



For further information on how to interpret these results or to get a copy of the MEME software please access <http://meme.nbcr.net>.

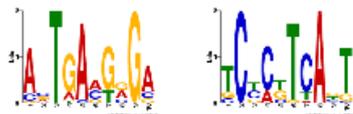
[DISCOVERED MOTIFS](#) | [BLOCK DIAGRAMS OF MOTIFS](#) | [PROGRAM INFORMATION](#) | [EXPLANATION](#)

DISCOVERED MOTIFS

Motif Overview

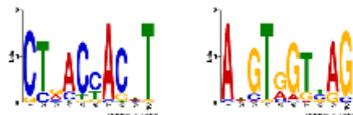
[Motif 1](#)

- 2.9e+007
- 23 sites



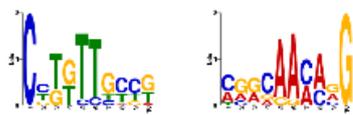
[Motif 2](#)

- 7.7e+006
- 23 sites



[Motif 3](#)

- 2.0e+011
- 23 sites



Further Analysis

Submit all motifs to [MAST](#) [?](#) [FIMO](#) [?](#) [GOMO](#) [?](#) [BLOCKS](#) [?](#) Mouse-over buttons for more information.

MOTIF 1

[Next Top](#)

Summary [?](#)

E-value 2.9e+007
Width 10
Sites 23

[show more](#)

Sequence Logo [?](#)



[Standard](#) | [Reverse Complement](#)

Download LOGO [?](#) Orientation: [standard](#) SSC: [off](#) Format: [web \(png\)](#) Width: [10](#)

cm Height: [7.5](#) cm [Download](#)

Regular expression [?](#)

A[CAG]TGA[AC][GT][AGC]GA

Further Analysis [?](#)

Submit this motif to [MAST](#) [?](#) [FIMO](#) [?](#) [TOMTOM](#) [?](#) [GOMO](#) [?](#) [BLOCKS](#) [?](#) Mouse-over buttons for more information.

Data Formats [?](#)

View the motif in PSPM Format [?](#) PSSM Format [?](#) BLOCKS Format [?](#) FASTA Format [?](#) Raw Format [?](#) or Hide

Sites [?](#)

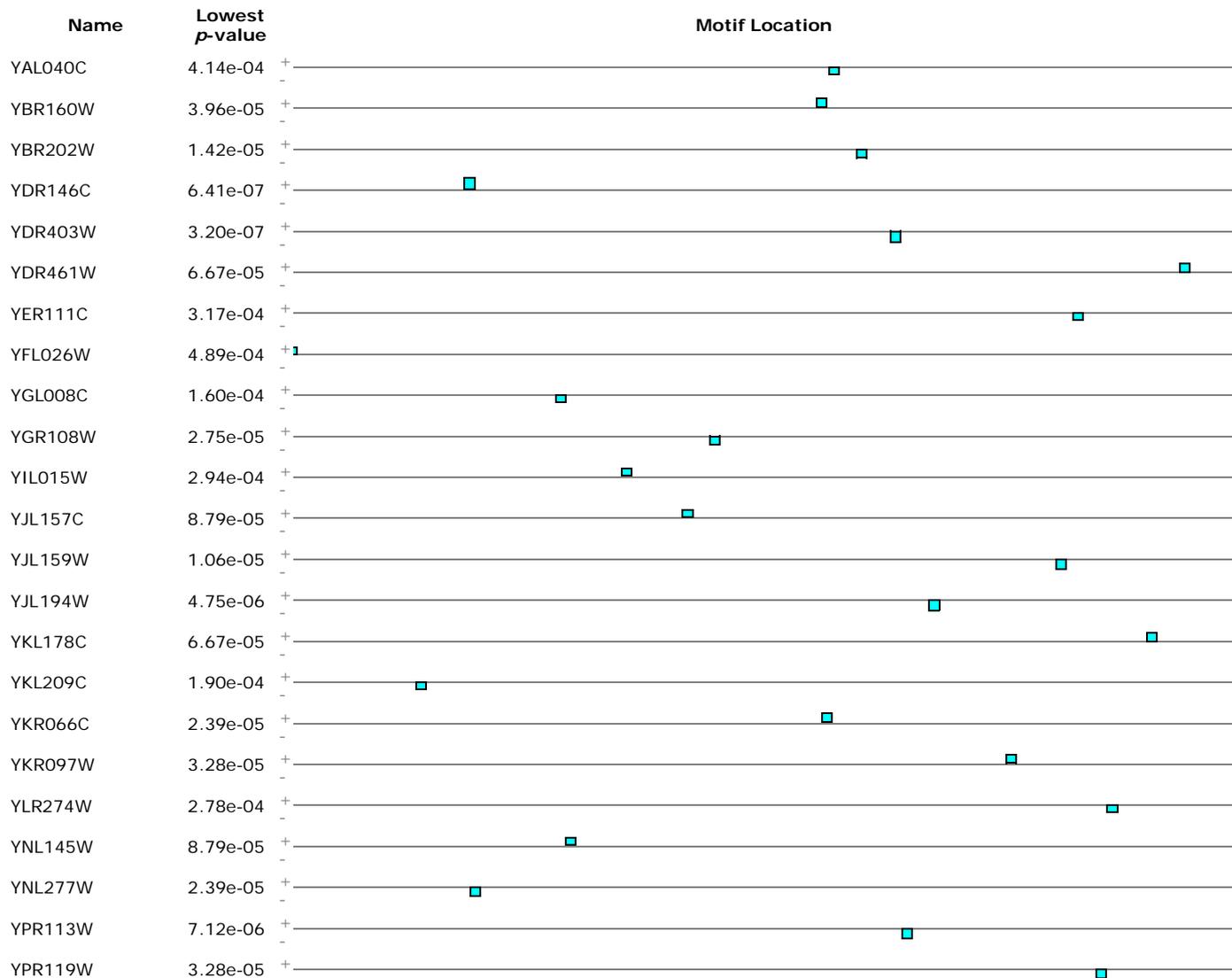
Click on any row to highlight sequence in all motifs.

