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Analysis of Codon Usage Bias in *Atractylodes Chinensis* (DC.) Koidz. Based on Transcriptome Data

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Abstract

To investigate the codon bias characteristics and influencing factors of *Atractylodes chinensis* (DC.) Koidz. based on the transcriptome, a total of 40,309 coding sequences from the transcriptome data were selected as the research objects. Programs and software such as Codon 1.4.2, R language, and EMBOSS were used to study the codon usage bias of the *A. chinensis* transcriptome. The results showed that the GC content of codons in the CDS sequences of the *A. chinensis* transcriptome was concentrated between 35% and 50%, with an average GC content of 44.6% and a GC3 content of 43.26%. The results of neutral mapping, bias, and ENC-Plot analyses indicated that selective pressure was the main driving force for the formation of codon bias in the *A. chinensis* transcriptome sequences. Based on RSCU analysis, a total of 28 codons were high-frequency codons, most of which had A or U as the terminal base. Finally, GCA, GAA, GGA, and GUG were determined as the optimal codons.

Keywords: *Atractylodes chinensis* (DC.) Koidz; Transcriptome; Codon; Usage Bias; Selective pressure

Abbreviations: Met: Methionine, Trp: Tryptophan, CUB: Codon Usage Bias, CDS: Coding Sequence, ENC: Effective Number of Codons, CAI: Codon Adaptation Index, RSCU: Relative Synonymous Codon Usage, A: adenine, U: uracil, G: guanine, C: cytosine, T: thymine

Introduction

Atractylodes chinensis (DC.) Koidz. belongs to the Atractylodes genus within the Asteraceae family and is the original plant source of Atractylodis Rhizoma. As a commonly used bulk medicinal herb, it was first documented in the Shennong Ben Cao Jing [1]. Widely distributed in northern China, including Hebei, Inner Mongolia, and Liaoning provinces, Hebei serves as the primary production region and is recognized as one of the "Top Ten Hebei Medicines". According to relevant studies [2], the core planting areas in Hebei are concentrated in the counties of Qinhuangdao and Chengde, where the herb yields the highest quality. The dried rhizome of A. chinensis, the main medicinal part, holds significant pharmaceutical value in traditional Chinese medicine, exhibiting effects of dispelling dampness, invigorating the spleen, relieving wind-cold, and improving eyesight [3,4]. Thriving in wild, cool, and humid environments, A. chinensis has seen increasing market demand due to its recognized potential in dietary therapy alongside social development and medical advancements. However, wild resources have become scarce due to long-term exploitation and ecological changes. Francis Crick's central dogma illuminates the flow of genetic information from DNA to RNA to proteins, with codons playing a pivotal role in this process [5,6]. As the bridge connecting DNA and proteins, codons are fundamental to gene transcription and translation [7,8]. In mRNA coding sequences, three nucleotides (a codon) specify a single amino acid [9].

Among the 20 basic amino acids, only methionine (Met) and tryptophan (Trp) are encoded by a single codon, while the remaining 18 amino acids are specified by 2 to 6 codons, illustrating the degeneracy of genetic codons [10]. Studies define multiple codons encoding the same amino acid as synonymous codons [11,12]. In organisms, the usage frequency of synonymous codons varies significantly, a phenomenon known as codon usage bias (CUB) [13,14]. The most frequently used codon among synonyms is termed the optimal codon [15], selected during gene expression to ensure encoding accuracy and efficiency. CUB is a universal phenomenon in nature, observed across diverse genomes. Due to codon wobble, bias typically manifests at the third codon position. Analyzing plant CUB helps characterize species-specific gene sequences and provides insights into evolutionary patterns and gene expression regulation [14]. Since the 1960s, CUB has drawn extensive attention as a key mechanism of gene expression regula-

tion. Advances in bioinformatics have driven methodological innovations and systematic summaries of CUB across species, deepening our understanding of its biological significance from multiple perspectives. Current research on A. chinensis primarily focuses on pharmacology and active components, with limited studies on its codon usage. This study aims to reveal CUB patterns, explore influencing factors, and identify optimal codons in the A. chinensis transcriptome, providing a basis for species improvement and therapeutic applications.

