

TABLE 3 Parameters pertaining to the macromolecular synthesis rates in exponentially growing *E. coli* B/r as a function of growth rate at 37°C

Parameter	Symbol	Units	At $\tau$ (min) and $\mu$ (doublings per h):					Observed parameter(s)	Footnote
			$\tau$ , 100 $\mu$ , 0.6	$\tau$ , 60 $\mu$ , 1.0	$\tau$ , 40 $\mu$ , 1.5	$\tau$ , 30 $\mu$ , 2.0	$\tau$ , 24 $\mu$ , 2.5		
RNA polymerase protein/total protein	$\alpha_p$	%	0.90	1.10	1.30	1.45	1.55	$\alpha_p$	a
RNA polymerase molecules/cell	$N_p$	$10^3$ RNAP/cell	1.5	2.8	5.0	8.0	11.4	$\alpha_p, P_C$	b
RNA polymerase activity	$\beta_p$	%	17	20	21	24	30	$r_s, r_m, c_r, G_m, N_p$	c
Active RNA polymerase per cell	$N_{ap}$	RNAP/cell	205	503	992	1,929	3,298		c
Stable RNA synthesized per total RNA synthesized	$r_s/r_t$	%	41	52	68	78	85	$r_s/r_t$	d
Active RNA polymerase synthesizing stable RNA	$\psi_s$	%	24	36	56	68	79	$r_s/r_t$	e
rRNA chain elongation	$c_s$	Nucl./s	85	85	85	85	85	$c_s/t_m$	f
mRNA chain elongation	$c_m$	Nucl./s	39	45	50	52	55	Indirect	g
Rate of stable RNA synthesis/cell	$r_s$	$10^7$ nucl./min/cell	3.0	9.9	29.0	66.4	132.5	RC	h
Rate of mRNA synthesis/cell	$r_m$	$10^5$ nucl./min/cell	4.3	9.2	13.7	18.7	23.4	$r_s, r_s/r_t$	i
ppGpp concentration	ppGpp/M	pmol/OD <sub>600</sub>	55	38	22	15	10	ppGpp/M	j
	ppGpp/P	pmol/10 <sup>17</sup> aa	8.5	6.6	4.2	2.9	2.0	$P_M$	j
r-Protein per total protein	$\alpha_r$	%	9.0	11.4	14.8	17.5	21.1	$P_M, R_M$	k
			9	11	13.5	18.0	21.6	$\alpha_r$	l
Ribosome activity	$\beta_r$	%	80	80	80	80	80	Indirect	m
Peptide chain elongation	$c_p$	aa residues/s	12	16	18	20	21	Indirect	n
Ribosomes/cell	$N_r$	$10^7$ ribosomes/cell	6.8	13.5	26.3	45.1	72.0	$R_C, f_s, f_t$	o
tRNA/cell	$N_t$	$10^7$ tRNA/cell	63	125	244	419	669	$N_r, f_t$	p
rrn genes/cell	$N_{rrn}$	Avg no./cell	12.4	15.1	20.0	26.9	35.9	C, D	q
rrn genes/genome	$N_{rrn}/G$	Avg no./genome	7.9	8.2	8.6	9.0	9.5	C	r
Initiation rate at rrn gene	$i_{rrn}$	Initiations/min/genome	4	10	23	39	58	$N_r, N_{rrn}$	s
Distance of ribosomes on mRNA	$R_m/N_r$	Nucl./ribosome	79	85	65	52	41	$r_m, c_m, N_r$	t
No. of translations per mRNA	$N_{trans}$	Ribosomes	27	33	49	70	93	$P_C, r_m$	u
DNA chain elongation	$c_d$	Nucl. residues/s	585	783	870	911	933	C	v
C period	C	min	67	50	45	43	42	Indirect	v
D period	D	min	30	27	25	24	23	Indirect	w

<sup>a</sup> The fraction of the total cell protein that is core RNA polymerase was calculated from the  $\beta$  and  $\beta'$  content determined by sodium dodecyl sulfate-gel electrophoresis (125).

<sup>b</sup> The number of core RNA polymerases per cell was calculated from  $\alpha_p$  (this table) and values of  $P_C$  (Table 2), using aa/pol (Table 1) and the relationship  $N_p = P_C \cdot \alpha_p / (\text{aa/pol})$ .

<sup>c</sup> The fraction of active RNA polymerase was calculated from values in this table, the relationship  $\beta_p = (r_s/c_s + r_m/c_m)/N_p$ , and the active RNA polymerase per cell,  $N_{ap} = \beta_p \cdot N_p$ .

<sup>d</sup> The fraction of the total RNA synthesis rate that is stable RNA was determined by hybridization of pulse-labeled total RNA to an rDNA probe and correction for tRNA (119). Since the pulse-labeling time (1 min) was similar in duration to mRNA lifetimes, the  $r_s/r_t$  values shown are somewhat overestimated. This results from the underestimate of the rate of mRNA synthesis due to decay of labeled mRNA during the pulse-labeling period.

