4.9 Thermodynamic data for protein-nucleic acid interactions

4.9.1 Introduction

4.9.1.1 General remarks

The interaction of a protein with a nucleic acid is of paramount importance to many essential biological processes. This is true whether the protein is a relatively "simple" nucleic acid binding protein or a more "complex" nucleic acid enzyme; in both instances, the ability to recognize and bind to the appropriate nucleic acid substrate is an essential first step. Consequently, a knowledge of the thermodynamic and kinetic parameters of the binding process is crucial to a complete understanding of those events.

This chapter will contain a summary of the known thermodynamic parameters for a variety of protein-nucleic acid interactions. The data included are the binding site size, intrinsic binding constant, and cooperativity parameter (all defined below) for various nucleic acid substrates. Where available, the variation of these parameters as a function of salt concentration, temperature and pH is reported. Included are proteins which show nucleic acid sequence specificity (specific binding) in their binding behavior, as well as proteins which show no sequence specificity (non-specific binding). Though many more proteins are known to bind nucleic acids than are reported in this chapter, only those systems for which the data were sufficiently quantitative to permit determination of intrinsic binding constants were included. No attempt has been made to summarize kinetic data (association or dissociation rate constants) or enzymatic data (e.g. K_m or k_{cat}).

4.9.1.2 Arrangement of data

All of the data are presented in Table 1 (section 4.9.3). Specific binding affinity constants are distinguished from non-specific affinity constants by the presence of an "S" or an "N", respectively, in the "Type" column of Table 1. For a protein which binds both specifically and non-specifically, the data for specific binding are presented in alphabetical order before the data for non-specific binding (also in alphabetical order).

The proteins are arranged in alphabetical order, followed by their source, the nucleic acid substrates (in alphabetical order, with the specific binding data presented first), the relevant thermodynamic parameters, experimental conditions, experimental method used, reference(s), and specific explanatory notes. A complete set of data was not available for each protein, and this is indicated in Table 1 by a blank space. Some of the entries in Table 1 were calculated from data provided in the original reference (e.g. some values for $d \lg K / d \lg [salt]$). In some cases, in order to facilitate comparison of different data sets, the values for K in Table 1 represent either extrapolation or interpolation of the original data. Finally, readers should consult the original reference for details of the experimental methods, for extinction coefficients employed, for specific composition of the buffer solutions used, and for the experimental uncertainties in the reported parameters. The values of n reported have not been adjusted for differences in extinction coefficients that different laboratories may have employed.

As mentioned earlier, Table 1 does not contain any kinetic data (see [86L1] for recent summary) or any enzymatic data (K_m or k_{cat}). Only binding data which were sufficiently quantitative to permit calculation of binding constants are included. Also, the binding data presented are limited to the interaction of intact, wild-type proteins to either specific nucleic acid binding sites or polynucleotides. Excluded are data on fragment proteins, on mutant variants of either proteins or specific nucleic acid binding sites, and on the non-specific binding of oligonucleotides to proteins (this is often different from polynucleotide binding). My apologies to anyone whose data I have overlooked.

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4.9.1.3 List of symbols and abbreviations

Symbols

Symbol	Unit	Description
a		number of anion binding sites involved in protein-nucleic acid complex formation
K	M^{-1}	intrinsic binding constant
L	M	ligand concentration
m'		number of ion pairs formed between the protein and the nucleic acid
n		binding site size
T	°C	temperature
[X]	M	concentration of X (molarity M = mol l^{-1})
v		binding density
ω		cooperativity factor

Abbreviations

CD	circular dichroism
DC	DNA-cellulose chromatography
EM	electron microscopy
FL	fluorescence
FP	footprinting
GC	gel exclusion chromatography
GR	gel retardation (electrophoresis)
NC	nitrocellulose filtration
S	sedimentation
TM	dsDNA melting temperature
UV	ultraviolet absorbance

Note: Symbols and abbreviations not listed here are explained in the section in which they appear.

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4.9.2 Thermodynamic formalism and experimental methods

4.9.2.1 Definition of sequence-specific nucleic acid binding parameters

The binding of a sequence-specific nucleic acid binding protein to its substrate is described by the following reaction:

$$P + S \rightleftarrows PS \quad (1)$$

where P is protein, S is specific binding site, and PS is protein-nucleic acid complex. The intrinsic binding constant for sequence specific binding is defined by:

$$K = [PS]/[P][S]. \quad (2)$$

If cast in the form of a Scatchard equation, Eq. (2) yields

$$v/L = K(1 - v) \quad (3)$$

where v is the binding density (moles bound per mole of total binding sites), $L \equiv [P]$.

4.9.2.2 Definition of non-specific nucleic acid binding parameters

The non-specific binding of a protein to a nucleic acid which is long enough to accommodate the binding of many (in theory, an infinite number) protein molecules is complicated by problems of "overlap" or "excluded site binding" (see [74M] for detailed discussion). In essence, the number of potential nucleic acid binding sites decreases non-linearly with increasing binding density. The theoretical formalism employed here is that developed by McGhee and von Hippel [74M]. Other mathematical approaches have been employed to derive equations which yield similar results (see citations in [74M]). In contrast to these approaches, the McGhee-von Hippel methodology yields a binding equation in closed analytic form. Recently, an alternative approach was used to yield a single analytic equation [89B].

The parameters used to describe the non-specific binding of a protein to a large nucleic acid are (see Fig. 1): *"n"*, the binding site size, *"K"*, the intrinsic binding constant (for non-specific binding), and *"ω"*, the cooperativity parameter [74M].

The site size, n, is defined as the number of nucleotide residues (for ssDNA), or the number of base pairs (for dsDNA) which are occluded, or covered, on the nucleic acid upon binding of the protein. Thus, the site size is a measure of the "size" of a protein in units of nucleotide residues or base pairs. Normally, in the absence of specific molecular information regarding the nature of the functional protein binding species, protein monomer is assumed to be the binding species. Note that the site size does not measure the number of residues (or base pairs) that actually make physical contact with the protein (see Fig. 2 for an illustration of binding to ssDNA). Instead, it only sets an upper limit to the number of residues that can be involved in the interaction.

The intrinsic binding constant, K, is described by the following equilibrium:

$$P + N \rightleftarrows PN \tag{4}$$

where P is a single isolated protein, N is a non-specific nucleic acid binding site, and PN is a non-specifically bound protein-nucleic acid complex. The intrinsic binding constant is defined by:

$$K = [PN]/[P][N]. \tag{5}$$

Note that the concentration of potential non-specific nucleic acid binding sites (at zero binding density) is the total molar concentration of nucleotide residues (for ssDNA) or base pairs (for dsDNA).

The cooperativity parameter, ω, is described by the following equilibrium (Fig. 1):

$$PNP \rightleftarrows PPN \tag{6}$$

where PNP represents two proteins which are bound non-specifically to nucleic acid *and* which are isolated from one another; PPN represents two proteins which are bound non-specifically *and* which are also located adjacent to one another (i.e. at contiguous binding sites). Note that only nearest neighbor interactions (i.e. protein-protein interactions) are permitted.

$$\omega = [PPN]/[PNP]. \tag{7}$$

For proteins that bind without cooperativity (non-cooperative binding), ω is equal to 1 (i.e. equal probabilities of contiguous vs. isolated binding, under standard state conditions). For proteins which display positive (i.e. favorable) cooperativity, ω is greater than 1; for negative cooperativity, ω is less than 1. Consequently, as depicted in Fig. 1, the apparent affinity of a free protein for a nucleic acid binding site which is immediately adjacent to a bound protein molecule, is defined by the product, $K\omega$. Interestingly, ω for all non-specific binding proteins examined to date is greater than or equal to 1 (Table 1).

For non-cooperative binding, the following equation applies:

$$v/L = K(1-nv)\left[\frac{1-nv}{1-(n-1)v}\right]^{n-1}. \tag{8}$$

For cooperative binding, the following equation applies:

$$v/L = K(1-nv)\left[\frac{(2\omega-1)(1-nv)+v-R}{2(\omega-1)(1-nv)}\right]^{n-1}\left[\frac{1-(n+1)v+R}{2(1-nv)}\right]^{2} \tag{9}$$

where

$$R = [[1-(n+1)v]^2 + 4\omega v(1-nv)]^{1/2}$$

(note in Eq. (9) that, due to a typographical error, the term "$(2\omega-1)$" was incorrectly printed in the original reference [74M]).

