

Chapter

The Role of Noncoding RNAs in the Response of Oil Palm Plants to Abiotic Stresses

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Abstract

The genus *Elaeis* comprises two species, *E. guineensis* Jacq. and *E. oleifera* (Kunth) Cortés, which are known as the African and the American oil palms, respectively. The African oil palm originated from West Africa and is the predominant species in commercial plantations. This oilseed crop is the number one source of consumed vegetable oil in the World. Several abiotic stressors affect the plant life cycle interfering with growth and productivity. Salinity and drought are abiotic stresses that affect plantations on all continents, resulting in the loss of billions of dollars annually. MicroRNAs (miRNAs) are small endogenous noncoding RNAs that impact almost all biological processes, affecting either the transcriptional or posttranscriptional regulation of gene expression. Here we describe the R&D initiatives on oil palm miRNAs, highlighting the current knowledge on miRNAs' involvement in oil palm response to abiotic stress and postulating possible miRNA-based strategies for the genetic improvement of oil palm salinity and drought stresses tolerance.

Keywords: abiotic stress, tolerance, transcription factor, transcriptome, noncoding RNA, oil palm, drought stress, salt stress

1. Introduction

Oil palm (*Elaeis guineensis* Jacq.) is known as the most productive oilseed crop in the World, bearing great economic importance due to its large-scale production and high efficiency of the extraction and refining processes to obtain palm oil and palm kernel oil [1, 2]. In 2021/2022, the World consumed approximately 82 million metric tons of palm oil and palm kernel oil, making this oilseed crop the number one source of consumed vegetable oil [3].

The oil palm industry faces criticism due to a series of unsustainable practices (deforestation and consequent biodiversity loss, increased greenhouse gas emissions, and environmental and aquatic pollution), finding itself under pressure to adopt new and innovative procedures that could help this sector reverse this negative public perception [4]. Darkwah and Ong-Abdullah [5] highlighted some of these procedures, such as choice for intensification over extensification, adoption of

precision agriculture technologies, support for smallholder farmers, sustainability certification, and circular economy.

Oil palm plantations are in areas with tropical forests in the equatorial belt, as they need high rainfall throughout the year [6]. In Brazil, for instance, there is an extensive area with favorable conditions for cultivating oil palm outside the Amazon rainforest; however, those areas experience long periods of drought when oil palm does not meet the physiological water requirement to maintain productivity [7], and, consequently, need to be artificially irrigated with proper management to avoid soil salinization. Approximately 30% of the irrigated land area in the World is affected by salt [8], which, to a certain extent, shows a link between drought and salinity stresses.

Studies have shown that the progression of abiotic stresses is limiting global agricultural production, with no sign of reversal shortly [9–11], making it necessary to develop crops that are resilient to different abiotic stresses, such as drought and salinity, ensuring food security. Therefore, it is currently a challenge for plant scientists to develop crops resistant or tolerant to these conditions, capable of withstanding climatic instabilities and environmental stresses, especially combinations of these stresses. So, the research community aiming to develop knowledge and technology to allow oil palm breeding programs in Brazil and elsewhere to breed for superior genotypes must consider that.

Plants respond to environmental stimuli in a complex and highly coordinated manner at biochemical, physiological, and molecular levels [11–13]. When exposed to stress, rapid and effective reprogramming at the molecular level is required to adapt to unfavorable conditions [12, 14, 15]. This reprogramming regulates the expression of stress-responsive genes, especially at transcriptional and posttranscriptional levels [14, 16, 17].

micro RNAs (miRNAs) are posttranscriptional and translational regulators frequently correlated with plant stress tolerance and modulating stress response [15, 18, 19]. miRNAs have enormous potential for crop improvement, being the focus of studies by scientists in recent years [18, 20–22].

Therefore, the main objectives of this review are to describe the R&D initiatives known to date on oil palm (*Elaeis* spp.) miRNAs, to report on their biogenesis and mode of action, to summarize the current knowledge on miRNAs' involvement in oil palm response to abiotic stress, and to postulate possible miRNA-based strategies on the genetic improvement of oil palm's tolerance to abiotic stress.

