

Genomewide SNP marker identification associated with drought tolerance in oil palm

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Abstract. *Yono D, Nugroho YA, Tanjung ZA, Utomo C, Liwang T. 2021. Genomewide SNP marker identification associated with drought tolerance in oil palm. Biodiversitas 22: 3138-3144.* Drought stress is one of the abiotic stresses that frequently occurred in the oil palm plantation and has a negative impact on fresh fruit bunch (FFB) production. Therefore, drought-tolerant palms are essential to be selected to mitigate this challenge. In Indonesia, several oil palm plantation areas have a dry climate, such as Lampung province. Distinct yield performance palms were identified from well-recorded agronomic trials in these areas, where the palms are frequently exposed to drought stresses every year and lead them to suffer from water deficit response. Group of high and low-yielding palms was selected based on FFB production of each palm for at least ten constitutive years. The double digest restriction amplified DNA (ddRAD) genotyping methods were used to capture the Single Nucleotide Polymorph (SNP) variant from pools of sample association datasets. At least, 538k SNPs were identified from these pooled datasets. A bulked segregant analysis with a Case-Control approach was implemented to screen the contrast SNP profiles between both pools. A total of 56 association signals was selected from sequential filtering. These SNP sites are located in 21 genes. Further SNP validation and phenotypic verification are necessary to obtain SNPs marker for drought-tolerant palm selections.

Keywords: bulked segregant analysis, ddRAD, drought stress, FFB production, SNP.

Abbreviations: FFB: Fresh fruit bunch, ddRAD: double digest restriction amplified DNA, SNP: single nucleotide polymorph, MAS: marker-assisted selection, tGBS: targeted genotyping by sequencing

INTRODUCTION

Abiotic stress conditions in oil palm plantations such as the drought condition could negatively affect palm growth and productivity. One of the climatic phenomena that are associated with drought conditions is El Niño. El Niño is a large-scale oceanic warming event in the tropical Pacific Ocean (Wang et al. 2017) and occurs with an interval of about 6 years (Trenberth 2020). El Niño was identified to occur in 2015 in Lampung Province. Drought stress condition in Lampung oil palm plantation was shown by the rainfall pattern (Figure 1), which could reduce oil palm yield (Murugesan et al. 2017) and increase sex ratio of oil palm (Cros et al. 2013).

Oil palm that is more tolerant to drought stress is required to reduce the loss of productivity during water stress conditions. The bunch production was influenced by male inflorescence production and female flower or fruit bunch abortion which was induced by stresses (Adam et al. 2011). A conventional palm selection for drought-tolerance is performed by a multilocation test of progeny trials in the dry and wet areas. The gap of regional water deficit between locations and the yield performance between progenies are used as parameters to select palm genotypes that are more tolerant to drought stress. A conventional breeding selection to obtain this trait needs over 20 years

(Cros et al. 2015) of one breeding cycle. It comprises parental population planting, crossing and generating hybrids or progenies from selected parents, planting the progenies trials at multi locations, yield recording, and palm selection.

The selection process in oil palm breeding can be accelerated through molecular marker-assisted selection (MAS). About 40 years for two breeding cycles in conventional selection can be reduced to 24 years with MAS (Cros et al. 2015). Molecular markers can be collected or mining by comparing the distinct palms samples which can be performed in the field or the nursery trials.

Several molecular markers like DNAs, RNAs, proteins, metabolites, enzymes, and hormones can be used for MAS. At DNA level, the single nucleotide polymorphism (SNP) variant is abundant in the genome (Nugroho et al. 2019). SNP markers become more effective and efficient to assist the palm selection, through mass genotyping like fluorescence-based genotyping (Jatayev et al. 2017) and targeted genotyping by sequencing (tGBS) technology (Ott et al. 2017). Other molecular markers in RNAs, proteins, metabolites, enzymes, and hormone levels can be used to verify the SNP markers, together with other phenotypes like bunch numbers and fresh fruit bunch (FFB) production.