Materials and Data

The test samples were collected from the Medicinal Botanical Garden of Chengde Medical University in Chengde City, Hebei Province. They were identified as Atractylodes chinensis (DC.) Koidz. by Professor Chunying Zhao from the Institute of Traditional Chinese Medicine, Chengde Medical University, and exhibited different plant phenotypes. Transcriptome sequencing was performed by Major bio (Shanghai, China). For the assembled Unigene sequences, coding sequence (CDS) analysis was conducted. Using Perl programs, 40,309 CDS sequences were screened with gene lengths exceeding 300 bp and redundant sequences removed. These sequences used ATG as the start codon and TAA, TAG, or TGA as the stop codon.

Methods

Base Content Analysis of Coding Sequences

CodonW1.4.2 software was used to analyze the effective number of codons (ENC), codon adaptation index (CAI), relative synonymous codon usage (RSCU), and optimal codon usage frequency in the CDS sequences of A. chinensis transcriptome. The GC content was determined using the cusp program of EMBOSS. Here, GC1, GC2, and GC3 denote the GC contents of the first, second, and third codon positions, respectively, while GC represents the mean of GC1, GC2, and GC3. Additionally, GC3s indicates the GC content at the third position of synonymous codons.

Neutrality Plot Analysis

Neutrality plot analysis was performed with GC3 as the abscissa and GC12 (the average of GC1 and GC2) as the ordinate, followed by linear regression analysis to examine the correlation between GC12 and GC3 for identifying the main factors influencing codon usage bias [16]. A regression coefficient close to 1 indicates a significant correlation between GC12 and GC3, suggesting mutational pressure dominance, whereas a coefficient close to 0 implies weak correlation and selective pressure dominance.

PR2-Plot Analysis (Parity Rule 2 Plot)

PR2-Plot analysis evaluated mutational equilibrium at the third codon position by plotting G3/(G3+C3) against A3/(A3+T3) with the central coordinate (0.5, 0.5). This analyzed the relationships among adenine (A), guanine (G), cytosine (C), and uracil (U) at the third position to infer factors affecting codon bias in *A. chinensis* [17]. When A=T and C=G, codon usage is unaffected by selection or mutation.

ENC-Plot Analysis

Using R language, a two-dimensional scatter plot was generated with GC3 values and effective number of codons (ENC) of A. chinensis CDS sequences as the x- and y-axes, respectively, along with a standard curve [18]. Genes close to the standard curve suggest mutational pressure-driven codon bias, while those far from it indicate regulation by natural selection. The standard curve formula is:

$$ENC = 2 + GC3 + 29/[GC3^2 + (1-GC3)^2].$$

Codon Adaptation Index (CAI) Analysis

CAI, a key tool for evaluating gene expression efficiency, ranges from 0 to 1. Higher CAI values (approaching 1) indicate higher expression levels, whereas lower values reflect reduced expression [5].

Relative Synonymous Codon Usage (RSCU) Analysis

RSCU measures codon usage frequency by calculating the relative probability of a specific codon among synonymous codons encoding the same amino acid. RSCU values typically range from 0 to 2: RSCU > 1 indicates a high-frequency codon with strong bias; RSCU = 1 denotes no bias; RSCU < 1 signifies low frequency and weak bias [19].

Optimal Codon Analysis

CDS sequences were sorted by ENC values to establish high- and low-expression gene libraries. RSCU values were calculated for each library, and codons with ΔRSCU (RSCU difference between libraries) > 0.08 were screened. Codons meeting both ΔRSCU > 0.08 and RSCU > 1 were identified as optimal codons in the A. chinensis transcriptome [20].

Data Processing

CodonW and EMBOSS were used to analyze transcriptome data for codon parameters. Neutrality plots, ENC-Plots, and PR2-bias Plots were generated using Excel and R language. Correlation analysis and heat maps of codon parameters were created with Origin Pro software.

