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Comprehensive evaluation of heat resistance in 68 *Vitis* germplasm resources

QIAN ZHA, XIAOJUN XI, YANI HE and AILI JIANG

Research Institute of Forestry and Pomology, Shanghai Academy of Agricultural Science, Shanghai, China

Summary

Temperature is a crucial factor limiting plant growth. Grapevine is frequently subjected to high temperature during its maturation stage, and this seriously influences grape growth and development. Here, we selected 68 grapevine varieties and examined the heat damage index, relative electrolyte leakage, and F_v/F_m after exposure to 50 °C. 'Red Seedless', 'Hong Yuli', 'At Suma', 'Hupei 3#', and 'Tamina' were tolerant to high-temperature stress; however, 'Brazil', 'Shenfeng', 'Gold Finger', 'Heimeixiang', 'Kaiji', and 'Zuijinxiang' varieties were sensitive to high-temperature stress and died after exposure to 50 °C. Our findings provide a valuable insight into resistance breeding programs for grapevine.

K e y w o r d s: evaluation; heat tolerance; variety; temperature.

A b b r e v i a t i o n s: PQ, plastoquinone; PSI, photosystem I; PSII, photosystem II; QA, quinone electron acceptors.

Introduction

Grapevine is the world's second largest fruit crop in terms of cultivated area and fresh weight production. Climate and viticulture practices markedly influence grapevine growth and development (DE ORDUNA 2010, KOYAMA *et al*. 2012). In many production regions, the maximum midday air temperature may reach 40 °C, and in some regions, it may exceed 45 °C (JONES *et al*. 2005, SALAZAR-PARRA *et al.* 2010). After fruit set, high temperatures are generally unfavorable for the synthesis of secondary metabolites such as phenolic compounds and aromatic volatiles (SCHULTZ 2000, SPAYD *et al*. 2002, MORI *et al.* 2007). However, high temperatures stimulate sugar accumulation and anthocyanin synthesis, contributing to the flower and fruit quality (SHAKED-SACHRAY *et al.* 2002, RIENTH *et al.* 2016). Therefore, there is a need for breeding new heat-tolerant grapevine varieties with effective physiological defenses against heat stress.

To assess heat tolerance based on plant physiological and biochemical indexes, plants are grown under natural or artificially induced heat conditions. The thermal stability of membranes and the parameters related to photosynthesis and other physiological processes are important indexes of heat injury in plants. The cell membrane is considered to be a site of primary physiological injury caused by heat stress. The injury inflicted on leaf tissues under conditions of high heat stress weakens the cell membrane, and this leads to leakage of electrolytes from the cell. Thus, measurement of electrolyte leakage is frequently used to evaluate heat injury. Photosynthesis is one of the most heat-sensitive processes in plants (BERRY and BJORKMAN 1980, WALBOT 2011), because temperature stress influences various aspects of photochemical reactions and can damage the oxygen-evolving complex and electron transfer in photosystem II (PSII; CAMEJO *et al.* 2005). STRASSER *et al.* (2000) developed a method for analyzing chlorophyll *a* fluorescence and demonstrated a polyphasic rise in fluorescence of oxygenic photosynthetic materials; this rise consisted of a sequence of steps, termed O, J, I, and P. The O-step reflects the minimum fluorescence - when all the primary quinone electron acceptors (QA) are oxidized - and the final P-step corresponds to the state in which all the QA are reduced. The transition from O to J reflects a reduction in QA and is associated with the primary photochemical reactions of PSII. The J to I phase parallels the reduction of the plastoquinone (PQ) pool, and the I to P phase depends on photosystem I (PSI) activity, representing the reduction of the ferredoxin pool in the presence of inactive ferredoxin-$NADP^+$-reductase (SCHREIBER *et al*. 1989, SCHANSKER *et al*. 2005). The OJIP transient is a rich but complex signal that has been verified as a sensitive and reliable tool for detection and quantification of heat-induced changes in PSII of plant leaves (CAMEJO *et al.* 2005, XU *et al.* 2014).