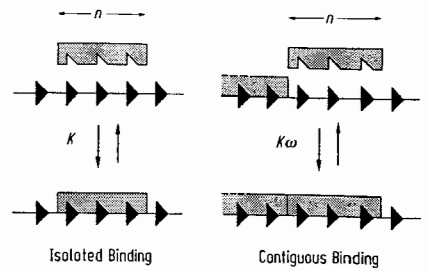

Fig. 1. Definitions of the thermodynamic parameters describing the interaction of a protein with a nucleic acid lattice. Each arrowhead represents a lattice site (i.e., either a nucleotide residue or a base pair) and the illustrated protein covers three such residues ($n=3$). K (in M^{-1}) is the intrinsic binding constant for protein binding to the lattice at an isolated site, and ω represents the cooperativity of binding. Thus $K\omega$ is the net binding constant per contiguously-bound protein molecule. (taken from [81K1])

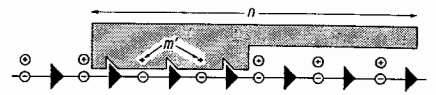

Fig. 2. Definitions of molecular binding (interaction) parameters. Here the arrowheads represent the nucleoside residue, the negative charges represent the backbone phosphates, the positive charges in the protein represent basic amino acid residues, and the positive charges in the solution represent monovalent counter-ions. The illustrated protein covers six nucleotide residues ($n=6$), but *directly* interacts with only three nucleoside residues, and forms two charge-charge interactions ($m'=2$) with the phosphate backbone. No anions are shown. (taken from [81K1])

The application of these equations is strictly valid only for homogeneous nucleic acids (with regard to binding sites) which are essentially of infinite length [74M]. The theoretical and experimental limitations, as well as their consequences, have been discussed [78E, 86K].

4.9.2.3 Effect of solution variables on protein-nucleic acid interactions

As might be expected, the interaction between molecules as complex as proteins and nucleic acids is affected by a variety of solution variables such as salt concentration, type of salt, pH, temperature, and nature of the nucleic acid substrate.

Experimentally, the affinity of proteins for nucleic acids is often found to be extremely sensitive to salt concentration. The molecular basis for this phenomenon has been proposed to result primarily from the competitive effects of added salt on the release of thermodynamically associated counter-ions (cations) from the nucleic acid upon binding of the protein (for review see [85RI]). A protein is envisioned (see Fig. 2) to possess m' ionic groups which form ion pairs with the nucleic acid phosphate backbone, resulting in the displacement of an equivalent of the thermodynamically bound counter-ions [76R, 77D2]. The value of m' must be less than or equal to n. In addition to cation displacement from the nucleic acid, displacement of anions from the protein upon complex formation may also occur.

Thermodynamic analysis predicts the following relationship for the variation of K with salt concentration [76R, 77D2]:

$$\frac{d \lg K}{d \lg [M^+]} = -m'\psi - \frac{aK_X[X^-]}{1+K_X[X^-]} \tag{10}$$

where K is the intrinsic binding constant (either specific or nonspecific), $[M^+]$ is the cation concentration, m' is the number of charge interactions formed between the protein and nucleic acid, ψ is the fraction of counter-ions thermodynamically bound to the nucleic acid (which varies from 0.71 to 0.93 for monovalent cations, depending on the nucleic acid species [76R]), *"a"* is the number of anion binding sites involved in the protein-nucleic acid interaction, and K_X is their intrinsic binding constant.

The effects of divalent ions and of pH on protein-nucleic acid complex stability have also been considered [77D2, 77R1]. In the absence of anion effects, $d \lg K / d \lg [M^{2+}]$ is approximately one-half (0.53) of the value given by Eq. (10) (since the equivalent value of ψ for Mg^{2+} association, which is ϕ, is 0.47 for native dsDNA). An equation describing the relationship between K and pH was also derived [77D2].

In the simplest case (i.e. in the absence of magnesium ions, anion displacement, and at constant pH), Eq. (10) predicts that the logarithm of the intrinsic binding constant decreases linearly with increasing logarithm of the monovalent cation concentration. The slope of this variation is $-m'\psi$. Thus, for this simple case, the number of charge interactions (m'), is readily obtained. Experimentally, nearly all protein-nucleic acid interactions display a linear $\lg K$ vs. $\lg[M^+]$ plot, provided that the salt concentration is not too low. However, many protein-nucleic acid affinity constants are also affected by the type of anion present (see Table 1). Where examined, effects on the absolute magnitude of the binding constants, with no effect on log–log slope, as well as effects on both the magnitude and the slope have been observed. This specific anion effect complicates the interpretation of such log–log plots.

For cooperative non-specific binding proteins, the values of K alone (not $K\omega$) should be used for analysis by Eq. (10) (since cooperativity appears to originate primarily from protein-protein interactions). However, for all proteins studied to date (see below), ω is found to be essentially *independent* of salt concentration (and also of nucleic acid type). Thus either $\lg K$ or $\lg K\omega$ (which is often more easily determined [86K]) can be used for the log–log plot.

The competitive effects of magnesium ions in buffers containing mixtures of monovalent and divalent cations have also been considered. The presence of Mg^{2+}, a common component of solutions employed, introduces curvature in $\lg K$ vs. $\lg[M^+]$ plots. A correction for this competitive effect has been described [77R1].

4.9.2.4 Experimental methods

A wide variety of experimental approaches can be used to determine binding affinities. Any procedures which permit physical separation of bound complex from free protein or nucleic acid can be employed (see below). In addition, a spectroscopic signal which is found to be proportional to complex formation can also be used (see below); spectroscopic procedures are indirect but are more convenient and rapid than the physical separation methods.

For sequence specific binding proteins, analysis of the binding data is usually straightforward. However, for non-specific binding proteins, the unambiguous extraction of n, K, and ω from the binding data requires some additional considerations [81K2, 81N, 86K, 83S]. A discussion of those considerations has been presented, as well as the means for determining these thermodynamic parameters from a combination of experimental procedures [86K].

The methods commonly used can be divided into two categories: physical separation methods and spectroscopic methods. Each category is comprised of a variety of experimental techniques. A brief description, any unique advantages or limitations, and citations to some examples are presented for each technique (see Table 1 and [81K1] for a more comprehensive list of citations).

4.9.2.4.1 Physical separation methods

Nitrocellulose filtration – is based on the observation that proteins and protein-nucleic acid complexes are retained on nitrocellulose filters, whereas free nucleic acids are washed through [70R]. This method has been used widely to study the affinity of sequence specific nucleic acid binding proteins. It is relatively fast, simple, and inexpensive. Its major limitation is limited applicability to non-specific nucleic acid binding proteins. Since the binding of one protein per nucleic acid is considered sufficient for retention, the study of non-specific binding to large nucleic acids is limited; several theoretical formulations which address this limitation are available ([82C, 83W] and citations contained within) and their applicability has been discussed [86S].

Sedimentation methods – the sedimentation coefficients of free and bound proteins and nucleic acids are generally different; thus differences in sedimentation velocities can be exploited. Several variations of the sedimentation methods exist [77J, 77R2, 79D, 79S, 80L, 81R]. Though generally not as convenient as other techniques, some of the procedures are thermodynamically rigorous (e.g. [81R]).

DNA-cellulose chromatography – DNA (either ss or ds) is covalently attached to cellulose (or agarose) and a nucleic acid binding protein is loaded on the column. Bound protein is retained on the column and subsequently eluted. Quantitative applications to date have been limited to non-specific binding proteins [77D1, 81K2], but should also be applicable to site-specific interactions as well. Since the concentration of DNA on the column is in great excess over the total protein concentration (i.e. the maximum binding density is very low), problems with excluded site effects or cooperativity are avoided [77D1, 86K]; this is also a drawback, since neither n nor ω can be determined from this procedure [86K].

Gel exclusion chromatography – is based on partition equilibria [85F]. This method is technically relatively simple, but it is slow, more applicable to enzymes than to binding proteins, and it is not as easy to scale down as the sedimentation methods.