2. miRNA biogenesis and mode of action

miRNAs are a class of endogenous, noncoding sRNAs transcribed from introns, exons, or intergenic regions [11]. They play a role in posttranscriptional RNA-mediated gene silencing and expression by complementary interaction with their mRNA target site [23, 24]. The biogenesis of plant miRNAs has been reported mainly in *Arabidopsis thaliana* (L.) Heynh. (**Figure 1**) [25].

Plant miRNAs range from 21 to 24 nucleotides in length [26]. Similar to protein-coding genes, miRNA genes (MIRs) are commonly transcribed by RNA polymerase II, forming a single-stranded precursor RNA called primary miRNAs (pri-miRNAs) that have imperfect self-complementary folding regions. Still in the nucleus, the 5' m7G-cap and 3' polyadenylation are added to promote better

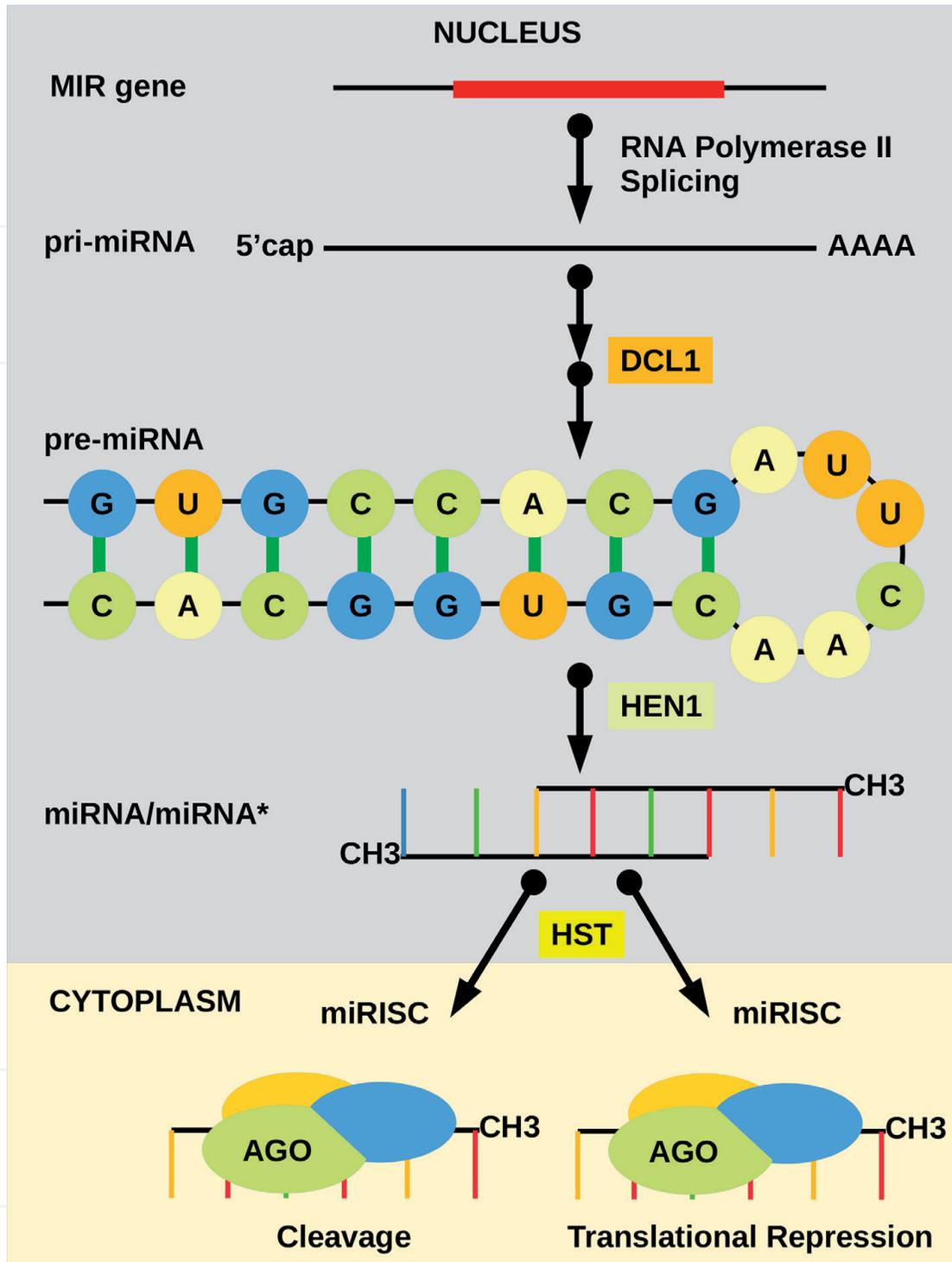


Figure 1. Biogenesis of plant miRNAs. A miRNA gene is transcribed by RNA polymerase II, giving rise to a primary transcript (pri-miRNA), which is then capped and polyadenylated. DCL1 processes pri-miRNA, perhaps in two or more steps, and HEN1 methylate it to produce the miRNA/miRNA* duplex. HST transports the duplex to the cytosol, and the miRNA strand gets incorporated into RISC. The nuclear export of miRNAs may occur before or after RISC assembly. According to the degree of complementarity with the target site, miRISC will either cleave the mRNA or inhibit its translation.

stability. Then the pri-miRNAs are converted into miRNA precursor sequences (pre-miRNA) by the action of DICER-LIKE 1 (DCL1) along with other associated proteins [15, 27].

The 3' end of the initial miRNA/miRNA* duplex is methylated by the nuclear protein HUA ENHANCER 1 (HEN1), thus preventing untemplated 3' polymerization that accelerates miRNA turnover [28]. The mature miRNA is then transported from the nucleus to the cytoplasm by the HASTY protein (HST), then loaded onto AGONAUTE (AGO) proteins and incorporated into an RNA-induced silencing complex (RISC), while often the star miRNA molecules (miRNA*) do undergo degradation. The AGO/miRISC complex search for RNA molecules through sequence complementarity, promoting posttranscriptional gene silencing through endonucleolytic cleavage or translation inhibition [25, 29]. The miRNA mechanisms of biogenesis and function are still unclear; however, studies have shown that they are involved in several cellular processes, including development, differentiation, division, and cell death [11, 26, 30].

An individual miRNA can regulate multiple transcripts, and a single transcript can be acted upon by several distinct miRNAs [11]. The miRNA can regulate the expression of its target gene using three strategies: (a) degradation of a target transcript through almost perfect complementarity; (b) inhibition of translation; or (c) DNA methylation. Regulation via degradation of the target transcript results in the degradation of intron sequences, and these cleaved sequences generate dsRNA molecules with the aid of RDR2 and then produce I-siRNA molecules of 21 and 22 nucleotides. Subsequently, the I-siRNA associated with the AGO-RISC complex directs the cleavage of the target mRNA sequence [31, 32].

Regarding the regulation via translation inhibition, only the roles of AGO1 and AGO10 have so far been understood [33, 34]. On the other hand, the miRNA-mediated inhibition mechanism remains unclear. At last, studies show that miRNAs in *A. thaliana* bind to AGO4, AGO6, and AGO9 to promote transcriptional gene silencing of target genes through RNA-directed DNA methylation (RdDM) [27].

3. miRNAs playing a role in plant response to abiotic-drought and salinity-stress

Abiotic stress, such as deprivation or excess of water, high salinity, low or high temperature, heavy metals, and ultraviolet radiation, is a negative impact caused by nonliving factors on living organisms [35, 36]. They are primary stresses that arise in the plantations limiting seed germination, plant growth, and plant development; and, in some cases, resulting in the death of the plants.

