Comparative identification and differential expression pattern of amino acid permease genes in *Elaeis guineensis*

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**ABSTRACT**

*Elaeis guineensis* is a tropical crop with high oil content, and the nutritional value of oil is very high. Amino acids not only affect the growth and development of plants but also act as intermediate metabolites of oils, which determine the final quality of oils. In this study, eleven amino acid permease genes (*EgAAPs*) in *E. guineensis* were identified from the amino acid transporter family. Real-time PCR results showed that seven *EgAAPs* (*EgAAP1, EgAAP2, EgAAP3, EgAAP4, EgAAP6, EgAAP9, and EgAAP10*) played an important role in vegetative growth because of their higher expression levels in roots and leaves, but *EgAAP5, EgAAP7, EgAAP8* and *EgAAP11* were also important for their higher expression levels in flowers or fruits. *E. guineensis* seedlings were treated with 20% PEG-6000 and 4°C to induce drought stress and cold stress, respectively. The expression of six *EgAAPs* (*EgAAP1, EgAAP2, EgAAP4, EgAAP6, EgAAP8* and *EgAAP11*) was decreased in both roots and leaves during cold treatment, and only the expression of *EgAAP5* was increased in both roots and leaves after 6h of cold treatment. The expression of six *EgAAPs* (*EgAAP2, EgAAP4, EgAAP7, EgAAP8, EgAAP10* and *EgAAP11*) was decreased in roots but increased in leaves under PEG treatment, indicating an opposite pattern of expression levels of these *EgAAPs* in roots and leaves. However, only *EgAAP5* had a similar pattern of expression levels between roots and leaves under PEG treatment. The findings provide information on how *EgAAPs* in *E. guineensis* are regulated during growth and development, and under various environmental stresses.

**Introduction**

*Elaeis guineensis* is an ancient tropical crop with high oil content, and its oil is rich in palmitic acid, β-carotene and vitamin E [1]. It has been reported that fertilization could promote the growth of *E. guineensis* under good watering conditions [2]. Nitrogen, including inorganic nitrogen and organic nitrogen, has important effects on plant growth and development and nutrition quality. Amino acids, as the most important form of organic nitrogen, are transported and utilized by plants and determine the final quality of oils.

Amino acids are transported from source to sink organs [3,4]. Amino acid transporters (AATs) are cellular membrane proteins that can transport amino acids. AATs play an important role in various plant processes, such as seedling development and responses to pathogen and abiotic stresses [5–7]. More than 60 *AtAATs* in *Arabidopsis* [4,8] and more than 80 *OsAATs* in rice [9,10] have been identified in model plants. Furthermore, AAT families have also been identified in poplar [11], *Solanum tuberosum* L. [12] and *Glycine max* L. [13]. Importantly, studies have shown that amino acid permeases (AAPs), which belong to the AAT family [14–16], played an important role in loading amino acids for nitrogen sink and supply [17]. Although the functions of many AAPs in *Arabidopsis* have been identified, few studies have investigated AAP family members in tropical crop *E. guineensis*. In this study, we identified 11 amino acid permease genes in *E. guineensis* and showed that these genes had differential expression patterns in various tissues. Furthermore, they had differential expression patterns in roots and leaves under cold and PEG stress. These data might provide insight for further understanding their roles in the growth and development of *E. guineensis* and give clues to understand how *E. guineensis* utilizes the expression of these amino acid permease genes to adapt to environmental stress.
Materials and methods
Identification of amino acid permease genes in E. guineensis

The EgAAP gene sequences in E. guineensis were acquired from the National Center for Biotechnology Information (NCBI, https://www.ncbi.nlm.nih.gov/), and the gene structures were analyzed. Protein structures were analyzed using ProtParam (http://web.expasy.org/protparam/). Their subcellular localization was predicted using Wolf PSORT (http://psort.hgc.jp/), and transmembrane domains were analyzed using TMHMM Server v. 2.0 (http://www.cbs.dtu.dk/services/TMHMM/). A phylogenetic tree of EgAAPs based on the amino acid sequence was drawn according to the results generated by MEGA4.0 analysis using the neighbour-joining method with an amino acid and the Poisson correction model. Bootstrap values calculated for 1000 replicates are indicated at corresponding nodes. The promoter sequence analysis of EgAAPs was conducted using Plant CARE (http://bioinformatics.psb.ugent.be/webtools/plantcare/html/).

