Reports

Normalization of genomic DNA using duplex-specific nuclease

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An application of duplex-specific nuclease (DSN) normalization technology to whole-genome shotgun sequencing of genomes with a large proportion of repetitive DNA is described. The method uses a thermostable DSN from the Kamchatka crab that specifically hydrolyzes dsDNA. In model experiments on human genomic DNA, we demonstrated that DSN normalization of double-stranded DNA formed during C_0t analysis is effective against abundant repetitive sequences with high sequence identity, while retaining highly divergent repeats and coding regions at baseline levels. Thus, DSN normalization applied to C_0t analysis can be used to eliminate evolutionarily young repetitive elements from genomic DNA before sequencing, and should prove invaluable in studies of large eukaryotic genomes, such as those of higher plants.

Introduction

Whole-genome sequencing is a powerful approach for obtaining reference sequence information for multiple organisms. The whole-genome shotgun (WGS) strategy has been applied to the study of several genomes. This approach generates enough sequence data to cover the genome several times over and is used for computational assembly of overlapping sequence reads into contigs. Contig assembly is achieved by aligning and orienting reads based on regions of shared identity; redundant reads are then used to produce a consensus sequence (1). However, in the case of large genomes, the presence of repetitive sequences, which constitute a considerable proportion of total genome size, makes WGS sequencing impractical. Effective strategies for eliminating these repetitive DNA sequences can facilitate sequencing analyses of large genomes by limiting redundant sequencing of repetitive elements.

Several approaches have been proposed for enrichment of genomic DNA with single-copy sequences and elimination of repetitive elements. Methylation filtration (MF), development of hypomethylated partial restriction (HMPR) libraries, and methylation-spanning linker libraries (MSLL) have been proposed for the analysis

of plant genomes. These methods are based on the tendency of repetitive sequences to be hypermethylated in higher plants (2–4). Thus, low-methylated, gene-rich fragments can be separated from most repetitive sequences by digestion with restriction enzymes sensitive to the 5'-methylation of cytosine (2,3) or by constructing genomic libraries in *Escherichia coli* strains with a McrBC restriction-modification system that prevents propagation of heavily methylated DNA (4). Unfortunately, these methods are clearly only applicable to a limited number of plant genomes that have the appropriate methylation character.

Another approach, high- C_0t analysis (where " C_0 " is DNA concentration at time zero and " t " is re-association time), is based on DNA renaturation kinetics. Because low-copy DNA sequences renature more slowly than repetitive sequences, a ssDNA fraction of high- C_0t DNA enriched with genes could be obtained under suitable conditions (5–7). In this technique, genomic DNA is sheared, heat-denatured, and slowly re-annealed. Then, the double-stranded (repetitive) DNA is separated from the single-stranded (low-copy) DNA by hydroxyapatite (HAP) chromatography. High- C_0t analysis can be applied to any genome; however, practitioners generally need a firm understanding of DNA reasso-

ciation kinetics and relatively advanced expertise in spectrophotometry.

In this study, we investigated the applicability of duplex-specific nuclease (DSN) normalization technology for eukaryotic genomic DNA. DSN normalization is a simple and effective method previously suggested for cDNA normalization before transcriptome sequencing (8, 9). The method is based on the properties of a DSN isolated from the Kamchatka crab. DSN is thermostable and specific to dsDNA (10).

Like high- C_0t DNA fractionation, DSN normalization is based on hybridization kinetics, but does not involve physical separation of ssDNA and dsDNA fractions. After re-association of denatured DNA, dsDNA comprising repetitive sequences is hydrolyzed by DSN and the ssDNA fraction containing low-copy molecules is amplified by PCR (8,9). DSN normalization has been successfully used for normalization of cDNA from different sources before sequencing of expressed sequence tags (ESTs) using both standard and high-throughput sequencing techniques (11). In addition, DSN normalization has been suggested for use in post-amplification normalization of microbial genomes obtained from individual cells using non-PCR-based, whole-genome amplification (WGA) methods (12).