Salinity and drought are two of the most prevalent abiotic stress worldwide, affecting plantations on all continents and resulting in the loss of billions of dollars annually. Plants have developed several mechanisms to combat drought stress, and several genes associated with the response of plants to this stress are known [12, 37]. One of these responses is the positive and/or negative regulation of several transcription factors (TF) related to numerous physiological and cellular functions [38].

The dehydration responsive elements (DREB) are TF related to the activation of genes responsive to drought stress tolerance, and its overexpression can result in tolerance to water deficit in plants. Similarly, the transcription factor MYB regulates negatively in plants during drought stress since it is related to stomata opening [11, 39]. However, the overexpression of other genes associated with drought stress in plants did not result in the expected drought tolerance, demonstrating the complexity of mechanisms responsible for plant tolerance to water stress [40].

Several research groups have identified and reported miRNAs responsive to water stress in several species, such as rice—*Oryza sativa* L. [41], soybean—*Glycine max* (L.) Merr. [42], barley—*Hordeum vulgare* L. [43], and Arabidopsis [44]. Those water stress-responsive miRNAs belong to three classes. The first class includes miRNAs targeting transcription factors that contribute to the gene regulation of the stress response, comprising miR156, miR159, miR165, miR169, miR171, miR172, miR319, and miR396 [21, 44, 45].

In the second class, the miRNAs are involved in the direct response to water stress, some of which are miR167, which is responsible for directing the auxin response factors ARF6 and ARF8 [46]; miR168, which targets the ARGONAUTE 1 (AGO1) mRNA [47]; and miR393 and miR394, which target F-box protein mRNAs that play roles in drought tolerance [45, 48, 49]. The last class contains miRNAs such as miR397 and miR408, which have hydrolase and oxidoreductase genes as their target gene [50, 51].

Zhou and colleagues [41] identified 30 miRNAs differentially expressed in rice under drought stress, 19 were new miRNAs. Regarding their expression, 14 were upregulated (miR159, miR169, miR171, miR319, miR395, miR474, miR845, miR851, miR854, miR896, miR901, miR903, miR1026, and miR1125) and 16 downregulated (miR156, miR159, miR170, miR171, miR172, miR319, miR396, miR397, miR408, miR529, miR896, miR1030, miR1035, miR1050, miR1088 and, miR1126). In soybean, upregulation of miRseq13, miR397ab, miR1513c, miR169-3p, and miR166-5p was observed in sensitive plants, while the same miRNAs were downregulated on tolerant crops [42].

When it comes to salinity stress, several genes are related to the plant's stress response, including those involved in ion channel activation, signal transduction, and modification regulated by plant growth factors, especially the morphological architecture of the root [52]. In *A. thaliana*, studies have shown increased expression of miRNAs miR156, miR158, miR159, miR165, miR167, miR168, miR169, miR171, miR319, miR393, miR394, miR396, and miR397 in response to salt stress, while miR398 was downregulated [21].

According to Ding and colleagues, when analyzing corn variants tolerant and sensitive to salt stress, members of the miR396, miR167, miR164, and miR156 families downregulated, while miRNAs miR474, miR395, miR168, and miR162 upregulated in the tolerant ones [18]. In radish (*Raphanus sativus*), 22 new and 49 already known miRNAs appeared under salt stress [53]. In young oil palm plants under saline stress, 27 new and 52 already known miRNAs appeared [15]. When analyzing the expression profile of these miRNAs, 72 of them showed negative differential expression and the remaining seven had no significant differential expression [15].

Recent studies allowed a better understanding of the mechanisms of action of miRNAs and their relationship in response to different abiotic stresses [38, 54, 55]. It is necessary to highlight that miRNAs are species-specific and present different expression levels when analyzed in distinct plant species or within a specific one under the same stress [15, 24].

4. miRNAs in oil palm (*Elaeis* spp.)

