Comparison of drought tolerance of banana genotypes

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Genet. Mol. Res. 19 (2): gmr18544

Received January 16, 2019

Accepted March 31, 2020

Published June 30, 2020

DOI <http://dx.doi.org/10.4238/gmr18544>

ABSTRACT. Banana is an important international economical crop, but drought is the most significant environmental stress in banana industry. Previous studies on banana drought tolerance evaluated just a few indicators, such as malondialdehyde (MDA) and plasma membrane permeability (PMP), with little or no systematic morphological and physiological information. We examined the morphological and anatomical structure characters of nine genotypes among 28 banana varieties from the variety resource nursery of China academy of tropical agricultural sciences, and combined physiological markers (PMP and MDA) with morphological data. Leaf thickness, upper leaf epidermis and cutin thickness, palisade tissue thickness, spongy tissue thickness, lower leaf epidermis and cutin thickness, cell tense ratio (CTR), PMP and MDA content were significantly different among these varieties. Banana varieties were divided into three groups by cluster analysis based on a CTR index or a MDA content index, and the varieties were divided into two groups by cluster analysis based on the PMP index. Based on discriminant functions, the original classification was confirmed, and the result of discriminant classification was 100% correct. Three discrimination models with superior distinguishing abilities were established.

Key words: Banana; Genotypes; Cluster Analysis; Drought Resistance

INTRODUCTION

Banana (*Musa* spp.) is grown in more than 120 countries throughout the world. They are cheap to produce, grow in a wide range of environments, and produce fruit year-round. China is one of centers of banana origin (Wu et al., 2013). Bananas are also food for more than 400 million people throughout the developing countries from tropical and subtropical areas, and are considered as the poor man's fruit crop in tropical and subtropical countries, with the annual production reaching 144 million tons (Christelová et al., 2017; Dale, 2017). The banana plant is sensitive to soil water deficit (Turner et al., 2007). Drought is a major abiotic stress affecting banana production worldwide, leading to yield losses of up to 65%. (Nansamba et al., 2020). To survive under water deficit conditions, plants respond by change in expression of many genes (Laraib et al., 2019). Because of the large leaf area, fibrous root system and rapid growth rate, bananas need a large amount of water for proper growth and development (Stover & Simmonds, 1987). Drought stress is one of the most serious yield-reducing stresses in banana industry, especially important in countries where crop agriculture is essentially rain-fed (Ghavami, 1976; Ekanayake, 1995; Bananuka et al., 1999; Carr, 2009; van Asten et al., 2011; Muthusamy et al., 2014). Cultivated bananas originated either from intraspecific hybridizations between wild diploid subspecies of *Musa acuminata*. ('A' genome), or from interspecific crosses between *M. acuminata* and the wild diploid *M. balbisiana*. ('B' genome) (Simmonds, 1995). Stover and Simmonds (1987) stated that bananas with the B genome were the most drought tolerant. Genotypes with "B" genome are more tolerant to abiotic stresses than those solely based on "A" genome (Ravi et al., 2013). Drought is an abiotic stress that strongly influences plant growth, development and productivity (Ye et al., 2013). Consequently, the relationship between different banana genotypes and their drought tolerance has become a hot research topic. Huang et al. (1999) and Bananuka et al. (1999) proposed that the more B genome the varieties are, the stronger drought tolerance they will be. While the more A genome those varieties are, the worse drought tolerance they may have. Cultivars with predominately A genomes and triploid cultivars may gave greater reductions in yield and yield components during moisture stress than cultivars with predominately B genomes and diploids and tetraploids (Ramadass et al., 1993). However, the correlation was not so tight because they selected only a few varieties as experimental materials, such as Huang et al. (1999) who examined three varieties [Williams (AAA), Zhongshanlongyajiao (AAB), Fenshajiao (ABB)] and Bananuka, et al. (1999) who texted six varieties [Nfuuka(AAA-EA), Sukalindizi(AB), French Plantain(AAB), Gros Michel(AAA), Lep Chang Kut(BBB), FHIA-2(AAAA)]. One variety could not represent all varieties in a corresponding genotype. Drought tolerance is a complex trait, the expression of which depends on action and interaction of different morphologies, physiologies and biochemistries. Morphological and physiological characters show different types of inheritance patterns (monogenic and polygenic) and gene actions (additive and non-additive), and very little is known about the genetic mechanisms that condition these characters (Mitra, 2001). In our study, we selected 28 banana varieties, including nine different genotypes, as experimental materials. Their drought tolerance and how they related to morphological and anatomical structure characters of leaves were observed by paraffin sectioning and the PMP, MDA content of leaves were measured. Cluster analysis is one of the analytic methods widely applied in quantitative taxonomy research, especially in the identification of plant germplasm