Materials and methods

DNA preparation

A total of 50 µg human genomic DNA (Clontech, Mountain View, CA, USA) was sheared using a Cole-Parmer CP750 Ultrasonic processor (Vernon Hills, IL, USA; 20 3-s cycles with 10 s between cycles) to a mean length of 500 kb (range 200–750 kb), as determined by agarose gel electrophoresis. The sheared DNA was purified by phenol:chloroform extraction, precipitated with ethanol, and redissolved in 50 µL 20 mM Tris-HCl (pH 8.0). A 1-µL aliquot of sheared DNA solution was treated with T4 DNA polymerase (Fermentas, Burlington, Canada) according to the manufacturer's instructions to create blunt ends, and then purified by phenol:chloroform extraction, precipitated with ethanol, and redissolved in 10 µL 20 mM Tris-HCl (pH 8.0) to a final DNA concentration of 100 ng/µL. The 5' ends of DNA fragments were phosphorylated by incubating 8 µL blunt-ended DNA sample with 1 µL 10× ligase buffer (Fermentas), riboATP (3 mM final concentration), and 0.7 µL T4 polynucleotide kinase (5 U/µL; Fermentas) at 37°C for 15 min, followed by heat inactivation of the enzyme at 60°C for 20 min. Phosphorylated DNA was ligated to the Not1S adapter (5'-GGT CGC GGC CGA GGT-3') by incubating 4 µL phosphorylation reaction mixture with 1 µL 10× ligation buffer (Promega, Madison, WI, USA), 2 µL 10 µM adapter, 2 µL Milli-Q water (Millipore, Billerica, MA, USA), and 1 µL T4 DNA ligase (3 U/µL, Promega) at 14°C overnight. The ligation mixture was then diluted 10× in Milli-Q water, and a 1-µL aliquot of the diluted sample was amplified by PCR using an Encyclo PCR kit (Evrogen,

Moscow, Russia) and Not1S primer in a total reaction volume of 100 µL, as described by the kit manufacturer. After preheating at 72°C for 2 min, 14 PCR cycles were performed on an MJ Research PTC-200 DNA Thermal Cycler (MJ Research, Inc., Waltham, MA, USA); each cycle consisted of 95°C for 7 s, 62°C for 20 s, and 72°C for 1 min. PCR products were purified using a PCR purification kit (Qiagen, Valencia, CA, USA), precipitated with ethanol, and diluted in Milli-Q water to a final DNA concentration of 75 ng/µL.

DNA normalization

A two-microliter aliquot of DNA solution containing ~250 ng DNA was mixed with 1 µL 4× hybridization buffer (200 mM HEPES pH 7.5, 2 M NaCl, 0.8 mM EDTA), and 1 µL human Cot-1 DNA (1 µg/µL; Invitrogen, Carlsbad, CA, USA). For normalizations performed without the Cot-1 fraction, 1 µL Milli-Q water was added in place of the Cot-1 fraction. Reaction mixtures were overlaid with mineral oil, denatured at 98°C for 3 min, and allowed to renature at 68°C for 5 h (C₀t ~ 50). After incubation, 5 µL 2× DSN buffer (100 mM Tris-HCl pH 8.0, 10 mM MgCl₂, 2 mM DTT), preheated to 70°C, was added to the reaction mixture. Next, 1 µL DSN solution (1 U/µL) was added to the reaction, and incubation was continued for 20 min at 65°C. DSN was then inactivated by addition of 10 µL 5 mM EDTA and diluted in 20 µL Milli-Q water.

Amplification of normalized DNA before sequencing

The normalized ssDNA fraction remaining after DSN treatment (5-µL aliquots) was amplified in five reaction tubes by PCR using an Encyclo PCR kit and Not1S primers in a total reaction volume of 50

µL. Thermocycling conditions used were 18 cycles of 95°C for 7 s, 62°C for 20 s, and 72°C for 1 min. PCR products were purified using a PCR purification kit (Qiagen), precipitated with ethanol, and diluted in Milli-Q water to a final DNA concentration of 50 ng/µL.

DNA library construction for conventional and automated sequencing

For DNA plasmid library construction, fresh amplified normalized and non-normalized DNA (~200 ng each) was cloned into the pGEM-T-Easy vector (Promega) as described by the manufacturer, and transformed into *E. coli* (XL-1 Blue strain) using electroporation with a Bio-Rad Micropulser (Hercules, CA, USA). From each library, 300 randomly selected white clones were used for plasmid purification and conventional sequencing.

For automated sequencing, ~3-µg aliquots of each DNA population were used. DNA fragmentation and adapter ligation were performed as described in (13), and fragments were sequenced at the Centre "Bioengineering" RAS using a 454 GS FLX Standard series automated sequencer (Roche, Basel, Switzerland). Sequences were analyzed using RepeatMasker software (www.repeatmasker.org/cgi-bin/WEBRepeatMasker).