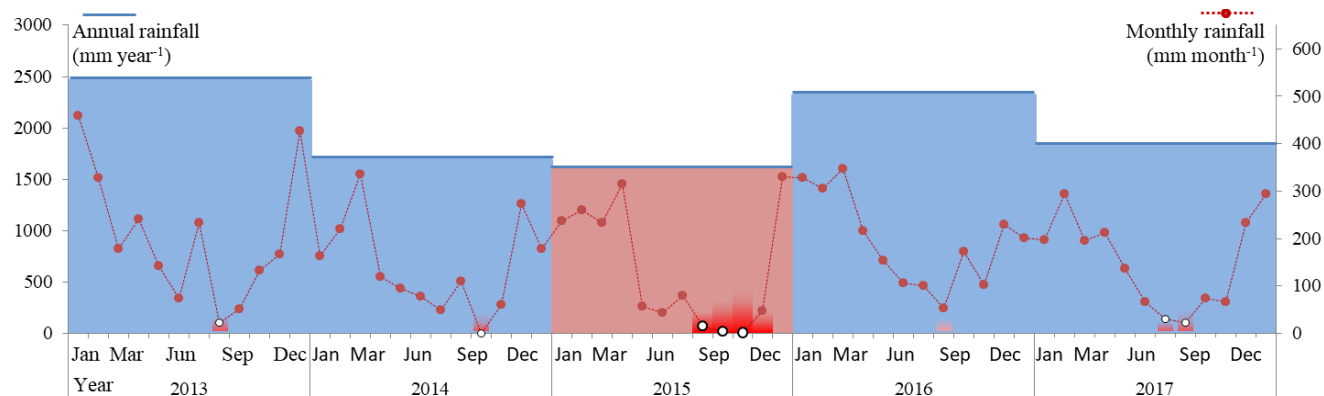


Figure 1. The rainfall distribution in Lampung-Indonesia (BPS 2015-1018). Three consecutive months in 2015 had very low rainfall, less than 17 mm month⁻¹, then considered as the water deficit period

MATERIALS AND METHODS

Palm selection

A set of association panels was generated from the individual mass selection of the palms from agronomic plot trials area in Lampung, Indonesia. This area was classified as a dry area with extensive agricultural drought conditions (Ma'rufah et al. 2017). The trial was established for over 18 years and the palms were severely exposed by water deficit in several years. The planting material was derived from commercial tenera (DxP) Marihat with unknown specific pedigree information. A total of 120 individual palms representing drought susceptible and drought-tolerant palms were selected from two identical trials based on the productivity recorded data. The average of bunch numbers (BN) and the fresh fruit bunch (FFB) weight were used as indicators to select both superior and inferior palms.

Tenera palms were selected based on fruit typing and shell thickness molecular markers (Singh et al. 2013). This selection retains 40 and 27 palms for the candidate of tolerant and susceptible palms, respectively (Table 1). This sample set was further used for the discovery of SNP marker associated with the drought stress response.

SNP mining and discovery

The genomic DNA (gDNA) was extracted from fresh mature leaves by the Nucleospin Plant II extraction kit (Macherey-Nagel; Düren, Germany). The quality and quantity of gDNA were checked using the NanoDrop 2000 (Thermo Scientific, USA) and run in 2% agarose gel electrophoresis. The gDNA was submitted to Novogene Laboratory (Beijing, China) for preparation of ddRAD-seq libraries and the Illumina HiSeq PE150 sequencing. Two restriction enzymes, *EcoRI* and *MseI* were used for DNA digestion (Nugroho et al. 2019). The DNA fragments were then ligated by a barcode adaptor in both DNA ends.

The raw sequencing reads were filtered and trimmed to get high-quality clean reads. To gain genetic variants, the clean reads of each sample were aligned to the EG05 reference genome of oil palm using BWA-MEM (Li 2013). SNPs were called with minimum quality >30 using

BCFtools programs: mpileup, call, and filter (Li et al. 2009). SNPs with the depth < 3, minor allele frequency (MAF) < 0.05, missing position < 10%, and number of alleles > 2 were removed using VCFtools (Danecek et al. 2011).