Results

Analysis of Codon GC Content Composition

Using CodonW1.4.2 software, GC content analysis was performed on approximately 40, 309 CDS sequences from the Atractylodes chinensis transcriptome. As shown in Figure 1A, the total GC content was concentrated between 35% and 50%, with an average of 44.6%. The average GC3s content (GC content at the third codon position) was 43.26%, and most genes exhibited GC3s values primarily ranging from 30% to 50% (Figure 1B), indicating a preference for adenine (A) and uracil (U) at the third nucleotide position.

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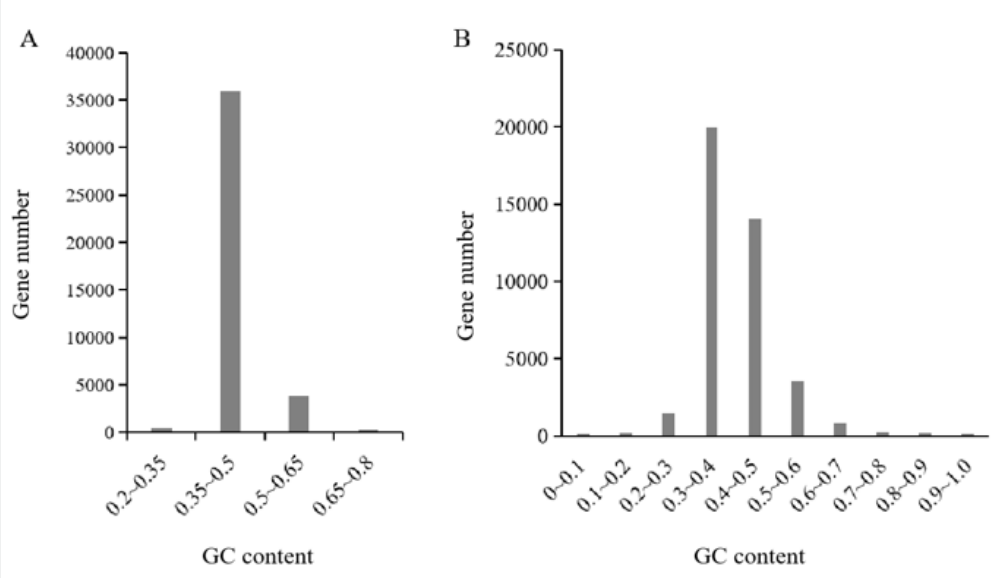

Figure 1: Composition of GC(A) and GC3s(B) content.

Neutrality Plot Analysis

Neutrality plot analysis showed that GC12 (the average of GC contents at the first and second codon positions) had a relatively concentrated distribution, mainly clustering between 0.3 and 0.6, while GC3 (GC content at the third position) exhibited a more dispersed range of 0.25-0.75. The regression curve equation was $y = 0.1005x + 0.4093$, with a slope of 0.1005, $R^2 = 0.0325$, and a correlation coefficient r of 0.1803. The weak correlation among the first, second, and third codon position bases indicated that codon usage bias in *A. chinensis* was primarily regulated by selective pressure (Figure 2).

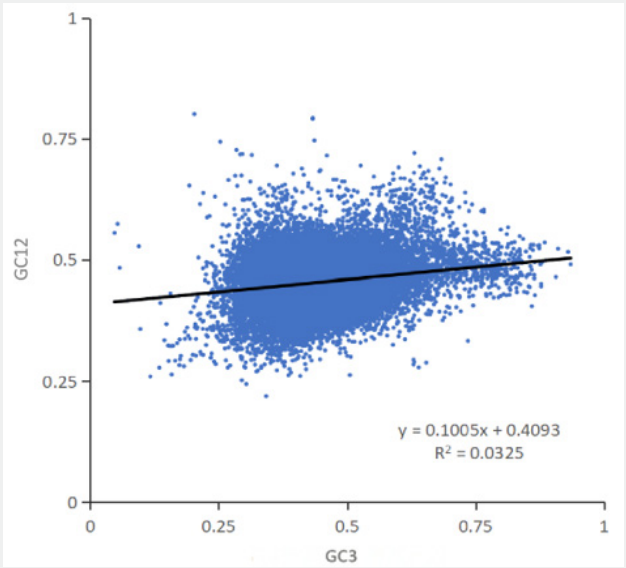

Figure 2: Neutrality plot analysis.