Gel electrophoresis (gel retardation) – protein-nucleic acid complexes migrate more slowly than free nucleic acids during either agarose or native polyacrylamide gel electrophoresis [81G2, 81F]. This method has found recent widespread use in the study of sequence specific binding proteins (see [86G]). In addition to being relatively rapid, simple, and inexpensive, little net dissociation of protein-nucleic acid complexes occurs during the course of separation, due to effects of the gel matrix. Though quantitative analysis of multiple binding sites is possible, applicability to non-specific binding is limited to qualitative observations (e.g. [86L2]).

Footprinting – is based on the differential sensitivity (usually protection) of a nucleic acid within a protein-nucleic acid complex to attack by either a nuclease [78G] or a chemical reagent [78J, 80S1], compared to the free nucleic acid. This is a very useful procedure for study of sequence-specific DNA binding proteins. Since individual site binding constants for a nucleic acid containing multiple binding sites can be resolved [86S], this method is readily applicable to studies of more complex sequence specific interactions (see [86B] for detailed methodology).

4.9.2.4.2 Spectroscopic methods

These methods are generally utilized to study nonspecific complex formation and all assume that the spectroscopic signal is proportional to extent of complex formation; a procedure for testing this assumption has been described [87B2].

Fluorescence – both intrinsic protein fluorescence and extrinsic probes have been used to detect complex formation (see [81K1] for citations). If changes in intrinsic protein fluorescence are observed, complex formation generally results in a quenching of the intrinsic fluorescence by as much as 80% (e.g. [75M]). Modification of DNA substrates to yield fluorescent derivatives has also proven to be useful (e.g. [81K2, 85M]). The fluorescence approaches are the most sensitive of the spectroscopic methods; however, quenching of intrinsic fluorescence is not observed for all proteins and care must be exercised when extrinsic probes are used.

Circular dichroism – upon complex formation, the circular dichroism spectrum of nucleic acids (generally single-stranded) is observed to change. This change is usually a decrease in signal. A drawback is that circular dichroism instrumentation is often not available.

UV absorbance – upon complex formation, the ultraviolet absorption spectrum of a single-stranded nucleic acid is sometimes altered [73D, 76J2, 77B] (see also [81K1]). The change is generally an increase in absorbance at 260 nm, but decreases also occur. Although the instrumentation for this method is much more readily available than for circular dichroism, the sensitivity of the UV method is poor.

dsDNA melting temperature – non-specific nucleic acid binding proteins affect the melting temperature, T_m, of dsDNA [76J1, 76J2]. Proteins with a net affinity for ssDNA will lower the T_m; those with a net affinity for dsDNA will increase the T_m [76M]. Though this method is best for determining the relative affinity for ss- vs. dsDNA, the drawbacks are that only relative affinities can be determined (unless the absolute affinity for ss- or dsDNA is known), rigorous quantitative analysis of the data requires knowledge of the enthalpy of binding, and the protein must be stable over the range of temperatures required to detect dsDNA melting. Due to the last reason, this approach has been generally limited to helix-destabilizing proteins.

Electron microscopy – is unique because it permits direct visualization of protein-nucleic acid complexes. Though electron microscopy is usually used to determine the morphology of protein-nucleic acid complexes, cooperativity of binding is readily detected as a clustering of bound protein molecules [75R, 88B]. Quantitative analysis of the average cluster sizes and cluster size distributions permits an evaluation of the cooperativity parameter, ω [86K, 88B]. Estimation of binding constants is possible though more difficult [80K].

4.9.3 Protein-nucleic acid binding parameters

Table 1. Protein-nucleic acid binding parameters.

Column 1: The protein and its origin is indicatd by bold faced letters. The interacting nucleic acid substrates are indicated by standard letters. The characterization of the nucleic acid substrates is self-explanatory, except for the following abbreviations:
Etheno M13 ssDNA = M13 phage ssDNA modified to contain 1,N^6-etheno-adenosine and 3,N^4-etheno-cytidine residues.
Poly(etheno rA) = poly-1,N^6-ethenoadenylic acid.
Poly(etheno A,U) = random co-polymer of 1,N^6-adenylic acid and uridylic acid residues, at the ratio indicated.

Column 2: The "Type" indicates whether binding is specific, S, or non-specific, N.

Column 3: n is the binding site size in numbers of nucleotide residues (for single-stranded, ss, nucleic acids) or basepairs (for double-stranded, ds, nucleic acids) per protein monomer.

Column 4: K is the intrinsic binding constant, given in M^{-1}. If the "Type" column contains the entry "S", then the values are for specific binding; if the entry is "N", then the values are for non-specific binding and were determined using either Eq. (8) or (9).

Column 5: ω is the unitless cooperativity parameter.

Column 6: $K\omega$ is the product of K and ω, given in M^{-1}.

Column 7: Salt: The numbers give the concentration of the listed salt at which the appropriate values of K and ω are defined.

Nucleic acid substrate	Type	n	K [M^{-1}]	ω	$K\omega$ [M^{-1}]	Salt [mM]
araC protein from *E. coli*						
AraI[1])	S		$5.6 \cdot 10^{11}$			100 NaCl
AraO[1])	S		$5.6 \cdot 10^{11}$			100 NaCl
Catabolite activator protein (CAP) from *E. coli*						
Gal promoter fragment[3])	S		$3 \cdot 10^8$			100 KCl
Lac promoter fragment (CRP1 site)[3])	S		$3 \cdot 10^9$			100 KCl
Lac promoter fragment (CRP2 site)[3])	S		$7.5 \cdot 10^7$			100 KCl
Lac promoter-operator region site 1[4])	S		$6.2 \cdot 10^8$			0
Lac promoter-operator region site 1[5])	S		$4.6 \cdot 10^9$			0
Lac promoter-operator region site 1[6])	S		$1.4 \cdot 10^{10}$			0
Lac promoter-operator region site 1[7])	S		$8.4 \cdot 10^{10}$			0
Gal promoter fragment[3])	S		$1.2 \cdot 10^9$			100 KCl
Calf thymus dsDNA	N	16	$6.7 \cdot 10^5$[8])	10	$6.7 \cdot 10^6$	0
Calf thymus dsDNA[9])	N	13	$9.9 \cdot 10^1$	100	$9.9 \cdot 10^3$	175 NaCl
λ DNA[9])	N	15	$7.4 \cdot 10^1$	100	$7.4 \cdot 10^3$	170 KCl
λ DNA[9,10])	N	15	$2.0 \cdot 10^3$	100	$2.0 \cdot 10^5$	170 KCl
λ DNA[9,11])	N	15	$1.4 \cdot 10^2$	100	$1.4 \cdot 10^4$	170 KCl
pBR322 digest[3])	N		$3.0 \cdot 10^5$			100 KCl
φX 174 ssDNA[9])	N	15	$3.8 \cdot 10^2$	100	$3.8 \cdot 10^4$	170 KCl
φX 174 ssDNA[9,10])	N	15	$3.2 \cdot 10^3$	100	$3.2 \cdot 10^5$	170 KCl
φX 174 ssDNA[9,11])	N	15	$3.4 \cdot 10^2$	100	$3.4 \cdot 10^4$	170 KCl
Poly(dA)	N	13	$1.6 \cdot 10^3$	600	$1.0 \cdot 10^6$	175 NaCl
Poly(dT)	N	13	$1.2 \cdot 10^3$	800[12])	$1.0 \cdot 10^6$	175 NaCl
Poly(dT)[13])	N	13	$6.5 \cdot 10^3$	260	$1.7 \cdot 10^6$	175 NaCl

[1]) In the presence of 50 mM arabinose.
[2]) 5 mM $MgCl_2$ has a 3-fold effect on K (at 100 mM KCl) whereas 5 mM KCl has no effect.
[3]) In the presence of 200 μM cAMP.
[4]) In the presence of 0.2 μM cAMP.
[5]) In the presence of 0.5 μM cAMP.
[6]) In the presence of 1.0 μM cAMP.
[7]) In the presence of 5.0 μM cAMP.
[8]) K and ω are approximately independent of cAMP concentration.
[9]) Based on CAP dimer concentration.

Column 8: d lg K/d lg[salt] indicates the slope, derived from a plot of lg K vs. lg[salt], for the salt listed.

Column 9: m' is the net number of ion pairs formed between protein and nucleic acid as derived from the log–log analysis (Eq. (10)); if no anion binding was assumed, it is indicated as such in the "a" column (column 10).

Column 10: a indicates the number of anions released from protein upon complex formation; if anion effects were not explicitly examined then the entry "0 (assumed)" occurs.