Name	Strand	Start	p-value	Sites ?
YDR403W	-	320	3.20e-07	TTAACACCAT ACTGACGGGA CGAAAATGCA

YDR146C	+	97	6.41e-07	CTCTTATGAA AGTGACGGGA ATTACGACTA
YJL194W	-	340	4.75e-06	GTAACGAAGA AATGACGGGA GGTCAGCCTG
YPR113W	-	326	7.12e-06	CATAGTACTC ACTGAAGCGA CAGTTCATTA
YJL159W	-	406	1.06e-05	ATTATGGAAT CCTGACGGGA AATCATGACA
YBR202W	-	302	1.42e-05	ATACGCGTCA AGTGAAGGGC ATGATAACAC
YNL277W	-	100	2.39e-05	ATATGTGATT CCTGACGAGA GGGACAATCT
YKR066C	+	284	2.39e-05	TCTATGGACT AGTGACGCGG CCCCCGATTCT
YGR108W	-	225	2.75e-05	AATTAGTCGA AATGAAGGGC TATTAACTCA
YPR119W	-	427	3.28e-05	AGTATACGAG AATGAGGAGA AAACATCTTG
YKR097W	+	380	3.28e-05	TAAAATCATG AATGAGGAGA GAACGTTGCC
YBR160W	+	281	3.96e-05	AAATAAATAA AATGACGAGG AGCATTAACC
YKL178C	+	454	6.67e-05	GAAAAGTTTC AGTGAGTGGG TTCACCTGTT
YDR461W	+	471	6.67e-05	AGTCCAAAGA ACTAACGGGC GCTGTAATAG
YNL145W	+	150	8.79e-05	ACCGATCTCT AGTGAATCGA TCTATACATT
YJL157C	+	211	8.79e-05	CAATCAGTCG ACTAAAGAGA TAATTAAAAA
YGL008C	-	145	1.60e-04	GTAGGCCTAA ATTGAAGCGA TAAGATGGAT
YKL209C	-	72	1.90e-04	CATACAAAGTC ACTGAATAGG GGAATATTAG
YLR274W	-	433	2.78e-04	CAATAAAACG ACTTAAGAGA TCTAGGATAT
YILO15W	+	179	2.94e-04	GAGTTATATA AATAAAGAGC AAGGAAGTCA
YER111C	-	415	3.17e-04	GTTAATATTA AGTAACTAGA GAGTTTGTCT
YAL040C	-	288	4.14e-04	GATAAAGCAA GGTGAGTGGG GAAGCAGATA
YFLO26W	+	4	4.89e-04	ACCG CATGCAGCGA TTTACGGTAT

Block Diagrams

The height of the motif "block" is proportional to $-\log(p\text{-value})$, truncated at the height for a motif with a p-value of $1e-10$. Click on any row to highlight sequence in all motifs. Mouse over the center of the motif blocks to see more information.

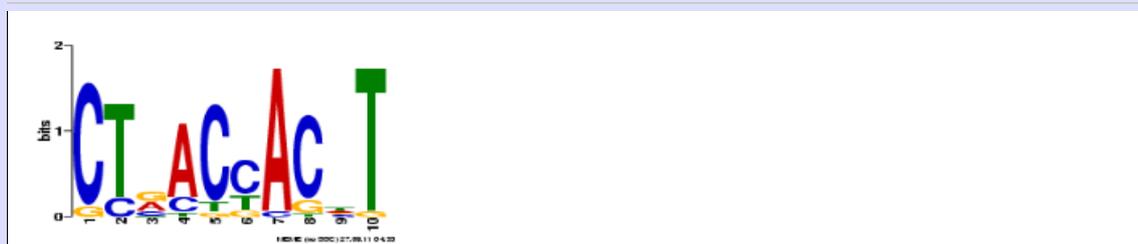


0 100 200 300 400 500

Time 14.1 secs.

MOTIF 2[Previous](#) [Next](#) [Top](#)**Summary**

E-value 7.7e+006
 Width 10
 Sites 23
[show more](#)

Sequence Logo
 Standard Reverse Complement

Download LOGO Orientation: SSC: Format: Width:
 cm Height: cm

Regular expression

CT[AG]AC[CT]AC[AT]T

Further Analysis

Submit this motif to Mouse-over buttons for more information.

