

Chapter 2

Study of Oil Palm Photosynthesis Using Omics Technologies

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2.1 Introduction

Improving crop yield to meet the demands of increasing human population is a critical issue to be addressed. The increase in yield of crop plants can come from many avenues, such as better adaptation to environmental conditions, greater resistance to pests and diseases, improved agronomic practice, increased genetic yield potential and interaction of the above-mentioned factors (Gifford and Evans 1981).

According to Yamori (2013), improvement of photosynthesis can be done through the following efforts: (1) improving the *ribulose 1,5-biphosphate carboxylase/ hydrogenase (RuBisCO)* performance via quality control and/or quantity control, (2) increasing the thermo tolerance of *RuBisCO activase* to sustain *RuBisCO* activity under high temperatures, (3) enhancing CO₂ levels around *RuBisCO* to maximize catalytic rate and minimize photorespiration, (4) enhancing rate of chloroplast electron transport, (5) enhancing the capacity of metabolite transport processes and carbon utilization, (6) enhancing enzyme activity of Calvin cycle and (7) other innovations such as quantitative trait locus (QTL) analyses, phenomic screening, manipulation of mitochondrial respiration and improving photosynthesis under fluctuating light conditions. In an earlier review by Zelitch (1982), researchers have shown that improving photosynthetic efficiency through photosynthetic energy transduction and carbon dioxide (CO₂) assimilation in crops may help to increase crop yield significantly. He also mentioned in his review that several attempts were made to relate seasonal changes in canopy photosynthesis with yield by constructing

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a carbon budget in relation to dry matter accumulation in the field studies of soybean, barley, wheat, sorghum, maize and tobacco. These investigations showed a clear positive correlation between net photosynthesis and yield. A 33% increase in leaf photosynthesis may be translated into an 18% increase in biomass (Sinclair et al. 2004). On average, a doubling of the current CO_2 concentration ($[\text{CO}_2]$) in the field or laboratory chambers results in no increase in leaf area, but can cause a 23–58% increase in leaf photosynthetic rate (Drake et al. 1997) and an average of 35% increase in crop yield (Kimball 1983). The increase in $[\text{CO}_2]$ has two effects on C_3 plants: an increase in leaf photosynthesis and a decrease in stomatal conductance to water vapour (gs) (Drake et al. 1997; Long et al. 2004). In addition, the elevated $[\text{CO}_2]$ increases net leaf photosynthetic rate primarily by (1) competitive inhibition of the oxygenase activity of RuBisCO and therefore photorespiration and (2) acceleration of carboxylation because the CO_2 binding site is not saturated with CO_2 at the current $[\text{CO}_2]$ (Long et al. 2006).

As oil palm appears to be generally a source-limited plant (Corley et al. 1971), information on the partitioning of nitrogen and carbon assimilated from photosynthetic (fully opened autotrophic) leaves to various sink organs, particularly developing mesocarp and non-photosynthetic (unopened spears/heterotrophic) leaves for reproductive and vegetative growth will be valuable to palm breeding and genomic studies. The correlation between the fat, sugars and protein nitrogen of olive leaves and fruits has been reported (Donaire et al. 1975), and supports that carbon and nitrogen are transported from leaves to fruit for lipid synthesis in the mesocarp. A study on oil palm leaf biomass, nitrogen, sugars and photosynthesis using leaf ranks –6 to 57 suggested that carbon isotope composition of heterotrophic spear leaves (<rank 0) was ^{13}C sugar-enriched due to remobilization of reserve carbon from source organs (Lamade et al. 2009). This indicated that in oil crops such as olive and oil palm, the carbohydrate source of fruit development and vegetative growth comes from photosynthesis.

In oil palm, bunch yield is in linear relationship to intercepted radiation per palm (Squire and Corley 1987), and the photosynthetic rate of individual leaves shows a curvilinear relationship with light intensity (Dufrene et al. 1990). At low light-intensity, light is the limiting factor, and the photosynthesis rate is directly related to light intensity. The “light compensation point” is the light intensity where photosynthesis and respiration are equal; below this light intensity, there is a net outflow of carbon dioxide from the leaf. At high light intensity, photosynthesis becomes light-saturated and the rate of carbon dioxide intake through stomata becomes the main limitation. Photosynthetic rate of leaves of young palms increases rapidly 2 months before the first bunch is harvested (Henson 1990). The rapid increase in photosynthesis rate of leaves of young palms coincides with the time where mesocarp commonly experiences intense growth and lipid accumulation (Corley et al. 1973; Corley and Tinker 2003; Badger 2009). It has been suggested that if the oil palm leaf had a longer period of high photosynthesis rate, that dry matter production and bunch yield would increase significantly (Suresh and Nagamani 2006).

The above-mentioned studies on oil palm photosynthesis suggested that the measurement of photosynthesis efficiency of seedlings and young palms may provide information on desired traits, such as yield, abiotic stress and disease tolerance.

However, direct photosynthesis measurement on individual adult palms may be difficult due to the large canopy and height, and therefore limit the number of measurements can be conducted per day. The problems arise when a large number of biological replicates are required for statistical significance. Therefore, Omics technologies may offer a solution to this problem by profiling the expression of photosynthesis-related genes, protein and metabolite concentrations to complement the physiological measurements related to photosynthesis.

