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RESEARCH ARTICLE

ANALYSIS OF THE CODON UTILIZATION PATTERN OF THE *lpxC* GENE FROM DIFFERENT HUMAN PATHOGENIC BACTERIA

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ABSTRACT

Antimicrobial drug resistance stand as a huge global challenge presently. The gram negative bacilli are on the rise and no new antimicrobial directed against these antibiotic resistant organisms have emerged in recent times. Six out of the nine Lipid A biosynthesis enzymes and their genes are highly significant and *lpxC* gene in particular because of its regulatory role has been reported to be conserved in a large majority of gram negative bacteria. Considering the conserved nature and universality of occurrence of the *lpxC* gene in the gram negative bacteria an in-depth codon utilization analysis of the *lpxC* gene was carried out from the genomic viewpoint in 16 different human pathogenic gram-negative bacteria. In this study, the emphasis has been laid to find out whether the codon usage pattern of the *lpxC* gene reflects the genomic codon usage design or does it possess some unique codon usage attributes. Codon usage study of the *lpxC* gene showed the gene to be under high degree of codon bias in most of the organisms considered in this study. The analysis of GC content of the *lpxC* gene demonstrated the gene to have varying GC content in comparison to their genomic GC content which probably suggests that horizontal gene transfer events may have played a significant role in the shaping up and accommodation of the *lpxC* gene within the genome of most of these pathogenic organisms.

INTRODUCTION

In the present time, antimicrobial drug resistance stand as a huge global challenge (Roberts *et al*., 2009). The gram negative bacilli (GNB) stand as a massive cause of concern. The marked increase in the incidence of infections due to antibiotic resistant GNB is of great concern, as patients infected by those isolates might initially receive antibiotics that are inactive against the responsible pathogens (Kang *et al*., 2005). GNB are recently on the rise (Wilson *et al*., 2011) and no new antimicrobial directed against these antibiotic resistant organisms have emerged in recent times (Piddock, 2012). GNB like *Acinetobacter baumannii*, *Klebsiella pneumonia*, *Pseudomonas aeruginosa*, *Proteus sp.* and others are linked with serious nosocomial infections and have surfaced as superbugs with high levels of resistance arising due to novel mechanisms of resistance like extended spectrum beta-lactamases, carbapenemases and the latest New Delhi metallo-beta-lactamase causing severe morbidity and mortality (Gupta, Limbago, Patel, & Kallen, 2011; Hawser *et al*., 2011; Kumarasamy, Toleman, & Walsh, 2010; Meir, Weber, Zbinden, Ruef, & Hasse, 2011; Naas, Cozon, Gaillot, Courcol, & Nordmann, 2011). The emergence of pathogenic bacteria resistant to the presently available antimicrobial agents has become a critical problem in modern medicine, particularly because of the parallel increase in immunosuppressed patients (Sulakvelidze, Alavidze, & Morris, 2001).

The development of relatively new approaches and technology in the form of microbial genomics and proteomics has ushered in a new era and paradigm shift in antimicrobial drug discovery. In the past two and a half decade there has seen a tremendous emphasis on the advancement of novel antimicrobials against drug resistant GNB by aiming at a vital bacterial pathway enzyme, the UDP-3-O-(R-3hydroxymyristoyl)–N-acetylglucosamine deacetylase or LpxC. This is the second enzyme in the Lipid A biosynthesis pathway and catalyzes the second step of Lipid A biosynthesis (M S Anderson, Bulawa, & Raetz, 1985; M S Anderson *et al*., 1993; M. S. Anderson, Robertson, Macher, & Raetz, 1988; Barb & Zhou, 2008; C. R. Raetz, Reynolds, Trent, & Bishop, 2007; Young *et al*., 1995). Lipid A is a powerful endotoxin causing bacterial sepsis, which in many cases has lethal consequences (Aderem & Ulevitch, 2000; Miller, Ernst, & Bader, 2005; C. R. Raetz, 1986, 1990; C R Raetz, 1993; Ulevitch & Tobias, 1995; Wyckoff, Raetz, & Jackman, 1998). Six out of the nine Lipid A biosynthesis enzymes and their