Association study of ddRAD result

A case-control study approach was applied to capture the associated SNPs with drought stress response for two groups of palm samples. SNP with minor allele frequency (MAF) more than 5%, has a biallelic variant type, and mapped into nuclear chromosomes was used for the association study. Two genotype parameters were observed, segregation in the samples and allelic odds ratio (Stare 2016). The significance of Odds ratio was calculated by standard normal distribution formula (Equation 1). The p-value was converted to the -Log₁₀ of p-value. The Manhattan plot of these -Log₁₀(p-value) was generated. Bonferroni threshold was calculated (Equation 2).

Equation 1. The p-value of odds ratio = $\text{NORM.S.DIST}(\text{LN}(\text{OR})/(\text{SQRT}((1/a)+(1/b)+(1/c)+(1/d))), \text{FALSE})$

Norm.s.dist = standard normal distribution, LN = natural logarithm, OR = odds ratio, Sqrt = the square root of a number, a;b;c;d = allele number in the two sample groups (Tolerant and Susceptible group) and two allele (the reference and alternate allele)

Equation 2. Bonferroni threshold = $-\log_{10}(0.05/\text{number of SNPs in the Manhattan plot})$

Table 1. Distinct palm samples from Lampung for SNP mining

	Tolerant samples (n=40 palms)		Susceptible samples (n=27 palms)	
	BN	FFB	BN	FFB
1 st Trial	10±1	206±15	6±1	115±12
2 nd Trial	9±1	208±11	6±1	129±10

Note: BN: bunch number (bunches/palm/year), FFB: fresh fruit bunch (kg/palm/year)

SNP with $-\text{Log}_{10}(\text{p-value})$ greater than or equal to the Bonferroni threshold was selected as associated and candidate markers. Heat map of the associated SNPs genotype in the samples was generated using the MS Excel™. The dendrogram of samples for selected SNPs was generated by DARwin software (Perrier and Jacquemoud-Collet 2006).

RESULTS AND DISCUSSION

SNP mining by ddRAD

The 538,093 SNP variants were detected by ddRAD genotyping that was distributed into 16 oil palm chromosomes. The 56 SNPs were detected with a higher association between distinct samples in drought response and have more than five of $-\text{Log}_{10}(\text{p-value})$ (Figure 2).

In the 4th chromosome, three SNPs groups have higher $-\text{Log}_{10}$ of Odds p-value (Figure 3). Four genes were related to the SNPs, consisting of MRL1, At1g35710, RNP1, and BDA1. In the 7th chromosome, five SNPs groups have higher $-\text{Log}_{10}$ of Odds p-value (Figure 4). Ten genes were related to the SNPs, consisting of PER7, SLAH2, SNRNP59, CYP74B2, NFD4, HK3, PUB1, LRP1, AKR2A, and β -gal.

In the 10th and 12th chromosomes, two SNPs groups have higher $-\text{Log}_{10}$ of Odds p-value (Figure 5). Four genes were related to the SNPs, consist of AHL1, PPD3, OVA3, and Uncharacterized gene (LOC105054577). In the 13th and 14th chromosomes, two SNPs groups have higher $-\text{Log}_{10}$ of Odds p-value (Figure 6). Three genes were related to the SNPs, consisting of CRY1, RNF1151, and CXP;2-31.

In total, there were 21 genes that areas located close to the associated SNPs with drought response from these oil palm samples. Six genes have SNP in the gene intron sequence and 15 genes were located close to these SNPs. Based on gene ontology, three genes were related to water deprivation, and four genes were related to signaling pathway, fatty acid metabolic process, H_2O_2 catabolic process, and root development respectively (Table 2).