resources and plant phylogenetic relationship (Zhang et al., 2013; Ai et al., 2014; You et al., 2014). Cluster and discrimination analysis techniques were used to study drought tolerance related characters of 28 different varieties of banana. The aim of this study was to examine the relationship between different genotypes and drought tolerance of banana and whether related genes distributed in the B chromosomes control drought tolerance or not. The ultimate purpose of this study was to provide a theoretical basis and practical methodology for drought tolerance breeding and cultivation.

MATERIAL AND METHODS

Materials (Table 1) were collected from the banana germplasm nursery of tropical crops genetic resources institute, Chinese academy of Tropical Agricultural Sciences. The third leaves from the top were cut as samples after the male flower cluster was cut off.

Table 1. Description of banana varieties in the study

Code	Variety	Genotype	Code	Variety	Genotype
1	'Babeiduo'	AAA	15	'Dongguan Gaobadajiao'	ABB
2	'Brazil'	AAA	16	'Dongguan Zhongbadajiao'	ABB
3	'Cros-Michel'	AAA	17	'Mengjiala Dajiao'	ABB
4	'Hongxiangjiao'	AAA	18	'Mengjiala Fendajiao'	ABB
5	'Baoting Aixiangjiao'	AAA	19	'Cachaco'	ABB
6	'Honghe Aijiao'	AAA	20	'Pisang Ceylan'	AAB
7	'Bawangling Yeshengjiao'	AA	21	'FHIA-17'	AAAA
8	'AACV Rose'	AA	22	'FHIA-25'	AAAA
9	'Pisang Jari Buaya'	AA	23	'FHIA-01'	AAAB
10	'Lingshui Yeshengjiao'	AA	24	'FHIA-18'	AAAB
11	'Baihualing Yeshengjiao'	BB	25	'FHIA-21'	AAAB
12	'Qujiang BB'	BB	26	'CRBP 39'	AAAB
13	'Yunnan BB'	BB	27	'FHIA-03'	AABB
14	'Shixing BB'	BB	28	'TMBx 5295-1'	ABBB

Measurements of anatomical structures

Measurement of characteristics of leaf anatomical structure was made with a paraffin sectioning method (Li, 2009). Thickness of leaf, thickness of upper leaf epidermis and cutin, thickness of palisade tissue, thickness of spongy tissue, thickness of lower leaf epidermis and cutin, cell tense ratio (CTR), spongy ratio (SR) were measured. Computational method for CTR and SR used Jian's method (1986).

Measurement of physiological characters

The PMP (plasma membrane permeability) reflects membrane injury. It was measured using the method of Bajji et al. (2001). Concisely, we cut the leaves (0.50 g) and incubated in 25 ml of distilled water at 25°C for 8 h. We measured the leakage of electrolyte to culture fluid with a conductivity meter (*Del Ta326, Mettler Toledo*, Switzerland).

Determination of membrane lipid peroxidation from malondialdehyde content (MDA), was made based on Hong et al. (2000). Approximately 0.5 g of the leaves were homogenized in 5 ml of 10% (m/v) trichloroacetic acid, and the homogenate was

centrifuged at 13 000 rpm for 15 minutes. The supernatant was mixed with an equal volume of thiobarbituric acid (0.5% in 20% trichloroacetic acid solution). The mixture was boiled at 100°C for 30 minutes, and then centrifuged. The absorbance of the supernatant was measured at 532 nm, and the non-specific turbidity was corrected by subtracting A600. The MDA content was calculated using the absorption coefficient of 155 mmol⁻¹ cm⁻¹. Four replicates were used for each treatment.