Data Formats

View the motif in PSPM Format PSSM Format BLOCKS Format FASTA Format Raw Format or Hide

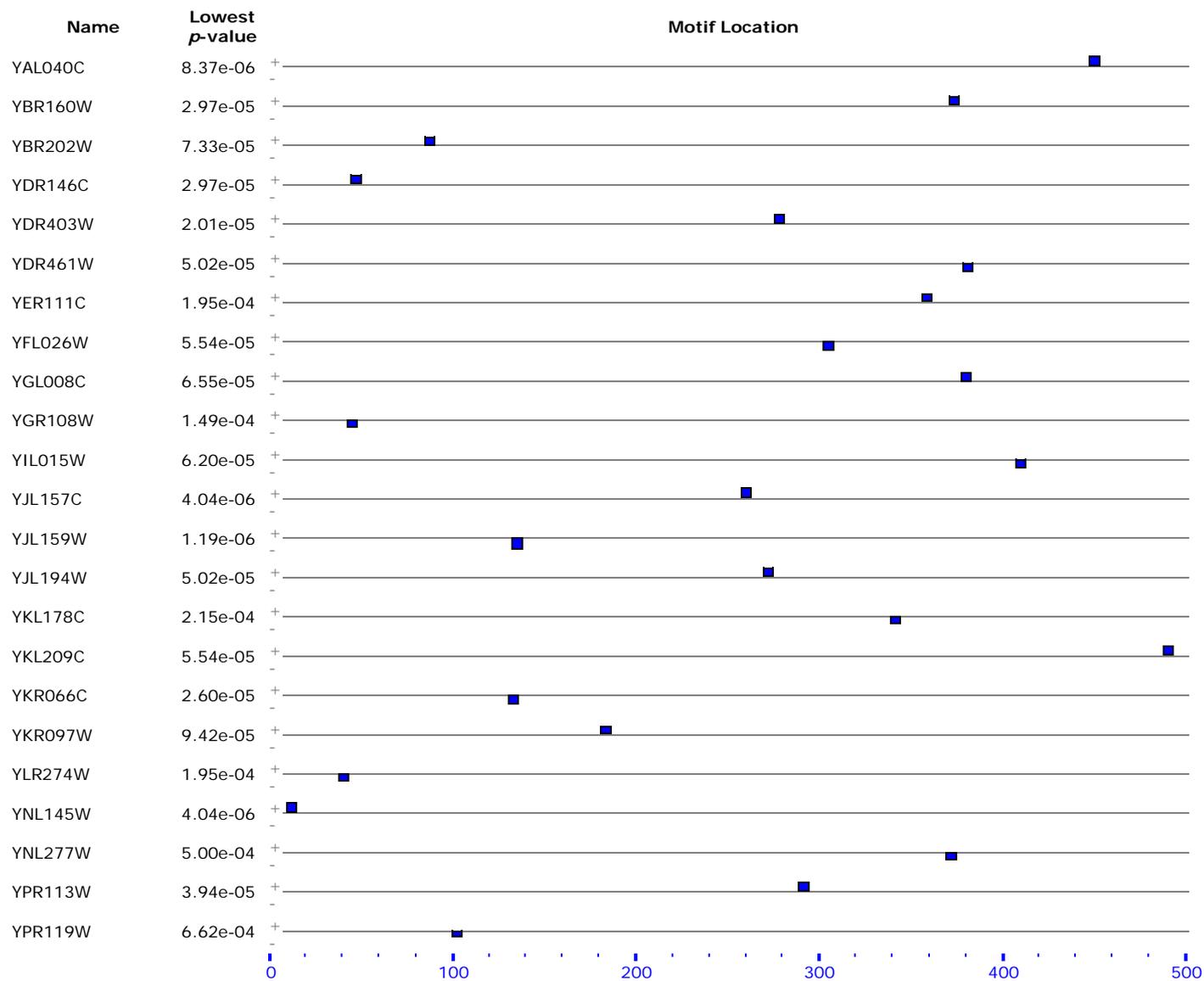
Sites

Click on any row to highlight sequence in all motifs.

Name	Strand	Start	p-value	Sites
YJL159W	-	133	1.19e-06	CTGGAACGAA CTGACCACCT TAAAAAGTCC
YNL145W	+	10	4.04e-06	GATTTGGGTA CTAACCACAT TTCTAGATAT
YJL157C	+	258	4.04e-06	AGACTTTATG CTAACCACAT GAAAGATATT
YAL040C	+	448	8.37e-06	ACTTAGTTAA CTAACCACCT TCTATTCCCT
YDR403W	+	276	2.01e-05	TAAAAATGAA CTCCCCACGT GAGTAAGGAT
YKR066C	-	131	2.60e-05	CCGCAGCACG CTAACTACTT ACTTTGAGAA
YDR146C	+	45	2.97e-05	AAGACTCAAT CTAACGACAT TAACAGTACA
YBR160W	+	371	2.97e-05	CGTCGAATAT CTAACGACAT AAATGTGAAC
YPR113W	+	289	3.94e-05	GGTCTTCAAT GTGACCACGT TTAACAATTA
YJL194W	+	270	5.02e-05	CAAAAACACC CTCACCAGAT TATAACCCCA
YDR461W	-	379	5.02e-05	CCGTGAGCCA CCCCCACAT TCTACCACCA
YKL209C	+	488	5.54e-05	ACTAATTCTC CTGCCTACCT AGTG
YFLO26W	-	303	5.54e-05	GTTACAGTTC CTTACCACCT TTTTGTTTCA
YILO15W	-	408	6.20e-05	ATTTCAATTC CTGATCACTT AACCTTTCTT
YGL008C	+	378	6.55e-05	TATTATTTAT CTGAGCACGT AAGTTATTTA
YBR202W	+	85	7.33e-05	CAACTACTTA CCAACTACTT AATACATCTG
YKR097W	+	181	9.42e-05	AAAGTACCGC CCGACCACAG TATACATTGA
YGR108W	-	43	1.49e-04	AAAGATATCG CTAATCACCT ATTGTGATCA
YLR274W	-	38	1.95e-04	ATCTATCTAA CCGACTAGTT ATAATTTACA
YER111C	+	356	1.95e-04	TATCTGTCCG CTGACCCGTT GTTCTATCAT
YKL178C	-	339	2.15e-04	AATTAGAAGG CTGTCTACTT GATACCGTCC
YNL277W	-	370	5.00e-04	TGAAGCACTT GTACCTACGT TAATTCCTGCT
YPR119W	-	100	6.62e-04	TTTAATTATA CTCACGATAT TAATTTTAAC