ENC-Plot Analysis

ENC-Plot analysis primarily serves to dissect the regulatory factors of codon usage bias, determining whether it is dominated by selective pressure or mutational pressure [21]. As shown by the distribution of data points for CDS sequences of *Atractylodes chinensis* transcriptome in Figure 3, most ENC values ranged from 35 to 61. Specifically, 367 sequences (0.9%) had ENC ≤ 35, indicating strong codon bias, while 1,839 sequences (4.6%) with ENC = 61 showed no codon bias. Additionally, the majority of genes were located below the standard curve, suggesting deviations between the actual ENC values and the ideal values, whereas a minori-

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ty were distributed along or near the standard curve, indicating close proximity between the actual and calculated ideal ENC values. These results suggest that although mutational pressure plays a role in the codon bias of *A. chinensis*, selective pressure is the key factor in shaping its codon usage bias (Figure 3).

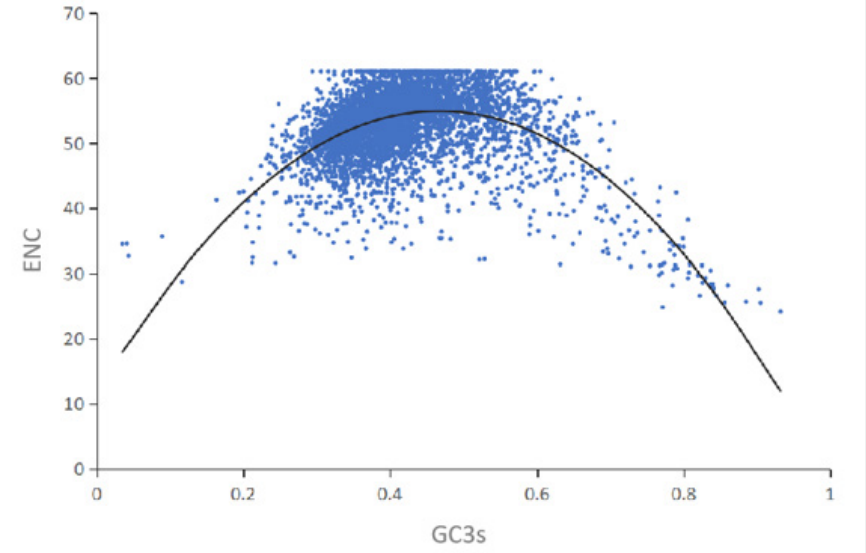

Figure 3: ENC-Plot mapping analysis of codon usage in the transcriptome.

PR2-Bias Analysis

The PR2-Plot (Figure 4) revealed uneven distribution of genes across the four quadrants, with a general concentration in the lower two quadrants. Specifically, uracil (U) was used more frequently than adenine (A), and guanine (G) more than cytosine (C) at the third codon position. This demonstrated a preference in the usage of the third codon base, with relatively higher contents of thymine (T), cytosine (C), and guanine (G). These findings indicate that the codon usage bias in Atractylodes chinensis is regulated by both mutational factors and selective pressure.