Column 11: Anion: The appropriate salt anions are listed.

Column 12: Reaction temperature, T, given in °C.

Column 13: The pH values of the solutions are listed.

Column 14: The experimental methods used to determine the thermodynamic parameters are listed. For the abbreviations see "List of symbols and abbreviations", section 4.9.1.3.

Column 15: References.

Special conditions and remarks are given in footnotes.

d lg K/d lg [salt]	m'	a	Anion	T[°C]	pH	Method	Ref.
−3.5	4	0[2])	Cl^-	37	7.4	GR	84H
−3.5	4	0[2])	Cl^-	37	7.4	GR	84H
				37	8.0	GR	83K
				37	8.0	GR	83K
				37	8.0	GR	83K
				20	8.0	GR	84F
				20	8.0	GR	84F
				20	8.0	GR	84F
				20	8.0	GR	84F
				37	8.0	GR	83K
				20	8.0	GR	84F
−4.9	5.5	0 (assumed)	Cl^-	22	7.9	S; CD	79S
−5.3	6	0 (assumed)	Cl^-	20	8.0	S; NC	79T
−4	4.5	0 (assumed)	Cl^-	20	8.0	S; NC	79T
−4.4	5	0 (assumed)	Cl^-	20	8.0	S; NC	79T
				37	8.0	GR	83K
−2.1	3	0 (assumed)	Cl^-	20	8.0	S	79T
−2.1	3	0 (assumed)	Cl^-	20	8.0	S	79T
−2.8	4	0 (assumed)	Cl^-	20	8.0	S	79T
−3.6	5	0 (assumed)	Cl^-	22	8.1	CD; S	81G1
−1.5	2	0 (assumed)	Cl^-	22	8.1	CD; S	81G1
				22	8.1	CD; S	81G1

[10]) In the presence of 50 μM cAMP.
[11]) In the presence of 50 μM cGMP.
[12]) ω determination represents a minimum value.
[13]) In the presence of 20 μM cAMP.

(continued)

Table 1, continued.

Nucleic acid substrate	Type	n	K [M^{-1}]	ω	$K\omega$ [M^{-1}]	Salt [mM]
cI repressor protein from λ phage						
OR1 (in OR-containing fragment)	S		$1.9 \cdot 10^8$			200 KCl
OR2 (in OR-containing fragment)	S		$1.4 \cdot 10^7$ [15]			200 KCl
OR3 (in OR-containing fragment)	S		$1.4 \cdot 10^7$ [16]			200 KCl
Coat protein from R17 phage						
21-nucleotide RNA binding site	S		$3 \cdot 10^8$			80 KCl [17]
21-nucleotide RNA binding site	S		$9.0 \cdot 10^6$			80 KCl
21-nucleotide RNA binding site	S		$1.8 \cdot 10^7$			80 KCl
21-nucleotide RNA binding site	S		$5 \cdot 10^8$			80 Na acetate
21-nucleotide RNA binding site	S		$1.3 \cdot 10^8$			80 NaBr
21-nucleotide RNA binding site	S		$8.5 \cdot 10^7$			80 $NaNO_3$
21-nucleotide RNA binding site	S		$2.1 \cdot 10^7$			80 NaSCN
21-nucleotide RNA binding site	S		$6.8 \cdot 10^6$			80 NaI
Cro repressor protein from λ phage						
Consensus operator	S		$8.3 \cdot 10^{11}$			100 KCl
OL1 21 bp fragment	S		$6.7 \cdot 10^{10}$			100 KCl
OL2 21 bp fragment	S		$3.7 \cdot 10^{10}$			100 KCl
OL3 21 bp fragment	S		$1.9 \cdot 10^{10}$			100 KCl
OR-containing 73 bp fragment	S		$5 \cdot 10^{11}$			100 KCl
OR-containing 193 bp fragment	S		$6.7 \cdot 10^{10}$ [19]			100 KCl
OR-containing 2410 bp fragment [19]	S		$7 \cdot 10^{10}$ [19]			100 KCl
OR1 (in OR-containing fragment)	S		$4.2 \cdot 10^7$			200 KCl
OR1 21 bp fragment	S		$1.2 \cdot 10^{11}$			100 KCl
OR2 (in OR-containing fragment)	S		$4.2 \cdot 10^7$			200 KCl
Or2 21 bp fragment	S		$8.3 \cdot 10^9$			100 KCl
OR3 (in OR-containing fragment)	S		$3.3 \cdot 10^8$			200 KCl
OR3 21 bp fragment	S		$5 \cdot 10^{11}$			100 KCl
Calf thymus dsDNA	N	7···15 [20]	$3.0 \cdot 10^4$	1	$3.0 \cdot 10^4$	200 KCl
DNA binding protein (DBP; N4 SSB) from N4 phage						
M13 ssDNA	N	11	$3.9 \cdot 10^4$	250	$9.8 \cdot 10^6$	300 NaCl
M13 ssDNA	N	11	$3.8 \cdot 10^4$	300	$1.1 \cdot 10^7$	220 NaCl
Poly(dA)	N	11	$2.3 \cdot 10^4$	300	$6.9 \cdot 10^6$	120 NaCl
Poly(dU)	N	11	$5.4 \cdot 10^4$	200	$1.1 \cdot 10^7$	600 NaCl
Poly(rA)	N	11	$6.5 \cdot 10^4$	150	$9.8 \cdot 10^6$	50 NaCl
EcoRI restriction endonuclease from *E. coli*						
EcoRI site (34 bp fragment)	S		$1 \cdot 10^{11}$			0
pBR 322	S		$9 \cdot 10^{10}$			100 NaCl
pBR 322 (containing 1 RI site) [22]	S		$1.9 \cdot 10^{11}$			0
pBR 322 without RI site	N		$7.4 \cdot 10^5$		$7.4 \cdot 10^5$	0
Estrogen receptor from calf						
Denatured calf thymus DNA	N		$2.2 \cdot 10^6$		$2.2 \cdot 10^6$	200 KCl
Denatured calf thymus DNA [23]	N		$1.0 \cdot 10^7$		$1.0 \cdot 10^7$	200 KCl
Denatured calf thymus DNA [23]	N		$5.0 \cdot 10^5$		$5.0 \cdot 10^5$	220 KCl
Denatured calf thymus DNA	N		$6.0 \cdot 10^5$		$6.0 \cdot 10^5$	220 KCl

[14]) The affinity decreases about 40-fold going from pH 6.5···8.0 and decreases about 3-fold from 4···38 °C.

[15]) In addition, there is a cooperative protein-protein interaction of −2 kcal/mol with protein bound at OR1.

[16]) In addition, there is a cooperative protein-protein interaction of −1.94 kcal/mol with protein bound at OR2, if OR1 is deleted.

[17]) K is not affected by substitution of either Li, Na, or ammonium cations.

[18]) The pH-dependence of K is bell-shaped with an optimum near pH 8.5; ΔH of binding is −19 kcal/mol at pH 7, 8, 8.5, and 9.

d lg K/d lg [salt]	m'	a	Anion	T[°C]	pH	Method	Ref.
				37 [14])	7.0 [14])	FP	79J, 80J, 82A
				37	7.0	FP	79J, 82A
				37	7.0	FP	79J
−4	4.7	0 (assumed)	Cl^-	2	8.5	NC	83C1, 83C2
				2 [18])	6.5 [18])	NC	83C1, 83C2
				2 [18])	9.5 [18])	NC	83C1, 83C2
				2	8.5	NC	83C1, 83C2
				2	8.5	NC	83C1, 83C2
				2	8.5	NC	83C1, 83C2
				2	8.5	NC	83C1, 83C2
				2	8.5	NC	83C1, 83C2
				0	7.4	NC	87K2
				0	7.4	NC	87K2
				0	7.4	NC	87K2
				0	7.4	NC	87K2
				0	7.4	NC	87K2
				0	7.4	NC	87K2
				0	7.4	NC	87K2
				37	7.0	FP	79J
				0	7.4	NC	87K2
				37	7.0	FP	79J
				0	7.4	NC	87K2
				37	7.0	FP	79J
				0	7.4	NC	87K2
−8.7	9	0 (assumed)	Cl^-	4	7.3	FL	82B
−5.2	7.3	0 (assumed)	Cl^-	25	8.0	FL	89L
−2.2	3.1	0 (assumed)	Cl^-	37	8.0	FL	89L
−2.2	3.1	0 (assumed)	Cl^-	25	8.0	FL	89L
−2.6	3.7	0 (assumed)	Cl^-	25	8.0	FL	89L
−1.8	2.5	0 (assumed)	Cl^-	25	8.0	FL	89L
				37	7.6	NC	83T
−7.1	8.1	0 (assumed)	Cl^-	37 [21])	7.6	NC	83T
				37	7.6	NC	83T
				37	7.6	NC	83T
−6.8	7.7	0 (assumed)	Cl^-	4	7.4	DC	85S
−11.5	13.1	0 (assumed)	Cl^-	4	7.4	DC	85S
−8.9	10.1	0 (assumed)	Cl^-	4	8.0	DC	85S
−6.7	7.6	0 (assumed)	Cl^-	4	8.0	DC	85S

[19]) K was identical, within experimental error, for 343, 516, 873, and 1475 bp fragments.

