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ORIGINAL ARTICLE

A high storage density strategy for digital information based on synthetic DNA

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Abstract

DNA has been recognized as a promising natural medium for information storage. The expensive DNA synthesis process makes it an important challenge to utilize DNA nucleotides optimally and increase the storage density. Thus, a novel scheme is proposed for the storage of digital information in synthetic DNA with high storage density and perfect error correction capability. The proposed strategy introduces quaternary Huffman coding to compress the binary stream of an original file before it is converted into a DNA sequence. The proposed quaternary Huffman coding is based on the statistical properties of the source and can gain a very high compression ratio for files with a non-uniform probability distribution of the source. Consequently, the amount of information that each base can store increases, and the storage density is also improved. In addition, quaternary Hamming code with low redundancy is proposed to correct errors occurring in the synthesis and sequencing. We have successfully converted a total of 5.2 KB of files into 3934 bits in DNA bases. The results of biological experiment indicate that the storage density of the proposed scheme is higher than that of state-of-the-art schemes.

Keywords DNA information storage · Quaternary Huffman code · Synthetic DNA · Storage density

Introduction

Global data are increasing explosively with the rapid development of the digital society, which is raising great challenges for information storage. Current technologies mainly rely on optical and semiconductor media to store data (Goda and Kitsuregawa 2012), which cannot satisfy current practical needs (Panda et al. 2018). Moreover, the production of monocrystalline silicon leads to serious environmental pollution and energy consumption. Therefore, there is an urgent need for an alternative storage medium. DNA has high information storage density and has attracted extensive attention. The binary storage capacity of a DNA molecule is about 4.2×10^{21} bits per gram, which is 420 billion times that of traditional storage media. DNA is also one of the most stable biomolecules, and thus can preserve information over extremely long periods.

The idea of storing information in DNA nucleotides has been proposed for decades, and the substantial progress achieved has been promising (Panda et al. 2018; Yazdi et al. 2015; Shipman et al. 2017; Akram et al. 2018). Joe Davis and a collaborator from MIT precisely encoded icons into DNA, which they called Microvenus (Davis 1996). Bancroft et al. (2001) successfully stored encoded words into DNA segments and utilized the four bases (A, T, C, and G) to encrypt information. Church and Kosuri made a remarkable breakthrough when they encoded images, an HTML draft, and a Java script (5.27 MB of files in total) into DNA molecules with higher efficiency and lower cost using the next generation of DNA synthesis and sequencing technology (Church and Kosuri 2012). A theoretical storage density of 1 bit/nt was achieved with one binary digit encoded per base. Goldman and his team exploited Huffman code to convert the binary digits of information into base-3 digits, which were then mapped to DNA bases according to the rotating code (Goldman et al. 2013). About 739 KB of data were stored in DNA, and the storage density was 0.33 bits/nt. Grass et al. (2015) proposed a special error correction scheme to cope with the errors in synthesis and sequencing.

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Bornholt et al. (2016) achieved a storage density of 0.88 bits/nt by taking the exclusive-or of two strands to form a third one. Blawat et al. (2016) developed a robust and efficient forward error correction scheme, which can deal with all types of errors in DNA synthesis, amplification, and sequencing. Notably, Erlich and Zielinski creatively developed a storage strategy called DNA Fountain, which applied fountain code to DNA information storage (Erlich and Zielinski 2017). They made one base corresponding to two binary digits and improved the coding potential and reliability of DNA nucleotides.

A high storage density can effectively reduce the cost and time of DNA synthesis and sequencing. Nevertheless, previous methods mainly tried to convert binary streams directly into DNA sequences without considering the characteristics of the original input data. Thus, the information storage densities were not greater than 2 bits/nt. Recently, Dimopoulou et al. (2019) applied a coding algorithm to the quantized wavelet coefficients of an image and conducted simulations on a Lena image with a size of 512 by 512 pixels . They achieved a nearly lossless compression and a coding potential of 2.14 bits/nt. They achieved a higher compression ratio using discrete wavelet decomposition (DWT) to take advantage of the spatial redundancies of the image, but they did not consider the statistical distribution of the input data.

This work presents a novel strategy for information storage in DNA that takes advantage of non-uniform data distributions to compress data through entropy-based coding, which results in higher coding density. We propose compressing the input binary streams with fully lossless quaternary Huffman coding before converting them into DNA bases. The quaternary Huffman coding is a type of entropy coding that can take full advantage of the statistical redundancy of the source and reduce the number of bits required to represent data. The compression allows us to make full use of the DNA bases and improve the storage density for files with a non-uniform probability distribution of the source, such as text, image, and audio. We also introduce an improved quaternary Hamming code based on the actual requirements for errors arising in the synthesis or sequencing process. Experimental results show that the improved quaternary Hamming code can robustly correct errors with low redundancy. Lastly, we design the carrier DNA strands while considering the difficulties in synthesizing long DNA sequences and the objective requirement of biological experiment. The results of biological experiment show that the original input files are synthesized and recovered perfectly by sequencing and decoding.