Block Diagrams

The height of the motif "block" is proportional to $-\log(p\text{-value})$, truncated at the height for a motif with a p-value of $1e-10$. Click on any row to highlight sequence in all motifs. Mouse over the center of the motif blocks to see more information.



Time 27.7 secs.

MOTIF 3

[Previous Top](#)

Summary

E-value 2.0e+011
Width 10
Sites 23

[show more](#)

Sequence Logo



Standard Reverse Complement

Download LOGO Orientation: SSC: Format: Width:
cm Height: cm

Regular expression

C[CTG][TG][GT]TTG[CT][CT][GT]

Further Analysis

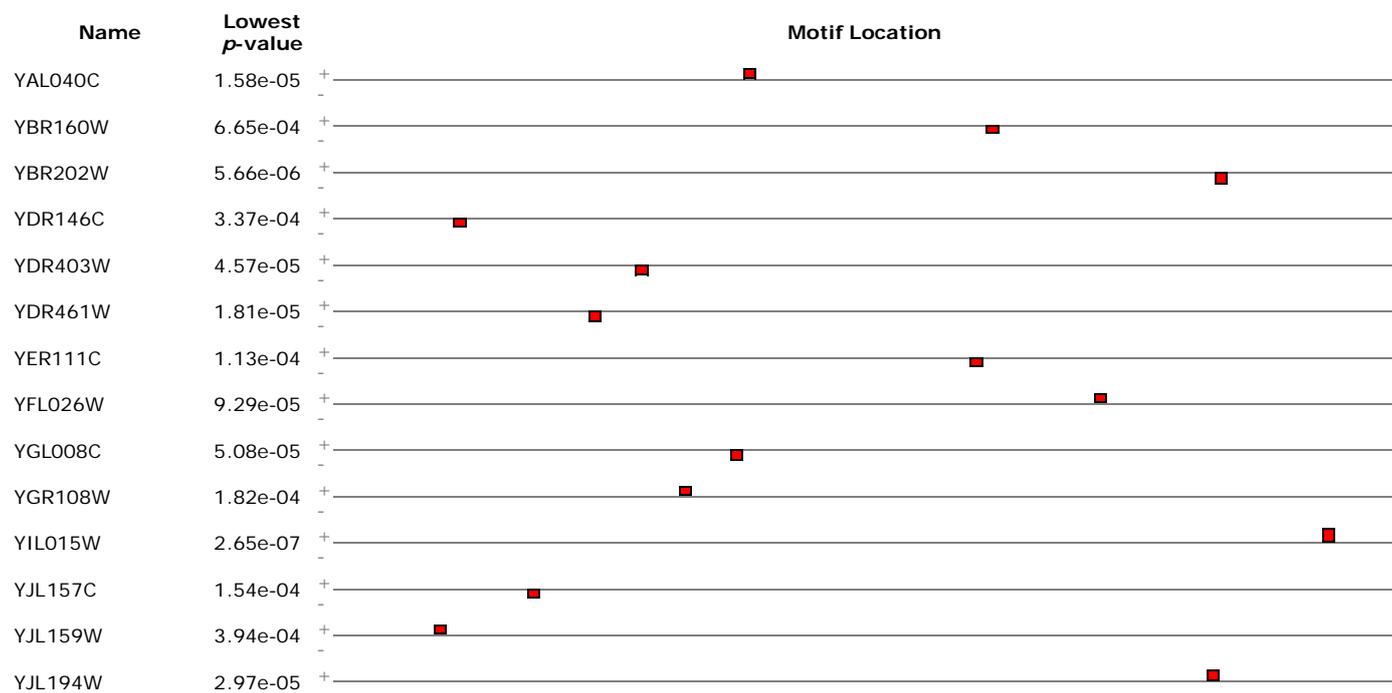
Submit this motif to

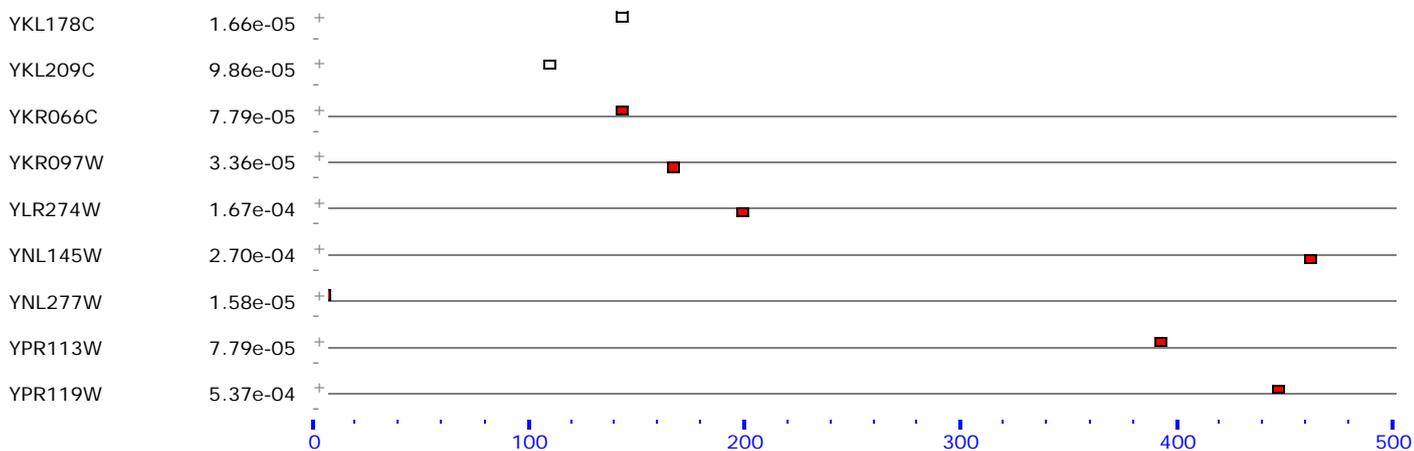
Mouse-over buttons for more information.

Data FormatsView the motif in PSPM Format PSSM Format BLOCKS Format FASTA Format Raw Format or Hide**Sites**

Click on any row to highlight sequence in all motifs.

Name	Strand	Start	p-value	Sites
YIL015W	+	466	2.65e-07	AGATGGACCT CCGGTTGCCG ATACTGGATA
YBR202W	-	416	5.66e-06	TATGTCTTTC CGTGTGTCG TTCTTTAGGA
YNL277W	+	3	1.58e-05	AGT CCTTTTGCTG ACCGTGTCAG
YAL040C	+	198	1.58e-05	TATACGATCC CCTTTTGCTG CCGACCTCTA
YKL178C	+	141	1.66e-05	GTGTAGGGTT CCTGTCGTCG TGTGTTATCA
YDR461W	-	126	1.81e-05	AGTGTGGACA CCTGTTCCCT ATGAAGGGAA