E. guineensis materials and treatments

For different tissue expression analyses of the EgAAP genes, male flower, female flower, lateral root, primary root, fruit and leaf tissues were sampled from African oil palm (pisifera, thin-shelled). Each type of tissue was collected on the same day from 15-year-old oil palms at the Coconut Research Institute, CATAS, China. Nine-week-old seedlings were grown in an artificial growth chamber with a constant photoperiod (16 h light/8 h darkness) and an average temperature of approximately 26 °C. The seedlings were treated with 20% PEG-6000 and 4°C to induce drought stress and cold stress, respectively. To obtain reliable experimental data and reduce experimental error, for each sample, we executed three repeated trials using the same stressor and carried out three biological replicates of expression analysis. For each induction treatment, spear leaves and roots were sampled at six time points (0, 1, 3, 6, 12, 24 and 48 h) and immediately stored at −80°C for RNA extraction. In addition, untreated plant materials (0 h) were used as the control group.

RNA extraction and real-time polymerase chain reaction (RT-qPCR) analysis

Approximately, 100 mg of tissue was utilized to extract total RNA using a MiniBEST plant RNA extraction kit (Takara, Japan). The RNA quantity was determined by a NanoDrop-2000 spectrophotometer (ThermoFisher, USA), and RNA integrity was confirmed by electrophoresis. The RNA from all tissues was used for reverse transcription (RT) using the PrimeScript™ RT reagent kit with genomic DNA eraser (Takara). The RT-qPCR mixture contained 1 μL diluted cDNA, 5 μL of 2 × PowerUp SYBR Green Master mix (Applied Biosystems, USA) and 0.5 μL of each gene-specific primer (10 μmol/L) in a final volume of 10 μL. All PCRs were performed using an ABI QuanStudio 6 machine under the following conditions: 10 min at 95 °C and 40 cycles of 5 s at 95 °C, 15 s at 55 °C and 20 s at 60 °C in 384-well clear optical reaction plates (Applied Biosystems, USA). The procedure ended with a melt curve ranging from 60 °C to 95 °C for 20 min to verify the PCR specificity. All qPCRs were carried out in biological and technical triplicate. The final Ct values were the means of nine measurements. Oil palm actin (GenBank accession number XP_010936865.1) was used as an internal control to normalize the expression of other genes. Gene-specific primers were designed with Primer Premier 5.0 (Table 1).

Table 1. Primers used for qRT-PCR of EgAAPs and Actin genes.