Methods

The framework of the proposed DNA information storage strategy

Similar to a communication system, the proposed DNA information storage framework includes DNA encoding, channel transmission, and DNA decoding, as shown in Fig. 1.

DNA encoding realizes the conversion from a target binary stream to carrier DNA strands, which can be further divided into source DNA encoding and channel DNA encoding. The encoding process is illustrated in Fig. 2. The source DNA encoding constructs the quaternary information stream with quaternary Huffman coding to compress the input binary stream. In channel DNA encoding, the quaternary information stream is segmented into several strings with a certain length, and then indexing and quaternary Hamming code are sequentially attached to these strings to obtain the quaternary strands. Next, the quaternary digits are mapped to DNA bases (0–A, 1–T, 2–C, and 3–G). The carrier DNA strands are synthesized, stored, and later retrieved.

Channel transmission corresponds to several biological processes based on DNA molecules, including synthesis, amplification, and sequencing. We use polymerase chain reaction (PCR) to amplify the strands and sequence the DNA library to recover the original information. All of these procedures are important for DNA information storage, but several errors may be introduced (Hughes and Ellington 2017; Mardis 2017).

DNA decoding is just the reverse of encoding, and completing the original information restoration. Similar to DNA encoding, DNA decoding contains channel DNA decoding and source DNA decoding. The reads acquired from DNA sequencing are scanned to obtain the carrier DNA strands. During channel DNA decoding, the quaternary strands are obtained according to the mapping rule between four bases and the quaternary digits. Strings with errors are corrected through the quaternary Hamming code, and then all fragments are connected to the full-length quaternary information stream based on the order inferred by the indexing bases. The source DNA decoding retrieves the binary stream by quaternary Huffman decoding.

Quaternary Huffman coding

As lossless coding methods with variable length, Huffman coding can produce the shortest codes as it represents more frequently appeared symbols by fewer bits. Huffman coding has a good compression capability and is the optimal method for multiple independent information sources.

DNA is a natural quaternary storage model with four bases: A, T, C, and G. Therefore, a coding method that can generate multi-ary code is required to make full use of the four bases. However, Huffman coding is mostly used for binary coding, which does not directly satisfy this requirement.