Data analysis

The data were statistically analyzed by analysis of variance (ANOVA). Averages of the main effects were compared by the Duncan test. The correlation between the characters was analyzed using by CORR process. Cluster analysis of each character used CLUSTER process and discrimination analysis of each character used DISCRIM process. All statistical analyses were performed by using SAS 9.0 software.

RESULTS

The differences between drought tolerance related characters of different banana varieties

Figure 1 showed the partial anatomical structures of leaves of different banana varieties. Figure 2 is the comparison of anatomical structure features of leaves among different banana genotypes. The results of variance (Table 2) showed that among the tested varieties, differences of thickness of leaf, thickness of upper leaf epidermis and cutin, thickness of palisade tissue, thickness of spongy tissue, thickness of lower leaf epidermis and cutin, CTR, SR, PMP, MDA content were highly significant. The mean thickness of leaf was 360.520 µm; the thickest variety was CRBP 39, and its thickness was 534.064 µm; the least thick variety was Pisang Jari Buaya, and its thickness was 253.009 µm. The mean of thickness of upper leaf epidermis and cutin was 52.657 µm, and the range was 30.179 µm to 77.366 µm. The variety with the greatest thickness of palisade tissue was FHIA-17, and its thickness was 124.539 µm; the least thick variety was Pisang Jari Buaya, and its thickness was 69.930 µm. The variety with the greatest thickness of spongy tissue was CRBP 39, and its thickness was 289.854 µm; the least thick variety was Cachaco, and its thickness was 92.859 µm. The mean thickness of lower leaf epidermis and cutin was 45.430 µm, and the range was 25.912 - 0.696 µm. The variety with the largest CTR was Cachaco, and its thickness was 62.76%; the least thick variety was Pisang Ceylan, and its thickness was 39.34%. The variety with the largest SR was Pisang Ceylan, and its thickness was 60.63%; the least thick variety was Cachaco, and its thickness was 37.19%. The mean of PMP was 27.472%, and the range was 17.568 - 37.384%. The mean of MDA content was 225.568 nmol/g, the range was 78.065 - 365.591 nmol/g, and the difference of maximum and minimum was 4.683 times.

Figure 1. The parts anatomical structures figure of leaves of different banana varieties. A: Cutin B: Upper leaf epidermis C: Palisade tissue D: Spongy tissue E: Aerenchyma F: Fibrovascular tissue G: Lower tight tissue H: Lower leaf epidermal.

Figure 2. The comparison of anatomical leaf structures figures among different banana genotypes (Scale bar = 100µm) A : Brazil banana (AAA); B : Pisang Jari Buaya (AA); C : Qujiang BB(BB) D : Pisang Ceylan (AAB) ; E : Cachaco (ABB); F : FHIA-25 (AAAA) G : FHIA-18 (AAAB); H : FHIA-03(AABB); I : TMBx 5295-1 (ABBB).

Table 2. Variance of drought tolerance related characters among banana varieties.

Item	Source of variance	DF	Sum of squares	Mean square	F value	Means	Range	CV
Thickness of leaf	Among varieties	27	2009608.26	74429.94	146.27**	360.52±22.58	253.01~534.06	6.26
	Error	247	125684.88	508.85				
	Total	274	2135293.14					
Thickness of upper leaf epidermis and cutin	Among varieties	27	32268.67	1195.14	34.82**	52.66±5.86	30.18~77.37	11.13
	Error	247	8478.17	34.33				
	Total	274	40746.84					
Thickness of palisade tissue	Among varieties	27	57598.97	2133.30	36.49**	90.59±7.65	69.93~124.54	8.44
	Error	247	14441.74	58.47				
	Total	274	72040.71					
Thickness of spongy tissue	Among varieties	27	982991.22	36407.08	93.06**	171.67±19.79	92.86~289.85	11.52
	Error	247	96626.92	391.20				
	Total	274	1079618.14					
Thickness of lower leaf epidermis and cutin	Among varieties	27	41515.31	1537.60	21.65**	45.43±8.43	25.91~70.67	18.55
	Error	247	17543.17	71.03				
	Total	274	59058.48					
CTR	Among varieties	27	11606.44	429.87	33.75**	53.50±3.57	39.34~62.76	6.67
	Error	247	3146.08	12.74				
	Total	274	14752.52					
SR	Among varieties	27	11663.73	431.99	33.92**	46.45±3.57	37.19~60.63	7.68
	Error	247	3145.75	12.74				
	Total	274	14809.48					
PMP	Among varieties	27	2344.19	86.82	11.34**	27.47±2.77	17.57~37.38	10.07
	Error	56	428.93	7.66				
	Total	83	2773.12					
MDA content	Among varieties	27	435645.26	16135.01	40.23**	225.57±20.026	78.07~365.59	8.88
	Error	56	22458.38	401.04				
	Total	83	458103.64					