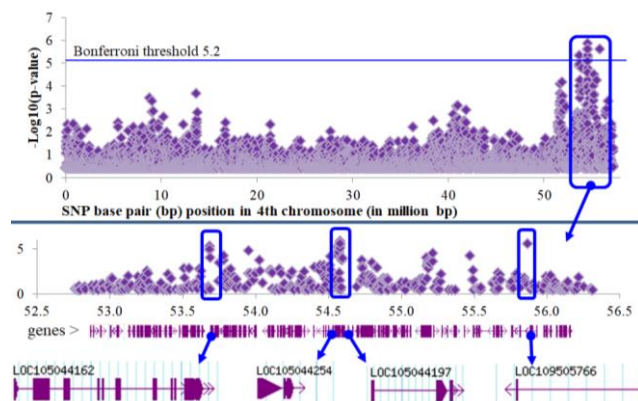


Figure 2. Associated SNPs in 4th Chromosome. Three SNPs clustered in 4th oil palm chromosome with $-\text{Log}_{10}$ of Odds p-value over the Bonferroni threshold

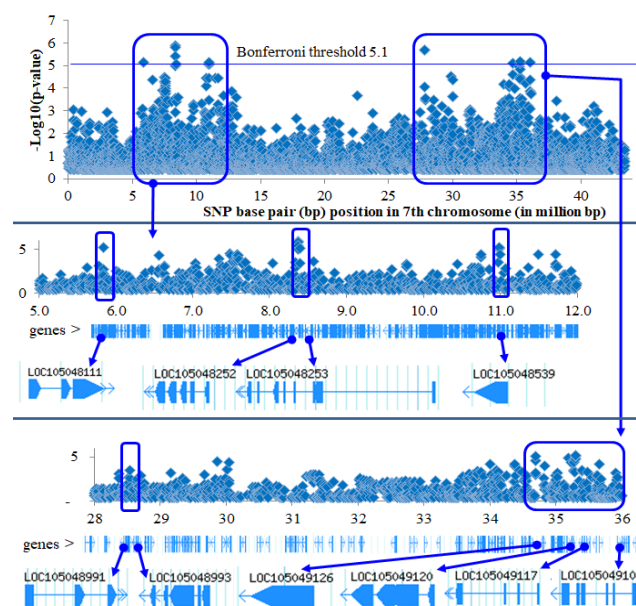


Figure 3. Associated SNPs in 7th Chromosome. Three SNPs groups in 7th oil palm chromosome with a higher $-\text{Log}_{10}$ of Odds p-value.

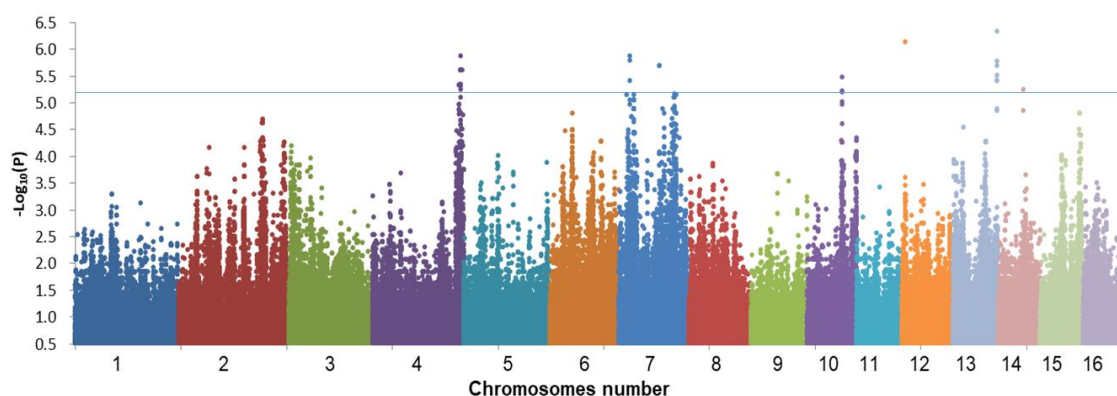


Figure 4. Allelic Manhattan plot. The p-value of odds ratio between alleles was converted to $-\text{Log}_{10}$. Higher significance of SNPs to the drought response was detected in 4th, 7th, 10th, 12th, 13th, and 14th chromosomes.