<sup>e</sup> The fraction of RNA polymerase synthesizing stable RNA was calculated using the relationship  $\psi_s = 1 / \{1 + [1/(r_s/r_t) - 1] / (c_s/c_m)\}$ .

<sup>f</sup> The stable RNA (or rRNA) chain growth rate was determined from 5S rRNA or tRNA labeling after rifampin addition (99, 120, 124).

<sup>g</sup> The mRNA chain elongation rate was determined by analysis of pulse-labeling kinetics of RNA after size fractionation (19) and by the time lag between induction of transcription of specific mRNAs (*lacZ*, *trpB*) and the appearance of specific hybridization to DNA probes from the 3' ends of the respective genes (139).

<sup>h</sup> The stable RNA synthesis rate per cell was determined from the data in Tables 1 and 2 and the rate equation  $r_s = R_C \cdot f_s \cdot \ln 2/t$ , where the factor  $f_s$  is equal to 1.2 and corrects for the 20% of the rRNA and tRNA primary transcripts that are unstable spacer or flanking sequences.

<sup>i</sup> The mRNA synthesis rate per cell was determined from the data in this table and the relationship  $r_m = r_s \{ [1/(r_s/r_t)] - 1 \}$ .

<sup>j</sup> Measurement of ppGpp was by  $A_{260}$  after separation of nucleotides by high-pressure liquid chromatography (119). ppGpp/P = (ppGpp/M)/ $P_M$ .

<sup>k</sup> The differential rate of r-protein synthesis was calculated from the data in Tables 1 and 2 and the relationship for  $\alpha_r$  (equation 6, Table 5).

<sup>l</sup> The differential rate of r-protein synthesis was determined from measurements of the protein content of ribosomes after labeling with radioactive leucine and uridine (44, 46).

<sup>m</sup> The fraction of active ribosomes was measured as ribosomes in polysomes with a correction for active 70S ribosomes (57).

<sup>n</sup> The peptide chain elongation rate,  $c_p$ , was calculated in amino acid residues per second per ribosome from the rate of protein synthesis ( $dP/dt$ ), the number of ribosomes ( $N_r$ ), and the fraction of active ribosomes ( $\beta_r$ ), using the relationship  $dP/dt = N_r \cdot \beta_r \cdot c_p$  (see also the equivalent equation 5 in Table 5; 44, 49).

<sup>o</sup> The number of ribosomes per cell was determined from values in Tables 1 and 2 and the relationship  $N_r = R_C \cdot f_s \cdot (1 - f_t) / (\text{nucl./rib})$ , where  $f_s, f_t$ , and nucleotides per ribosome are defined Table 1.

<sup>p</sup> The number of tRNAs per cell was determined from values in Tables 1 and 2 and the relationship  $N_t = R_C \cdot f_s \cdot f_t / (\text{nucl./tRNA})$ , where  $f_t$  and nucleotides per tRNA are defined in Table 1.

<sup>q</sup> The number of rRNA genes per cell was calculated from the number of *rrn* genes per genome (this table) and the number of genomes per cell (Table 2):  $N_{rrn} = (N_{rrn}/G) \cdot G$ .

<sup>r</sup> The number of rRNA genes per genome was determined from the value of the C period (footnote v, this table) and the locations of the seven *rrn* genes (87, 89.5, 85, 72, 90.5, 57, and 5 min, respectively), using equations 11 and 12 from Table 5 below.

<sup>s</sup> The transcription initiation rate at each *rrn* gene was calculated from the number of ribosomes per cell and the number of *rrn* genes per cell, using the relationship  $i_{rrn} = N_r \cdot (\ln 2/\tau) / N_{rrn}$ .

<sup>t</sup> The nucleotide distance between ribosomes on mRNA was calculated from data in this table and the relationship  $R_m/N_r = r_m \cdot t_m / (\beta_r \cdot N_r)$ , where  $R_m$  is the amount of mRNA and  $t_m$  is the average functional life of mRNA, assumed to be 1.0 min (5, 25).

<sup>u</sup> The number of translations per mRNA was calculated from data in Table 2 and this table using the relationship  $N_{trans} = 3 \cdot (dP/dt) / r_m$ . The factor 3 in the numerator is the coding ratio, i.e., 3 mRNA nucleotides per amino acid residue.

<sup>v</sup> The C period was determined from age-fractionated cultures (70), synchronized cultures (13), flow cytometric data (128), and perhaps most accurately in nonsynchronous exponential cultures by measuring the increase in the amount of DNA in the culture after treatment with rifampin or chloramphenicol (26). The values obtained by these different methods agree to within 10%. The values shown are considered to be the best average of the reported data.

<sup>w</sup> Like the C period, the D period was determined in age-fractionated and synchronized cultures, as well as from flow cytometric data (13, 70, 129). The D period was also determined by measuring the increase in cell number after treating exponential cultures with sodium azide; this treatment stops replication, but does not prevent the division of cells that were already in the D period at the time of the replication stop (14).