** means significant at 1% level. Abbreviations: MDA, malondialdehyde; CTR, cell tense ratio; PMP, plasma membrane, permeability; SR, spongy ratio.

Linear regression of CTR, plasma membrane permeability and MDA

The scatter distribution between CTR and PMP is shown in Figure 3a. By the linear regression analysis, their equation was $y = -0.4854x + 53.505$ (x means CTR, and y means PMP), and their correlation coefficient was -0.5986, which gave a highly significant negative correlation by the F test. The linear regression equation of CTR and MDA was $y = -6.3407x + 565.6$ (x means CTR, and y means MDA), and their correlation coefficient was -0.5735, which gave a highly significant negative correlation (Figure 3b). The linear regression equation of PMP and MDA was $y = 11.918x - 101.86$ (x means PMP and y means MDA), and their correlation coefficient was 0.8743, which gave an highly significant positive correlation (Figure 3c).

Figure 3. Line regression relationships between CTR, PMP and MDA. Abbreviations: MDA, malondialdehyde; CTR, cell tense ratio; PMP, plasma membrane permeability.

Cluster Analysis of CTR

The results showed that (Table 3) 28 different banana varieties could be divided to 3 groups by the dendrogram (Figure 4). Cluster 1 consisted of 16 species (two AAA genome types, three AA genome types, four BB genome types, three ABB genome types, one AAAA genome type, two AAAB genome types, one AABB genome type), their CTR were large, and their drought tolerance were strong; Cluster 2 consisted of 10 species (four AAA genome types, one AA genome type, two ABB genome types, one AAAA genome type, one AAAB genome type, one ABBB genome type), their CTR were moderate, and their drought tolerance were moderate; Cluster 3 consisted of 2 species (one AAB genome type, one AAAB genome type), their CTR were low, and their drought tolerance were inferior.

Table 3. Classification for CTR of different banana varieties.

Cluster	Code of variety	Number of varieties	Frequency (%)	Mean of cluster	Range
1	2, 3, 7, 8, 9, 11, 12, 13, 14, 17, 18, 19, 22, 24, 25, 27	16	57.15	58.90±0.34 A	54.59~62.64
2	1, 4, 5, 6, 10, 15, 16, 21, 26, 28	10	35.71	48.17±0.37 B	45.35~51.06
3	20, 23	2	7.14	40.98±0.68 C	39.39~42.57

Figure 4. Dendrogram of banana varieties based on the CTR data. (Variety code 1 - 28, see Table 1).

Cluster Analysis of plasma membrane permeability

The results showed that (Table 4) 28 different genotypes varieties of banana could be divided into 2 groups by the average class (Figure 5). Cluster 1 consisted of 17 species (one AAA genome type, three AA genome types, four BB genome types, three ABB genome types, one AAAA genome type, four AAAB genome types, one AABB genome type), their PMP were low, and their drought tolerance were strong; Cluster 2 consisted of

11 species (five AAA genome types, one AA genome type, two ABB genome types, one AAB genome type, one AAAA genome type, one ABBB genome type), their PMP were large, and their drought tolerance were inferior.

Table 4. Classification based on PMP of different banana varieties.

Cluster	Code of variety	Number of varieties	Frequency(%)	Mean of cluster	Range
1	2, 7, 8, 9, 11, 12, 13, 14, 17, 18, 19, 22, 23, 24, 25, 26, 27	17	60.71	23.68±0.41 B	17.60~26.59
2	1, 3, 4, 5, 6, 10, 15, 16, 20, 21, 28	11	39.29	33.33±0.68 A	28.71~37.38

Figure 5. Dendrogram of banana varieties based on the relative conductivity data. (Variety code 1 - 28, see Table 1).