[20]) n is dependent on the salt concentration.

[21]) Temperature-dependence of K yields the following at 37 °C: $\Delta H = -4.7$ kcal/mol; $\Delta G = -15.9$ kcal/mol; $\Delta S = 36.2$ cal/mol K.

[22]) The affinity for a methylated RI site was estimated to be at least 3-fold lower than for the unmodified recognition site.

[23]) Determined in the presence of 5 nM estradiol.

(continued)

Table 1, continued.

Nucleic acid substrate	Type	n	K [M^{-1}]	ω	$K\omega$ [M^{-1}]	Salt [mM]
Gene 32 protein from T4 phage						
Calf thymus dsDNA	N	5	$8.0 \cdot 10^3$	1	$8.0 \cdot 10^3$	50 NaCl
φX 174 ssDNA	N	7			$1 \cdot 10^9$	200 NaCl
Poly[d(A−T)]	N	7.5	$1.0 \cdot 10^7$	1000	$1 \cdot 10^{10}$	10 NaCl
Poly(dA)	N	7	$2.0 \cdot 10^2$	6000	$1.2 \cdot 10^6$	490 NaCl
Poly(dA)	N	7			$2 \cdot 10^8$	200 NaCl
Poly(dC)	N	7			$1.6 \cdot 10^9$	200 NaCl
Poly(dT)	N	10			$5.0 \cdot 10^5$	2100 NaCl
Poly(dU)	N	7			$5 \cdot 10^8$	200 NaCl
Poly(etheno rA)	N	6	$3.5 \cdot 10^3$	4000	$1.4 \cdot 10^7$	400 NaCl
Poly(etheno rA)	N	6	$6.8 \cdot 10^3$	5000	$3.4 \cdot 10^7$	400 NaCl
Poly(etheno rA)	N	6	$2.2 \cdot 10^3$	2000	$4.4 \cdot 10^6$	400 NaCl
Poly(rA)	N	7	$8.5 \cdot 10^2$	2000	$1.7 \cdot 10^6$	350 NaCl
Poly(rA)	N	7			$1.7 \cdot 10^5$	450 NaCl
Poly(rA)	N	7			$1.7 \cdot 10^6$	450 Na acetate
Poly(rA)	N	7			$1.0 \cdot 10^7$	450 NaF
Poly(rC)	N	7			$3.2 \cdot 10^5$	200 NaCl
Poly(rU)	N	7			$4.0 \cdot 10^7$	200 NaCl
Gene 5 protein from fd phage						
M13 ssDNA	N	4			$1.3 \cdot 10^7$	100 NaCl
Poly(dA)	N	4	$2.5 \cdot 10^3$	800	$2.0 \cdot 10^6$	100 NaCl
Poly(dA)	N	4	$3.0 \cdot 10^4$	130 [25]	$4.0 \cdot 10^6$	100 NaCl
Poly(dI)	N	4			$5.0 \cdot 10^7$	100 NaCl
Poly(dT)	N	4	$6.4 \cdot 10^6$	500	$3.2 \cdot 10^9$	100 NaCl
Poly(dU)	N	4			$6.3 \cdot 10^9$	100 NaCl
Poly(rA)	N	4	$7.6 \cdot 10^3$	500	$3.8 \cdot 10^6$	100 NaCl
Poly(rA)	N	4	$5.7 \cdot 10^4$	110 [28]	$6.3 \cdot 10^6$	100 NaCl
Poly(rC)	N	4	$1.2 \cdot 10^3$	400	$4.8 \cdot 10^5$	100 NaCl
Poly(rC)	N	4	$1.6 \cdot 10^4$	100	$1.6 \cdot 10^6$	100 NaCl
Poly(rI)	N	4			$5.0 \cdot 10^7$	100 NaCl
Poly(rU)	N	4	$2.1 \cdot 10^4$	400	$8.4 \cdot 10^6$	100 NaCl
Poly(rU)	N	4	$2.7 \cdot 10^5$	120 [29]	$3.2 \cdot 10^7$	100 NaCl
Gene 5 protein from IKe phage						
Poly(dA)	N	4	$6.3 \cdot 10^2$	300	$1.9 \cdot 10^5$	200 KCl
Poly(dI)	N	4	$9.3 \cdot 10^4$	300	$2.8 \cdot 10^7$	200 KCl
Poly(rA)	N	4	$4.3 \cdot 10^3$	300	$1.3 \cdot 10^6$	200 KCl
Poly(rA)	N	4	$6.3 \cdot 10^3$	300	$1.9 \cdot 10^6$	200 KCl
Poly(rA)	N	4	$4.0 \cdot 10^3$	300	$1.2 \cdot 10^6$	200 KCl
Poly(rA)	N	4	$2.3 \cdot 10^3$	300	$6.8 \cdot 10^5$	200 NaCl
poly(rC)	N	4	$2.8 \cdot 10^2$	300	$8.3 \cdot 10^4$	200 KCl
Poly(rU)	N	4	$8.3 \cdot 10^4$	300	$2.5 \cdot 10^7$	200 KCl
HB protein from B. globigii						
pBR 322 (linear)	N	11	$7.3 \cdot 10^6$	258	$1.9 \cdot 10^9$	100 NaCl
Poly(dA) · poly(dT)	N	9	$4.6 \cdot 10^6$	120	$5.5 \cdot 10^8$	100 NaCl
poly(dA)	N	12	$3.5 \cdot 10^6$	150	$5.3 \cdot 10^8$	100 NaCl
poly(dT)	N	11	$3.0 \cdot 10^6$	130	$3.9 \cdot 10^8$	100 NaCl
Poly(rA)	N	11	$4.0 \cdot 10^6$	110	$4.4 \cdot 10^8$	100 NaCl
Helix-destabilizing protein-1 from mouse						
Denatured calf thymus	N	6	$4.3 \cdot 10^5$	1	$4.3 \cdot 10^5$	20 NaCl

[24]) Enthalpies of binding determined at 280, 330, and 420 mM NaCl are +0.5, −0.4, and −2.2 kcal/mol, respectively.
[25]) ω may be as large as 500.
[26]) Enthalpies of binding determined at 175 and 210 mM NaCl are +2 and −2 kcal/mol, respectively.
[27]) Enthalpy of binding determined at 700 mM NaCl is −17.2 kcal/mol.
[28]) ω may be as large as 770.
[29]) ω may be as large as 270.