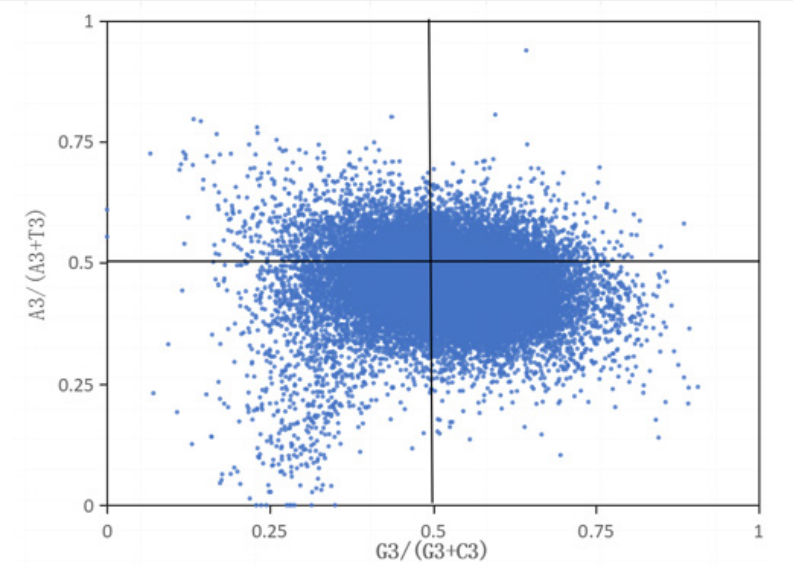

Figure 4: PR2-Bias plot analysis.

Relative Codon Adaptation and Correlation Analysis of Transcriptome Parameters

CAI (Codon Adaptation Index) is commonly used to evaluate gene expression levels [22]. In this study, CAI values ranged from 0.071 to 0.474, with the highest concentration around 0.2 (Figure 5), indicating low expression levels of Atractylodes chinensis tran-

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scriptome genes. This suggests that among the factors influencing codon bias in A. chinensis, natural selection exerts a stronger regulatory effect than mutational pressure. Correlation analysis of codon-related parameters in A. chinensis transcriptome sequences showed that GC1, GC2, and GC3 all exhibited significant correlations with the total GC content, but no significant correlations were observed among GC1, GC2, and GC3 themselves. Additionally, strong correlations were also observed between GC3, GC3s, GC and CAI, CBI (Codon Bias Index), FOP (Frequency of Optimal Codons). However, GRAVY (grand average of hydropathicity) showed no significant correlations with other parameters, even negative correlations in some cases, and ENC also showed no significant correlations with other parameters (Table 1).

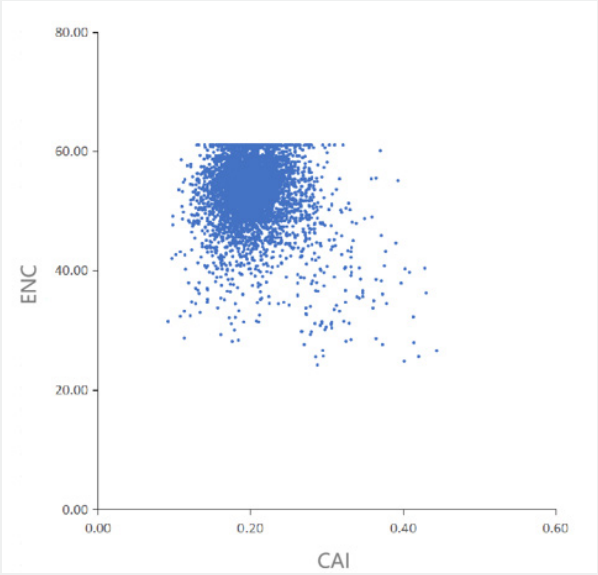

Figure 5: Relative fitness of codons in the transcriptome of A. Chinensis.

Table 1: Correlation analysis of *A.chinensis* gene-related parameters.

	GC1	GC2	GC3	GC	GC3s	CAI	CBI	FOP	ENC	GRAVY
GC1	1									
GC2	0.226**	1								
GC3	0.163**	0.120**	1							
GC	0.625**	0.619**	0.740**	1						
GC3s	0.198**	0.137**	0.992**	0.757**	1					
CAI	0.121**	0.139**	0.514**	0.431**	0.514**	1				
CBI	0.225**	0.204**	0.533**	0.516**	0.553**	0.316**	1			
FOP	0.219**	0.232**	0.510**	0.511**	0.533**	0.428**	0.965**	1		
ENC	0.065**	-0.007	0.031**	0.040**	0.033**	-0.177**	0.022**	0.001	1	
GRAVY	-0.210**	-0.109**	0	-0.137**	-0.027**	-0.461**	0.071**	-0.096**	0.053**	1