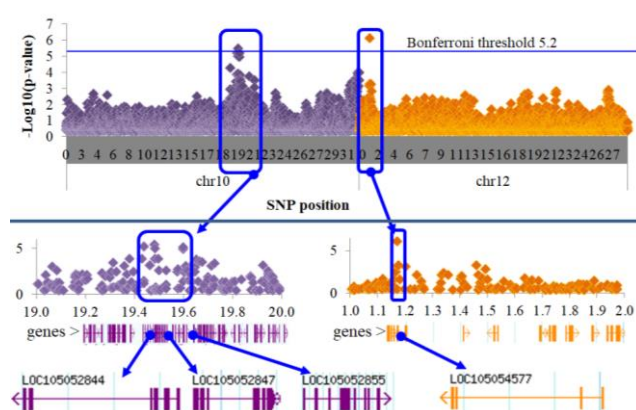


Figure 5. Associated SNPs in 10th and 12th Chromosome. One SNPs group in each 10th and 12th oil palm chromosome with a higher -Log10 of Odds p-value.

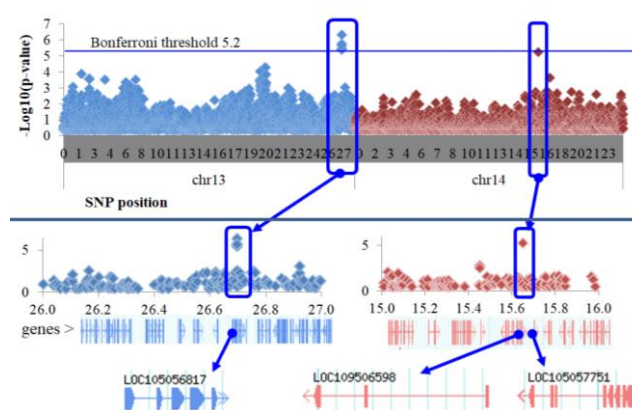


Figure 6. Associated SNPs in 13th and 14th Chromosome. One SNPs group in each 13th and 14th oil palm chromosome with a higher -Log10 of Odds p-value

Discussion

Palm response to drought stress is complex from a genomic perspective (Blum 2011; Xiong et al. 2006). Oil palm breeders have been trying to discover molecular markers for better drought-tolerant oil palm selection (Wang et al. 2020; Yono et al. 2019). In the root system, some mechanisms for abscisic acid (ABA) signal production begins that are triggered by rhizosphere water deficit. ABA signaling is delivered to some tissue and organ for next adaptations and other gene activations. These adaptations are important to maintain the osmolyte balance in the cells or for the ROS scavenging. The carbohydrate, amino acid, phenylpropanoid metabolism, and antioxidant enzymes were involved in plant drought stress response (Wang et al. 2019). Some associated genes in this study were involved in that mechanism (Table 2).

The internal plant signals are key factors for physiological adaptation mechanisms and induce the response to mitigate the non-optimal conditions around them, likewise the drought stress (Golldack et al. 2014). Several associated SNPs were located near the signaling pathway-related genes. These genes consisted of Atlg35710, CRY1, HK3, and CYP74B2 genes. An associated SNP was closely located to Atlg35710 gene that has a significant RNA transcription change in drought stress conditions (Klaas et al. 2019). Seven SNPs were located close to CRY1 (Cryptochrome-1) gene. The Cryptochrome gene was related to the abiotic stress response in the plant (Amico-damião and Carvalho 2018), like stomatal opening (Mao et al. 2005). Two SNPs were located near HK3 (histidine kinase) gene. A signal was triggered by the histidine kinase gene, leading to a plant adaptation in stress conditions (Osakabe et al. 2013). Ten SNPs were located close to hydroperoxide lyase (CYP74B2) genes. The hydroperoxide lyase gene functioned in oxylipin (Taurino et al. 2013) that as a signaling pathway (Savchenko et al. 2014). This hydroperoxide lyase gene was more expressed in drought-stress plants (Domenico et al. 2012). Some of these genes

are related to abscisic acid (ABA) hormone (Li et al. 2016) and the ABA was a key plant regulator in abiotic stresses condition like drought (Sah et al. 2016).