PCR with gene-specific primers

Non-normalized and normalized DNA were diluted in PCR mixture to a final concentration of 15–20 pg/µL and amplified using gene-specific primer pairs (Supplementary Table S2) and an Encyclo PCR kit, according to the manufacturer's instructions. Depending on the gene being amplified, 28–34 PCR cycles were performed on an MJ Research PTC-200 DNA Thermal Cycler; each cycle consisted

Table 1. Representation of repetitive elements in normalized and non-normalized samples of human genomic DNA.

Repetitive element families	Non-normalized DNA			Normalized DNA		
	bp	%	Mean divergence (%)	bp	%	Mean divergence (%)
Total nucleotides sequenced	6643277	100	—	6269460	100	—
LINE L1P	371253	5.6	9	69670	1.1	15
ERV-K	20597	0.3	8	6575	0.1	12
Simple sequence repeats	68367	1.0	10	18499	0.3	11
Alu	631112	9.5	12	6572	0.1	16
Satellite sequences	293827	4.4	15	7915	0.1	20
ERV1	165461	2.5	15	105155	1.7	17
ERV-L	323437	4.9	19	245039	3.9	22
LINE L1M/HAL	496398	7.5	19	605965	9.7	21
DNA transposons	161304	2.4	19	170331	2.7	21
MIR	118927	1.8	27	142060	2.3	27
LINE L2	104535	1.6	28	147241	2.3	28
LINE CR1/L3	10226	0.1	29	13318	0.2	29
LINE L4-L5	3508	0.05	33	3701	0.05	30

Figure 1. Schematic outline of genomic DNA normalization. Black and gray lines represent repetitive and low-copy sequences, respectively. The rectangles represent the adapter sequences and their complements. The normalization process results in equalization of concentrations of sequences with different abundance; therefore, concentrations of repetitive sequences are decreased to the level of low-copy sequences.

of 95°C for 7 s, 63°C for 20 s, and 72°C for 20 s.

Results and discussion

The normalization procedure is illustrated in Figure 1. Following DNA denaturation and re-association, the double-stranded fraction of repetitive sequences is degraded using

DSN, and the ssDNA fraction enriched for low-copy sequences is amplified by PCR. Because DSN normalization includes a PCR step to amplify the ssDNA fraction, a specific sequence is introduced into the ends of sheared DNA by ligation of double-stranded adapters.

The protocol was evaluated on human genomic DNA. Although the human

genome is less enriched for repetitive elements than are genomes of higher plants, it is well characterized with respect to the frequency and composition of repetitive elements (14), and thus allows for an accurate analysis of normalization results. Human genomic DNA was sheared, ligated to adapters, and normalized, as described in Materials and Methods. To achieve a more robust normalization, a human Cot-1 fraction, added as a driver, was included in the sample being normalized. Normalized DNA and non-normalized control samples were then sequenced side by side using an automated gene sequencing system to estimate the degree of reduction in high-abundance sequences during normalization. In total, 29,240 and 31,789 reads were obtained for normalized and non-normalized samples, yielding 6,269,460 and 6,643,277 nucleotides, respectively.

The sequence sets were tested using RepeatMasker software (www.repeat-masker.org/cgi-bin/WEBRepeatMasker) to quantify the levels of different repeated elements. Overall, ~40% of sequences from the non-normalized sample were found in the library of repetitive elements, whereas repetitive elements constituted only 25% of the sequences in the normalized sample. Table 1 shows the representation levels of different families of repetitive elements in non-normalized and normalized DNA samples. There was a significant decrease in the level of *Alu*, LINE L1P, ERV-K, and ERV1 repeats, as well as satellite sequences in the normalized DNA, whereas the levels of other repeats were unaltered by the normalization procedure. All repetitive elements whose levels were unchanged by normalization shared a higher mean divergence among nucleotide sequences than sequences that were efficiently normalized. Moreover, the mean divergence of nucleotide sequences in the group of repeats that were successfully normalized was increased during normalization.