In the present study, we evaluated the applicability of heat-tolerance assessment methods for determining heat tolerance and heat-tolerance mechanisms in grapevine. The specific objectives were (1) to identify the most appropriate method for assessing heat injury in grapevine and (2) to evaluate the heat tolerance of 68 grapevine varieties. Our findings provide a valuable insight into resistance breeding programs for grapevine.

Material and Methods

P l a n t m a t e r i a l a n d t r e a t m e n t s: Stem cuttings of 68 grapevine varieties (43 varieties of *Vitis vinifera* × *V. labrusca*; 20 varieties belonging to *V. vinifera*; two varieties belonging to *V. davidii*; and three varieties of the rootstock (Tab. 1), hereinafter termed the VL, VV, VD, and R groups; Tab. 1) were rooted in 15 cm × 40 cm (radius × height) plastic containers containing a mixture of peat moss and perlite in a 1:1 (v/v) ratio. The rooted cuttings

Correspondence to: Dr. AILI JIANG, Research Institute of Forestry and Pomology, Shanghai Academy of Agricultural Science, Shanghai 201403, China. E-mail: putaojal@163.com

Table 1

Grapevine varieties used in this study

Mark	Genotype	Varieties	Number
VL	*V. vinifera* × *V. labrusca*	Canadice(1), Golerula(2), Himrod Seedless(3), Hupei 2#(4), Hupei 1#(5), Pione(6), Aki Queen(7), Shennong Shuofeng(8), Shenhua(9), Shinano Smile(10), Takao(11), Zuirenxiang(12), Shennong Golden Queen(13), Red Seedless(14), Shenong Xiangfeng(15), Brazil(16), Zaoheibao(17), Hong Yuli(18), Hong Shuangwei(19), Juxuan(20), Zenju(21), Shenxiu(22), At Suma(23), Bai Fushi(24), Jingya(25), Honghou(26), Jingyou(27), Shengfeng(28), Shengyu(29), Kyoho(30), Gold Finger(31), Shine Muscat(32), Jinxiangyu(33), High Ruby(34), Jingchao(35), Guobao(36), Heimeixiang(37), Jumeigui(38), G26(39), G18(40), Zuijinxiang(41), Summer Black(42), Hupei 3#(43)	43
VV	*V. vinifera*	Sugraone(44), Italy(45), Yuehong Seedless(46), Melissa(47), Aishen Rose(48), Takachiho(49), Christmas Rose(50), Ruidu Xiangyu(51), Ruidu Wanxia(52), Kaiji(53), Centennial Seedless(54), Tamina(55), Muscat Hamburg (56), Zaokangbao(57), White Muscat Hamburg(58), Fuefuki(59), Fukushima(60), Guifei Rose(61), Autumn Red(62), Zizhenxiang(63)	20
VD	*V. davidii*	Downy Grape(64), Spine Grape(65)	2
R	Rootstock	Beta (*V. riparia*; 66), 1103 (*V. rupestris* × *V. berlandieri*, 67), Huajia 8# (*V. pseudoreticu lata.*, 68)	3

were grown in a greenhouse in Shanghai, China (31°96' N, 121°48' E). Young grapevines at the same growth stage (15-20 leaves) were acclimated in an environment room laboratory (65-70 % relative humidity, 25 °C temperature, and a photoperiod of 14 h light provided by a cool-white fluorescent light source at 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$). Grapevines were exposed to 50 °C at 09:00, and fully expanded mature leaves were tested at 0, 2, and 6 h after treatment. Relative electrolyte leakage and chlorophyll *a* fluorescence parameters were measured at 2 h, and the heat damage index was measured at 6 h after the inception of high-temperature treatment. All the experiments were performed on three biological replicates, each with three technical replicates.