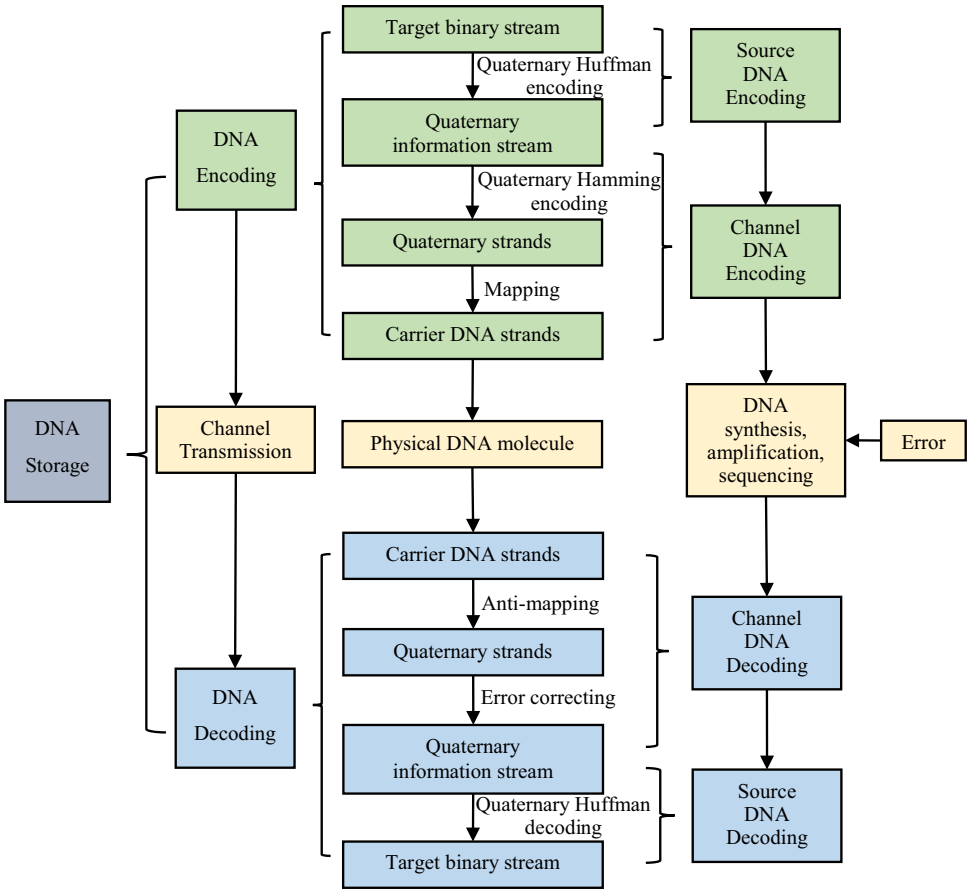


Fig. 1 The framework of the proposed DNA information storage strategy

There are two works on Huffman code for DNA information storage to the best of our knowledge. Ailenberg used the principles of the Huffman code to define DNA codons for unambiguous information coding (Ailenberg and Rotstein 2009). They did not directly use the Huffman code to compress the original file. The second work adopted the Huffman code to convert the binary digits of information into base-3 digits. However, due to the not full consideration for the four bases of DNA, the storage density achieved by this ternary Huffman coding was very low, with 0.33 bits/nt (Goldman et al. 2013).

Considering the natural characteristic of DNA and the shortcomings of the above works, the proposed method keeps the tree construction idea of Huffman coding, while the output code revised to quaternary, and the output quaternary digits are mapped to the four bases of DNA. As a result, DNA nucleotides can be taken full advantages of, and the information storage density increases.

According to the Huffman coding process, it is necessary to build a complete Huffman tree to make the average length of the output codes the shortest. For D-variants Huffman coding, D of $n+1$ order leaves is divided from one n order node, and the number of increased leaf nodes by one split is $D-1$. Therefore, the total number of leaves is:

$$s = D + (D-1)m, \tag{1}$$

where m is a non-negative integer that represents the number of times the node splits from the first order of D-ary tree. That is, the total number of symbols l in a system with p bases is:

$$l = p + (p-1)q, \tag{2}$$

where q represents the number of combinations during the coding process. If this equivalence cannot be satisfied, t additional symbols with a probability of zero should be added to obtain:

$$l + t = p + (p-1)q. \tag{3}$$

An example of quaternary Huffman coding with eight source symbols is shown in Fig. 3. The original number of source symbols l is eight, and the number of bases p is four. Two (i.e., t) additional symbols with a probability of zero are added since there is no positive integer q that can satisfy Eq. (2), and thus the value of q is two.

The binary stream converted from the source file is divided into segments with length i called scanning bits. A larger value of i can lead to more efficient coding. However, the value of i cannot be increased indefinitely due to its high influence on the complexity of the algorithm. The upper bound of i (i.e., $i_{\max}$) in this work is set to 52 to guarantee reasonable algorithm complexity. The process of quaternary Huffman coding is shown in Fig. 4, and the detailed steps are listed in Algorithm 1.