| Name            | Sequence (5’-3’)                          |
|-----------------|-------------------------------------------|
| EgAAP1-F        | GGCACCTTGGAGATATCCGATTGTCG               |
| EgAAP1-R        | ATCCAGGCGACCACACGAGTACGCGT              |
| EgAAP2-F        | ACCACAGCAGGAATTTCTACCCCA                 |
| EgAAP2-R        | ATACCAGCTGGACCCGATCGAC                 |
| EgAAP3-F        | GTGGACTGTTATGCGTCCGAGAG                |
| EgAAP3-R        | TGGTATCCAAATGGCGACT                   |
| EgAAP4-F        | TGGTGCTCTCCTATGCTTGCTGTCGCA           |
| EgAAP4-R        | GGTGAGGTCTACGTCGCCCT                  |
| EgAAP5-F        | CTTATGGGGGTATGATGCTGCTGCG              |
| EgAAP5-R        | ACCTCCACACACTACATAGGCA                 |
| EgAAP6-F        | TTGGAAGCATCAGCTATGCGCTGT              |
| EgAAP6-R        | CCAACAGCCTGTAATGGCCTCCCA              |
| EgAAP7-F        | TACACCCAGAACCACTCTGGAC                 |
| EgAAP7-R        | TCCGCGAGACTCGTGGCA                    |
| EgAAP8-F        | TACACCAAGAACCACTCTGGAC                 |
| EgAAP8-R        | CTCCGAGGACCATCAGCTGGAC                 |
| EgAAP9-F        | ATGGGACGATCCTCAATGCGC                  |
| EgAAP9-R        | CATGTTCTGTGTTTCAGGTGGGT               |
| EgAAP10-F       | GCTCTTGAGAATACCTCTCAGGGA              |
| EgAAP10-R       | TCTTGGCGGTTCCTGCGAGCA                 |
| EgAAP11-F       | CTCTGACGAGGACTGCTGCGA                   |
| EgAAP11-R       | TCAACCACAAAGGCCATCGTGGA              |
| Actin-F         | TCAACCACAAAGGCCATCGTGGA              |
| Actin-R         | GTGTTGGTGACACCACATCCTCAGCCAG         |
from ammonium to glutamine by glutamine synthetase [20]. The amino acid permease genes in *E. guineensis* were identified by searching the sequences from NCBI. Eleven putative amino acid permease genes were found (Table 2), and the exon number of the 11 *EgAAP* genes varied from 3 to 8 (Table 2). Furthermore, the results demonstrate that the corresponding proteins for 11 *EgAAP* genes had 457–513 amino acid residues (Table 2), indicating that these proteins are relatively similar in size. In addition, these proteins were predicted to all be localized at the membrane and to contain 9–11 transmembrane helices (Table 3). Although the number of amino acid residues was found to be similar to the predicted value, the number and arrangement of transmembrane helices were different (Figure 1). Many proteins did not have transmembrane helices in a large region after the fourth or fifth transmembrane helices (Figure 1). To further confirm the phylogenetic relationship of the proteins encoded by the 11 *EgAAP* genes, we compared their amino acid sequences, and the results showed that *EgAAP1*/*EgAAP6*, *EgAAP2*/*EgAAP3*, *EgAAP4*/*EgAAP5*, *EgAAP6*/*EgAAP11*, *EgAAP7*/ *EgAAP9* and *EgAAP8*/*EgAAP10* were clustered (Figure 2). Furthermore, we analyzed the promoter sequences of all *EgAAPs* and found that all the promoters of these genes have many light-responsive elements and

### Table 2. Gene information of the amino acid permease genes in *E. guineensis*.

| Gene name | Locus       | Number of introns | Number of exons | Prediction function     |
|-----------|-------------|-------------------|-----------------|-------------------------|
| *EgAAP1*  | NC_025995.1 | 6                 | 7               | Amino acid permease     |
| *EgAAP2*  | NC_025994.1 | 6                 | 8               | Amino acid permease     |
| *EgAAP3*  | NC_025994.1 | 6                 | 6               | Amino acid permease     |
| *EgAAP4*  | NC_025996.1 | 9                 | 8               | Amino acid permease     |
| *EgAAP5*  | NC_025994.1 | 5                 | 7               | Amino acid permease     |
| *EgAAP6*  | NC_025993.1 | 6                 | 7               | Amino acid permease     |
| *EgAAP7*  | NC_026000.1 | 4                 | 7               | Amino acid permease     |
| *EgAAP8*  | NC_025994.1 | 5                 | 6               | Amino acid permease     |
| *EgAAP9*  | NC_026000.1 | 6                 | 7               | Amino acid permease     |
| *EgAAP10* | NW_011550942.1 | 5             | 6               | Amino acid permease     |
| *EgAAP11* | NW_011582070.1 | 2            | 3               | Amino acid permease     |