Classification of heat injury symptoms and measurement of heat damage index: At 6 h after the inception of high-temperature treatment, the degree of plant wilting and water loss in leaves was observed and used to grade heat injury symptoms according to the following scale: level 0, no heat injury symptoms; level 1, plant slightly wilting, leaf damage up to 10 %; level 3, plant wilting and 50 % of leaves with obvious damage; level 5, plant wilting and 67 % of leaves with obvious damage; level 7, 100 % of leaves with obvious damage. The heat damage index was calculated according to the formula: Heat damage index =

$$(0*N1 + 1*N2 + 3*N3 + 5*N4 + 7*N5)/7*(N1 + N2 + N3 + N4 + N5);$$

N1…N5 means the number of level 0…7 plants

Measurement of polyphasic chlorophyll a fluorescence transient OJIP: The polyphasic chlorophyll a fluorescence transient was measured (OJIP test) using a Plant Efficiency Analyzer (Hansatech Instruments Ltd., King's Lynn, UK) to provide information on the photochemical activity of PSII and the status of the PQ-pool (STRAUSS *et al*. 2006). Before measurements, leaves were acclimated to darkness for 20 min. The parameters and their descriptions are presented in Tab. S1.

Measurement of relative electrolyte leakage: Leaf discs (10 mm diameter) were punched from five whole leaves, placed in a beaker with 10 mL of ddH_2O, and shaken continuously for 3 h. The initial electrolyte leakage value (OD_1) and the value measured after boiling the sample for 10 min (OD_2) were determined using an electrolyte leakage measurer (DDS-6110; Chendu Ruizi Analysis and Control Instrument Co., Ltd., Chendu, China). The electrolyte leakage of ddH_2O blank samples (OD_0) was determined simultaneously. The relative electrolyte leakage (L) of each sample was determined as:

$$L\,(\%) = (OD_1 - OD_0) \times 100/(OD_2 - OD_0)$$

Data analysis: Pearson correlation coefficients (*r*) were determined with SPSS18.0 (SPSS Inc., Chicago, IL, USA) to determine the degree of linear correlation between two variables. The greater the absolute value of *r*, the stronger the correlation. K-means cluster analyses were determined with SPSS18.0 (SPSS Inc., Chicago, IL, USA).

The variation in indexes between different cultivars was analyzed with Microsoft Excel 2010 software. Boxplots were used to display the range, median, and distribution density of the variables in the samples. The lower and upper quartile values were indicated by the height of the box or the interquartile range (IQR). Whiskers indicated the range of the data and were represented as vertical lines ending in a small horizontal line. Approximately 99 % of the data were inside the whiskers.

Fuzzy membership function value method was adopted to improve the comprehensive evaluation; the calculation method of the membership function value was as follows:

$$Z_{ij} = (X_{ij} - X_{imin})/(X_{imax} - X_{imin})$$

If the index was negatively related to heat tolerance, the membership function value was calculated using the equation:

$$Z_{ij} = 1 - (X_{ij} - X_{imin})/(X_{imax} - X_{imin})$$

Z_{ij} is the membership function value of i varieties with j parameters; X_{ij} is the value of i varieties with j parameters; and X_{imin} and X_{imax} are the minimum and maximum values, respectively.

Table 2

Pearson correlation analysis of heat damage index, relative conductivity, and F_v/F_m.

	Heat damage index	Relative conductivity	Fv/Fm
Heat damage index	1	0.645**	0.520**
Relative conductivity		1	0.349**
Fv/Fm			1

Results

After 6 h of high-temperature treatment, damage was observed in all 68 grapevine varieties, albeit at various levels. The heat tolerance differed significantly between different varieties (Fig. S1). In some varieties, only the young leaves wilted slightly, and mature leaves remained healthy after 6 h of high-temperature treatment (Fig. 1A). In other varieties, the leaves displayed signs of dehydration followed by sudden death after 2 h of high-temperature treatment (Fig. 1B).

We used the heat damage index, relative electrolyte leakage, and F_v/F_m to evaluate the heat tolerance of the 68 grapevine varieties (Tab. S1). If the mean Pearson product-moment correlation coefficient was significant, the correlation between two variables was good. The good correlations between the heat damage index, relative electrolyte leakage, and F_v/F_m (Tab. 2) indicated that the three indexes were reliable and applicable for data analysis in the present study.