d lg K/d lg [salt]	m'	a	Anion	T[°C]	pH	Method	Ref.
−1.7	2	0 (assumed)	Cl^-	24	7.7	S	76J1
−6.3			Cl^-	25	7.7	FL	81N
				24	7.7	TM	76J1
−5.7	3	4	Cl^-	25	7.7	UV	81K2, 81N
−5.9			Cl^-	25	7.7	FL	81N
−7.1			Cl^-	25	7.7	FL	81N
−3.5			Cl^-	25	7.7	UV	81N
−5.5			Cl^-	25	7.7	FL	81N
−6.5	3	4	Cl^-	25	7.7	FL	81K2, 81N
				17	7.7	FL	81K2
				35	7.7	FL	81K2
−7	3	4	Cl^-	25	7.7	UV	81K2, 81N
−6.5	3	4	Cl^-	25	7.7	FL	81K2, 81N
−5.1	3	2	acetate	25	7.7	FL	81K2, 81N
−3.5	3	0	F^-	25	7.7	FL	81K2, 81N
−7			Cl^-	25	7.7	FL	81N
−7.5			Cl^-	25	7.7	FL	81N
−3.3	3.7	1	Cl^-	5 [24])	7.0	FL	83A, 85B
				20	6.7	FL	83P
−4.7	5	1	Cl^-	5 [26])	7.0	FL	83A, 85B
−3.3	3	1	Cl^-	5	7.0	FL	83A, 85B
−3.4	5	0 (assumed)	Cl^-	20	6.7	FL	83P
−4.6	5.5	1	Cl^-	5 [27])	7.0	FL	83A, 85B
−4.3	5.5	0 (assumed)	Cl^-	20	6.7	FL	83P
−4.6	5	1	Cl^-	5	7.0	FL	83A, 85B
				20	6.7	FL	83P
−3.5	4	1	Cl^-	5	7.0	FL	83A, 85B
−3.6	3.6	1	Cl^-	5	7.0	FL	83A, 85B
−3.3	4.8	0 (assumed)	Cl^-	20	6.7	FL	83P
−3.5	3.5	1	Cl^-	5	7.0	FL	83A, 85B
−2.7	3.5	0 (assumed)	Cl^-	3.7	6.8	FL	87D1
−3.3	4.2	0 (assumed)	Cl^-	3.3	6.8	FL	87D1
−3	3.8	0 (assumed)	Cl^-	3.4	6.8	FL	87D1
−3.5	4.5	0 (assumed)	Cl^-	12.5	6.8	FL	87D1
−3.1	4	0 (assumed)	Cl^-	19.3	6.8	FL	87D1
−3.4	4.4	0 (assumed)	Cl^-	12.5	6.8	FL	87D1
−2.6	3.8	0 (assumed)	Cl^-	3.4	6.8	FL	87D1
−2.6	3.8	0 (assumed)	Cl^-	4.3	6.8	FL	87D1
−0.7	1	0 (assumed)	Cl^-	20	7.5	FL	84W
				20	7.5	FL	84W
				20	7.5	FL	84W
				20	7.5	FL	84W
				20	7.5	FL	84W
				24	8.8	S	80P

(continucd)

Table 1, continued.

Nucleic acid substrate	Type	n	K [M^{-1}]	ω	$K\omega$ [M^{-1}]	Salt [mM]	d lg K/d lg [salt]	m'	a	Anion	T [°C]	pH	Method	Ref.
HinfI restriction endonuclease from *H. influenzae*														
pBR 322	S		$2 \cdot 10^{10}$			50 NaCl	−3	3.4	0 (assumed)	Cl^-	21	7.5	GC	85F
pBR 322 HinfI fragments	N		$5.2 \cdot 10^{4}$		$5.2 \cdot 10^{4}$	50 NaCl					21	7.5	GC	85F
hnRNP complex protein A1 from rat														
Poly (etheno rA)	N	12	$1.5 \cdot 10^{5}$	30	$4.5 \cdot 10^{6}$	400 NaCl	−1	1	0 (assumed)	Cl^-	22	7.5	FL	88C
Lac repressor protein from *E. coli*														
Lac operator – 21 bp fragment	S		$7.1 \cdot 10^{10}$			160 KCl	−1.6	1.8	0 (assumed)	Cl^-	22 [30]	7.4	NC	77G
Lac operator – 26 bp fragment	S		$1 \cdot 10^{11}$			160 KCl	−1.5	1.7	0 (assumed)	Cl^-	22 [30]	7.4	NC	77G
Lac operator – 29 bp fragment	S		$2.6 \cdot 10^{10}$			150 KCl	−1.6	1.8	0 (assumed)	Cl^-	20	7.5	NC	80O
Lac operator – 29 bp fragment [31]	S		$1.7 \cdot 10^{7}$			150 KCl	−1.2	1.4	0 (assumed)	Cl^-	20	7.5	NC	80O
Lac operator – 203 bp fragment	S		$2.3 \cdot 10^{11}$			200 KCl	−6.9	7.8	0 (assumed)	Cl^-	23	7.5	NC	81W
Lac operator – 6700 bp fragment	S		$1.3 \cdot 10^{12}$			200 KCl	−5.1	5.8	0 (assumed)	Cl^-	23	7.5	NC	81W
Lac operator – λ plac5 DNA	S		$1 \cdot 10^{11}$			150 NaCl	−4.4	5	0 (assumed)	Cl^-	20	7.5	NC	80O
Lac operator – λ plac5 DNA	S		$1.1 \cdot 10^{12}$			200 KCl	−6	6.8	0 (assumed)	Cl^-	23	7.5	NC	81W
Lac operator – λ plac5 DNA	S		$8 \cdot 10^{12}$			130 NaCl	−7.7	8.8	0 (assumed)	Cl^-	20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$6 \cdot 10^{12}$			130 NaCl	−9.3	10.6	0 (assumed)	Cl^-	20	7.4 [32]	NC	81B1
Lac operator – λ plac5 DNA	S		$1.6 \cdot 10^{14}$			130 NaCl	−7.5	8.5	0 (assumed)	Cl^-	20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$2.3 \cdot 10^{13}$			10 $MgCl_2$	−4.1	8.7	0 (assumed)	Cl^-	20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.7 \cdot 10^{13}$			130 CsCl					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.1 \cdot 10^{13}$			130 KCl					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$7 \cdot 10^{12}$			130 NH_4Cl					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1 \cdot 10^{12}$			130 LiCl					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.5 \cdot 10^{14}$			130 $NaHCO_3$					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.3 \cdot 10^{14}$			130 Na acetate					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.3 \cdot 10^{14}$			130 NaF					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$2.3 \cdot 10^{13}$			130 Na_3PO_4					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.1 \cdot 10^{13}$			130 Na_2SO_4					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$9 \cdot 10^{12}$			130 Na citrate					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$9 \cdot 10^{11}$			130 NaBr					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.2 \cdot 10^{11}$			130 $NaNO_3$					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.8 \cdot 10^{10}$			130 NaSCN					20	8.0	NC	81B1
Lac operator – λ plac5 DNA	S		$1.3 \cdot 10^{10}$			130 NaI					20	8.0	NC	81B1
Calf thymus dsDNA	N		$1.3 \cdot 10^{5}$	1	$1.3 \cdot 10^{5}$	130 NaCl	−12	11.5	0 (assumed)	Cl^-	20	7.4	DC	77D1
Calf thymus dsDNA	N		$1.8 \cdot 10^{4}$	1	$1.8 \cdot 10^{4}$	160 NaCl	−10	11	0···1	Cl^-	4	8.0	DC	77D2
Calf thymus dsDNA	N		$7.0 \cdot 10^{5}$	1	$7.0 \cdot 10^{5}$	160 Na acetate	−9.1	10	0	acetate	4	8.0	DC	77D2
Calf thymus dsDNA	N		$4.6 \cdot 10^{5}$	1	$4.6 \cdot 10^{5}$	10 $MgCl_2$	−5.8	12 [33]	0	Cl^-	4	8.0	DC	77D2
Calf thymus dsDNA	N		$1.4 \cdot 10^{5}$	1	$1.4 \cdot 10^{5}$	130 NaCl					4	8.0 [34]	DC	77D2
λ DNA	N	12	$2.4 \cdot 10^{5}$	1	$2.4 \cdot 10^{5}$	150 NaCl	−10	11	0 (assumed)	Cl^-	20	7.5	S; CD	77B, 77R2
λ DNA	N	12	$1.2 \cdot 10^{6}$	1	$1.2 \cdot 10^{6}$	150 NaCl					20	7.2	S	77R2
λ DNA	N	12	$1.4 \cdot 10^{5}$	1	$1.4 \cdot 10^{5}$	150 NaCl					20	7.8	S	77R2
λ DNA	N	12	$3.8 \cdot 10^{5}$	1	$3.8 \cdot 10^{5}$	150 NaCl					10	7.5	S	77R2
λ DNA	N	12	$1.9 \cdot 10^{5}$			150 NaCl					30	7.5	S	77R2
Poly[d(A−T)]	N	12	$1.4 \cdot 10^{6}$	1	$1.4 \cdot 10^{6}$	150 NaCl	−8.2	9.5	0 (assumed)	Cl^-	20	7.5	S	77B, 77R2
T7 DNA	N	[35]	$4.8 \cdot 10^{3}$	1	$4.8 \cdot 10^{3}$	200 NaCl	−8.7	10	0 (assumed)	Cl^-	20	7.5	S	80L
lexA repressor protein from *E. coli*														
Colicin E1 operator fragment	S		$2.5 \cdot 10^{9}$			200 KCl					37	7.0	FP	83E
lexA operator fragment	S		$5.0 \cdot 10^{7}$			200 KCl					37	7.5	FP	81B2
recA operator fragment	S		$5 \cdot 10^{8}$			200 KCl					37	7.5	FP	81B2
umuDC operator fragment	S		$5 \cdot 10^{9}$			200 KCl					37	7.0	FP	85K
uvrA operator	S		$7.0 \cdot 10^{7}$			100 NaCl	−6.3	5.5	0 (assumed)	Cl^-	37	7.9	[36]	87B1