Analyses of the representation of repeats with different sequence divergences revealed that, in non-normalized DNA samples, ~10% of sequences shared 100–91% identity with each other; 20% shared 90–81% identity; 10% shared 80–71% identity; and the remaining sequences were <70% identical. In the normalized sample, there was a 15× reduction in the levels of elements with a high degree of nucleotide identity (100–91%), and a 2× reduction in the levels of elements that shared 81–90% sequence identity. The representation of sequences with higher degrees of diver-

Figure 2. Representation of repetitive elements in samples of non-normalized and normalized human genomic DNA. Black bars, non-normalized DNA; gray bars, normalized (in the presence of Cot-1 driver).

gence remained roughly the same or was slightly increased compared with the non-normalized sample (Figure 2, Supplementary Table S1).

To demonstrate that the representation of unique gene sequences did not change during normalization, we analyzed 11 different genes by PCR using gene-specific primers. All genes tested (see Supplementary Table S2) were found in both samples at similar levels.

In addition, to estimate the contribution of the Cot-1 fraction to normalization efficacy, we constructed a library of human genomic DNA normalized without the driver, and sequenced 300 randomly selected clones; clones from a control (non-normalized) DNA library were sequenced in parallel. The normalization results obtained in the absence of the Cot-1 driver were similar to those in the presence of the Cot-1 fraction for all repeat groups except for those sequences with 100–91% identity (Supplementary Table S1), which showed only a 7-fold decrease in concentration. These data indicate that the addition of driver DNA comprising undesired sequences increases normalization efficacy.

Our results indicate that DSN normalization is highly effective against abundant, evolutionarily young, repetitive sequences with high sequence identity, like *Alu* elements and satellite repeats. It has been shown that, unlike most mammalian repeats, the genomes of many higher plants contain a large number of highly conserved repetitive elements. For example, ~80% of maize and wheat genomes are composed of repetitive DNA, mainly retrotransposons (15–20). In maize, most of these LTR-retrotransposons share more than 95% sequence identity and are the result of vigorous retrotransposon activity during the past 1–3 million years (15, 21). Similarly, wheat small nonautonomous CACTA (SNAC) elements show 91–95% identity within a subfamily (22). Our results indicate that DSN normalization can efficiently reduce the concentration of

such highly-conserved repetitive sequences in genomic DNA to be sequenced.

On the other hand, DSN normalization did not decrease the levels of repetitive elements that were substantially divergent. It is likely that this outcome reflects the stringency of the hybridization conditions used in the model experiment. The hybridization conditions used in the normalization protocol were the same as those used for cDNA normalization, and allow effective hybridization of sequences that are substantially identical. It has previously been shown that cDNA sequences with 87% sequence identity do not cross-hybridize under these conditions (23). Thus, the sequences representing divergent repetitive elements behave as unique sequences under the hybridization conditions used. Modification of hybridization conditions—most notably increasing the C_{ot} value—to which a sample is allowed to reassociate prior to DSN treatment, should increase the proportion of the DNA molecules that form duplexes, and thus improve the ability of the method to enrich for low-copy (slow-reannealing) sequences. Reducing the stringency of hybridization (e.g., by decreasing reassociation temperature and/or increasing the cation concentration of the buffer) would also result in enhanced duplex formation, although such an approach likely would result in a loss of unique sequences due to nonspecific hybridization.

The amount of DSN used for degradation of dsDNA fraction did not appreciably affect the normalization efficacy when 0.8–1.2 units DSN were added to the reaction. The addition of smaller amounts of DSN led to insufficient normalization that was evaluated by PCR analysis of *Alu* repeat abundance in the samples, while the increase of DSN amount to 2 units per reaction resulted in loss of the average length of normalized DNA. Moreover, additional PCR cycles were required to amplify the sample in this case (data not shown).

Some increase in normalization efficacy can be achieved by the inclusion of driver DNA comprising sequences to be eliminated from the sample. In the model experiment, we used a commercially available Cot-1 fraction of human DNA; however, the driver can be prepared from the cloned DNA population of undesired sequences, as described in Bogdanova et al. (23).

Thus, DSN normalization is applicable for reducing the concentration of highly abundant, evolutionarily young genomic repetitive elements with the low sequence diversity that is so problematic in genomic sequence assembly. It should be noted that elimination of “old” highly diverged repeat sequences is not necessary in many cases, as they are sometimes found in genes and occasionally form protein-coding regions (24).

In contrast to high- C_{ot} analysis and MF approaches, DSN normalization does not include steps to physically separate DNA fractions; thus, all DNA populations are maintained in the sample. However, DSN normalization leads to smaller reduction of repetitive DNA overall than the high- C_{ot} approach and fails to accomplish the complete separation of fractions based on sequence complexity.

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Competing interests

The authors declare no competing interests.

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