) to a
final concentration of 30 μCi/ml and 1 μg/ml.
Nucleotides were extracted by rapidly transferring and mixing 10-
μl aliquots of the culture into 10 μl of 2.6 M HCOOH in an ice bath.
Adenine nucleotides were separated by chromatography on poly-
ethyleneimine thin layer plates (20 cm, Machery-Nagel and Co.).
After application of a sample the plates were washed with methanol
to remove Tris buffer. The plates were run in water three times
followed by a run in 1.4 M LiCl (10). The spots were cut out on the
basis of the positions of markers, placed in plastic vials, and the
radioactivity was determined by liquid scintillation counting; a typi-
chal chromatogram is shown in Fig. 1A. Energy charge is calculated
from the three adenine phosphate spots.
Measurement of Nicotinamide Nucleotides - (Catabolic Reduction
Charge and Anabolic Reduction Charge) - Nicotinamide (Amersham,
England) was added to a volume of the main culture, to a final concentration of 1 μCi/ml and 1 μg/ml.
Nucleotides were extracted by rapidly transferring and mixing 10-
μl aliquots of the culture into 10 μl of 2.6 M HCOOH in an ice bath.
Adenine nucleotides were separated by chromatography on poly-
ethyleneimine thin layer plates (20 cm, Machery-Nagel and Co.).
After application of a sample the plates were washed with methanol
to remove Tris buffer. The plates were run in water three times
followed by a run in 1.4 M LiCl (10). The spots were cut out on the
basis of the positions of markers, placed in plastic vials, and the
radioactivity was determined by liquid scintillation counting; a typi-
chal chromatogram is shown in Fig. 1A. Energy charge is calculated
from the three adenine phosphate spots.
Measurement of Adenine Nucleotides - (Adenylate Energy
Charge) - The adenine nucleotides were labeled with 12-HAdenine;
3H label in the 2 position is lost during conversion of adenine nucleo-
tides to guanine nucleotides in the cell. [2-3H]Adenine (Amersham,
England) is added to a volume of the main culture (A,,, = 0.1) to a
final concentration of 50 μCi/ml and 1 μg/ml.
Nucleotides were extracted by rapidly transferring and mixing 10-
μl aliquots of the culture into 10 μl of 2.6 M HCOOH in an ice bath.
Adenine nucleotides were separated by chromatography on poly-
ethyleneimine thin layer plates (20 cm, Machery-Nagel and Co.).
After application of a sample the plates were washed with methanol
to remove Tris buffer. The plates were run in water three times
followed by a run in 1.4 M LiCl (10). The spots were cut out on the
basis of the positions of markers, placed in plastic vials, and the
radioactivity was determined by liquid scintillation counting; a typi-
chal chromatogram is shown in Fig. 1A. Energy charge is calculated
from the three adenine phosphate spots.
RESULTS
Evaluation of Reduction Charge Measurements - Nicotina-
mide is taken up by Escherichia coli and incorporated into the
nicotinamide nucleotides (11). The Kₚ for uptake of nicotin-
amide was estimated to 0.2 μM (results not shown) (5). Total
incorporation, determined after filtration of the cells, showed a
biphasic uptake (Fig. 2A), indicating a rapid equilibration of the
total nicotinamide pool. Virtually all of the labeled material
in the cells was acid soluble, indicating that it consisted of
small molecules. The sum of the four nicotinamide nucleotides
measured by the chromatographic method was equal to the
total incorporation measured by filtration (Fig. 2B), showing
that almost all radioactive material in the cell had been incor-
porated exclusively into the four nicotinamide nucleotides, as
reported previously (12).
NADH and NADPH are labile in acid, which makes acid
extraction impossible for measurements by fluorescence and
enzymatic methods. The reaction of hydrogen ions with the
reduced nicotinamide nucleotides forms products (13) which
are not fluorescent. However, acid-treated NADH and
NADPH are found at the same positions as the untreated
compounds in the chromatographic system, determined by
ultraviolet detection of the spots of pure markers (5).
The result of this method for determination of nicotinamide
charges are in general agreement with enzymatic measure-
ments (14) on cell extracts as indicated in Table I.
Charges during Exponential Growth - E. coli was grown
with different carbon sources, which gave growth rates rang-
ing from 0.2 to 2.4, doubling per h. As shown in Table II, all
charges had the same values regardless of growth rate; energy
charge, 0.91 ± 0.04; catabolic reduction charge, 0.05 ± 0.02;
and anabolic reduction charge, 0.45 ± 0.04. The distribution of
total nicotinamide nucleotides between nicotinamide adenine
dinucleotide phosphates and nicotinamide adenine dinucleo-
tides also remained constant; the nicotinamide adenine dinu-