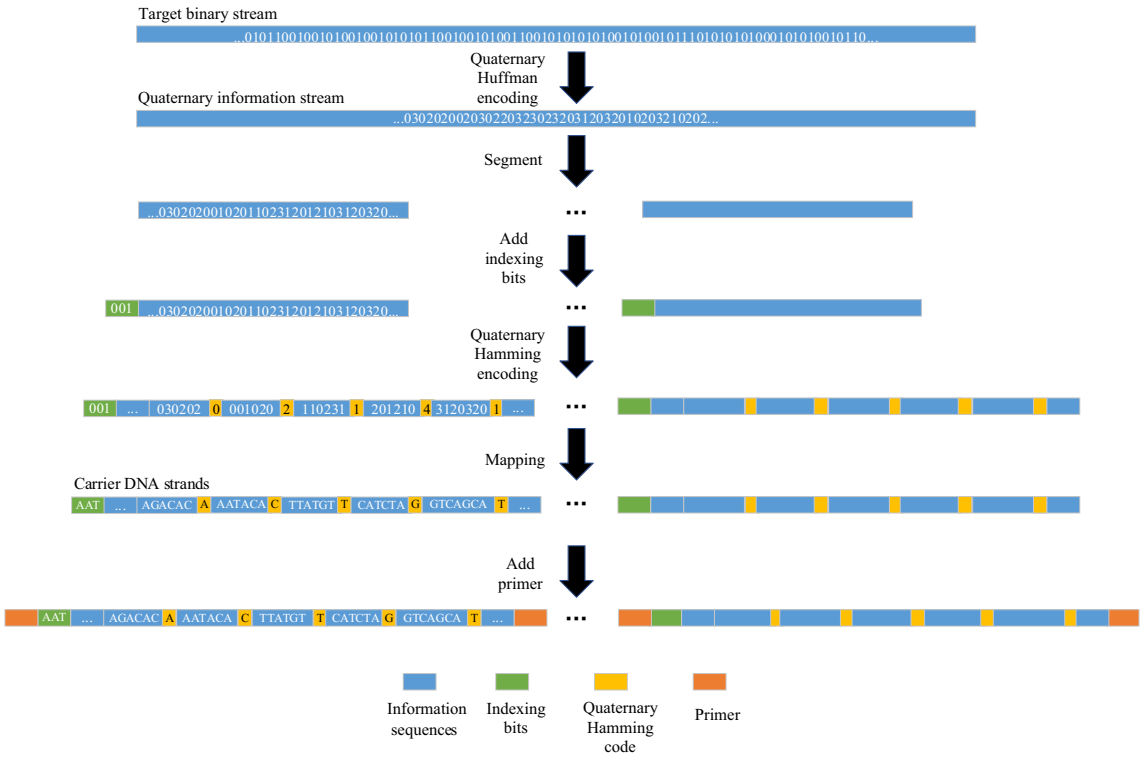


Fig. 2 The proposed DNA encoding process

Fig. 3 An example of quaternary Huffman coding with eight source symbols

Source symbols	Probability	Coding process			Code	Code length
a_1	0.30		0.30	0.30 0	0	1
a_2	0.29		0.29	0.29 1	1	1
a_3	0.18		0.18	0.23 2 → 1	2	1
a_4	0.07		0.07 0	0.18 3	30	2
a_5	0.05		0.06 1		22	2
a_6	0.05		0.05 2		23	2
a_7	0.05	0	0.05 3		210	3
a_8	0.01	1			211	3
a_9	0	2			212	3
a_{10}	0	3			213	3

Algorithm 1 The process of quaternary Huffman coding

1. Convert target storage file to binary stream.
2. Set $i = 4$ and $i_{\max} = 52$.
3. Scan the stream thoroughly, take i bits as a source symbol, and count the number and probabilities of symbols.
4. Encode the symbols with quaternary Huffman code, and calculate the average code length m_i and coding density d_i ($d_i = \frac{i}{m_i}$).
5. Check whether i is less than $N+1$. If yes, return to step 3; if not, go to the next step.

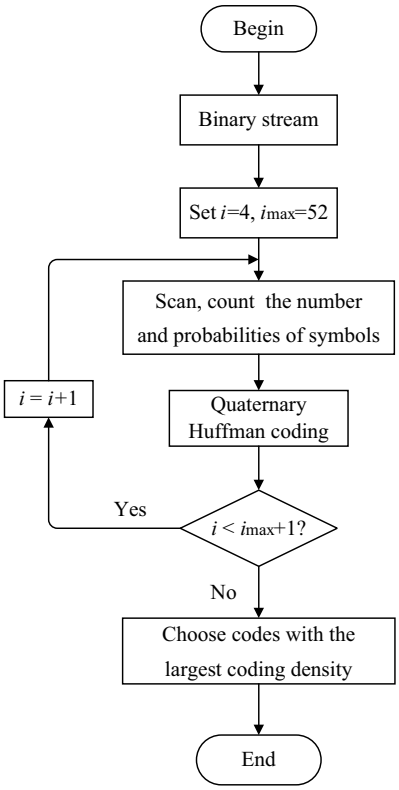


Fig. 4 The process of quaternary Huffman coding

Quaternary Hamming code

Hamming code is one of the most widely used channel codes. The relevant theories and techniques have matured after years of research and applications since the concept was put forward in 1950. It is widely used in communication, data storage (Borchert et al. 2013), image encoding, and digital circuit (Rajaei et al. 2017). Hamming code is the most efficient single error correcting complete block code and is an optimal alternative with low redundancy when the channel environment is appropriate (Babu et al. 2017). Therefore, we use Hamming code to correct errors while considering the situation of specific errors arising in DNA synthesis and sequencing. Although Hamming code was chosen in this study, other error correction codes such as RS code can also be compatible with the proposed quaternary Huffman coding strategy.

The information is divided into several groups based on a certain rule when correcting errors. Parity check bits are arranged in each group, and then tests are done to determine the location of errors. The codes with errors can be corrected by reversing the wrong bits.

The Hamming code is generally represented by (n, k), which satisfies the inequality function as follows:

$$2^r - 1 \geq n = r + k, \tag{4}$$

where n is the number of transmission bits, k is the number of information bits, and $r = n - k$ is the number of check bits.

According to Eq. (4), the relationship between k and r can be derived as shown in Table 1.

However, Hamming code cannot be directly used in our scheme because parity check is not applicable to quaternary code. Therefore, we make modifications to define a new value of the check bits in this study. Taking quaternary Hamming (7, 4) code as an example, we set the check bits matrix to:

$$p = [4\,4\,4]^T - Qd, \tag{5}$$

where Q is a matrix indicating the relationship between check bits and information bits, and d is a matrix of the information bits.

If errors occur, the location of errors is determined first. Non-zero values of the syndrome are subtracted from the error bits in quaternary (allowing borrowing) to obtain the correct bits. That is, error correction is completed by the quaternary Hamming code.