2.2 Contribution of Omics Technologies to Photosynthesis Study

Various omics-based approaches are now being deployed to complement conventional breeding, and to improve the understanding and selection efficiency for specific physiological traits, including photosynthesis.

2.2.1 Genomics

Plant genomics is a study in genetics that applies DNA sequencing approaches combined with bioinformatics approaches to sequence, assemble, and analyse the function and structure of plant genomes. Chloroplasts are photosynthetic intracellular organelles, hence it is important to sequence the plant chloroplast genome. Our understanding of plant chloroplast genome evolution has greatly advanced through genomic sequencing and comparative analysis of chloroplast genomes from different species. For example, Uthapaisanwong et al. (2012) characterized the oil palm chloroplast genome by using 454-pyrosequencing and the features of the characterized genome were then compared with those from date palm and rice. Consequently, they identified 32 RNA editing events in 19 chloroplast protein-coding genes of oil palm. Information from analysis of the chloroplast genome of natural population is useful for obtaining desirable agronomic traits, such as yield enhancement and resistance to pathogens (Daniell et al. 2016). This can be achieved by the discovery of useful alleles from genomic analysis as well as identification of regions of the genome in which diversity has been lost in domestic breeding. Desirable agronomic traits can then be achieved by breeding cultivated crops with their wild relatives (Brozynska et al. 2015).

2.2.2 Transcriptomics

Transcriptomics is a study of a complete set of RNA transcripts that are produced by the genome by using high-throughput methods, such as microarray analysis and RNA sequencing. To close the gap between the real and potential photosynthetic

rates under field conditions, genome-wide identification and characterization of the nuclear genes for photosynthetic traits in a segregating population of poplar was performed using microarray and bulked segregant analysis (Wang et al. 2014a). A total of 515 differentially expressed genes were identified in the study revealing that photosynthesis regulation mainly involved genes in transport, metabolism and response to stimulus functions. Those differentially expressed genes were *ATP-binding cassette*, major facilitator superfamily protein (transport), *glucanase*, *beta-D-xylosidase*, *NADH dehydrogenase* (metabolism), *WRKY* and *chitinase* (stress response). Additionally, they suggested that stress responses could be a factor to be considered for photosynthetic improvement in the field.

With the reduction in cost of next generation sequencing (RNA-seq), many comparative transcriptomes for photosynthesis studies have recently been reported on different plant species such as maize (Chang et al. 2012; Ding et al. 2015), *Cleome* spp. (Bräutigam et al. 2011), *Staria* spp. (Xu et al. 2013; Rao et al. 2016), *Megathyrus* spp. (Bräutigam et al. 2014), switchgrass (Serba et al. 2016), *Brassica* spp. (Mushtaq et al. 2016), foxtail, rice and sorghum (Ding et al. 2015). Many transcriptome comparative studies set out to investigate gene regulation differences between C₃ and C₄ plant species (Bräutigam et al. 2011, 2014; Xu et al. 2013; Ding et al. 2015; Rao et al. 2016). The leaves of C₄ crops such as maize and sorghum normally have better CO₂ fixation, along with better water and nitrogen use efficiencies compared to C₃ species such as rice. C₄ photosynthesis therefore affords higher efficiency of carbon conversion that enables plants to accumulate biomass at a faster rate compared to C₃ species. Understanding the C₄ photosynthesis pathway and mechanism may help to improve crop productivity; these pathway and mechanism can even be transferred to C₃ plants. Comparative transcriptome analysis provides a useful platform for candidate gene identification related to photosynthesis in C₄ plants, for examples, *mitochondrial decarboxylate carrier* and *phosphoenolpyruvate/phosphate translocator* (transport protein) (Bräutigam et al. 2011). Several recent transcriptome studies related to photosynthesis are summarized in Table 2.1.

2.2.3 Proteomics

Proteomics is the large-scale study of proteomes. A proteome is defined as the set of proteins found in a particular cell, tissue or organism. It is the aim of proteomics to elucidate all the proteins in a proteome, including protein abundances, protein modifications and protein–protein interactions. The proteomes of chloroplast, including its envelope, stroma and thylakoid membrane fractions, of several higher plants have been analysed (Friso et al. 2004; Pineda et al. 2010; de Luna-Valdez et al. 2015). In addition, the chloroplast proteomes of plant growing under various biotic and abiotic stresses have been described for rice, wheat, pea, as well as for the plant model *Arabidopsis thaliana* (Aro et al. 2005; Cui et al. 2005; Curto et al. 2006; Zhou et al. 2006; Wang et al. 2016). In their studies on the effect of 8 h darkness on *Arabidopsis* chloroplasts, Wang and colleagues identified 81 darkness-responsive