**P＜0.01

Relative Synonymous Codon Usage (RSCU) and Optimal Codon Analysis

RSCU represents the ratio of the observed usage frequency of a specific codon to its expected frequency under random usage [23]. RSCU analysis of Atractylodes chinensis transcriptome sequences (excluding stop codons UAA, UAG, UGA) identified 28 high-frequency codons (RSCU > 1), including AUG, UGG, AAG, GUG, GAA, UAU, UUU, CAA, AAU, UGU, GGA, ACU, ACA, AUU, GGU, CAU, GCA, UCA, GAU, CCA, CCU, AGG, CUU, UCU, UUG, GCU, GUU, and AGA. Notably, most high-frequency codons ended with adenine (A) or uracil (U), indicating a terminal base preference for A/U. CDS sequences were sorted by ascending ENC values, and the top and bottom 10% were selected to construct high- and low-expression gene libraries. ΔRSCU (RSCU difference between libraries) was calculated, and codons with ΔRSCU > 0.08 were screened [24]. By integrating ΔRSCU > 0.08 with RSCU > 1 criteria, four optimal codons were identified: GCA, GAA, GGA, and GUG. This confirms a strong preference for adenine at the third codon position in A. chinensis (Table 2).

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Table 2: Optimal codons of *A. chinensis* genes based on the RSCU.

Amino acid	Codon	High expression RSCU (number)	Low expression RSCU (number)	ΔRSCU
Ala	GCA*	1.1803 (17477)	1.0613 (13060)	0.119
	GCC	0.9193 (13612)	1.0862 (13366)	-0.1669
	GCG	0.5899 (8735)	0.3361 (4136)	0.2538
	GCU*	1.3105 (19405)	1.5164 (18661)	-0.2059
Cys	UGC	0.9037 (7964)	0.815 (6049)	0.0887
	UGU*	1.0963 (9661)	1.185 (8796)	-0.0887
Asp	GAC	0.7562 (17543)	0.758 (14744)	-0.0018
	GAU*	1.2438 (28853)	1.242 (24156)	0.0018
Glu	GAA*	1.0713 (28875)	0.9631 (22442)	0.1082
	GAG	0.9287 (25033)	1.0369 (24162)	-0.1082
Phe	UUC	0.9536 (19415)	0.9027 (14924)	0.0509
	UUU*	1.0464 (21304)	1.0973 (18143)	-0.0509
Gly	GGA*	1.1744 (17329)	1.0862 (14437)	0.0882
	GGC	0.789 (11643)	0.8008 (10644)	-0.0118
	GGG	0.8717 (12862)	0.6054 (8047)	0.2663
	GGU*	1.1649 (17189)	1.5075 (20036)	-0.3426
His	CAC	0.8281 (9621)	0.8246 (7833)	0.0035
	CAU*	1.1719 (13614)	1.1754 (11165)	-0.0035
Ile	AUA	0.7806 (12997)	0.6216 (8451)	0.159
	AUC	1.0746 (17891)	1.1325 (15396)	-0.0579
	AUU*	1.1448 (19059)	1.2459 (16938)	-0.1011
Lys	AAA	0.9815 (26836)	0.8375 (21513)	0.144
	AAG*	1.0185 (27846)	1.1625 (29862)	-0.144
Trp	UGG	1 (13454)	1 (10564)	0
Leu	CUA	0.709 (10136)	0.5207 (5647)	0.1883
	CUC	0.9609 (13736)	1.1345 (12303)	-0.1736
	CUG	0.8219 (11749)	0.6936 (7521)	0.1283
	CUU*	1.2812 (18316)	1.3486 (14624)	-0.0674
	UUA	0.8172 (11682)	0.7929 (8598)	0.0243
	UUG*	1.4098 (20154)	1.5097 (16371)	-0.0999
Met	AUG*	1 (24645)	1 (20840)	0
Arg	AGA*	1.4251 (11422)	1.858 (12246)	-0.4329
	AGG*	1.2767 (10233)	1.4341 (9452)	-0.1574
	CGA	0.9518 (7629)	0.6436 (4242)	0.3082
	CGC	0.6143 (4924)	0.7609 (5015)	-0.1466
	CGG	0.8025 (6432)	0.3603 (2375)	0.4422
	CGU	0.9295 (7450)	0.9431 (6216)	-0.0136
Ser	AGC	0.8894 (10977)	0.7319 (7569)	0.1575
	AGU	0.9013 (11124)	0.9071 (9381)	-0.0058
	UCA*	1.1685 (14423)	1.2703 (13137)	-0.1018
	UCC	0.9487 (11710)	0.9913 (10252)	-0.0426
	UCG	0.8565 (10571)	0.5687 (5881)	0.2878
	UCU*	1.2356 (15251)	1.5306 (15829)	-0.295
Thr	ACA*	1.1317 (13318)	1.1296 (11117)	0.0021
	ACC	1.079 (12698)	1.2694 (12493)	-0.1904