Cluster Analysis of MDA

The results showed that (Table 5) 28 different genotypes varieties of banana could be divided into 3 groups by the average class (Figure 6). Cluster 1 consisted of 3 species (one AAA genome type, two AAAB genome types), their MDAs were low, and their drought tolerance was strong; Cluster 2 consisted of 18 species (one AAA genome type, three AA genome types, four BB genome types, five ABB genome types, one AAAA genome type, two AAAB genome type, one AABB genome type, one ABBB genome type), their MDA were moderate, and their drought tolerance were moderate; Cluster 3 consisted of 7 species (four AAA genome types, one AA genome type, one AAB genome type, one AAAA genome type), their MDA were large, and their drought tolerance were inferior.

Table 5. Classification for MDA of different banana varieties.

Cluster	Code of variety	Number of varieties	Frequency(%)	Mean of cluster	Range
1	2, 24, 26	3	10.71	111.40±9.46 C	78.07~128.82
2	1, 7, 8, 9, 11, 12, 13, 14, 15, 16, 17, 18, 19, 22, 23, 25, 27, 28	18	64.29	203.14±3.98 B	161.08~255.27
3	3, 4, 5, 6, 10, 20, 21	7	25.00	332.17±7.44 A	284.95~365.59

Figure 6. Dendrogram of banana varieties based on the MDA data. (Variety code1-28, see Table 1).

Cluster Analysis of CTR, plasma membrane permeability and MDA

The results showed that (Table 6) 28 different genotypes varieties of banana could be divided to 3 groups by the average class (Figure 7). Cluster 1 consisted of 15 species (one AAA genome type, three AA genome types, four BB genome types, three ABB genome types, one AAAA genome type, two AAAB genome types, one AABB genome type), their CTR were large, plasmamembrane permeability and MDA were low, and their drought tolerance were strong; Cluster 2 consisted of 11 species (five AAA genome types, one AA genome type, two ABB genome types, one AAB genome type, one AAAA genome type, one ABBB genome type), their CTR were low, plasmamembrane permeability and MDA were large, and their drought tolerance were inferior; Cluster 3 consisted of 2 species (two AAAB genome types), their CTR were low, and plasmamembrane permeability and MDA were also low. By discrimination analysis after using cluster analysis, we used CTR, plasmamembrane permeability and MDA as discriminant variables to establish a discrimination function. According to discrimination function, we re-classified the original. Discrimination classification result was zero misjudgment. We considered that this research method established three discrimination models with better distinguishing abilities.

Table 6. Classification and discriminatory for CTR plasma membrane permeability and MDA of different banana varieties.

Cluster	Code of variety	Number of varieties	Frequency (%)	Discriminatory model	Mean of cluster		
					CTR	Plasmamem brane permeability	MDA
1	2, 7, 8, 9, 11, 12, 13, 14, 17, 18, 19, 22, 24, 25, 27	15	53.57	$Y = 8.7751CTR + 2.6921PP + 0.3003MDA - 318.6620$	59.07±0.34 A	23.88±0.44 B	183.61±4.45 B
2	1, 3, 4, 5, 6, 10, 11, 16, 20, 21, 28	11	39.29	$Y = 7.6128CTR + 4.1515PP + 0.2860MDA - 294.7513$	47.95±0.45 B	33.33±0.68 A	299.37±9.24 A
3	23, 26	2	7.14	$Y = 6.4407CTR + 3.0195PP + 0.1871MDA - 187.9265$	44.04±0.80 C	22.21±0.84 B	134.30±25.74 C

Figure 7. Dendrogram of banana varieties based on the CTR, plasma membrane permeability and MDA data. Abbreviations: MDA, malondialdehyde; CTR, cell tense ratio; PMP, plasma membrane permeability.