**Figure 1.** Transmembrane helices of *EgAAPs* (A–K) in *E. guineensis* based on amino acid sequences. The transmembrane helices were acquired from TMHMM Server v. 2.0 ([http://www.cbs.dtu.dk/services/TMHMM/](http://www.cbs.dtu.dk/services/TMHMM/)). The red line represents the transmembrane, the blue line represents the inside, and the pink line represents the outside of the transmembrane helices.
enhancer regions (Table 4). In addition, the promoters of four genes (EgAAP1, EgAAP7, EgAAP9 and EgAAP10) have low temperature-responsive elements (Table 4). Almost all promoters of EgAAPs have abscisic acid-responsive elements except EgAAP3 (Table 4).

Different tissue expression profiles of amino acid permease genes in E. guineensis

Expression profiles can reflect the activity of genes in tissues, and the expression profiles of AATs have been identified in Arabidopsis [21]. In the present study, we used qRT-PCR to monitor the expression levels of different tissues in an important oil crop, E. guineensis (Figure 3). Since the root is one of the main sources of nutritional uptake, the results indicate that the expression of EgAAP1 was higher in lateral roots than in other tissues (Figure 3(a)). It was reported that AtAAP1 transports amino acids at the roots of Arabidopsis [22] and regulates amino acids in developing embryos [23]. In our study, only the expression of EgAAP5 in lateral roots was very low (Figure 3(e)), and the expression of seven EgAAPs (EgAAP3, EgAAP4, EgAAP5, EgAAP6, EgAAP9, EgAAP10 and EgAAP11) was higher in the primary root (Figure 3(c–f, i–k)), indicating that most EgAAPs played an important role in the amino acid transport in roots. Moreover, our results showed that none of the EgAAP genes had very low expression in the primary root (Figure 3).

The leaves are the primary tissue that is a rich source of nitrogen and that remobilizes nutrients to developing seeds or fruits. Free amino acids can be transported from leaves to sink tissues [23]. The expression of amino acid permease genes is essential for efficient nutrient transportation to developing fruits. A previous study reported that rice OsAAP5 is highly expressed in the leaves [10]. Our results indicated that the expression levels were different among these EgAAP genes and that the expression levels of EgAAP2, EgAAP7, EgAAP8, EgAAP9, EgAAP10 and EgAAP11 were higher in the leaves of E. guineensis (Figure 3(b, g–k)). However, few genes were expressed at a higher level in female flowers, except EgAAP11 (3K). EgAAP7, EgAAP8 and EgAAP11 were expressed at slightly higher levels in male flowers than in other tissues (Figure 3(g, h, k)). Furthermore, the expression of EgAAP1, EgAAP4, EgAAP6, EgAAP9 and EgAAP10 was lower than that of other tissues (Figure 3(a, d, f, i, j)), but the expression of four genes (EgAAP5, EgAAP7, EgAAP8 and EgAAP11) was highly expressed in the fruits (Figure 3(e, g, h, k)). These findings suggest that different EgAAPs play different roles during E. guineensis growth and development.

Cold stress effects on the expression profiles of amino acid permease genes in E. guineensis

Tropical crops are affected negatively by climate change [24], and the fresh fruit of palm oil is easily affected by temperature [25]. The best average temperature for oil palm is approximately 27°C, with a

Table 3. Protein information and transmembrane helices of the amino acid permease genes in E. guineensis.