Despite many advancements in the prediction and characterization of miRNAs in plants, there are only a few studies where researchers report the identification and characterization of miRNAs in oil palm, either under abiotic stress conditions or not. Currently, there are 10 published studies reporting miRNAs identification

and characterization in oil palm [15, 30, 56–63]. Considering the great economic importance of oil palm, the number of miRNA studies reported on this oilseed crop is relatively low (**Table 1**).

Nasaruddin and colleagues found five potential miRNA encoding sequences in oil palm by a combined homology and structural analysis approach, having roles in regulating the auxin response, floral development, and basal transcription [30]. Mehrpooyan, Othman, and Harikrishna [56] identified in oil palm six paralogs of miR172, a regulator of the APETALA2 (AP2)-like family transcription factors. Their results suggested that the expression of different miR172 precursor paralogs is tissue-specific and showed that each of the two mature miR172 isoforms had different expression patterns during floral development.

Low and colleagues identified 14 miRNAs in contigs assembled from sequences generated from the hypomethylated or gene-rich regions in the genomes of both species from the *Elaeis* genera [57]. Target prediction of these miRNAs identified just one putative target gene, similar to the Rab21-family small GTPase, a small GTP-binding protein of the Ras superfamily. Silva and colleagues identified 57 mature miRNAs in *E. guineensis* and 52 in *E. oleifera*, respectively, revealing that majority of them are transcription factors involved in the plant development process [58].

According to Somyong et al. [59], miRNA159 is related to the determination of females in oil palm trees, which is directly related to the higher production of oil palm trees, since palm oil with high number of female inflorescence and of clusters is most favorable. Noting that no expression of EgmiR159a was found in male flowers in their study, confirming its role in female sexual differentiation (**Table 1**). Ho and colleagues identified 15 oil palm-specific miRNA candidates when investigating microRNA expression in female inflorescence at two stages of floral [60].

In Gao et al. [61], the micro RNA EgmiR179 regulates the biosynthesis of metabolites through the negative regulation of its target gene NDT1, increasing oil content in palm oil [61]. Zheng and colleagues identified 452 microRNAs (miRNAs), including 170 conserved miRNAs and 282 new miRNAs, when gaining insights into the oil palm regulatory mechanisms of lipid and fatty acid metabolism. They found 37 fatty acid synthesis-related genes as putative miRNA-target genes and indicated that 22 conserved miRNAs and 14 new ones might be involved in fatty acid metabolism pathways. Tregear et al. [63] reported finding 30 previously unreported oil palm miRNA genes in a molecular study of the process of sexual differentiation in the immature inflorescence of oil palm.

Our research group reported prospecting and characterizing miRNAs in oil palm plants under salinity stress (**Table 1**) [15]. That was the first step in a study prospecting and characterizing miRNAs in oil palm plants under salinity [64] or drought stress and looking for insights on commonalities—miRNAs and putative miRNA-target genes—on the molecular response of young oil palm plants to these two abiotic stresses.

We did find 81 miRNAs—52 known ones and 29 new ones (**Figure 2**)—and 139 differentially expressed putative miRNA-target genes [15, 64]. In Salgado et al. [15], miR166, miR169, miR319, miR396, miR529, and egu-miR24sds showed altered expression profiles in young oil palm plants subjected to salt stress, both targeting TF, indicating a miRNA-dependent posttranslational regulation during the plant's response to the environment.

All miRNAs identification and characterization studies done so far in oil palm allowed the identification of 55 miRNA families or groups of miRNAs that derive from a common ancestor (**Figure 3**).