After internal signals were produced, some pathways take action to maintain the plant metabolism. Several associated SNPs were located around the DNA-RNA related genes, namely: MRL1, RNP1, SNRNP59, and AHL1. Four SNPs were located upstream of pentatricopeptide repeat (MRL1) gene. The pentatricopeptide repeat protein was has a stabilisation function of RNA (Prikryl et al. 2011). A SNP was located in the intron sequence of each RNP1 and SNRNP59. These genes were nuclear ribonucleoprotein, that have mRNA processing function in the plant (Shih et al. 2019). Two SNPs were located in the intron of AHL1 gene. The AHL gene was indicated in the regulation of some genes target in plant growth (Kim et al. 2011).

Other associated SNPs were located close to some genes in carbohydrates, amino acids, and photosynthesis pathways. Some modifications in carbohydrate stock were important to maintain plant life in stress conditions (Chuste et al. 2019; Cui et al. 2015). A SNP was located at the upstream of β -gal gene. This gene was related to the carbohydrate metabolic process and has a function in galactose metabolism (EC 3.2.1.23) and is related to cell wall modification (Liu et al. 2013). Amino acids have important roles in sustaining the plant cellular function under stress (Farooq et al. 2012). Several SNPs were located near amino acid-related genes, OVA3 (Haider et al. 2017) and CXP;2-31 (Prinsi et al. 2018). In the plant under drought stress conditions, the photosynthesis will be reduced, along with the increase of stomatal closure adaptation (Farooq et al. 2012). One SNP was located in the intron of PPD3 gene which was involved in the photosynthesis pathway (Liu et al. 2012).

The heat map and similarity dendrogram of these samples and associated SNPs were generated (Figure 7). From the heat map, there were some samples have the opposite genotype to the sample group. About 80%-94% of the samples were correctly clustered in a dendrogram.

Table 2. Description and regulation of genes with the associated SNP to drought stress response