Table 2.1 Comparative transcriptome analysis summary

Reference	Plant species	Highlighted finding
Bräutigam et al. (2011)	<i>Cleome spinosa</i> and <i>Cleome gynandra</i>	Large quantities of Asp, Ala and pyruvate in C ₄ leaves compared to C ₃ . The genes involved in transport and metabolism were also expressed higher in C ₄ leaves including genes for <i>phosphate translocator</i> , <i>mitochondrial dicarboxylate carrier</i> and <i>adenylate kinase</i> family protein. The genes for transcription factors such as <i>AP2-EREBP</i> , <i>bZIP</i> and <i>zinc finger</i> also showed higher expression level in C ₄ leaves
Chang et al. (2012)	<i>Zea mays</i>	Pathway analyses revealed differences between mesophyll and bundle sheath cells of maize in various functional categories. Mesophyll plays more important roles including light reaction, protein synthesis and folding. Bundle sheath cells play a role in transport, signalling, protein degradation etc. Potential candidate genes identified include those for <i>phosphoenolpyruvate carboxylase</i> , <i>NADP-MDH</i> and <i>dicarboxylate transporter</i> . The genes for many transcription factors were found to be differentially expressed, including <i>WRKY</i> , <i>NAC</i> , <i>MYB</i> , <i>bHLH</i> and <i>GRAS</i>
Xu et al. (2013)	<i>Setaria viridis</i>	Whole transcriptome analysis revealed 7056 simple sequence repeats from 60,751 transcripts assembled. Many genes related to C ₄ photosynthesis were identified, including those for <i>PEPC</i> , <i>NADP-ME</i> , <i>MDH</i> and <i>PCK</i> from the study
Wang et al. (2014a)	<i>Populus</i>	The microarray study identified 163 up-regulated and 352 down-regulated genes. Gene enrichment identified 48 significant GO terms in biological processes and cell components. The candidate genes identified were mainly involved in transport, metabolism and response to stimulus function including <i>ATP-binding cassette</i> , major facilitator superfamily protein, <i>oligopeptide transport</i> , <i>S-type anion channel</i> , <i>NADPH oxidases</i> , <i>NADH dehydrogenase</i> , <i>WRKY</i> and <i>MYB</i>
Bräutigam et al. (2014)	<i>Megathyrsus maximus</i> , <i>Dichantheium clandestinum</i>	The study indicated that the core C ₄ cycles are similar between two species with only a few exceptions including subcellular location of acid production and up-regulation of genes in C ₄ enzymes. Sucrose and starch synthesis are critical component in C ₄ metabolism. <i>M. maximus</i> appears to have simpler C ₄ metabolism compared to other plants with less adjustment involved within intercellular transport capacity and electron transfer

(continued)

Table 2.1 (continued)

Reference	Plant species	Highlighted finding
Ding et al. (2015)	<i>Zea mays</i> , <i>Sorghum bicolor</i> , <i>Oryza sativa</i> , <i>Setaria viridis</i>	From gene co-expression and differentially co-expression network analysis, 128 genes were found to be specific to C ₄ . Many genes which are associated with light reaction, starch and sucrose metabolism, transportation and transcription regulation were identified to be involved in C ₄ photosynthesis. They include <i>PEPC</i> , <i>PPDK</i> , <i>NADP-MDH</i> , <i>NADP-ME</i> , <i>PPDK-RP</i> , <i>aspartate aminotransferase</i> , <i>triphosphate phosphate translocator</i> , <i>FBA</i> , <i>FBP</i> , <i>phosphoglucan phosphatase</i> and <i>sucrose transporter 1/2</i>
Serba et al. (2016)	Switchgrass	The comparison of lowland and upland genotypes revealed that transcripts related to photosynthesis efficiency and development, and photosystem reaction centre subunits were up-regulated in lowland genotype. These transcripts for <i>fatty acid desaturase</i> , <i>cupin superfamily protein</i> , <i>elongation factor</i> , <i>glycine-rich protein</i> , <i>membrane protein</i> and <i>zinc finger</i> transcription factor. However, <i>catalase isozymes</i> , <i>late embryogenesis abundant group I</i> , <i>photosulphokinases</i> , <i>S-adenosyl methionine</i> and <i>HLH</i> transcription factor were up-regulated in upland genotype. The SNPs markers detected in the study will be useful for trait mapping for breeding improvement
Mushtaq et al. (2016)	<i>Brassica</i> spp.	From the comparison of leaf transcriptome analysis on Brassica, almost all late biosynthetic genes of anthocyanin such as <i>dihydroflavonol four-reductase</i> , <i>anthocyanin synthase</i> and <i>transparent Testa 19</i> were up-regulated in all purple leaves. Three genes related to degradation of photo-damaged protein in <i>photosystem II</i> and light respiration were down-regulated including <i>FTSH protease 8</i> , <i>glycolate oxidase 1</i> and <i>glutamine synthetase 1;4</i> . The accumulation of anthocyanin might have potential physiological function related to photosynthesis

proteins (Wang et al. 2016). Most of the identified proteins are nucleus-encoded, thus suggesting that darkness response in chloroplast is closely controlled by the nucleus. Incidentally, the abundance of 17 ribosomal proteins that are known to be involved in protein synthesis decreased after the dark treatment. The findings revealed that darkness triggers the inhibition of protein translation in the chloroplast, inhibition of *Photosystem II (PSII)* resulting in preferential cyclic electron flow around *Photosystem I (PSI)* and starch degradation, as well as enhancement of redox capacity. The study has improved our knowledge of molecular regulatory mechanisms in chloroplasts under light-limiting conditions.