Technology	Condition	miRNA	Species	Oil palm material	Publication
Small RNA-seq	Normal	miR159a	<i>E. guineensis</i>	Female flower	Somyong et al. [59]
3730 sequencing technology/ Blast	Normal	miR2911, miR2916, miR156j, miR2914, miR2910, miR319f, miR167g, miR319e, miR845a, miR845b	<i>E. guineensis</i> and <i>E. oleifera</i>	Leaf	Low et al. [57]
Blast	Normal	miR156, miR157, miR159, miR160, miR164, miR166, miR167, miR168, miR169, miR171, miR172, miR319, miR390, miR393, miR394, miR395, miR396, miR397, miR398, miR399, miR528, miR529, miR530, miR535, miR815, miR1428, miR1432, miR2118, miR2275, miR5148, miR5179, miR5532, miR5801	<i>E. guineensis</i> and <i>E. oleifera</i> and <i>Phoenix dactylifera</i>	Genome	da Silva et al. [58]
Blast	Normal	miR156, miR157, miR159, miR160, miR854	<i>E. guineensis</i>	Genome	Nasaruddin et al. [30]
RNA-seq	Normal	miR5179	<i>E. guineensis</i>	Fruit	Gao et al. [61]
Small RNA-seq	Salt stress	miR156, miR391, miR395a, miR536, miR156, miR160, miR166, miR167, miR169, miR171, miR172, miR395, miR396, miR399, miR528, miR156, miR159, miR166, miR319, miR393, miR535, miR156, miR162, miR169, miR529, miR530, miR168, miR319, miR159. egumiR01, egumiR02, egumiR03, egumiR04, egumiR05, egumiR06, egumiR07, egumiR08, egumiR09, egumiR10, egumiR11, egumiR12, egumiR13, egumiR14, egumiR15, egumiR16, egumiR17, egumiR18, egumiR19, egumiR20, egumiR21, egumiR22, egumiR23, egumiR24, egumiR25, egumiR26, egumiR27.	<i>E. guineensis</i>	Leaf	Salgado et al. [15]
Small RNA-seq	Normal	miR1432, miR160, miR163, miR166, miR168, miR172, miR1859, miR1873, miR2199, miR2654, miR396, miR4365, miR528, miR535, miR827, miR835, miR858, miR894, egumiR3, egumiR5, egumiR6, egumiR7, egumiR8, egumiR9, egumiR10, egumiR11, egumiR12, egumiR13, egumiR14, egumiR15.	<i>E. guineensis</i> Tenera hybrid palms (<i>Dura</i> × <i>Pisifera</i>)	Female Inflorescence	Ho et al. [60]

Technology	Condition	miRNA	Species	Oil palm material	Publication
Small RNA-seq	Normal	miR156, miR160, miR164, miR172, miR444, miR5179, miR528, miR167, egumiR259, egumiR223, egumiR218, egumiR255, egumiR43, egumiR132, egumiR172, egumiR113, egumiR273, egumiR158, egumiR275, egumiR138, egumiR59, egumiR201, egumiR209, egumiR116, egumiR129, egumiR211, egumiR7, egumiR210, egumiR274.	<i>E. guineensis</i>	Mesocarp	Zheng et al. [62]
Small RNA-seq	Normal	miR319, miRN1, miR168, miR482, miR2118, miR159, miR171, miR167, miR397, miR160, miR156, miR535, miR396, miR536, miR169, miR319, miR179, miR166, miR394, miR399, miR172, miR164, miRN4, miR390, miR393, miRN5, miRN6, miR162, miR827, miR398, miRN7, miR395, miRN8, miRN9, miRN10, miR408, miR528, miRN11.	<i>E. guineensis</i>	Immature Inflorescence	Tregear et al. [63]
Blast	Normal	miR172	<i>E. guineensis</i>	Inflorescence	Mehrpooyan et al. [56]

Table 1.
Summary of miRNA studies reported on oil palm.

by overexpression or knocking down strategies. This step attempts to gain further insights that could allow the development of distinct ways to generate superior genotypes harboring tolerance to those stresses, either by vertical or horizontal transfer of genes or even by genome editing [8].