![Fig. 2. Uptake of [carbonyl-14C]nicotinamide and its recovery in nicotinamide nucleotides. Glucose cultures (1.4 doublings/l) were labeled at the arrow as described under Materials and Methods.](http://www.jbc.org/Downloaded from)
ucleotide phosphates were 19% of the total. The constancy of energy charge over growth rate has been reported previously (15, 16) with values from different measurements ranging from 0.8 to 0.95. The two reduction charges were previously measured by separate extraction of the reduced compounds (alkaline extraction) and the oxidized compounds (acid extraction). Catabolic reduction charges have been reported in the range 0.02 to 0.3 for aerobically grown E. coli, Klebsiella aerogenes, and Pseudomonas spingidae (12-19). The anabolic reduction charge has been reported as ranging from 0.5 to 0.9 (12, 17, 19). Fluorometric measurements have been made on intact cells, but this method has the capability to detect changes in the total amount of reduced nicotinamide nucleotides (NADH + NADPH) (17, 20) rather than their absolute amounts.

**Charges during Changes in Availability of Carbon Source**—As the primary event by changes of the availability of carbon source on the cell, the rates of production of NADH and NADPH would be effected, and secondarily the rate of ATP production, through the oxidative phosphorylation.

**Table I**

Reduction charges measured by enzymatic method*  
Escherichia coli was grown in glucose medium with vigorous aeration in a fermentor. Samples were taken at A 540 between 1 and 4, directly into cold perchloric acid, or at KOH at 100° and analyzed as described by Estabrook and Maitra (14).

| Nucleotide | Concentration/μmol cell dry weight | Number of analyses |
|------------|-----------------------------------|--------------------|
| NAD⁺       | 8.6 ± 2.0                         | 7                  |
| NADH       | 1.1 ± 0.2                         | 3                  |
| NADP⁺      | 1.0 ± 0.2                         | 4                  |
| NADPH      | 1.3 ± 0.3                         | 4                  |

* Anabolic reduction charge, 0.57. Catabolic reduction charge, 0.11. Amount of the two nicotinamide adenine dinucleotide phosphates, 0.19, as fraction of the total four nicotinamide nucleotides.

**Table II**

Charge values for cultures grown on various carbon sources

| Carbon source | Growth rate† | Catabolic reduction charge | Anabolic reduction charge | NADPH/ (NADH + NADPH) | Adenylate energy charge |
|---------------|--------------|---------------------------|--------------------------|------------------------|-------------------------|
| Glucose + 1% casamino acids | 2.39 | 0.04 | 0.44 | 0.17 | 0.85 |
| Casamino acids, 1% | 2.00 | 1.43 | 0.05 | 0.46 | 0.22 | 0.89 |
| Glucose | 1.42 | 1.25 | 0.04 | 0.49 | 0.18 | 0.85 |
| Galactose | 1.30 | 1.27 | 0.04 | 0.49 | 0.18 | 0.85 |
| Arabinose | 1.29 | 1.29 | 0.04 | 0.49 | 0.18 | 0.85 |
| Lactose | 1.15 | 1.90 | 0.04 | 0.46 | 0.20 | 0.95 |
| Fructose | 1.10 | 1.10 | 0.04 | 0.46 | 0.20 | 0.95 |
| Xylose | 1.06 | 1.06 | 0.04 | 0.46 | 0.20 | 0.95 |
| Sorbitol | 1.00 | 1.00 | 0.04 | 0.46 | 0.20 | 0.95 |
| Lactate | 0.71 | 0.90 | 0.05 | 0.48 | 0.18 | 0.87 |
| Glucose + 3% α-methyl glucose | 0.68 | 0.75 | 0.06 | 0.39 | 0.19 | 0.92 |
| Mannose | 0.43 | 0.58 | 0.05 | 0.48 | 0.18 | 0.87 |
| Succinate | 0.53 | 0.53 | 0.05 | 0.48 | 0.18 | 0.87 |
| Fumarate | 0.36 | 0.36 | 0.05 | 0.48 | 0.18 | 0.87 |
| Acetate | 0.30 | 0.30 | 0.05 | 0.48 | 0.18 | 0.87 |
| 2-Ketoglutarate | 0.22 | 0.22 | 0.05 | 0.48 | 0.18 | 0.87 |

† Measurements of reduction charges and adenylate energy charge were performed in different experiments with slightly varying growth rates; first column gives the growth rates in reduction charge measurements; second column gives the growth rates in adenylate energy charge measures. Cultures were labeled at A 540 0.1 and measurements performed at A 540 0.4.