| Gene name | Accession | Amino acid number | Molecular weight | Theoretical pI | Number of transmembrane helices |
|-----------|-----------|-------------------|------------------|---------------|---------------------------------|
| EgAAP1    | XP_010915382.1 | 485               | 53048.62         | 8.45          | 9                               |
| EgAAP2    | XP_010911284.1 | 489               | 53669.73         | 8.59          | 9                               |
| EgAAP3    | XP_010912574.1 | 488               | 54111.33         | 8.69          | 9                               |
| EgAAP4    | XP_010920126.1 | 513               | 56790.41         | 9.14          | 9                               |
| EgAAP5    | XP_010911832.1 | 458               | 49871.44         | 9.11          | 11                              |
| EgAAP6    | XP_010943299.1 | 473               | 52058.73         | 8.84          | 9                               |
| EgAAP7    | XP_010927999.1 | 458               | 50742.15         | 8.52          | 10                              |
| EgAAP8    | XP_010911831.1 | 461               | 50962.01         | 8.03          | 11                              |
| EgAAP9    | XP_010928207.1 | 466               | 51547.94         | 6.26          | 9                               |
| EgAAP10   | XP_010904713.1 | 459               | 50313.55         | 9.02          | 9                               |
| EgAAP11   | XP_010911645.1 | 457               | 49971.39         | 8.98          | 9                               |
minimal growth temperature of 15 °C [26]. Low temperature is an important ecological factor that affects the distribution and cultivation of oil palms [27]. It was revealed that the C-repeat binding factor (CBF) mediated the gene expression pattern in *E. guineensis* under cold stress via RNA-Seq analysis [26]. Other reports indicated that the *PtAAT* genes might play a critical role in the abiotic stress signaling in *Populus* because their expression was either increased or repressed after the cold and PEG treatments [11]. However, little is known about the role of *EgAAPs* in response to environmental signals. *E. guineensis* is an economic crop in the tropics, and its growth and oil quality are affected when it suffers from cold stress. The comprehensive roles of the amino acid permease genes in *E. guineensis* in response to cold stress were determined by investigating their expression patterns by using qRT-PCR (Figure 4). The results showed that the expression level of seven *EgAAPs* (*EgAAP1, EgAAP2, EgAAP4, EgAAP6, EgAAP8, EgAAP9* and *EgAAP11*) was decreased during the cold treatment duration and that the expression level of *EgAAP5* was increased after 6 h of cold treatment (Figure 4). At 12 h of cold treatment, only one gene, *EgAAP7*, was expressed at a level similar to that with no treatment, but it was down-regulated at 24 h in both roots and leaves (Figure 4(g)). It has been reported that AAPs are highly regulated by environmental signals [28], and the promoters of four genes (*EgAAP1, EgAAP7, EgAAP9* and *EgAAP10*) have a low temperature-responsive element (Table 3). Here, we also found that the expression of most *EgAAPs* was affected by cold treatment.

Leaves subjected to cold treatment showed the downregulation of eight amino acid permease genes (*EgAAP1, EgAAP2, EgAAP4, EgAAP6, EgAAP7, EgAAP8, EgAAP10* and *EgAAP11*), and only two amino acid permease genes (*EgAAP5* and *EgAAP9*) showed upregulation in response to cold stress (Figure 4). Interestingly, the expression of *EgAAP3* was almost unchanged at the beginning but decreased at 6 h and increased at 24 h after cold treatment (Figure 4(c)). However, the expression of *EgAAP9* was upregulated after cold treatment at 3 and 6 h but downregulated after cold treatment at 12 and 24 h (Figure 4(i)).

**Table 4.** Promoter cis-element analysis of the amino acid permease genes in *E. guineensis*.

| Gene     | MeJA responsive element | Light responsive element | Low temperature responsive element | Cold responsive element | Abscisic acid responsive element | Auxin responsive element | Zein metabolism response | Salicylic acid responsive element |
|----------|-------------------------|--------------------------|------------------------------------|-------------------------|----------------------------------|--------------------------|--------------------------|-----------------------------------|
| *EgAAP1* | 2                       | 4                        | 2                                  | 4                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP2* | 4                       | 2                        | 4                                  | 2                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP3* | 2                       | 4                        | 2                                  | 4                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP4* | 4                       | 2                        | 4                                  | 2                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP5* | 2                       | 4                        | 2                                  | 4                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP6* | 14                      | 1                        | 1                                  | 1                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP7* | 14                      | 1                        | 1                                  | 1                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP9* | 81                      | 41                       | 61                                 | 1                       | 1                                | 1                        | 1                        | 1                                 |
| *EgAAP10*| 29                      | 41                       | 16                                 | 1                       | 1                                | 1                        | 1                        | 1                                 |