Results and discussion

We validate the performance of the proposed DNA information storage framework by performing three sets of experiments. First, coding experiments are conducted with text, image, audio, and compressed file. Second, experiments are performed with different lengths of quaternary Hamming code to compare their correction capabilities. Third, a biological experiment based on synthesis DNA is carried out.

Coding performance of quaternary Huffman coding

We perform coding experiments to assess the coding performance of the proposed quaternary Huffman code, and introduce the compression ratio as a measurement. The experimental results are given for the case of even scanning bits since results for odd bits are relatively poor. The coding environment comprises Windows 10 64 bit as the operating system, an i7-7500u processor, 8 GB of running memory, and MATLAB R2017a.

Table 1 The relationship between the number of information bits and check bits

The number of information bit (bits)	1	2–4	5–11	12–26	27–57	58–120	…
The number of check bit (bits)	2	3	4	5	6	7	…

Table 2 Input data for encoding, size, and type

Size	Type	Name
6.24 KB	Text	medicalcase.txt
26.6 KB	Text	writtenjudgment.txt
796 B	Text	SongofMulan.txt
392 B	Text	LittleStar.txt
1.37 MB	Text	PilgrimagetotheWest.txt
4.02 KB	Monochrome image	circbw.tif
43.5 KB	Gray image	rice.png
94.7 KB	Color picture	kids.tif
44 KB	Audio	sp01.wav
67.7 KB	Zipped file	file.rar
69.2 KB	Zipped file	file.zip

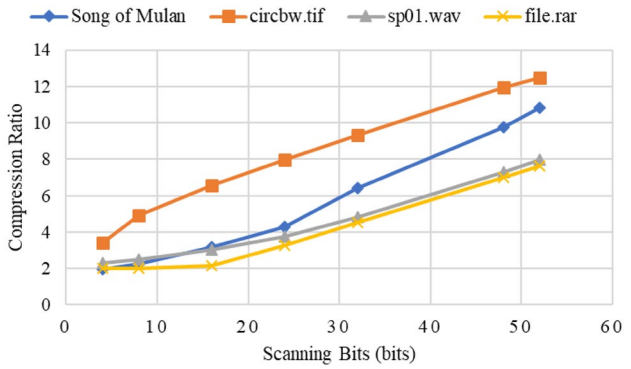


Fig. 5 Compression ratios of *Song of Mulan*, circbw.tif, sp01.wav, and file.rar with different scanning bits

To validate the generality of the proposed quaternary Huffman coding, different formats of files are provided as the input data, including texts, images, compressed files, etc., as shown in Table 2. The formats of the compressed files are .rar and .zip, which are used to package the first three text files and an image file called kids.tif.

Figure 5 shows the compression ratios of *Song of Mulan*, circbw.tif, sp01.wav, and file.rar with different scanning bits. The highest compression ratios for these files are 10.81, 12.48, 7.9, and 7.62, respectively. Thus, our encoding scheme achieves high performance on text, image, audio, and compressed file. In addition, the compression ratio increases with the number of scanning bits. This occurs because the types of source symbols increase and the probabilities of each symbols become more diverse as the scanning bits increase, leading to better performance of the Huffman coding.

Figure 6 shows the relationship between the scanning bits and coding time. There are very different patterns for the four files. The coding time is proportionally related to the number of source symbols since the coding object is the probability of source symbols. Theoretically, the number of source symbols is 2^i when the scanning bits are i. However, there are usually not that many symbols in each file in practice, which will lead to reduced coding time. The number of source symbols of each type of file shows different trends when the scanning bits increase due to the files' unique binary stream characteristics. Consequently, the patterns of the coding time differ for different types of files.

In particular, for file.rar, the number of source symbols is 2^i before i is 16, so the coding time increases steadily. But after that, the number of source symbols decreases, and so does the coding time.