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genes are highly significant and *lpxC* gene in particular because of its regulatory role (Luo *et al*., 2006; Sorensen *et al*., 1996) has been reported to be conserved in a large majority of gram negative bacteria. Considering the conserved nature and universality of occurrence of the *lpxC* gene in the gram negative bacteria an in-depth codon utilization analysis of the *lpxC* gene was carried out from the genomic viewpoint in 16 different human pathogenic gram-negative bacteria. Codon usage bias along with GC content variation is known to play a prominent role in genome evolution and is known to have varied biological consequences (Pal, Banerjee, Mondal, Mukhopadhyay, & Bothra, 2015). The sixteen different species considered in this study represent some of the most potent human pathogens and include organisms such as *Acinetobacter baumanii, Bordetella pertussis, Escherichia coli, Haemophilus influenza, Salmonella* and others. A table showing the organisms selected for this study along with the diseases caused by them is given in Table 1. A thorough comparative study of the degree of codon bias pattern together with the primary sequence structure analysis of the *lpxC* protein coding gene was carried out to explore the characteristic features of this particular gene which may provide sufficient insights for looking into other structural genes of prokaryotic pathways and exploring them as novel antibacterial targets. In this study, the emphasis has been laid to find out whether the codon usage pattern of the *lpxC* gene reflects the genomic codon usage design or does it possess some unique codon usage attributes.

MATERIALS AND METHODS

The *lpxC* gene and amino acid sequences of sixteen human pathogenic GNB were downloaded from the IMG (Markowitz *et al*., 2012) and GenBank (Benson *et al*., 2013) sequence database together with their whole genome sequences. Utilizing these sequences, the effective number of codons (Nc), which is a measure of synonymous codon usage bias (Wright, 1990), was calculated for each nucleotide sequence encoding enzymes of the amino acid biosynthetic pathway followed by the frequency of guanine and cytosine at the synonymous third position of codon (GC3). CodonW (Peden, 1999) was used to carry out both these calculations. Information regarding inter-species synonymous codon usage variation can be accounted for by studying the variation in G+C content in the third position of a codon (GC3). The Nc-plot (Wright, 1990) was used to explore such inter-specific synonymous codon usage patterns. Correlation analysis between the different primary sequence analysis parameters was carried out to examine the association between the different variables of codon usage such as, Nc GC, GC3 content and amino acid length.

RESULTS AND DISCUSSION

Codon usage bias is reported to be a major driver in genome evolution (Pal *et al*., 2015). In order to comprehend the codon usage architecture of the *lpxC* gene, a comprehensive codon usage analysis was carried out. Looking at the universality of this vital gene in gram negative bacteria there is a curiosity to know how the *lpxC* gene behaves and adjusts with the whole genome codon usage pattern in different bacterial species. For this, a thorough analysis of the codon usage pattern prevalent within the *lpxC* gene of the selected 16 highly pathogenic species was carried out. The average whole genome Nc of each of the species was compared with the Nc of their respective *lpxC* gene sequence and majority of the species were found to possess Nc value less than their mean whole genome Nc, suggesting the existence of greater codon bias within the *lpxC* gene. The *lpxC* gene of *Veillonella parvula* was an exception in this regard with 12.21% greater Nc score than its mean whole genome Nc. The *lpxC* gene of *Aggregatibacter aphrophilus* (Nc=39.09) demonstrated greater codon bias compared to its mean genomic effective number of codons (Nc=45.45). The *lpxC* genes from *Chlamydia trachomatis*, *Legionella pneumophila*, *Microcystis aeruginosa* and *Acinetobacter baumannii* demonstrated Nc values closer to their mean genomic Nc (Figure 1).

Table 1 The 16 gram negative bacterial species whose *lpxC* gene is selected for this study along with the diseases caused by them

Organism	Diseases	Relevance
Acinetobacter baumannii ATCC 17978	Septicemia, Meningitis, Pneumonia, Nocosomial infection	Human Pathogen, Medical
Aggregatibacter aphrophilus NJ8700	Periodontal infection, Periodontitis	Human Pathogen, Animal Pathogen, Medical
Bordetella pertussis CS	Respiratory infection	Pathogen, Medical
Chlamydia trachomatis L2/434/BU	Lymphogranuloma vernerum, Respiratory infection, Pharyngitis, Pneumonia, Bronchitis	Human Pathogen, Medical, Animal Pathogen
Chlamydophila pneumoniae TW-183	Heart disease, Bronchitis, Pneumonia, Respiratory infection, Pharyngitis	Human Pathogen, Medical
Coxiella burnetii Dugway 5J108-111	Q fever, Food poisoning	Medical, Human Pathogen, Animal Pathogen, Biothreat
Escherichia coli O157:H7 EC4115	Hemorrhagic colitis, Diarrhea	Comparative analysis, Medical, Human Pathogen
Francisella tularensis holarctica LVS	Tularemia	Human Pathogen, Medical, Biothreat
Haemophilus influenzae R2846	Septicemia, Sinusitis, Otitis media, Meningitis	Medical, Human Pathogen
Klebsiella pneumoniae pneumoniae MGH78578	Pneumonia, Bacteremia, Urinary tract infection	Cattle Pathogen, Human Pathogen, Animal Pathogen, Medical
Legionella pneumophila Paris	Pneumonia, Legionellosis	Human Pathogen, Medical, Animal Pathogen
Microcystis aeruginosa NIES-843	Gastroenteritis, Hepatic inflammation, Skin irritation	Medical, Environmental, Human Pathogen, Animal Pathogen
Neisseria meningitidis M04-240196	Meningitis, Septicemia	Medical, Comparative analysis, Human Pathogen
Rickettsia rickettsii Sheila Smith	Rocky Mountain Spotted Fever	Medical, Human Pathogen
Salmonella enterica enterica sv Typhi Ty2	Salmonellosis, Food poisoning, Typhoid fever, Gastroenteritis	Human Pathogen, Medical
Veillonella parvula Te3, DSM 2008	Bacteremia, Opportunistic infection, Endocarditis	Human Pathogen, Tree of Life, GEBA, Medical