YJL194W	+	412	2.97e-05	ATAATTATCA CTTTTGTCG CATCGGTGAT
YKR097W	-	165	3.36e-05	TCGGGCGGTA CTTTTCGCCG GTAAGATTTA
YDR403W	-	148	4.57e-05	ATTTCGACCT CTGGTTTCCG TTGAAACATC
YGL008C	-	192	5.08e-05	ACTTCGAATA CGGGTTGTCT AATTGCAAAA
YPR113W	+	391	7.79e-05	GGTATGCTAA CTTGTTCTCTG TGCATAAGAA
YKR066C	+	141	7.79e-05	AAGTAGTTAG CGTCTGCGG AGAATAAAGC
YFLO26W	+	360	9.29e-05	ACGTGCTGAT CGTTTTGTGG AATTTAGCTA
YKL209C	+	108	9.86e-05	ATCATTACGT CCTGTTGCTA TTTATTTGTG
YER111C	-	303	1.13e-04	ATAGCGCAAA CCGGTTGGCT GATATTAGAT
YJL157C	-	98	1.54e-04	TAACGGCTGA CTTTTGTGT CAAAATAAAT
YLR274W	-	197	1.67e-04	CCTAGTCAGA CTGGTTGACG ATTAATTTTT
YGR108W	+	168	1.82e-04	GAGTTTGTA CTTTTGTCA TTCATTTGCT
YNL145W	-	460	2.70e-04	CTTCGATCGT CGGTTTTCCG GGCAAAAAAAA
YDR146C	-	64	3.37e-04	GTGGTACGAA CTTGCTCTCT GACTGTAA
YJL159W	+	55	3.94e-04	ATTCTCGTTA CCTGCTCTCT ACGTTATTTA
YPR119W	+	445	5.37e-04	TTCTCGTATA CTGTTTCCTT ACAGGATAAC
YBR160W	-	310	6.65e-04	ACAGTCCATT CTTTTTCTT TCATGAGCCG

Block DiagramsThe height of the motif "block" is proportional to $-\log(p\text{-value})$, truncated at the height for a motif with a p-value of $1e-10$. Click on any row to highlight sequence in all motifs. Mouse over the center of the motif blocks to see more information.