According to Hajyzadeh et al. [69], the overexpression of miR408 in chickpea (*Cicer arietinum* L.) resulted in improved drought tolerance. Plants overexpressing the pre-miR408 from *A. thaliana* were without wilting and drying after 8 days of undergoing the drought treatment, unlike the control plants [69]. Arabidopsis plants overexpressing miR408 showed resilience to multi-stress environments—salinity and drought [70]. Through biochemical analysis and fluorescence imaging with measures of the photosystem efficiency, it was reported tolerance of the transformants compared to control ones [70].

Transgenic lines of creeping grass (*Agrostis stolonifera* L.) overexpressing rice pre-miR393 showed a better tolerance response to saline stress (at 250 mM for 10 days), drought (15 days), and heat (40°C at day, 35°C at night, 13 days), confirming that miR393 is a potent candidate to confer resistance to multiple stresses [71]. According to Baek and colleagues, the overexpression of miR399f in Arabidopsis promoted greater tolerance to salinity and treatment with abscisic acid (ABA) [72]. Arabidopsis' putative miRNA-target genes—ABF3 and CSP41b—had low expression levels in transgenic plants, and these genes are related to stress due to their participation in ABA signaling [72].

Although the strategy of overexpression of miRNAs is dominant among the studies to obtain plants resistant to different stresses, the inhibition approach is also being promoted through the use of the short tandem target mimic (STTM) approach, causing loss of function [11]. Although there has been an increase in studies on the use of miRNAs to obtain plants resistant to multi-stress, there is still a long way to go.

According to Ferdous and colleagues, the overexpression of Hv-miR827 in barley (*H. vulgare* cv. “Golden Promise”) influenced the grain weight and allowed the plants to recover after drought treatment, in addition to providing an improvement in the efficiency of the use of water [73]. Such behavior is also in transgenic Arabidopsis plants overexpressing the miRNA Ath-miR827 [74, 75].

miR319 is one of the oldest and most conserved miRNA families in plants, responsive to several stresses, including drought and salinity, based on high-throughput sequencing [76]. Studies have shown that its overexpression in transgenic creeping grass resulted in tolerance to salt and drought stresses; and it was linked to downregulation of at least four putative target genes of miR319 (AsPCF5, AsPCF6, AsPCF8, and AsTCP14) [77].

So far, no studies are known reporting on successfully horizontally transferring (or editing) miRNAs to or from oil palms aiming at achieving tolerance to abiotic stresses. Our research group prospected stress-responsive miRNAs and putative target genes that are good candidates for such endeavor [15, 64]. miRNAs and their putative target genes responsive to both stresses at once are the priority candidates for further studies.

Among putative target genes responsive to both stresses identified by our group in oil palm, there are some lncRNAs. Several studies have shown that lncRNAs play essential roles and different functions in the biological processes of plants. They can play a role as sRNA precursors to produce sRNAs, such as miRNAs and siRNAs. In response to different stresses, lncRNAs also play a role in the RNA-directed DNA methylation (RdDM) pathway [78–80].

6. Conclusions and future perspectives

Due to a series of unsustainable practices used by the oil palm industry, there is criticism pressuring it to adopt new and innovative procedures, including getting away from the tropical rain forests.

Predictably, primary stresses (abiotic and biotic) will arise once the industry establishes itself in those new areas for oil palm cultivation, forcing it to search for tools to deal in an economically sustainable way with them. Salinity and drought are on the top of such a list of primary abiotic stresses. Many studies report successful attempts to increase plants' tolerance to such stresses by altering the expression levels of miRNAs, either by overexpression or knocking down strategies. Despite the great economic importance of oil palm, we found only 10 published studies reporting miRNAs identification and characterization in this oilseed crop. When considering abiotic stresses, the scenario is even worst; only one published study so far. In this sense, it is clear that further studies are necessary on the role of miRNAs - and their putative target genes - in oil palm's response to abiotic stress. Besides that, as candidate genes become available from those studies, it will be necessary to validate their potential as tools to generate superior genotypes harboring tolerance to those stresses, either by vertical or horizontal transfer of genes or even by genome editing.

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Conflict of interest

The authors declare no conflict of interest.

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