**PEG stress effects on the expression profiles of amino acid permease genes in *E. guineensis***

*E. guineensis* requires sufficient sunlight and water for growth and production. Breeding drought tolerant varieties of *E. guineensis* is the goal of breeders [29]. Previous research revealed that the proline content...
increased in vegetative tissues in response to drought [30], while the total soluble protein content was affected by increasing drought severity [31]. Previous results showed that boron (B) and silicon (Si) application could induce physiological resistance of oil palm seedlings to drought stress [32]. The genes involved in cellular nitrogen compound metabolic processes and transmembrane transport are differentially expressed during drought treatments [33]. Therefore, we investigated the expression pattern of the amino acid permease genes in the root and leaf tissues in *E. guineensis* in response to PEG treatment by using qRT-PCR (Figure 5). When the expression of the amino acid permease genes was compared, there was a lower expression level of *EgAAP2*, *EgAAP3* and *EgAAP6* in the root (Figure 5(b, c, f)). No gene was expressed at a level similar to that in the non-treatment group (Figure 5). *EgAAP5*, *EgAAP9* and *EgAAP10* showed higher expression in the root under PEG treatment (Figure 5(e, i, j)). In leaves subjected to PEG treatment, the expression of five *EgAAPs* (*EgAAP1*, *EgAAP4*, *EgAAP7*, *EgAAP8* and *EgAAP11*) was downregulated in the first few hours and was then subsequently further downregulated with treatment duration. Surprisingly, the results indicate that the expression of amino acid permease genes did not increase at the beginning of the experiment and then decreased later (Figure 5(a, d, g–k)). It was reported that water stress inhibited the
growth of oil palm seedlings [34]; similarly, we hypothesize that simulated drought treatment with PEG affected the expression of most EgAAP genes, thereby affecting nutrient transport.

The expression of EgAAP4, EgAAP7, EgAAP8 and EgAAP11 decreased in the leaf during the PEG treatment from 0 to 48 h (Figure 5(d, g–k)). No elevated gene expression was observed under PEG treatment. The expression of EgAAP1, EgAAP2 and EgAAP9 decreased at the early stage of PEG treatment and then increased at the late stage (Figure 5(a, b, i)). However, the expression of three genes, EgAAP3, EgAAP6 and EgAAP10, increased at the beginning of PEG treatment but then decreased when PEG treatment continued (Figure 5(c, f, j)).

In plants, many stress-related genes generated a series of stress responses to meet the adverse environmental condition during growth and development.
Overall, our data showed that the eleven identified EgAAP genes exhibited differential expression in adapting to developmental conditions and environmental stress. These data might provide insight for further understanding the functions of EgAAP genes and their roles in E. guineensis growth and development.

Conclusions

We performed qRT-PCR to investigate the expression patterns of EgAAP genes under PEG and cold treatment. The EgAAP members showed significantly differential expression patterns under the two abiotic stresses examined. Most EgAAP genes were upregulated by the two abiotic stress treatments, suggesting that EgAAP genes may play crucial roles in abiotic stress responses in E. guineensis. For instance, EgAAP5 was highly expressed (over 40-fold that of the control level) in roots under PEG (drought) stress treatment. Furthermore, two paralogous pairs (EgAAP1/EgAAP2, EgAAP8/EgAAP11) had similar expression levels and behaviour under cold and PEG treatment. These results might suggest that homologous genes had similar putative functions in the processes of plant growth and development.
Disclosure statement
No potential conflict of interest was reported by the authors.

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