Comparative proteomics of tea leaves of normal and abnormal colours revealed differential protein abundance for proteins related to photosynthesis machinery, including *PSI*, *PSII*, *cytochrome b6/f complex*, photosynthetic electron transport, light-harvesting complex and *F-type ATPase* (Ma et al. 2016). The decrease of

photosynthetic protein abundance was suggested to be associated with the colour changes in tea leaves. In another comparative study, the proteome of chloroplast envelope of pea (C_3 plant) was compared with that of maize (C_4 plant) (Bräutigam et al. 2008) revealing specific adaptations of the plastid envelope to C_4 photosynthesis and the proteins that were possibly required for maintaining C_4 metabolite fluxes. The data could be useful for improving the efficiency of photosynthesis in future C_4 crops. The information obtained from proteomics studies would help in gaining insights into roles and functions of proteins associated with photosynthesis. The knowledge may prove vital for crop modification, particularly in engineering better crops to cope with various stresses in the future.

2.2.4 Metabolomics

Metabolomics is a large-scale study of chemical processes involving metabolites by using various analytical platforms such as liquid chromatography–mass spectrometry, capillary electrophoresis–mass spectrometry, and gas chromatography–mass spectrometry (Sumner et al. 2003). Comparative analyses of C_4 and C_3 photosynthesis in developing leaves of maize and rice were previously conducted by using both integrated metabolomics and transcriptomics approaches (Wang et al. 2014b). Since C_4 and C_3 photosynthesis exhibit different efficiency in water and nitrogen consumption, the study was conducted to investigate whether C_3 plants having C_4 photosynthesis could have improved carbon fixation in a hot and arid situation. Metabolomics analysis of photosynthesis and the related primary metabolites were also conducted in transgenic rice plants with both overexpressed and knockout leaf *RuBisCO* using capillary electrophoresis–time-of-flight mass spectrometry (Suzuki et al. 2012). In rice seedlings with reduced *RuBisCO* content, Suzuki et al. (2012) found that there was a decrease in photosynthesis, starch and carbohydrate levels with a substantial accumulation of ribulose biphosphate, diphosphate and triphosphate compounds of other nucleosides, ATP, ADP and amino acids. In addition, starch and carbohydrate levels decreased in these plants. Thus, genetic manipulation of *RuBisCO* widely affected C and N metabolism in rice. A lipidomics approach has been deployed for comprehensive analysis of lipid composition in crude palm oil and showed that galactolipids such as monogalactosyldiacylglycerol, digalactosyldiacylglycerol and sulphoguinovosyl diacylglycerol are crucial for maintaining the function of the photosynthesis machinery and involved in photosynthesis and metabolic regulation under various stress conditions (Cheong et al. 2014).

2.2.5 Phenomics

Plant phenomics is the study of plant growth, architecture, performance, and composition using high-throughput methods of imaging, data acquisition and analysis (Araus et al. 2015; Walter et al. 2015). The phenotyping approach in studying

photosynthesis involves the application of fluorescence imager in high-throughput estimation of leaf chlorophyll content and photochemical yield of *PS II* (Baker and Rosenqvist 2004). Leaf chlorophyll content is a valuable indicator of plant health since its content is affected by both biotic and abiotic stresses. According to Gitelson et al. (2003), the F735/F700 ratio of chlorophyll fluorescence at 735 nm (F735) to that in the range of 700 nm and 710 nm (F700) shows a good linear relationship with the chlorophyll content ($R^2 > 0.95$). Therefore, this ratio seems to be a suitable measurement for the estimation of chlorophyll content of leaves.

Phenomic data is essential to plant breeding programmes for yield enhancement. However, the process of obtaining phenotypic data is the most time consuming, costly and labour intensive step of many biological experiments (Flood et al. 2016). In addition, the precision of phenotypic data is compromised due to lack of uniformity and reproducibility of the measurements. Moreover, the complex multidimensional nature of phenotypes especially in the field environment poses additional challenges. Hence, high-throughput and precise phenotyping is needed to complement other omics-based approaches. High precision screening of plants under nursery or field conditions can be aided by using innovative agricultural technologies such as drone or fieldcopter with measuring system and image capture function (van der Wal et al. 2013). The information from transcriptomics, proteomics, metabolomics and other omics technologies will be precise only if proper phenotyping is done. The integration of all omics data will help to further enhance our understanding of plant photosynthesis.

2.3 Investigation of Photosynthesis in Oil Palm Using Omics Technologies

In this chapter, we review studies conducted on oil palm photosynthesis, focusing on the potential role of omic technologies in oil palm yield enhancement.

2.3.1 Yield

Overall palm oil yield can be attained by the combination of several positive bunch traits: bunch number per year, bunch weight, fruit per bunch, ratio of mesocarp thickness to fruit (M/F) and oil content in dry mesocarp (O/DM) (Appleton et al. 2014a, 2014b). Of these, two key contributors of yield that are highly heritable are ratios of M/F and O/DM.