Related Genes	Gene Code	Gene Ontology (UniProt and QuickGO)	Associated SNP	Location (±)
Pentatricopeptide repeat-containing MRL1 protein (LOC105044162)	MRL1	GO:0048255, mRNA stabilization	4	6.5 kbp from gene (upstream)
Probable leucine-rich repeat receptor-like protein kinase At1g35710 (LOC105044254)	At1g35710	GO:0009755, hormone-mediated signaling pathway	1	3.4 kbp from gene (downstream)
Heterogeneous nuclear ribonucleoprotein 1 (LOC105044197)	RNP1	GO:2000070, regulation of response to water deprivation	12	1 SNP in intron, 11 SNPs in the downstream of gene (3.1 kbp)
Ankyrin repeat-containing BDA1-like protein (LOC109505766)	BDA1	GO:0009751, response to salicylic acid	1	Intron
Peroxidase P7 (LOC105048111)	PER7	GO:0042744, H ₂ O ₂ catabolic process	1	1.2 kbp from the gene (downstream)
S-type anion channel SLAH2 (LOC105048252)	SLAH2	GO:0055085, transmembrane transport	4	6.2 kbp from the gene (downstream)
U11/U12 small nuclear ribonucleoprotein 59 kDa protein-like (LOC105048253)	SNRNP59	GO:0008380, RNA splicing	1	Intron
Probable inactive linolenate hydroperoxide lyase (LOC105048539)	CYP74B2	GO:0006631, fatty acid metabolic process	10	~1.6 kbp from the gene (upstream)
NUCLEAR FUSION DEFECTIVE 4-like Protein (LOC105048991)	NFD4	GO:0009651, response to salt stress	2	~48 kbp from the gene (upstream)
Probable histidine kinase 3 (LOC105048993)	HK3	GO:0009414, response to water deprivation		67 kbp from the gene (upstream)
U-box domain-containing protein 1 (LOC105049126)	PUB1	GO:0061630, ubiquitin-protein ligase activity	1	0.8 kbp from the gene (upstream)
LATERAL ROOT PRIMORDIUM 1 Protein (LOC105049120)	LRP1	GO:0048364, root development	1	37 kbp from the gene (upstream)
Ankyrin repeat domain-containing protein 2A (LOC105049117)	AKR2A	GO:0045036, protein targeting to the chloroplast	2	~7.5 kbp from the gene (upstream)
Beta-galactosidase (LOC105049109)	β-gal	GO:0009341, beta-galactosidase complex	1	21 kbp from the gene (upstream)
AT-hook motif nuclear-localized protein 1 (LOC105052844)	AHL1	GO:0043565, sequence-specific DNA binding	2	Intron
psbP domain-containing protein 3, chloroplastic (LOC105052847)	PPD3	GO:0015979, photosynthesis	2	1 SNP in intron, and 1 in 3'UTR
Glutamate--tRNA ligase, chloroplastic/mitochondrial (LOC105052855)	OVA3	GO:0004818, glutamate-tRNA ligase activity	2	~4 kbp from the gene (upstream)
Uncharacterized (LOC105054577); similar to Small Nucleolar RNA R71 (99%)	snoRNAR71	GO:0006396, RNA processing	1	Intron
Cryptochrome-1 (LOC105056817)	CRY1	GO:0009414, response to water deprivation	7	~14 kbp from gene (upstream)
E3 ubiquitin-protein ligase RNF115-like (LOC109506598)	RNF1151	-	1	22 kbp from gene (upstream)
Serine carboxypeptidase II-3-like (LOC105057751)	CXP;2-31	GO:0004185, serine-type carboxypeptidase activity		25 kbp from the gene (downstream)
Total			56	SNP

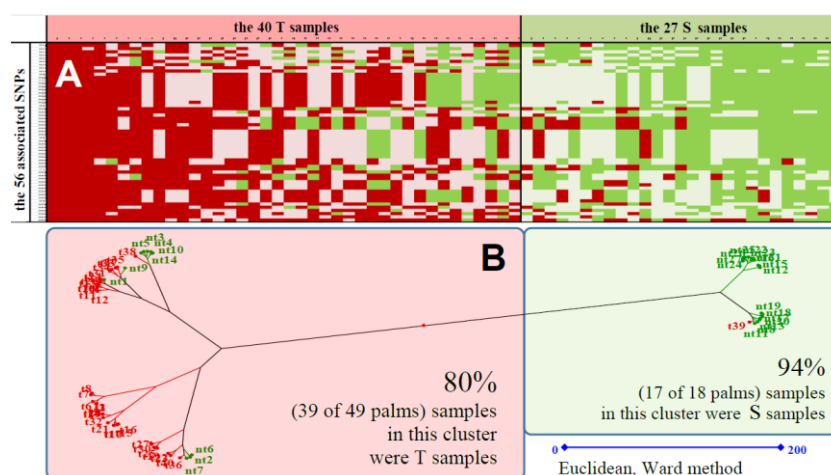


Figure 7. Distinct Samples heat map (A) and dendrogram (B). The heat map and dendrogram were generated from distinct samples with 56 associated SNPs. T: more tolerant palm to drought stress, S: susceptible palm. Cell color in heat map: Red: more tolerant genotype, green: more susceptible genotype, pink and light green: moderate genotype

A total of 56 association signals was identified according to the case-control bulked segregant analysis approach. Several SNPs are closely located to the drought response-related genes, although they need to be verified further in different sample datasets and genetic backgrounds to generate the common markers for drought tolerance. In parallel, the validation using targeted gene expression and phenotypic observation for drought stress response will be also essential to be observed further.

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