Starvation for succinate, reached after growth in media with a limiting succinate concentration (Fig. 3), represents a total starvation for substrate. Energy charge fell from the exponential growth level to 0.6 during this starvation and rose again to 0.85 upon succinate readdition. The catabolic reduction charge was constant, with the value 0.05, but was seen in Fig. 3 transiently to rise 0.05 unit upon succinate addition. The anabolic reduction charge decreased immediately from 0.5 to 0.2 as a result of the starvation and returned to 0.5 upon succinate readdition.

Starvation for glucose after consumption of a limiting amount of glucose is not a total starvation, since the cells during glucose growth excrete acetate, which can be used as a secondary metabolite after the glucose is consumed (21). The energy charge was shown in this case to fall from 0.8 to 0.6 upon the starvation (16). Fig. 4 shows the reduction charges. While the catabolic reduction charge stayed constant, around 0.05, the anabolic reduction charge fell from 0.45 to 0.25 ini-
duced down shift described above (5).

Fig. 4. Charges during glucose starvation and readdition: anabolic reduction charge (○), catabolic reduction charge (●), adenylate energy charge (▲), and A_50 of the cultures (+); labeling at zero time. The initial culture medium contained 0.02% w/v glucose; 0.2% glucose was readded at 260 min (arrow after a starvation period of 140 min.)

Fig. 5. Charges after α-methylglucoside addition (arrow) to a glucose culture (A) and a glucose to mannose shift (B): anabolic reduction charge (○), catabolic reduction charge (●), adenylate energy charge (▲), and A_50 of the cultures (+); labeling at zero time. In A, 2.5% w/v α-methylglucoside was added at 90 min to a culture growing in medium containing 0.2% glucose. In B the initial culture medium contained 0.02% w/v glucose and 0.2% mannose.

Fig. 6. Oxygen starvation of succinate (A) and glucose (B) cultures: anabolic reduction charge (○), catabolic reduction charge (●), adenylate energy charge (▲), and A_50 of the cultures (+); labeling at zero time. Aerated cultures were bubbled through with N_2 (freed from oxygen with alkaline pyrogallol) at 70 min (A) and 80 min (B). At 130 and 140 min, respectively, oxygen was rebubled with air.

Metabolic Control

Charges during Changes of Respiration Rate—An experiment with oxygen starvation during succinate growth is shown in Fig. 6A. Since succinate cannot be fermented this shift leads to a total termination of the ATP production and NADH utilization. The energy charge dropped from 0.9 to 0.65 as under the other conditions like carbon source starvation leading to energy starvation. The catabolic reduction charge was here constant, with the value 0.05. During the oxygen starvation the anabolic reduction charge slowly decreased from 0.55 to 0.5. This result is difficult to interpret since the rate of NADPH production is possible both coupled to the respiration via the energy-dependent transdehydrogenase (3) and to the catabolism via the NADP-dependent isocitrate dehydrogenase (2).

In case of oxygen starvation during growth on glucose fermentation will result. Energy charge in this case has been reported to drop from 0.8 to 0.7 and to rise slowly to 0.8 during the starvation (16). The latter can be seen as a result of the adaptation to fermentation. The catabolic reduction charge stayed constant, at a value of 0.05; the anabolic reduction charge dropped transiently from 0.5 to 0.35 upon the oxygen starvation, as shown in Fig. 6B. The catabolic reduction charge has been reported to rise from 0.2 to 0.6 during anaerobiosis of E. coli grown in rich media (18), measured enzymatically, and the sum of reduced nicotinamide adenine nucleotides (NADH, NADPH) has been shown by the in vivo fluorescence technique to rise during anaerobiosis (17, 20).

Charges during Changes of Anabolism—Anabolism is effected by stopping translation with chloramphenicol (Fig. 7A) or by stopping transcription with rifampicin (Fig. 7B); both conditions should lead to a stop of the rate of utilization of NADPH and ATP. Energy charge was constant, at 0.8 to 0.85 during rifampicin treatment and possibly rose by 0.05 unit
during chloramphenicol treatment. The anabolic reduction charge rose in both cases moderately, from 0.4 to 0.6. After prolonged treatment with either inhibitor the energy charge and anabolic reduction charge decreased, probably because of damage to the cells from secondary effects of the drugs. The catabolic reduction charge was constant at 0.05.