	Nc_avg (WG)	Nc (*lpxC*)	Difference	%age change
AAP	45.4500	39.0900	6.36	13.99%
ABA	45.2478	45.9100	-0.66	-1.46%
BPE	33.3891	34.1700	-0.78	-2.34%
CBU	51.5605	46.4300	5.13	9.95%
CPN	49.9705	47.1000	2.87	5.74%
CTR	48.9575	49.1100	-0.15	-0.31%
ECO	47.1347	43.3700	3.76	7.99%
FTU	41.0721	38.8400	2.23	5.43%
HIF	43.3115	39.1900	4.12	9.52%
KPN	41.0755	42.7000	-1.62	-3.95%
LPN	50.5305	50.7700	-0.24	-0.47%
MAE	49.1544	48.7100	0.44	0.90%
NME	43.5997	41.9600	1.64	3.76%
RRI	42.5869	44.8100	-2.22	-5.22%
SEN	46.7990	44.7400	2.06	4.40%
VPA	43.8558	49.2100	-5.35	-12.21%

Figure 1 A comparative account of the difference in Nc at the whole genome and the individual *lpxC* gene level in the selected sixteen bacterial species.

The analysis of GC content at the third position of the codon (GC3) demonstrated that the *lpxC* gene from *Klebsiella pneumoniae* has 11.56% lower GC3s compared to its genomic GC3. On the other hand, *Chlamydia trachomatis* (GC3=0.42) and *Neisseria meningitidis* (GC3=0.66) has 9.17% and 8.28% greater GC3 respectively, compared to their genomic GC3. The GC3 values of *lpxC* sequences from organisms like *Salmonella enterica*, *Veillonella parvula*, *Francisella tularensis* and *Coxiella burnetii* were quite similar to their genomic GC3 scores (Figure 2).

	GC3_avg (WG)	GC3 (*lpxC*)	Difference
AAP	0.3830	0.3120	7.10%
ABA	0.2819	0.2630	1.89%
BPE	0.8717	0.8420	2.97%
CBU	0.3866	0.3790	0.76%
CPN	0.3264	0.2760	5.04%
CTR	0.3263	0.4180	-9.17%
ECO	0.5160	0.5630	-4.70%
FTU	0.1914	0.1880	0.34%
HIF	0.2604	0.1800	8.04%
KPN	0.6856	0.5700	11.56%
LPN	0.3035	0.2710	3.25%
MAE	0.3744	0.3310	4.34%
NME	0.5762	0.6590	-8.28%
RRI	0.2060	0.2180	-1.20%
SEN	0.5570	0.5560	0.10%
VPA	0.2745	0.2790	-0.45%

Figure 2 A comparative account of the difference in GC3 at the whole genome and the individual *lpxC* gene level in the selected sixteen bacterial species.

A Pearson product moment correlation analysis of the genomic GC and the individual *lpxC* GC content depicted a significant positive correlation between the two (r=0.97, p=1×10^{-9}). The GC content of the *lpxC* gene of *Klebsiella pneumoniae* and *Chlamydia trachomatis* demonstrated an interesting property. Both of these have GC content that deviates from their genomic GC content. The *lpxC* gene of *Klebsiella pneumoniae* had 6.28% lower whereas, *Chlamydia trachomatis* had about 4% higher GC content compared to their mean genomic GC content. Out of the 16 selected species, the *lpxC* sequence of *Legionella pneumophila* exhibited GC content very much similar to its genomic GC level. A comparative account of the GC levels in the 16 species is given in Figure 3.