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	ACG	0.7358 (8659)	0.3543 (3487)	0.3815
	ACU*	1.0535 (12398)	1.2467 (12270)	-0.1932
Val	GUA	0.6836 (10536)	0.5568 (6882)	0.1268
	GUC	0.8227 (12680)	1.022 (12631)	-0.1993
	GUG*	1.1511 (17741)	0.9218 (11393)	0.2293
	GUU*	1.3427 (20694)	1.4994 (18531)	-0.1567
Trp	UGG*	1 (13454)	1 (10564)	0
Tyr	UAC	0.9894 (13642)	0.9689 (10632)	0.0205
	UAU*	1.0106 (13935)	1.0311 (11314)	-0.0205
Asn	AAC	0.9712 (18477)	0.9708 (16250)	0.0004
	AAU*	1.0288 (19573)	1.0292 (17228)	-0.0004
Pro	CCA*	1.2483 (14135)	1.3574 (11904)	-0.1091
	CCC	0.7369 (8344)	0.879 (7709)	-0.1421
	CCG	0.8078 (9147)	0.4092 (3589)	0.3986
	CCU*	1.207 (13667)	1.3544 (11878)	-0.1474
Gln	CAA*	1.147 (18373)	1.1258 (15727)	0.0212
	CAG	0.853 (13665)	0.8742 (12212)	-0.0212

Discussion

Codon usage bias (CUB), a pivotal biological phenomenon, extends beyond fundamental science to exhibit profound applied implications. This study illuminates evolutionary trajectories, offering critical insights into biological evolution, genetic characteristics, and practical applications in germplasm improvement and therapeutic development. CUB emerges from organisms' long-term interaction with the environment, governed by multiple regulatory factors-predominantly selective pressure and mutational bias [25-26]. However, debates persist in the field regarding the relative dominance of these forces in shaping codon bias.

Our analysis of 40, 309 coding sequences from the *A.chinensis* transcriptome revealed an average GC content of 44.6% (ranging 35%-50%) and a third-codon-position GC3s content of 43.26% (30%-50%), indicating weak codon bias with a pronounced preference for adenine (A) or uracil (U) at the third position. These findings align with studies on Ananas comosus [26], Camellia oleifera [27], and Canarium album [28], as the third codon baseless constrained by functional constraints-often serves as a key marker for CUB analysis [29]. Neutrality plot, ENC-Plot, and PR2-Plot analyses consistently validated selective pressure as the primary driver of CUB, echoing results from Dalbergia odorifera [30], Medicago sativa [31], and Sphaerophysa salsula [32].

The CAI values (0.071-0.474) reflected low gene expression levels in *A. chinensis*. RSCU analysis identified 28 high-frequency codons (RSCU > 1), of which 22 terminated with A/U and 6 with C/G. Notably, the optimal codons (GCA, GAA, GGA, GUG) also exhibited A/U endings, reinforcing the third-base preference. While CUB is influenced by multifaceted factors including selective pressure, mutational bias [33], gene expression levels [34], gene length [35], protein structure [36], tRNA abundance [37], and others [38-39], our data unequivocally demonstrate that selective pressure constitutes the primary regulatory mechanism in *A. chinensis*. This study characterizes the weak CUB and low expression profiles in *A. chinensis*, identifying optimal codons and regulatory determinants. These insights deepen our understanding of genomic architecture and encoding mechanisms, providing a robust theoretical framework for future genetic research and biotechnological exploitation of this medicinal species.

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