Plant resistance is frequently evaluated using the membership function method based on several indexes. This method avoids the use of a single index when evaluating the accuracy, and the results are scientific and integrated. In our present study, we used the membership function method to evaluate the thermal indexes of the 68 grapevine varieties. The average values of the membership function were calculated based on several parameters (Tab. 3); the higher the ranking, the stronger the tolerance to heat stress. The highest tolerance to heat stress was detected in 'Hong Yuli', 'At Suma', 'Red seedless' and 'Hupei 3#' varieties from the VL group and 'Tamina' varieties from the VV group.

The heat damage index, relative electrolyte leakage, and F_v/F_m in different grapevine groups were represented using boxplots (Fig. 2). The graphical representation of the median and the distribution of the heat damage index in the four grapevine categories - VL, VV, VD, and R - were widely distributed. The mean heat damage index among the four categories differed significantly; the lowest value was detected in VV. The range of relative electrolyte leakage was similar between VL and VV and low in VD and R. The F_v/F_m range was larger in VL than in VV, VD, and R; however, it did not differ significantly among the four grapevine categories.

A

B

Fig. 1: Phenotypes of 11 grapevine varieties subjected to high-temperature treatment. **A**: 5 varieties were tolerance to heat stress; **B**: 6 varieties were sensitive to heat stress. 14: 'Red seedless'; 18: 'Hong Yuli'; 23: 'At suma'; 43: 'Hupei 3#'; 55: 'Tamina'; 16: 'Brazil'; 29: 'Shenfeng'; 31: 'Golden Fingers'; 37: 'Heimeixiang'; 53: 'Kaiji'; 63: 'Zizhenxiang'.

Table 3

Membership function values and ranking in the investigated grapevine varieties

		Membership function value				
No.	Variety	Heat damage index	Relative electrolyte leakage	F_v/F_m	Average value	Rank
1	Canadice	0.19	0.50	0.10	0.27	58
2	Golerula	0.98	0.81	0.46	0.75	19
3	Himrod Seedless	0.91	0.71	0.17	0.60	35
4	Hupei 2#	0.38	0.51	0.50	0.46	44
5	Hupei 1#	0.40	0.77	-0.01	0.39	50
6	Pione	0.89	0.70	0.89	0.82	9
7	Aki Queen	0.74	0.57	0.45	0.59	39
8	Shennong Shuofeng	0.10	0.05	0.07	0.07	66
9	Shenhua	0.89	0.67	0.66	0.74	21
10	Shinano Smile	0.14	0.42	0.20	0.25	59
11	Takao	0.91	0.82	0.59	0.77	13
12	Zuirenxiang	0.89	0.18	0.47	0.51	42
13	Shenong Golden Queen	0.16	0.42	0.45	0.34	51
14	**Red Seedless**	0.97	0.93	0.70	0.87	**3**
15	Shennong Xiangfeng	0.86	0.75	0.62	0.74	20
16	Brazil	0.00	0.11	0.09	0.07	43
17	Zaoheibao	0.43	0.22	0.70	0.45	45
18	**Hong Yuli**	0.81	0.94	1.00	0.92	**1**
19	Hong Shuangwei	0.94	0.58	0.97	0.83	8
20	Juxuan	0.75	0.70	0.34	0.60	36
21	Zenju	0.90	0.47	0.59	0.65	26
22	Shenxiu	0.88	0.63	0.56	0.69	24
23	**At Suma**	0.97	0.75	0.97	0.90	**2**
24	Bai Fushi	0.57	0.86	0.44	0.62	31
25	Jingya	0.89	0.82	0.45	0.72	23
26	Honghou	0.71	0.78	0.45	0.65	28
27	Jingyou	0.43	0.78	0.45	0.55	41
28	Shenyu	0.93	0.42	0.97	0.77	15
29	Shenfeng	0.00	0.07	0.05	0.04	68
30	Kyoho	0.38	0.37	0.46	0.40	48
31	Gold Finger	0.00	0.26	0.09	0.12	64
32	Shine Muscat	0.10	0.22	0.02	0.11	65
33	Jinxiangyu	0.81	0.58	0.38	0.59	37
34	High Ruby	0.29	0.28	0.32	0.29	55
35	Jingchao	1.00	0.77	0.75	0.84	6
36	Guobao	0.14	0.07	0.47	0.23	61
37	Heimeixiang	0.00	0.36	0.37	0.25	60
38	Jumeigui	0.48	0.11	0.08	0.22	62
39	G26	0.21	0.76	0.87	0.62	33
40	G18	0.88	0.55	0.52	0.65	27
41	Zuijinxiang	0.12	0.76	0.33	0.40	47
42	Summer Black	0.38	0.60	0.28	0.42	46
43	**Hupei 3#**	1.00	0.94	0.62	0.85	**4**
44	Sugraone	0.90	0.82	0.56	0.76	17
45	Italy	0.95	0.97	0.55	0.82	10
46	Yuehong Seedless	0.89	0.83	0.77	0.83	7
47	Melissa	0.93	0.92	0.61	0.82	11
48	Aishen Rose	1.00	0.91	0.28	0.73	22
49	Takachiho	0.89	0.67	0.31	0.62	32
50	Christmas Rose	0.90	0.76	0.26	0.64	29
51	Ruidu Xiangyu	0.38	0.42	0.00	0.27	57