[30] Temperature was not reported; assumed to be room temperature: 22 ··· 23 °C.
[31] In the presence of 1 mM IPTG.
[32] From a pH-dependence, the slope of lg K vs. pH is −0.9 at 130 mM NaCl.
[33] 6 magnesium ions are released upon complex formation.
[34] From a pH-dependence, the slope of a lg K vs. pH plot is −2.1.
[35] Knowledge of n not required for data analysis.
[36] Competition with RNA polymerase using abortive initiation assays; K based on monomer binding.

(continued)

Table 1, continued.

Nucleic acid substrate	Type	n	K [M^{-1}]	ω	$K\omega$ [M^{-1}]	Salt [mM]	d lg K/d lg [salt]	m'	a	Anion	T[°C]	pH	Method	Ref.
p10 from murine leukemia														
Poly(etheno rA)	N	6	$3.0 \cdot 10^5$	1	$3.0 \cdot 10^5$	200 NaCl	−2.3	3	0 (assumed)	Cl^-	22	7.0	FL	87K1
Poly(U)	N	6	$1.0 \cdot 10^4$	1	$1.0 \cdot 10^4$	200 NaCl	−2.1	3	0 (assumed)	Cl^-	22	7.0	FL	87K1
recA protein from *E. coli*														
Etheno M13 ssDNA	N	8[37]	$3.4 \cdot 10^5$	50[38]	$1.7 \cdot 10^7$	220 NaCl	−10.5	0	10	Cl^-	25	7.5	FL	85M, 87M, 90M
Etheno M13 ssDNA[39]	N	8	$1.4 \cdot 10^4$	50[40]	$7.0 \cdot 10^5$	220 NaCl	−3.2	0	3	Cl^-	25	7.5	FL	85M, 87M, 90M
Etheno M13 ssDNA	N	8	$1.1 \cdot 10^7$	125[40]	$1.3 \cdot 10^9$	220 Na acetate	−4.8	0	4.8	acetate	25	7.5	FL	90M
Etheno M13 ssDNA[39]	N	8	$2.3 \cdot 10^5$	125[40]	$2.9 \cdot 10^7$	220 Na acetate	−3.6	0	3.6	acetate	25	7.5	FL	90M
Etheno M13 ssDNA	N	8			$1.0 \cdot 10^7$[41]	1500 Na glutamate	0	0	0	glutamate	37	7.5	FL	90M
Etheno M13 ssDNA	N	8	$1.9 \cdot 10^5$	125[40]	$2.4 \cdot 10^7$	220 NaCl[42]	−9	0	9	Cl^-	37	7.5	FL	88M2, 90M
Etheno M13 ssDNA[43]	N	8	$6.8 \cdot 10^3$	125[44]	$8.5 \cdot 10^5$	220 NaCl[42]	−3.3	0	3	Cl^-	37	7.5	FL	88M2, 90M
rho protein from *E. coli*														
Poly(etheno A, C) 1:1	N	13[45]		46]	$1 \cdot 10^9$	100 KCl					25	7.5	FL	88M1
Poly(etheno A, C) 1:4	N	13[47]		48]	$3 \cdot 10^9$	100 KCl					25	7.5	FL	88M1
Poly(etheno A, U) 1:1	N	13[45]			$2 \cdot 10^8$	100 KCl					25	7.5	FL	88M1
Poly(etheno A, U) 1:4	N	13[45]		49]	$1 \cdot 10^8$	100 KCl					25	7.5	FL	88M1
Poly(dC)	N	13[45]		50]	$2 \cdot 10^9$	100 KCl					25	7.5	FL	88M1
Poly(rC)	N	13[45]	$5.3 \cdot 10^6$	380[51]	$2 \cdot 10^9$	100 KCl					25	7.5	FL; EM	88M1, 88B
Poly(rU)	N	13[45]		52]	$1 \cdot 10^8$	100 KCl					25	7.5	FL	88M1
Ribonuclease A from bovine														
Calf thymus dsDNA	N	8	$1.4 \cdot 10^3$	1	$1.4 \cdot 10^3$	52 NaCl	−3.5	4	0 (assumed)	Cl^-	24[53]	7.7	S	76J2
T7 DNA	N	35]	$6.4 \cdot 10^3$	1	$6.4 \cdot 10^3$	35 NaCl	−3.7	4.2	0 (assumed)	Cl^-	20	7.7	S	80L
Denatured calf thymus DNA	N	11	$5.7 \cdot 10^5$	1	$5.7 \cdot 10^5$	50 NaCl	−4.5	5.8	0 (assumed)	Cl^-	24	7.7	S	76J2
Ribosomal S1 protein from *E. coli*														
Denatured λ DNA[54]	N	5	$3.0 \cdot 10^6$	1	$3.0 \cdot 10^6$	100 NaCl					5	7.7	FL; S	77D3, 79D
Poly(dA)[54]	N	5	$1.7 \cdot 10^6$	1	$1.7 \cdot 10^6$	100 NaCl	−1.6	2.1	0 (assumed)	Cl^-	25	7.7	FL	78D2
Poly(dC)[54]	N	5	$6.0 \cdot 10^6$	1	$6.0 \cdot 10^5$	100 NaCl	−1.6	2.1	0 (assumed)	Cl^-	25	7.7	FL	78D2
Poly(rA)[55]	N	10	$3.6 \cdot 10^5$	1	$3.6 \cdot 10^5$	100 NaCl	0.8				25	7.7	FL	78D3
Poly(rC)[56]	N	10	$1.0 \cdot 10^6$	31	$3.1 \cdot 10^7$	100 NaCl	0.4				25	7.7	FL	78D3
Ribosomal S4 protein from *E. coli*														
α mRNA leader region	S		$1.6 \cdot 10^7$			250 K_2SO_4	−3.2	57]			0	7.6	NC	87D2
α mRNA leader region	S		$1.6 \cdot 10^7$			250 K acetate	−3.2	57]			0	7.6	NC	87D2
α mRNA leader region	S		$8.3 \cdot 10^6$			250 KNO_3	−4.3	57]			0	7.6	NC	87D2
α mRNA leader region	S		$8.1 \cdot 10^6$			250 KBr	−1.4	57]			0	7.6	NC	87D2
α mRNA leader region	S		$2.0 \cdot 10^7$			250 KCl	0	57]			0	7.6	NC	87D2
tRNA	N		$8.7 \cdot 10^5$		$8.7 \cdot 10^5$	250 KCl	−4.4	57]			0	7.6	NC	87D2

[37]) n was adjusted to 8 after change in the extinction coefficient used.
[38]) ω assumes monomer binding and represents a lower limit.
[39]) In the presence of 100 μM ADP.
[40]) ω assumes monomer binding and is a lower limit if the binding species is an aggregate [86T].
[41]) $K\omega$ represents a minimum value at this salt concentration.
[42]) In the presence of $CaCl_2$.
[43]) In the presence of 500 μM ADP.
[44]) ω assumes monomer binding.
[45]) Per monomer;
[46]) Cooperativity between hexamers is estimated to range between 10 ··· 400.
[47]) Per monomer; n is unchanged in the presence of either 1 mM ATP or ADP.
[48]) Cooperativity between hexamers is estimated to range between 1 ··· 500.
[49]) Cooperativity between hexamers is estimated to range between 1 ··· 200.
[50]) Cooperativity between hexamers is estimated to range between 4 ··· 30.
[51]) Cooperativity between hexamers is estimated to range between 10 ··· 250.
[52]) Cooperativity between hexamers is estimated to range between 10 ··· 200.
[53]) Temperature dependence of K at 12 mM NaCl yields a ΔH value of approximately −5 kcal/mol.
[54]) For "site I".
[55]) For "site II"; log−log data for $A(pA)_9$.
[56]) For "site II"; log−log data for $C(pC)_9$.
[57]) ψ is not defined for RNA molecules possessing secondary structure; consequently, m' cannot be evaluated.