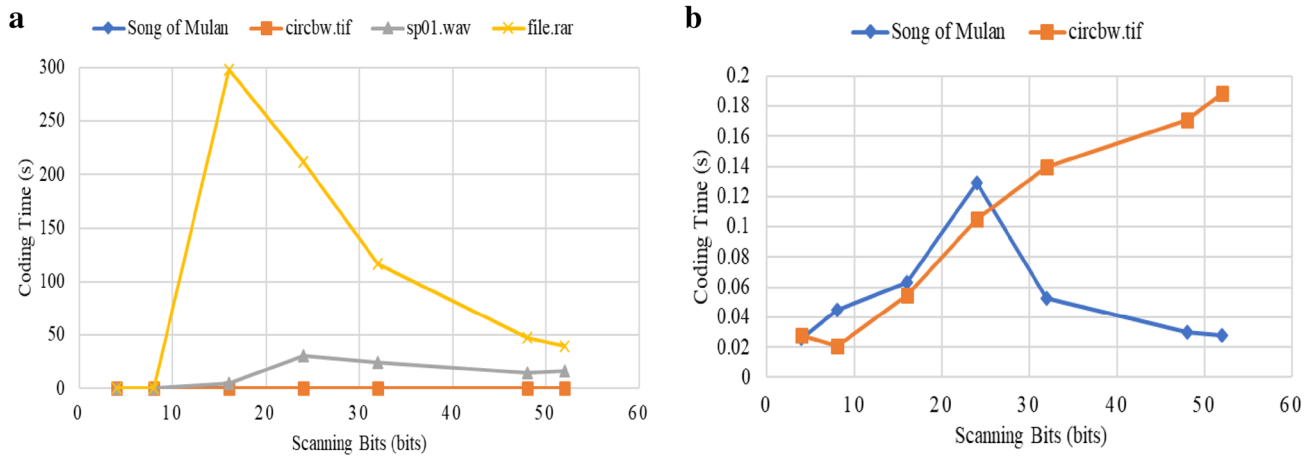


Fig. 6 **a** Coding time of *Song of Mulan*, circbw.tif, sp01.wav, and file.rar with different scanning bits. **b** Coding time of *Song of Mulan* and circbw.tif with different scanning bits

Error correction performance of quaternary Hamming code

The error correction capability is compared between different quaternary Hamming codes: Hamming (15, 11) code, Hamming (31, 26) code, and Hamming (63, 57) code. The codes are applied to the same file, circbw.tif. Random errors with probabilities of 1/10,000, 1/5000, 1/2500, and 1/1000 are introduced to simulate different situations of practical errors. The corrected DNA sequences are compared with the actual one to evaluate the number of bits unable to be rectified and corresponding frequencies. Trials with the same error probability are all carried out 100 times, and the average values are presented as the results in Table 3.

As shown in Table 3, the redundancy of Hamming code gradually decreases as the number of bits increases. The error rate in biological experiments is generally less than 1/10,000 if the operation is rigorous and advanced DNA synthesis and sequencing techniques are used. Therefore, all three codes provide reasonably good error correction performance. However, longer Hamming code bits result in, a greater probability of errors occurring since errors in DNA sequences are random. Consequently, the error frequency after correcting increases correspondingly.

We eventually select quaternary Hamming (31, 26) code after considering the trade-off between redundancy and error correction performance of the Hamming code and the specific errors arising in DNA synthesis and sequencing. The quaternary Hamming (31, 26) code performs well in error correction without introducing too much redundancy. Therefore, the channel bandwidth is relatively narrow in this case.

Table 3 Experimental results of quaternary Hamming code

Code	Transmission redundancy (%)	Probability of errors	Error frequency after correcting
Hamming (15, 11)	26.67	1/10,000	0
		1/5000	0
		1/2500	0
		1/1000	0.013‰
Hamming (31, 26)	16.13	1/10,000	0
		1/5000	0.003‰
		1/2500	0.002‰
		1/1000	0.012‰
Hamming (63, 57)	9.52	1/10,000	0
		1/5000	0.003‰
		1/2500	0.002‰
		1/1000	0.037‰

Real oligonucleotide synthesis and sequencing

We carry out a biological experiment to verify the feasibility of the proposed scheme. Files of *Song of Mulan*, *Twinkle Twinkle Little Star*, and circbw.tif (Fig. 7), are chosen as input data for the experiment (5.2 KB in total). Specifically, the length of carrier DNA strands is 465 nt due to difficulties in synthesizing long DNA sequences. The information stream encoded by quaternary Huffman code with 32 scanning bits is segmented into eight fragments of 380 bits (although the last one can be less than 380 bits). Next, 10 bits for indexing and 75 bits of quaternary Hamming (31, 26) code are added to each fragment in order. The obtained quaternary fragments are converted into carrier DNA strands, and two 25 nt primers are attached to both ends of them during DNA synthesis. Consequently, a total of 3934 DNA bases are obtained.

The biological experiment includes three steps: synthesis of the carrier DNA strands, PCR amplification and sequencing of the short strands, and the recovery of information by decoding DNA strings. The carrier DNA strands in the stored pool (Fig. 8a) are amplified using PCR. Primers are first designed and amplified, and then target sequences could be obtained by colony PCR. After the preparation, the amplification results are detected by enzyme identification. The electrophoretograms of the enzyme samples show that the acquired sequences are consistent with the expected one (Fig. 8b, c). We use Sanger method to sequence DNA library, and eight carrier DNA strands are acquired after reading a group of backup sequences. The decoder corrects errors based on quaternary Hamming (31, 26) code and then retrieves the original information through quaternary Huffman decoding.