Tab. 3, continued

		Membership function value				
No.	Variety	Heat damage index	Relative electrolyte leakage	F_v/F_m	Average value	Rank
52	Ruidu Wanxia	0.81	0.87	0.57	0.75	18
53	Kaiji	0.00	0.60	0.01	0.20	63
54	Centennial Seedless	0.98	0.93	0.44	0.78	12
55	**Tamina**	0.91	0.92	0.71	0.85	**5**
56	Muscat Hamburg	0.33	0.62	0.57	0.51	43
57	Zaokangbao	0.88	1.00	0.42	0.77	16
58	White Muscat Hamburg	0.98	0.93	0.40	0.77	14
59	Fuefuki	0.10	0.45	0.41	0.32	53
60	Fukushima	0.43	0.00	0.37	0.27	56
61	Guifei Rose	0.71	0.76	0.20	0.56	40
62	Autumn Red	0.74	0.48	0.54	0.59	38
63	Zuizhenxiang	0.00	0.41	0.49	0.30	54
64	Downy Grape	0.93	0.75	0.33	0.67	25
65	Spine Grape	0.20	0.28	0.69	0.39	49
66	Beta	0.93	0.69	0.23	0.62	33
67	1103	0.29	0.62	0.11	0.34	52
68	Huajia 8#	0.71	0.67	0.49	0.63	30

Note: The top five ranked varieties are indicated in bold. The Membership function value of heat damage index is 0.00 indicated the variety was sensitive to high temperature stress.

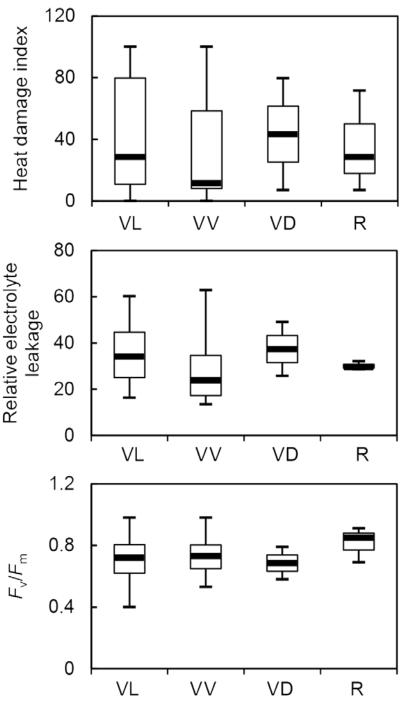

Fig. 2: Heat damage index, relative electrolyte leakage, and F_v/F_m in different grapevine varieties.