The metabolite profiles of oil palm leaves have contributed to a distinct clustering of photosynthetic and non-photosynthetic leaves in principal component analysis (Neoh et al. 2013). It was found that the differences between these two leaf types were caused by differential abundance of several groups of metabolites such as sugars,

amino acids and nucleosides. In the non-photosynthetic leaves, the relative abundance of sugar content was 21.3% lower than the photosynthetic leaves, presumably to support leaf growth during the fast elongation stage (Lamade et al. 2009; Kusano et al. 2011). Concordant with the lower amount of extract as a percentage of dry tissue weight obtained from the non-photosynthetic leaves, higher wet biomass was assumed compared to the photosynthetic leaves. The rapid increase in spear leaf biomass requires a carbon allocation presumably from both trunk apex and photosynthetic leaves. Total sugar content produced from photosynthesis may vary and is believed to be related to leaf rank (non-photosynthetic to photosynthetic) (Kusano et al. 2011; Ibrahim and Jaafar 2012). Adenine and many amino acids such as arginine, asparagine, proline, valine and tyrosine are more concentrated in non-photosynthetic compared to the photosynthetic leaves. In leaves, the biosynthesis of amino acids is developmentally regulated, usually being most active in young leaves (Galili 1995; Zhu-Shimoni 1997; Teija Ruuhola et al. 2003). This trend is similar to that observed in developing mesocarp tissue before lipid biosynthesis commences. It has been reported that nucleosides in young leaves were converted to salvage products (nucleotides and nucleic acids), degradation products and purine alkaloids, such as caffeine (Koyama et al. 2003). In coffee, almost 75% reduction of purine alkaloids is observed during leaf development (Deng and Ashihara 2010). The concentration of nucleosides is also found to be markedly lower in photosynthetic leaves (Neoh et al. 2013). The regulation of nucleosides also appears to play an important role in fruit development and lipid production in mesocarp (Neoh et al. 2013; Teh et al. 2013).

From our unpublished data, we observed that the photosynthetic-related genes were differentially expressed between high- and low-yielding palms with different M/F and O/DM traits. The differentially expressed genes included those encoding *chlorophyll a-b binding protein (CAB)*, *PSI* and *ferredoxin*. All these genes encoded for the main functional proteins in the upstream of photosynthesis mechanism. They exhibited higher expression in the high-yielding population as compared to the low-yielding population (Fig. 2.1a).

The differential expression of these genes indicates that high-yielding palms may have high abundance of these proteins, suggesting they are better in light energy harvesting and electron transfer during photosynthesis, which then lead to higher lipid production in this population. It has been reported that the Single Nucleotide Polymorphisms (SNPs) in gene encoding *CAB* in barley were associated with at least one of the six agronomic traits including plant height, spike length, a number of grains per spike, 1000 grain weight, flag leaf area and leaf colour (Xia et al. 2012).

A higher concentration of G6P and sucrose was found in higher yielder palms analysed using CE-MS (G6P) and GC-MS (Sucrose) metabolomics platform (Neoh et al. 2013). In the same experiment, several metabolites in photosynthetic leaves were found to be associated to O/DM. In photosynthetic leaves, both glucose 6-phosphate (G6P) and sucrose, two of the products of photosynthesis, were found to show significant difference ($pV < 0.05$) between high- and low-yielding palms (Fig. 2.1b). Both G6P and sucrose were found to be more concentrated in high O/DM palms. Several studies reported the presence of a close correlation between the G6P concentration in the cytosol and photosynthetic sucrose production in wheat

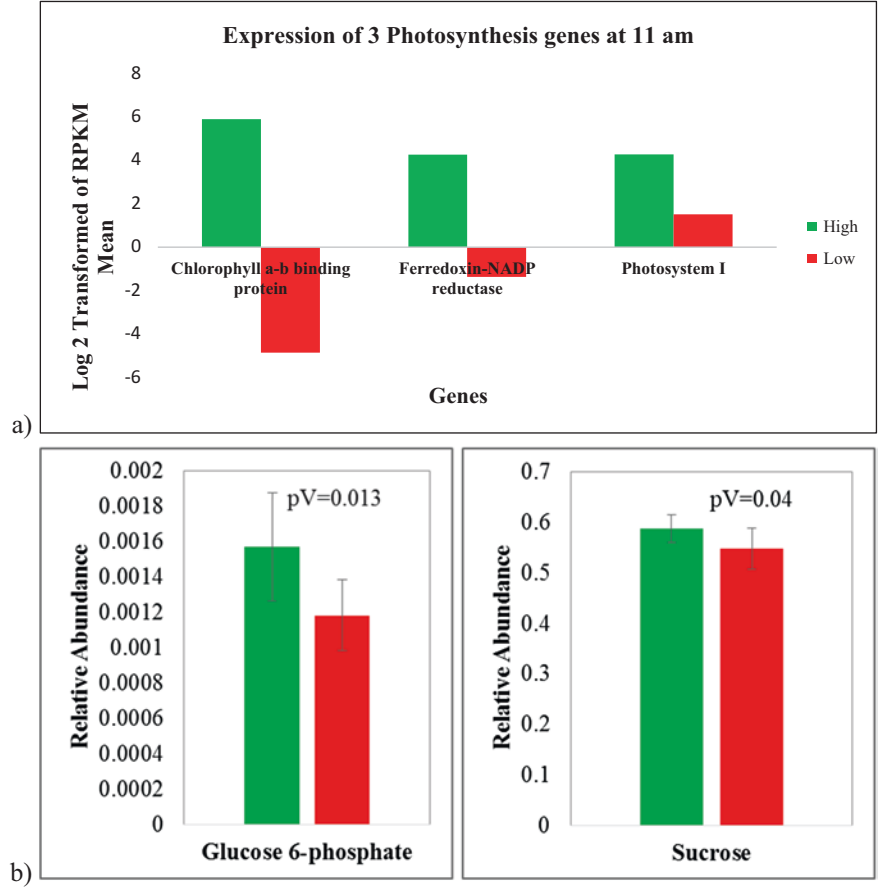


Fig. 2.1 Expression of photosynthesis-related genes and metabolites in oil palm leaf. **(a)** Differential expression of three photosynthesis-related genes in high and low yielder palms by RNAseq. Significant $Q > 0.85$ is explained by the probability of equivalent expression in Noiseq (Zheng and Moriyama 2013); **(b)** Abundance of G6P and sucrose in high and low yielder palms. pV indicated the p -value between high- and low-yielding palms, $pV < 0.05$ is considered significantly difference