Table 4 shows the experimental results of comparing the previous schemes for information storage in DNA and the proposed method. A more intuitive comparison of the storage density is shown in Fig. 9. The theoretical storage density and the actual density of the proposed scheme are both significantly greater than those of the other methods. The theoretical storage density is the information content per base without considering indexing, error correction bits, and primers; while, the actual storage density is the information content per base in consideration these conditions. Notably, our storage density does not include video files (Table 4). The quaternary Huffman coding is less effective for video files. This is because arithmetic coding that makes full use of the statistical properties of the source, such as CABAC, has already been used when obtaining the binary video streams, which makes the advantages of entropy-based coding less obvious. Error correction represents the presence of error correction code to deal with synthesis and sequencing errors. Full recovery denotes whether all information is restored without any error. Random access refers to whether the

Fig. 7 Input data for the biological experiment: **a** *Song of Mulan*, **b** *Twinkle Twinkle Little Star*, and **c** circbw.tif

a

唧唧复唧唧，木兰当户织。不闻机杼声，惟闻女叹息。
问女何所思，问女何所忆。女亦无所思，女亦无所忆。昨夜见军帖，可汗大点兵，军书十二卷，卷卷有爷名。阿爷无大儿，木兰无长兄，愿为市鞍马，从此替爷征。
东市买骏马，西市买鞍鞯，南市买辔头，北市买长鞭。旦辞爷娘去，暮宿黄河边，不闻爷娘唤女声，但闻黄河流水鸣溅溅。旦辞黄河去，暮至黑山头，不闻爷娘唤女声，但闻燕山胡骑鸣啾啾。
万里赴戎机，关山度若飞。朔气传金柝，寒光照铁衣。将军百战死，壮士十年归。
归来见天子，天子坐明堂。策勋十二转，赏赐百千强。可汗问所欲，木兰不用尚书郎，愿驰千里足，送儿还故乡。
爷娘闻女来，出郭相扶将；阿姊闻妹来，当户理红妆；小弟闻姊来，磨刀霍霍向猪羊。
开我东阁门，坐我西阁床，脱我战时袍，著我旧时裳。当窗理云鬓，对镜帖花黄。出门看火伴，火伴皆惊忙：同行十二年，不知木兰是女郎。
雄兔脚扑朔，雌兔眼迷离；双兔傍地走，安能辨我是雄雌？

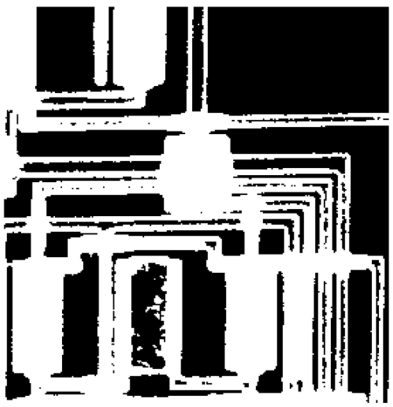
b

Twinkle, twinkle, little star,
How we wonder what you are.
Up above the world so high,
Like a diamond in the sky.

When the glorious sun has set,
And the grass with dew is wet,
Then you show your little light,
Twinkle, twinkle, all the night.

When the golden sun doth rise,
Fills with shining light the skies,
Then you fade away from sight,
Shine no more 'till comes the night

c



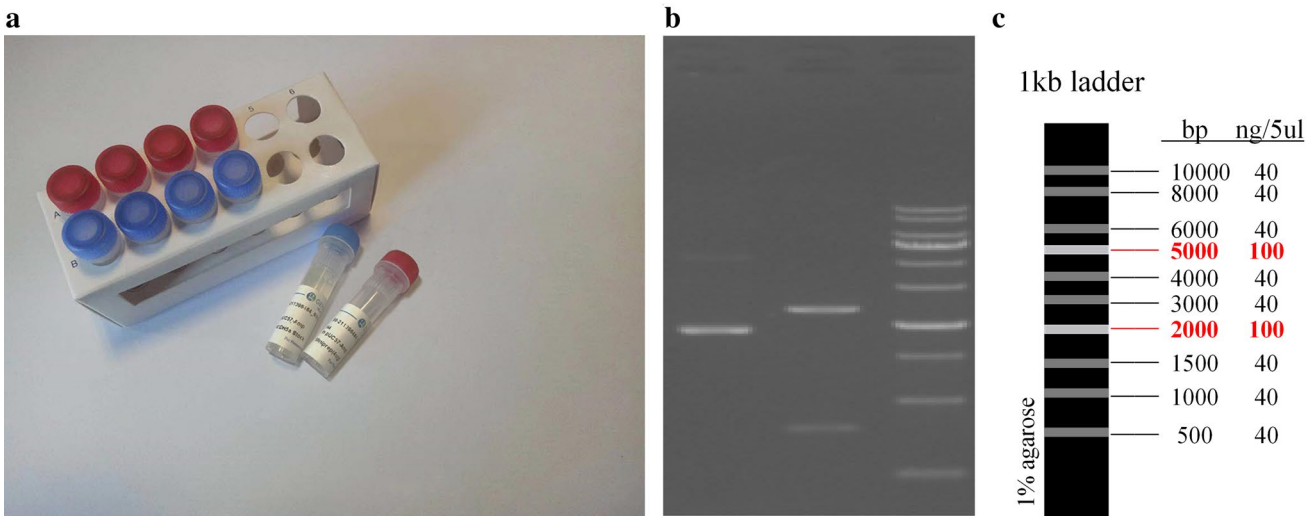


Fig. 8 Biological experiment: **a** DNA pool, **b** the electrophoretogram of enzyme samples, and **c** marker