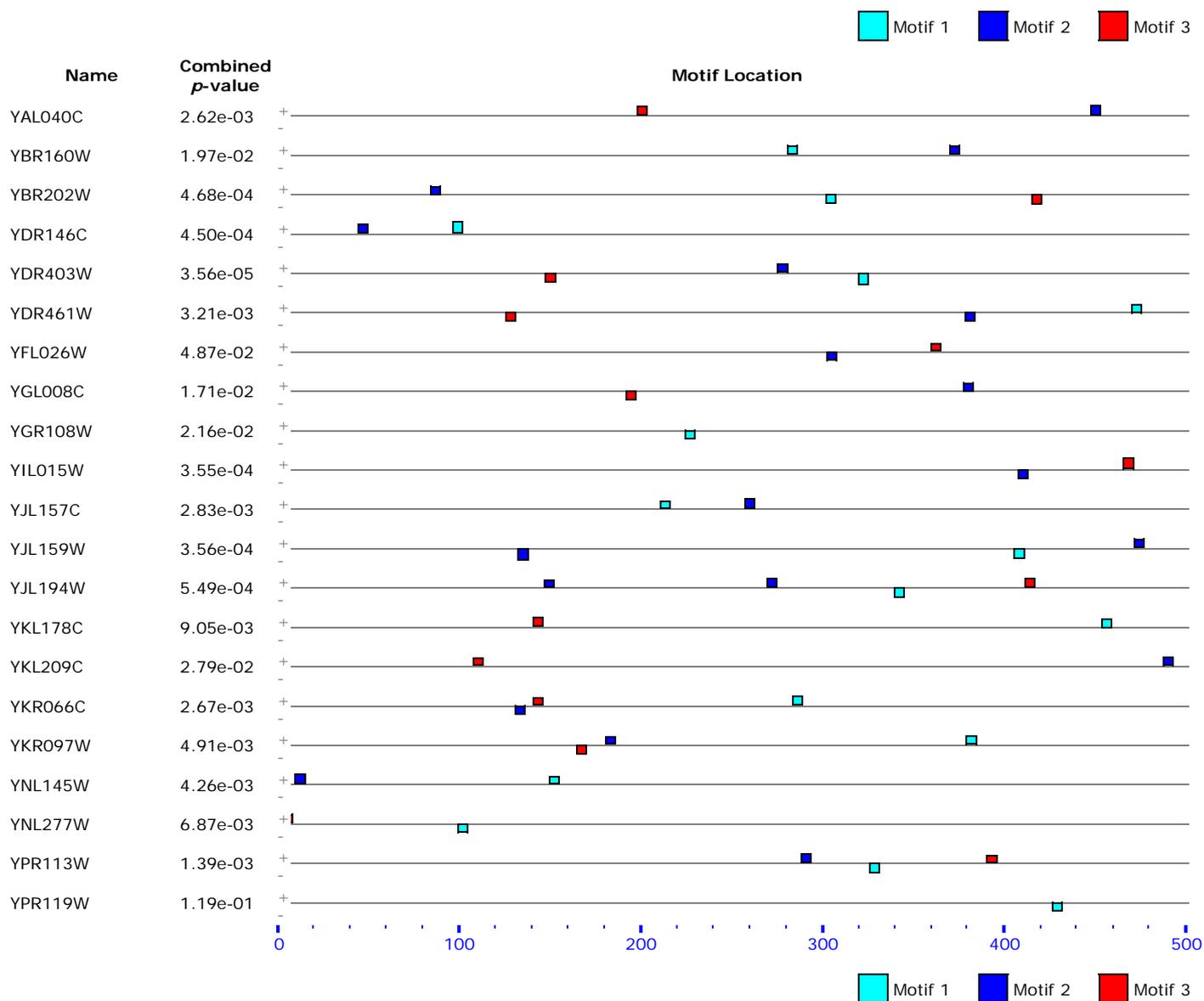
Time 41.5 secs.

ALL MOTIFS[Top](#)**Combined Block Diagrams**

Non-overlapping sites with a p -value better than 0.0001.

The height of the motif "block" is proportional to $-\log(p\text{-value})$, truncated at the height for a motif with a p -value of $1e-10$.

Click on any row to highlight sequence in all motifs. The motif blocks have tool tips with more information.



[Top](#)**MEME version**

4.6.1 (Release date: Mon Mar 21 13:41:45 EST 2011)

Reference

Timothy L. Bailey and Charles Elkan, "Fitting a mixture model by expectation maximization to discover motifs in biopolymers", Proceedings of the Second International Conference on Intelligent Systems for Molecular Biology, pp. 28-36, AAAI Press, Menlo Park, California, 1994.

[show training set...](#)**Command line summary**

```
meme sequences -sf promoters.txt -dna -mod oops -nmotifs 3 -minw 10 -maxw 20 -time 7200 -maxsize 60000 -revcomp -oc . -
```

Letter frequencies in dataset

A: 0.325 C: 0.175 G: 0.175 T: 0.325

Background letter frequencies (from dataset with add-one prior applied):

A: 0.325 C: 0.175 G: 0.175 T: 0.325

Stopping ReasonStopped because nmotifs = 3 reached. Program ran on *compute-0-16.local*.[show model parameters...](#)**EXPLANATION OF MEME RESULTS**[Top](#)**The MEME results consist of**

- The [overview](#) of all discovered motifs.
- Information on each of the [motifs](#) MEME discovered, including:
 1. A [summary table](#) showing the width, number of contributing sites, log likelihood ratio, statistical significance, information content and relative entropy of the motif.
 2. A [sequence LOGO](#).
 3. Downloadable [LOGO files](#) suitable for publication.
 4. A [regular expression](#) describing the motif.
 5. Some [further analysis](#) that can be performed on the motif.
 6. A list of [data formats](#) describing the motif.
 7. The [contributing sites](#) of the motif sorted by p -value and aligned with each other.
 8. The [block diagrams](#) of the contributing sites of the motif within each sequence in the training set.
- A [combined block diagram](#) showing an optimized (non-overlapping) tiling of all of the motifs onto each of the sequences in the training set.
- The [version](#) of MEME and the date it was released.
- The [reference](#) to cite if you use MEME in your research.
- A description of the [sequences](#) you submitted (the "training set") showing the name, "weight" and length of each sequence.
- The [command line summary](#) detailing the parameters with which you ran MEME.
- The reason why MEME [stopped](#) and the name of the CPU on which it ran.
- This [explanation](#) of how to interpret MEME results.