(continued)

Table 1, continued.

Nucleic acid substrate	Type	n	K [M^{-1}]	ω	$K\omega$ [M^{-1}]	Salt [mM]
RNA polymerase – core from *E. coli*						
Calf thymus dsDNA	N		$2.0 \cdot 10^6$	1	$2.0 \cdot 10^6$	200 NaCl[59]
Calf thymus dsDNA	N		$1.0 \cdot 10^4$	1	$1.0 \cdot 10^4$	200 NaCl[60]
T7 DNA	N	[35]	$1.3 \cdot 10^6$	1	$1.3 \cdot 10^6$	200 NaCl
Denatured wheat germ DNA	N		$8.0 \cdot 10^7$	1	$8.0 \cdot 10^7$	200 NaCl
RNA polymerase – holoenzyme from *E. coli*						
Lac L8UV5 promoter (open complex)	S		$1.9 \cdot 10^7$[61]			0
λ PR promoter (open complex)	S		$4.1 \cdot 10^{10}$			210 NaCl
λ PR promoter (open complex)	S		$1.2 \cdot 10^{11}$			120 KCl
T7 A1 and D promoters	S		$9.4 \cdot 10^8$			200 NaCl
T7 A1 and D promoters	S		$1 \cdot 10^8$			200 NaCl
Calf thymus dsDNA	N		$1.0 \cdot 10^5$	1	$1.0 \cdot 10^5$	200 NaCl
Calf thymus dsDNA	N		$3.0 \cdot 10^3$	1	$3.0 \cdot 10^3$	200 NaCl[60]
P22 dsDNA	N	42	$7.8 \cdot 10^4$	1	$7.8 \cdot 10^4$	200 NaCl
P22 dsDNA	N	42	$1.1 \cdot 10^5$	1	$1.1 \cdot 10^5$	200 NaCl
P22 dsDNA	N	42	$5.5 \cdot 10^4$	1	$5.5 \cdot 10^4$	200 NaCl
P22 dsDNA	N	42	$1.1 \cdot 10^5$	1	$1.1 \cdot 10^5$	200 NaCl
P22 dsDNA	N	42	$5.9 \cdot 10^4$	1	$5.9 \cdot 10^4$	200 NaCl
T7 DNA	N	[35]	$5.8 \cdot 10^4$	1	$5.8 \cdot 10^4$	200 NaCl
T7 DNA fragment	N		$4.5 \cdot 10^3$	1	$4.5 \cdot 10^3$	200 NaCl[60]
Denatured wheat germ DNA	N		$2 \cdot 10^{11}$	1	$2 \cdot 10^{11}$	200 NaCl
RNA polymerase III from yeast						
Denatured calf thymus DNA	N		$8.2 \cdot 10^7$			200 KCl
Denatured calf thymus DNA	N		$1.9 \cdot 10^{11}$			200 K acetate
Single-stranded DNA binding protein (SSB) from *E. coli*						
Poly(dA)	N	65[66]	$1.8 \cdot 10^4$	50[67]	$1.8 \cdot 10^5$	200 NaCl
Poly(dA)	N	65[66]	$7.3 \cdot 10^3$	350[68]	$2.6 \cdot 10^6$	200 NaCl
Poly(dT)	N	41		50[69]		300 NaCl
Poly(dT)	N	65[66]	$2 \cdot 10^9$	130[68]	$2.6 \cdot 10^{11}$	350 NaBr
Poly(rA)	N	65[66]	$6.8 \cdot 10^2$	450[68]	$3.1 \cdot 10^5$	200 NaCl
Poly(rU)	N	65[66]	$1.0 \cdot 10^5$	40[67]	$4.0 \cdot 10^6$	200 NaCl
Poly(rU)	N	65[66]	$5.9 \cdot 10^4$	380[68]	$2.2 \cdot 10^7$	200 NaCl
Poly(rU)	N	65[66]	$3.8 \cdot 10^2$	460[68]	$1.7 \cdot 10^5$	350 KCl
Poly(rU)	N	65[66]	$1.0 \cdot 10^3$	380[68]	$3.8 \cdot 10^5$	350 NaCl
Poly(rU)	N	65[66]	$8.1 \cdot 10^4$	370[68]	$3.0 \cdot 10^7$	350 Na acetate
Poly(rU)	N	65[66]	$1.9 \cdot 10^5$	440[68]	$8.4 \cdot 10^7$	350 NaF
Poly(rU)	N	65[66]	$5.0 \cdot 10^5$	380[68]	$1.9 \cdot 10^8$	350 K glutamate
Poly(rU)	N	65[66]	$9.0 \cdot 10^1$	380[68]	$3.4 \cdot 10^4$	350 NaBr

[58]) The pH dependence of K yields a slope for lg K vs. pH of −0.3.
[59]) Similar data obtained with KCl, but not shown.
[60]) In the presence of 10 mM $MgCl_2$; the log−log plot is non-linear.
[61]) K is relatively insensitive to temperature from 20···37 °C.
[62]) The slope of the log−log plot is corrected for magnesium ion concentration; the value of −15 represents a minimum estimate.
[63]) The pH dependence of K yields a slope for lg K vs. pH of 2 above pH 7.
[64]) The pH dependence of K yields a slope for lg K vs. pH of −0.4.
[65]) Slope of log−log plot is not corrected for magnesium ion concentration.
[66]) Site size per tetramer; n is very dependent on solution conditions.
[67]) ω determined using McGhee-von Hippel formalism.
[68]) ω determined using the tetramer-octomer model [87B3].
[69]) ω was estimated to range from 50···250.
[70]) Net cation release; m' is actually 14···16 since there is compensating cation uptake [88O].

d lg K/d lg [salt]	m'	a	Anion	T[°C]	pH	Method	Ref.
−21.2	24	0 (assumed)	Cl^-	4	7.8[58])	DC	78D1
				4	7.8	DC	78D1
−18.2	21	0 (assumed)	Cl^-	20	7.8	S	80L
−17.6	18			4	7.8	DC	78D1
				37	8.0	GR	87S
				25	7.5	NC	85R2
−20						NC	84R
−15[62])	18	0 (assumed)	Cl^-	37	8.0	NC	80S2
−14.7	16.7	0 (assumed)	Cl^-	37	7.4[63])	NC	80S2
−10.5	12	0 (assumed)	Cl^-	0	7.5[63])	DC	78D1
−10.8	12	0 (assumed)	Cl^-	4	7.8[64])	DC	78D1
				4	7.8	S	81R
−6.2	7	0 (assumed)	Cl^-	20	7.9	S	81R
−6.2	7	0 (assumed)	Cl^-	5	7.9	S	81R
−5.5	6.3	0 (assumed)	Cl^-	35	7.9	S	81R
−8.4	9.6	0 (assumed)	Cl^-	20	7.4	S	81R
−6.4	7.3	0 (assumed)	Cl^-	20	8.4	S	80L
−8.1	9	0 (assumed)	Cl^-	20	7.7	S	80K
−1[65])	1	0 (assumed)	Cl^-	0	8.0	EM	78D1
−17.6	18			4	7.8	DC	
−13.3	18	0	Cl^-	4	7.9	DC	84G
−13.8	18	0	acetate	4	7.9	DC	84G
				25	8.1	FL	86L2
				25	8.1	FL	88O
−6.1				22	7.5	EM	87G
				25	8.1	FL	88O
−5.7				25	8.1	FL	88O
−6.2				25	8.1	FL	86L2
				25	8.1	FL	88O
−7.4				25	8.1	FL	88O
−7.2	4[70])	3	Cl^-	25	8.1	FL	88O
−7	4[70])	3	Cl^-	25	8.1	FL	88O
−6.6	4[70])	2	acetate	25	8.1	FL	88O
−4.8	4[70])	0	F^-	25	8.1	FL	88O
−5.7	4[70])	2	glutamate	25	8.1	FL	88O
−6.7	4[70])	3	Br^-	25	8.1	FL	88O

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