scheme supports the writing and reading of specific content. Redundancy represents the excess oligonucleotides that do not store original information. Cost indicates the amount of money required to store 1 MB of information with the assumption that the price of DNA synthesis is 1.5 *yuan* per base.

Conclusions

This study proposes a novel DNA information storage scheme that can effectively improve the storage density and correct errors with low redundancy. The digits encoded per base dramatically increase using quaternary Huffman code to compress the input binary streams for files with

Table 4 Comparison of experimental results of different storage schemes

Parameter	Input data (MB)	Theoretical storage density (bits/nt)	Actual storage density (bits/nt)	Error correction	Full recovery	Random access	Redundancy (%)	Cost (*yuan*/bit)
Church and Kosuri (2012)	0.65	1	0.83	No	No	No	17.00	1.81
Goldman et al. (2013)	0.63	1.58	0.33	Yes	No	No	79.11	4.55
Grass et al. (2015)	0.08	1.78	1.14	Yes	Yes	No	35.96	1.32
Bornholt et al. (2016)	0.15	1.58	0.88	No	No	Yes	44.30	1.70
Blawat et al. (2016)	22	1.6	0.92	Yes	Yes	No	42.50	1.63
Erlich and Zielinski (2017)	2.11	1.98	1.57	Yes	Yes	No	20.71	0.96
Dimopoulou et al. (2019)	0.26	2.14	1.71	Yes	Yes	No	19.36	–
Proposed method	0.005	13.68	10.83	Yes	Yes	No	20.00	0.27

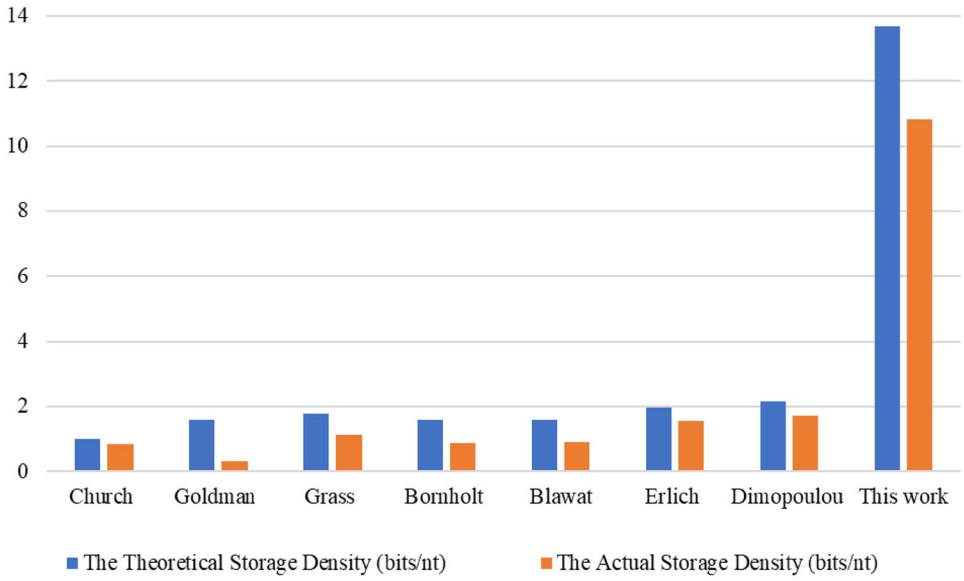


Fig. 9 Theoretical and actual storage densities of previous storage schemes and the proposed scheme

a non-uniform probability distribution of the source. The challenges of expensive DNA synthesis and low utilization of DNA molecules are addressed. The Hamming code is improved to meet the needs of quaternary sequence error correction and can correct errors occurring in the synthesis and sequencing with low redundancy. The biological experiment shows that texts and images stored in synthetic DNA molecules can be successfully recovered through DNA sequencing and decoding. The actual storage density obtained in the biological experiment is 10.83 bits/nt, which is better than that of the state-of-the-art schemes. Nevertheless, it should be noted that although the information storage density has been greatly improved in our scheme, it is not applicable to files with evenly probability distributed source, such as video. This issue shall be addressed in future work. In addition, the proposed scheme does not support random access. Even if only a part of the information is requested, all information must be sequenced. Further studies are required to enable random access of the information.

Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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