Motifs

For each motif that it discovers in the training set, MEME prints the following information:

Summary Table

This summary table gives the main attributes of the motif.

 E -value

The statistical significance of the motif. MEME usually finds the most statistically significant (low E -value) motifs first. The E -value of a motif is based on its log likelihood ratio, width, sites, the background letter frequencies (given in the [command line summary](#)), and the size of the training set. The E -value is an estimate of the expected number of motifs with the given log likelihood ratio (or higher), and with the same width and site count, that one would find in a similarly sized set of random sequences. (In random sequences each position is independent with letters chosen according to the background letter frequencies.)

Width

The width of the motif. Each motif describes a pattern of a fixed width as no gaps are allowed in MEME motifs.

Sites

The number of sites contributing to the construction of the motif.

Log Likelihood Ratio

The log likelihood ratio of the motif. The log likelihood ratio is the logarithm of the ratio of the probability of the occurrences of the motif given the motif model (likelihood given the motif) versus their probability given the background model (likelihood given the null model). (Normally the background model is a 0-order Markov model using the background letter frequencies, but higher order Markov models may be specified via the **-bfile** option to MEME.)

Information Content

The information content of the motif in bits. It is equal to the sum of the **uncorrected** information content, $R()$, in the columns of the [LOGO](#). This is equal relative entropy of the motif relative to a uniform background frequency model.

Relative Entropy

The relative entropy of the motif, computed in bits and relative to the background letter frequencies given in the [command line summary](#). It is equal to the log-likelihood ratio (llr) divided by the number of contributing sites of the motif times $1/\ln(2)$,

$$re = llr / (\text{sites} * \ln(2)).$$

Sequence LOGO

MEME motifs are represented by position-specific probability matrices that specify the probability of each possible letter appearing at each possible position in an occurrence of the motif. These are displayed as "sequence LOGOS", containing stacks of letters at each position in the

motif. The total height of the stack is the "information content" of that position in the motif in bits. The height of the individual letters in a stack is the probability of the letter at that position multiplied by the total information content of the stack.

Note: The MEME LOGO differs from those produced by the [Weblogo](#) program because a **small-sample correction is NOT applied**. However, MEME LOGOS in PNG and encapsulated postscript (EPS) formats **with small-sample correction (SSC)** are available by clicking on the download button with "SSC" set to "on" under [Download LOGO](#). The MEME LOGOs without small sample correction are similarly available. Error bars are included in the LOGOs with small-sample correction.

Modern web browsers supporting the canvas element and it's text manipulation functions as described in the html 5 standard, can render the sequence LOGOs without needing the images. The browsers which work with this feature are:

- Firefox 3.5 and above
- Safari 4 and above
- Google Chrome 4 and above

Unfortunately Internet Explorer 8 does not support any html 5 features.

The information content of each motif position is computed as described in the paper by Schneider and Stephens, "Sequence Logos: A New Way to Display Consensus Sequences" but **the small-sample correction, $e(n)$, is set to zero for the LOGO displayed in the MEME output**. The corrected information content of position i is given by

$$R(i) \text{ for amino acids} = \log_2(20) - (H(i) + e(n)) \quad (1a)$$

$$R(i) \text{ for nucleic acids} = \log_2(4) - (H(i) + e(n)) \quad (1b)$$

where $H(i)$ is the entropy of position i ,

$$H(i) = - \left(\sum f(a,i) * \log_2[f(a,i)] \right). \quad (2)$$

Here, $f(a,i)$ is the frequency of base or amino acid a at position i , and $e(n)$ is the small-sample correction for an alignment of n letters. The height of letter a in column i is given by

$$\text{height} = f(a,i) * R(i) \quad (3)$$

The approximation for the small-sample correction, $e(n)$, is given by:

$$e(n) = (s-1) / (2 * \ln(2) * n), \quad (4)$$

where s is 4 for nucleotides, 20 for amino acids, and n is the number of sequences in the alignment.

The letters in the logos are colored as follows.

For DNA sequences, the letter categories contain one letter each.

NUCLEIC ACIDS	COLOR
A	RED
C	BLUE
G	ORANGE
T	GREEN

For proteins, the categories are based on the biochemical properties of the various amino acids.

AMINO ACIDS	COLOR	PROPERTIES
A, C, F, I, L, V, W and M	BLUE	Most hydrophobic[Kyte and Doolittle, 1982]
NQST	GREEN	Polar, non-charged, non-aliphatic residues
DE	MAGENTA	Acidic
KR	RED	Positively charged
H	PINK	
G	ORANGE	
P	YELLOW	
Y	TURQUOISE	

J. Kyte and R. Doolittle, 1982. "A Simple Method for Displaying the Hydropathic Character of a Protein", J. Mol Biol. 157, 105-132.

Note: the "text" output format of MEME preserves the historical MEME format where LOGOS are replaced by a simplified probability matrix, a relative entropy plot, and a multi-level consensus sequence.

Download LOGO

Logos can be generated on the fly by the meme webservice and you may specify a number of options to customize them to your needs. The options are:

Orientation

Only valid for nucleotide motifs. Generate the standard view or the reverse complemented view of the motif.