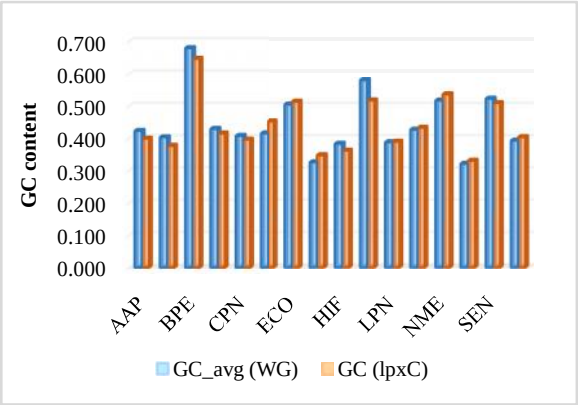

Figure 3 A comparative account of the GC content at the whole genome and the individual *lpxC* gene level in the selected sixteen bacterial species.

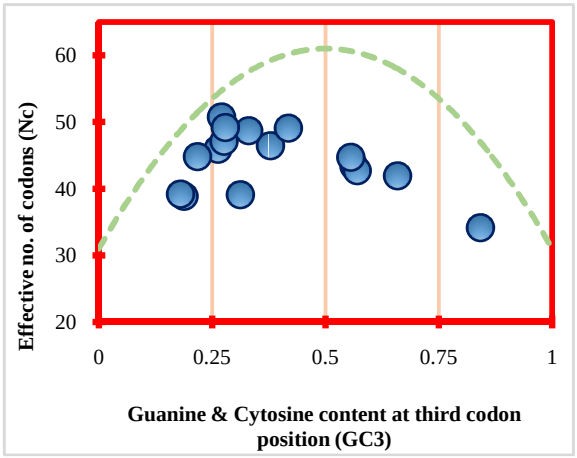

Figure 4 An Nc-plot showing the relation between Nc and GC3 of the *lpxC* gene in the sixteen pathogenic gram negative bacterial species. The dotted line represents the null hypothesis curve that the GC bias at the synonymous site is solely due to mutation but not selection.

An Nc-plot, shown in Figure 4, was constructed by plotting the Nc values of the 16 *lpxC* sequences against their GC3s. The *lpxC* sequence of *Bordetella pertussis* and *Neisseria meningitidis* existed as isolated points on the right hand side of the Nc-plot. The *lpxC* sequences of *Klebsiella pneumoniae*, *Escherichia coli*, and *Salmonella enterica* were present as an overlapping cluster on the Nc-plot. The codon usage study thus demonstrate that the *lpxC* sequences of *Klebsiella pneumoniae*, *Escherichia coli*, and *Salmonella enterica* share a similar evolutionary lineage and demonstrate quite identical codon usage pattern.

Correlation analysis showed that the length of the LpxC enzyme was negatively correlated with its effective codon number or Nc (r=-0.5, p<0.05) suggesting the fact that LpxC proteins having more amino acid residues have their respective genes under higher degree of codon usage bias. Another correlation study showed that the GC content of the *lpxC* gene was significantly anti-correlated with the frequency of the hydrophilic residues (r=-0.6, p<0.01) and positively correlated with the frequency of the total number of hydrophobic residues (r=0.53, p=0.03) constituting the LpxC enzyme. All these observations are quite interesting, considering the fact that, the amino acid compositional properties of the LpxC enzyme

protein is majorly influenced by the GC content and the codon usage bias of the *lpxC* gene.

Based on the type of amino acyl tRNA synthetases charging the various tRNA's for participation in the translation process it was observed that Class I tRNA synthetases are less utilized compared to the Class II synthetases. This is indicative of the feature that in a vital enzyme like LpxC, in terms of participation, the two different classes of tRNA synthetases shares a strong and perfect anti-correlation (r=-1.0, p<<0.001).

CONCLUSION

The *lpxC* gene is a vital component of the Lipid A biosynthetic pathway existing universally in all the gram negative bacterial species. The LpxC enzyme performs the first committed step of the Lipid A biosynthetic pathway providing structural and physiological integrity to the gram negative eubacteria. Codon usage study of the *lpxC* gene showed the gene to be under high degree of codon bias in most of the organisms considered in this study. The analysis of GC content of the *lpxC* gene demonstrated the gene to have varying GC content in comparison to their genomic GC content which probably suggests that horizontal gene transfer events may have played a significant role in the shaping up and accommodation of the *lpxC* gene within the genome of most of these organisms.

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