protoplasts (Stitt et al. 1983). The increase in G6P and sucrose is attributed to increasing light intensities and CO₂ concentration, where both are key sources for photosynthesis. In oil palm, the elevated CO₂ concentration and interception radiation have led to the increase of biomass and bunch dry matter production (Squire and Corley 1987; Ibrahim et al. 2010).

2.3.2 Diurnal Cycle

Plants are exposed to changing environmental conditions, and one of the most common is the daily alternation between light and darkness. In an effort by Rees (1961) in monitoring midday closure of stomata in oil palm in Nigeria, he found that diurnal stomatal opening differed during the wet and the dry seasons. In the wet season, stomata opened early in the morning and remained wide open throughout the day before closing in the early evening. While in the dry season, partial closure of stomata occurred during the middle of the day (Rees 1961; Carr 2011). In Malaysia, Henson (Henson and Chang 1990; Henson 1991) found that stomatal conductance peaked in mid-morning and then progressively declined in the afternoon. The same diurnal pattern was obtained under clear sky conditions regardless of the age of the palms, although actual conductance increased with age.

Metabolic processes in plants and most other organisms operate in concert with day/night cycles. This coordination is accomplished by diurnal oscillations in transcriptional and posttranscriptional activities integrated with light, temperature, carbon status and circadian signalling (Usadel et al. 2008). Through this arrangement, metabolic pathways in the cell can sense and anticipate environmental cues (Mangelsen et al. 2010).

In our study, sampling of 20 adult palms was carried out at five time points (7 am, 11 am, 3 pm, 7 pm and 7 am the following day) to monitor the metabolites and expression changes in relation to the diurnal cycle. In the diurnal expression study, we observed the abundance of transcript encoding chlorophyll a-b binding protein reached its peak at 11 am and decreased slowly throughout diurnal cycle. The expression of the transcript encoding ferredoxin reached its peak, slightly later at 3 pm (supplementary data) and remained constant for several hours before eventually decreasing after sunset. As there was no measurement taken between 11 am and 3 pm, actual peak expression of these genes may occur during midday time. *CAB* which forms a complex structure with *PSI* and *II* captures solar energy for the excitation of the photosystems. The released electron from photosystems will be used to reduce $NADP^+$ to *NADPH* via *ferredoxin* and *ferredoxin-NADP reductase (FNR)*. The energy generated (ATP) is then transferred into the Calvin cycle, which is required by ribulose-biphosphate to capture carbon dioxide via *RuBisCO*. From our diurnal expression study, the expression of the gene encoding *CAB* reached the peak early into the sunlight hours, suggesting its importance in the capture of solar energy for photosynthesis under light-limiting conditions. The expression then appeared to decrease once light intensity was not a limiting factor. The expression continued to decrease until the beginning of the following diurnal cycle. *PSI* and *ferredoxin* were expressed at lower levels during the early stages of the diurnal cycle and increased gradually once light intensity increased and reached the peak expression at light saturation when photosynthesis reached its maximum (11 am–3 pm). When light intensity increases and more electrons are being transferred away from the photosystems, it is suggested that more *ferredoxin* and *FNR* are needed to reduce $NADP^+$ to *NADPH* and enter into Calvin cycle together with energy produced

through *ATP synthase* complex. Study by Chang et al. (2017) also concluded that overexpression of *ferredoxin*-like protein improves production of rice by enhancing the capacity of photosynthetic carbon assimilation through higher efficiency of electron transport and gas exchange rate.

Metabolites such as sugar and sugar phosphates displayed a diurnal trend that was low during limited light (7–11 am), and peaked at midday (peak photosynthesis) at 11 am to 3 pm, and decreased as light reduced (3–7 pm) (Fig. 2.2). This is in agreement with the findings of Bläsing et al. (2005) whereby the photosynthetic carbon fixation in leaves supports the synthesis and export of sucrose to the remainder of the plant to support metabolism, storage, and growth during the day. At night, the plant becomes a net consumer of carbon. The supply of sugars from photosynthesis can increase the rates of nitrate and ammonium uptake and assimilation, the synthesis of organic acid acceptors, and the synthesis of amino acids (Stitt and Krapp 1999).

We also observed the accumulation of amino acids with the increase of sugars early in the day. The diurnal trend for Gln was similar to sugar where it peaked at 3 pm, whereas the concentration for other amino acids decreased after 11 am but increased again after 3 pm till the next morning (Fig. 2.2). In agreement with previous reports by Kovtun and Daie (1995) and Lam et al. (1995), we found the concentration of several amino acids (Fig. 2.2) were higher at night (except for Gln) compared to during the day time when photosynthesis was active. These amino acids are presumably important for nitrogen storage and transport for the allocation of nitrogen resources between source and sink organs, especially at the beginning of the night (Kovtun and Daie 1995; Lam et al. 1995). In oil palm, amino acids were found to be highly concentrated in high-yielding palms during mesocarp (sink) development (Teh et al. 2013), where 35% larger mesocarp was recorded in high-yielding palms compared to a low-yielding population. Teh et al. (2013) highlighted that the accumulation of amino acids at this stage could possibly support the production of proteins necessary for lipid biosynthesis and cell division required for mesocarp development.