SSC

Use small sample correction and show errorbars on the image. Small sample correction is used by the [Weblogo](#) program.

Format

The format of the generated image. If the image is to be used on the web then png is recommend. If the image is to be published then eps is recommended.

Width

The width of the generated image in centimetres.

Height

The height of the generated image in centimetres.

Regular Expression

This is a regular expression (RE) describing the motif. In each column, all letters with observed frequencies greater than 0.2 are shown; less-frequent letters are not included in the RE. MEME regular expressions are interpreted as follows: single letters match that letter; groups of letters in square brackets match any of the letters in the group. Regular expressions can be used for searching for the motif in sequences (using, for example, [PatMatch](#)) but the search accuracy will usually be better with the PSSM (using, for example [MAST](#).)

Further Analysis

Either as a group or individually the motifs have a number of options for further analysis.

MAST

Finds the best matching positions for a set of motifs in each sequence provided to it, ranked by the combined score of each sequence. For more information about MAST please read the [introduction](#).

FIMO

Finds all matches for a motif. For more information about FIMO please read the [introduction](#).

TOMTOM

Compares a single motif to a database of motifs. For more information about TOMTOM please read the [introduction](#).

GOMO

Identifies possible roles of DNA binding motifs. For more information about GOMO please read the [introduction](#).

BLOCKS

Submit to Blocks Multiple Alignment Processor where you can do several things like create phylogeny trees and search the blocks against a database of other blocks (protein only). For more information about BLOCKS Multiple Alignment Processor please visit the [website](#).

Data Formats

The extracted data is available in the following formats.

PSPM Format

The motif itself is a position-specific probability matrix giving, for each position in the pattern, the observed frequency ("probability") of each possible letter. The probability matrix is printed "sideways"--columns correspond to the letters in the alphabet (in the same order as shown in the simplified motif) and rows corresponding to the positions of the motif, position one first. The motif is preceded by a line starting with "letter-probability matrix:" and containing the length of the alphabet, width of the motif, number of occurrences of the motif, and the *E*-value of the motif.

Note: Earlier versions of MEME gave the posterior probabilities--the probability after applying a prior on letter frequencies--rather than the observed frequencies. These versions of MEME also gave the number of *possible* positions for the motif rather than the actual number of occurrences. The output from these earlier versions of MEME can be distinguished by "n=" rather than "nsites=" in the line preceding the matrix.

PSSM Format

The position-specific scoring matrix corresponding to the motif is printed for use by database search programs such as MAST. This matrix is a log-odds matrix calculated by taking 100 times the log (base 2) of the ratio p/f at each position in the motif where p is the probability of a particular letter at that position in the motif, and f is the background frequency of the letter (given in the [command line summary](#) section.) This is the same matrix that is used above in computing the p -values of the occurrences of the motif in the [Sites](#) and [Block Diagrams](#) sections. The scoring matrix is printed "sideways"--columns correspond to the letters in the alphabet (in the same order as shown in the simplified motif) and rows corresponding to the positions of the motif, position one first. The scoring matrix is preceded by a line starting with "log-odds matrix:" and containing the length of the alphabet, width of the motif, number of characters in the training set, the scoring threshold (obsolete) and the motif *E*-value.

Note: The probability p used to compute the PSSM is *not* exactly the same as the corresponding value in the Position Specific Probability Matrix (PSPM). The values of p used to compute the PSSM take into account the motif prior, whereas the values in the PSPM are just the *observed* frequencies of letters in the motif sites.

BLOCKS Format

For use with [BLOCKS tools](#).

FASTA Format

The FASTA format as described [here](#).

Raw Format

Just the sites of the sequences that contributed to the motif. One site per line.

Sites

MEME displays the occurrences (sites) of the motif in the training set. The sites are shown aligned with each other, and the ten sequence positions preceding and following each site are also shown. Each site is identified by the name of the sequence where it occurs, the strand (if both strands of DNA sequences are being used), and the position in the sequence where the site begins. When the DNA strand is specified, '+' means the sequence in the training set, and '-' means the reverse complement of the training set sequence. (For '-' strands, the 'start' position is actually the position on the **positive** strand where the site ends.) The sites are **listed in order of increasing statistical significance** (p -value). The p -value of a site is computed from the the match score of the site with the [position specific scoring matrix](#) for the motif. The p -value gives the probability of a random string (generated from the background letter frequencies) having the same match score or higher. (This is referred to as the **position p -value** by the MAST algorithm.)

Block Diagrams

The occurrences of the motif in the training set sequences are shown as coloured blocks on a line. One diagram is printed for each sequence showing all the sites contributing to that motif in that sequence. The sequences are **listed in the same order as in the input** to make it easier to compare multiple block diagrams. Additionally the best p -value for the sequence/motif combination is listed though this may not be in ascending order as with the sites. The p -value of an occurrence is the probability of a single random subsequence the length of the motif, generated according to the 0-order background model, having a score at least as high as the score of the occurrence. When the DNA strand is specified '+', it means the motif appears from left to right on the sequence, and '-' means the motif appears from right to left on the complementary strand. A sequence position scale is shown at the end of each table of block diagrams.

Combined Block Diagrams

The motif occurrences shown in the motif summary **may not be exactly the same as those reported in each motif section** because only motifs with a position p -value of 0.0001 that don't overlap other, more significant motif occurrences are shown.

See the documentation for [MAST output](#) for the definition of position and combined p -values.