**DISCUSSION**

Charge levels during steady state growth showed constant values, independent of the absolute rate of growth. These values were: energy charge, 0.85 to 0.95; catabolic reduction, 0.03 to 0.07; and anabolic reduction charge, 0.4 to 0.5. The free energy of cleavage of the phosphoric bonds in the adenine phosphates is thus maintained at a high level, which would provide additional driving force in ATP-utilizing reactions. The catabolic reduction charge is kept at a low value, which would pull NAD-linked reactions toward delivery of reduction equivalents, as is characteristic of many catabolic reactions. In comparison the anabolic reduction charge was higher, which would allow NADP-linked reactions to receive reduction equivalents; this is in agreement with the well known utilization of NADPH in many synthetic reactions. Although NADP and NAD have almost the same standard reduction potentials (24), the different charges serve as different potential levels to which respective anabolic and catabolic reactions can be coupled. The difference in charge is maintained by coupling to different reactions accepting reduction equivalents, or by the use of energy in the energy-dependent transhydrogenase reaction (3). During aerobic growth the respiration chain and oxidative phosphorylation serve to maintain the high energy level of ATP and to accept reduction equivalents in a low energy stage.

**Charge Regulation in Transients** — In the experiments shown the rates were affected at different positions in the cell metabolism: (a) catabolism, (b) respiration, and (c) anabolism. This was done in intention only to change either the rate of utilization or the rate of the production of the examined nucleotides. According to the charge regulation hypothesis described, information is thus obtained for the regulation pattern of the corresponding reactions.

Regulation of the ATP utilization rate was primarily seen during oxygen starvation. This rate is regulated between a high value at an energy charge of 0.9, characteristic of steady growth (Fig. 6A), and a low value at an energy charge of 0.6, characteristic of the interrupted growth. A regulation pattern for protein synthesis has recently been reported within this region of energy charge (25). The same characteristics are seen upon carbon source starvation which acts secondarily via the oxidative phosphorylation system. The rate of ATP production is possibly regulated in a narrow range of energy charge. Production is high during steady state growth at the energy charge 0.9, and is possibly decreased when the charge is increased by 0.05 unit, as seen from the chloramphenicol experiment (Fig. 7A). Uncoupling of the ATP utilization is conceivable in the presence of such inhibitors (26); this would interfere with this interpretation.

The rates of NADH utilization and production can be interpreted as being regulated in a very narrow range around the steady state value of the catabolic reduction charge of 0.05; no substantial changes are seen during starvation for carbon source or oxygen (Figs. 3 to 6). The value for the steady state charge is in general agreement with previous reports, but changes have been reported previously during oxygen starvation (17, 18) in contrast to this present observation.

Regulation of the NADPH utilization rate is seen during carbon source starvation or shift experiments. The rate of utilization in steady state growth is concerted with the anabolic reduction charge of 0.4 to 0.5, whereas the rate is decreased at an anabolic reduction charge of 0.1 to 0.2 (Fig. 3). Intermediate values of the rate of NADPH utilization (proportional to the growth rate) and anabolic reduction charge are seen during the glucose starvation and α-methylglucoside-induced shift (Fig. 4, Fig. 5A). The rate of NADPH production seems to be regulated within a range of the anabolic reduction charge of 0.2 to 0.3 unit; production is high (steady state growth value) at an anabolic reduction charge of 0.4 to 0.5 and low at an anabolic reduction charge of 0.6 to 0.7, as indicated by the experiments with chloramphenicol and rifampicin (Fig. 7, A and B).

**Regulation Characteristics** — To obtain a very narrow range of regulation of the rate of NADH utilization and ATP synthesis, the respective regulation curve between high steady state and stopped rate have to be rather steep. In terms of enzyme kinetics this requirement can be met by a saturated enzyme system, with (a) a considerably lower $K_m$ value for substrates (NADH or ADP) than for products (NAD$^+$, ATP), and (b) with a high reaction energy in these reactions (6, 27).

When these characteristics are established in the cell (during aerobic growth by the respiration chain and the oxidative phosphorylation system) the corresponding enzyme systems may have a large freedom of regulatory characteristics ($K_m$ values and reaction energies); this is seen for the rate of ATP consumption. The NADH-producing reactions seem, although, also to be regulated in a narrow charge range; this can be explained by a high energy of reaction, or by a lower $K_m$ value for product than for substrate, or by both.

The regulation pattern of reactions consuming or producing NADPH can be explained without strong requirements on reaction energy or $K_m$ values. The anabolic reduction charge during steady state growth is in the middle of the charge scale, and these rates are each regulated in broad ranges of charge values.

**Regulation of Enzyme Production** — During changes of growth conditions, the cells adapt slowly to the new conditions and establish a new steady growth rate (if growth is not totally blocked). The cells adapt from one set of balanced nucleotide utilizing and producing rates regulated by the steady state charges, toward a new set of rates controlled by the same steady state charges, as seen in Fig. 4, Fig. 5, A and B, Fig. 6B. Since the maximal rates of metabolic reactions are determined by the total amount of enzymes present, these results suggest that the amounts of enzymes charging and discharging the transfer nucleotides may be regulated by the relevant charge, by induction, or repression of synthesis of the enzymes.

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K B Andersen and K von Meyenburg

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