2.3.3 Abiotic Stresses

Abiotic stresses in oil palm range from nutrient deficiency, flooding, climate change, drought and high salinity. In the oil palm industry, the El Nino weather effect is a serious concern, and prolonged drought can attribute to an 8% reduction in palm oil production in Malaysia (Shean 2016). The changes in weather pattern and low rainfall lead to soil water deficit and reduce bunch yield (Bakoumé et al. 2013; Gawankar et al. 2003). Reduced leaf production due to water stress by as much as 30% during the early growth phase and by 12.5% in the later growth phase has been observed (Gawankar et al. 2003). In addition, early closure of stomata due to moisture stress may reduce net photosynthesis, and ultimately fresh fruit bunch (FFB) production (Smith 1989). Other than that, photosynthesis-related parameters, such as content of

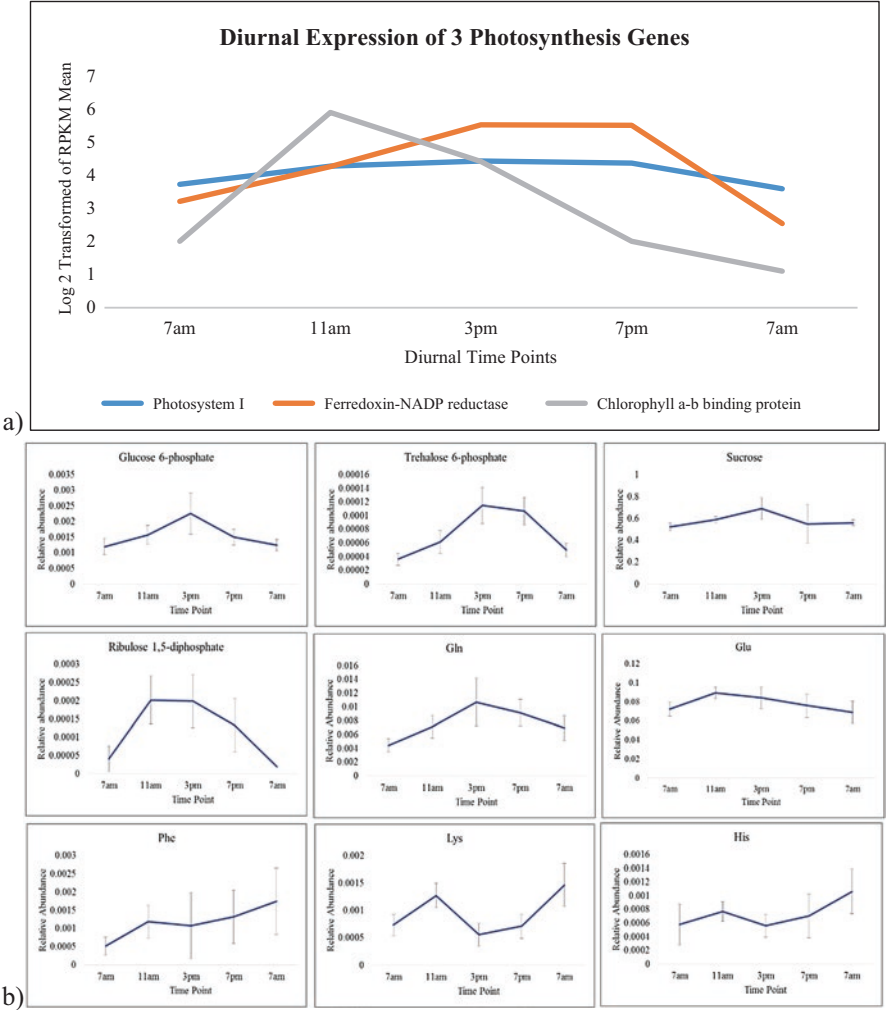


Fig. 2.2 Diurnal changes of photosynthesis-related genes and metabolites. **(a)** Expression of *Photosystem I*, *chlorophyll a-b binding protein* and *ferredoxin-NADP reductase* throughout diurnal cycle; **(b)** different trends of metabolites changes monitored throughout diurnal cycle from limited light to peak and back to limited light

chlorophyll a (chla), chlorophyll b (chlb) and total chlorophyll (chl), along with density, length and width of stomatal aperture, stomatal conductance and transpiration rate, photosynthetic rate and photosynthetic activity per plant have been reported to be used for selecting drought tolerant material for oil palm breeding (Kallarackal 1996; Suresh et al. 2010, 2012; Chaum et al. 2012; Méndez et al. 2012; Cha-um et al. 2013; Jazayeri et al. 2015; Putra and Purwanto 2015; Azzeme et al. 2016). According to Méndez et al. (2012), the selection of potential genotype for