DISCUSSION

Currently, classification of bananas mostly follows the morphological classification proposed by Simmonds (1995). Subsequently some others also conducted on research on banana morphological markers (Ortiz, 1997; Osuji et al., 1997; Pilar et al., 1997; Karamura et al., 1998; Lai et al., 2007). However, these morphological characteristics are controlled by various genes and are influenced by environmental conditions simultaneously, so they could not exactly compare various germplasms. Chromosome number, karyotype, banding and behavior of meiotic division could be classified as one of strong evidences of resource classification and genetic relationships (Qin et al., 2007). Ravi et al. (2013) phenotyped bananas for drought resistance. Wang et al. (1994) found that none of the banana genomes came from AA genotype. Besides, AAA genotype was not all autotriploid, and AAB and

ABB genotypes were not necessarily allotriploid. Chen (2002) carried on the chromosome analysis to the part wild bananas and discovered that the germplasm of the wild bananas was diploid; the chromosome number had three kinds of situations of 18, 20 and 22. Our results showed that, according to the cluster analysis results of CTR, plasma membrane permeability and MDA, the drought resistant of Hongxiangjiao (AAA) was strong, and it was strictly separated from other AAA varieties. By researching karyotype of Hongxiangjiao, Gong et al. (2002) founded that it ($3n = 33$) and wild banana ($2n = 22$) were a kind of similarity between them and closely genetic relationship. Ji et al. (2007) showed that although the peel of Xinglong Hongxiangjiao was red, and it was easy to separate to other AAA varieties in the field, the genetic relationship between them were very similar with the SSR markers detection. Li (2002) could make it be separated from other AAA with field test and AFLP markers detection. AACV Rose (AA), Pisang Jari Buaya (AA) and FHIA-25 (AAAA) were strong drought resistance, and in the same genotype with them respectively Lingshui Yeshengjiao (AA) and FHIA-17 (AAAA) were sensitive drought tolerance varieties. Ji et al. (2007) found modern cultivated banana varieties were narrow genetic base and their genetic diversity were relatively low, but the genetic differences between AACV Rose, Pisang Jari Buaya, FHIA-25 and modern cultivated banana varieties (AAA genotype) were highlighted, which had important referential value for banana breeding. There is no significant association between the geographical origin (Yuan et al., 2018). Dongguan Zhongbadajiao, Dongguan Gaobadajiao, Mengjiala Fendajiao, Jianfenling Dajiao and Cachaco belonged to ABB genotype were completely different drought tolerance kinds, Dongguan Zhongbadajiao and Dongguan Gaobadajiao were strong drought resistance, and Mengjiala Fendajiao, Jianfenling Dajiao and Cachaco were sensitive drought resistance. Discussing classification location of Guangdong Dajiao, Wang et al. (1995) argued that Dajiao (ABB) is homologous triploid, and is ABB genotype. Baihualing Yeshengjiao, Qujiang BB, Yunnan BB, and Shixing BB belonged to BB the same BB genotype and were in the same strong drought tolerance group. Although FHIA-01, FHIA-18, FHIA-21 and CRBP39 belonged to the same AAAB genotype, their drought tolerance was different. FHIA-18 and FHIA-21 is strong drought resistance, and not only CTR of FHIA-01 and CRBP39 was small, but also the plasmamembrane permeability and MDA of them were small. Pisang Ceylan, FHIA-03 and TMBx5295-1 respectively belonged to AAB, AABB, and AB BB genotypes and their drought tolerance were divided into two groups. FHIA-03 was strong drought resistance, and Pisang Ceylan and TMBx5295-1 were sensitive drought tolerance varieties.

As more experimental materials, in my experiment, the varieties including more B genome were not the very strong drought tolerance types, and the varieties including more A genome were not the very sensitive drought tolerance type. But throughout the 28 banana varieties, there was a tendency that the more B genome the varieties had, the stronger their drought tolerance was; the more A genome the varieties had, the worse their drought tolerance was; drought tolerance in tetraploids was stronger than in diploids and triploids. In this study, we discuss whether the genes about controlling drought tolerance were distributed in the B chromosomes only from the aspects of the banana leaves' morphological and anatomical structures and physiology. As for its genetic mechanism, genetics and molecular biology need more study.

ACKNOWLEDGMENTS

This work is supported by the National Natural Science Foundation of China (31760549,30860170) and Hainan Postgraduate Innovation Research Project (Hys2019-91).

CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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