drought tolerant breeding material should encompass the following criteria: (1) highest photosynthetic rate, (2) the lowest respiratory rate, (3) highest efficiency to move its assimilates mainly towards the roots and (4) the ability to adjust its water potential (active accumulation of sugars) during stress. The reduction of chl content and the ratio of chl_a to chl_b (chl_a:chl_b) were significant in drought-stressed oil palm seedlings (Azzeme et al. 2016). The significant reduction of chl_a was closely related to *PSII* deficiency. Genes encoding ethylene responsive binding protein, *late embryogenesis abundant (LEA)*, *dehydrin (DHN)*, cold-induced, *heat shock protein 70* and *metallothionein type 2* were differentially up-regulated in the leaves, while in the roots, only genes encoding *LEA* and *DHN* were up-regulated. The proline content increased in both vegetative tissues, while the total soluble protein content was affected by increasing drought severity. The activity of catalase was highest in the roots during severe drought, while guaiacol peroxidase activity was shown to be the highest in the leaves under mild drought (Azzeme et al. 2016). In a polyethylene glycol induced drought stress, maximum quantum yield of *PSII* (F_v/F_m) and photon yield of *PSII* in the oil palm seedlings under water deficit conditions dropped significantly in comparison to the control group, leading to a reduction in net-photosynthetic rate (*P_n*) (Cha-Um et al. 2010b). Although some of the above-mentioned drought symptoms were similar to nutrient stress, it was reported that the water stress had a greater influence on oil palm (Sun et al. 2011).

In a salinity stress study on oil palm seedlings, photosynthesis phenotypes including chl_a, chl_b, chl, total carotenoids, maximum quantum yield of *PSII*, photon yield of *PSII* and quantum efficiency of *PSII* in the seedlings under salt stress dropped significantly in comparison to those of the control group, leading to a reduction in net-photosynthetic rate (*P_n*) and growth (Cha-Um et al. 2010a). A positive correlation between physiological and growth parameters (including sodium ion, relative electrolyte leakage, photosynthetic pigments, *P_n* and water oxidation in *PSII*) and plant dry weight was found, in which, the salt stress affected photosynthesis mechanism thus lowering the oil palm biomass.

2.3.4 Diseases (*Ganoderma* and *Fusarium*)

Using a proteomics approach, Daim et al. (2015) found oil palm leaves infected with *Ganoderma boninense* revealed changes in proteins involved in photosynthesis. The abundance of photosynthesis-related enzymes such as *RuBisCO*, *RuBisCO* activase, *CAB* several different subunits of *ATP synthase* and *oxygen evolving enhancer protein 1 (OEE1)* of the light-harvesting complex were reduced in infected palms. Previous plant–fungi interaction studies have shown that reduction in photosynthesis rate during the infection process is attributed to a sugar-mediated repression of photosynthetic genes (Biemelt and Sonnewald 2006). However, the protein abundance of *FNR* from *PSI* was found to be increased two-fold by Daim et al. (2015). *Ferredoxin* may participate in other reactions in the chloroplast, including nitrogen and sulphur assimilation, amino acid, and fatty acid synthesis and also

redox regulation (Bilgin et al. 2010). The increase of *ferredoxin* may reflect its participation in pathogen defence. De novo transcriptomics study of host–fungal interactions in oil palm was carried out by comparing the root transcriptomes of untreated oil palm seedlings with those inoculated with *G. boninense* and *T. harzianum*, respectively (Ho et al. 2016). Ho et al. (2016) found that among the down-regulated genes in *Ganoderma*-treated oil palm roots were those related to the generation of precursor metabolites and energy, photosynthesis, electron transport chain, ribosome biogenesis, *xyloglucan:xyloglucosyl transferase* activity and others. Both findings showed that the photosynthesis-related genes were down-regulated in *Ganoderma* infected palm.

Unlike *Ganoderma* which is prevalent in Malaysia coastal areas, *Fusarium* wilt is the most destructive disease of oil palm in Africa and causes severe losses in Côte d’Ivoire, Nigeria, Ghana, Cameroon and Congo (Flood 2006). To date, the photosynthesis of oil palms infected with *Fusarium* wilt has not been thoroughly studied. According to Mepsted et al. (1995), the stomata conductance and internal CO₂ decreased along with an increase of photosynthesis in *Fusarium* infected oil palm seedlings. According to the author, the result might be due to non-uniform stomata closure, as reflected in the negative correlation of stomata conductivity to photosynthesis rate. Therefore, further study is needed to determine if the cause of photosynthesis rate changes in *Fusarium* wilt is entirely due to by stomatal closure or the other environmental effects.

2.4 Conclusion

Photosynthesis is a mechanism that fuels plant growth and development through the conversion of light energy, carbon dioxide and water into sugars and carbohydrates. The effort to increase photosynthesis efficiency in oil palm is an important initiative to improve oil yield potential through the selection of genotypes with higher expression of photosynthesis genes such as *CAB*, *FNR* and *PSI*. Omics platforms can contribute to the selection of breeding materials that can perform better under light-limiting conditions, such as shading from neighbouring palms and cloud cover, and that have overall increases in photosynthesis early and late in the day. In fact, photosynthesis is also a useful tool to phenotype and determines the condition of palms under abiotic or biotic stresses. Omics studies can complement marker assisted breeding by providing more accurate or physiologically linked traits. Identification of selection markers associated with these traits can then increase the accuracy of drought and *Ganoderma* tolerant breeding material identification and selection, which is critical to the oil palm industry in Malaysia.

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