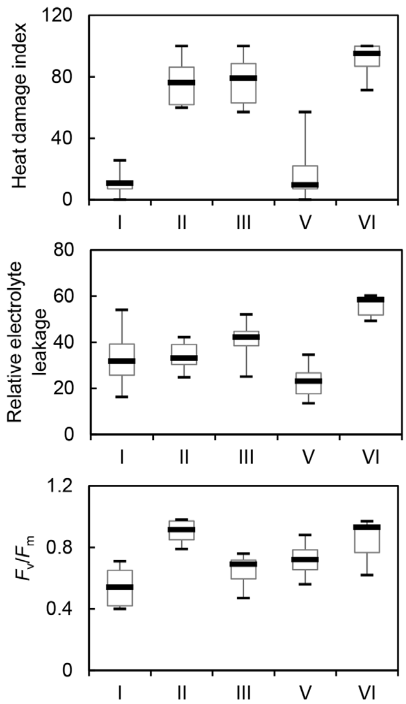

Fig. 3: Classification of different grapevine varieties.

Based on cluster analysis, the 68 grapevine varieties were grouped into five major classes - I, II, III, V, and VI. The classification of grapevine varieties was represented using boxplots (Fig. 3). The range and medium of the heat damage index in classes I and V were significantly lower than those in classes II, III, and VI. The distribution patterns of the relative electrolyte leakage in class V were lower than those in classes I, II, III, and VI, and the distribution patterns and medium of the relative electrolyte leakage in class VI were higher than those in classes I, II, III, and V. Class I had a significantly lower mean F_v/F_m value than classes II, III, V, and VI, and class II had the highest mean F_v/F_m value among the five classes of grapevine varieties.

Table 4

Cluster analysis of the 68 investigated grapevine varieties

Cluster	Varieties	Number
I	Pione, Shenhua, Zuirenxiang, Yuehong Seedless, **Hong Yuli**, Hong Shuangwei, Zenju, Shenxiu, **At Suma**, Shenyu, Autumn Red, Jingchao, G18	13
II	Canadice, Hupei 1#, Shinano Smile, Ruidu Xiangyu, Kaiji, Zuijinxiang, 1103, Summer Black	8
III	Hupei 2#, Shenong Golden Queen, Meiguixiang, Zaokangbao, Fuefuki, Kyoho, Zizhenxiang, Heimeixiang, G26, Spine Grape	10
V	Golerula, Himrod Seedless, Sugraone, Aki Queen, Italy, Takao, Melissa, **Red Seedless**, Aishen Rose,Takachiho, Shennong Xiangfeng, Christmas Rose, Ruidu Wanxia, Centennial Seedless, **Tamina**, Zaokangbao, White Muscat Hamburg, Juxuan, Bai Fushi, Jingya, Honghou, Jingyou, Guifei Rose, Jingxiangyu, Downy Grape, Beta, Huajia 8#, **Hupei 3#**	28
VI	Shennong Shuofeng, Brazil, Fukushima, Shenfeng, Gold Finger, Shine Muscat, High Ruby, Guobao, Jumeigui	9

Discussion

The optimum temperature for grapevine growth is 25-35 °C (FEIL and PURCELL 2001; HENDRICKSON *et al.* 2004). High temperature - as an abiotic stress - directly or indirectly influences grapevine production; hence, there is a need for evaluation of high-temperature sensitivity of grapevine. Recent observations showed that the highest summer temperature in the field can reach 45 °C in China (ZHA *et al.* 2016). To avoid diseases and insect pests prevalent in a rainwater environment, growers cultivate grapevines by using a greenhouse. The temperature inside the grapevine canopy is often 3-5 °C higher than that outside the grapevine canopy (CRISOSTO *et al.* 1995); hence, in our present study we selected 50 °C for the high-temperature treatment.

Under conditions of high-temperature stress, plant physiological and biochemical processes are influenced to varying extents (ORCUTT 2000, WAHID *et al.* 2007). The plant response to heat stress is influenced by many factors, and different varieties of plants have different heat-resistance mechanisms. Thus, plant heat-stress tolerance is rarely inferred from a single index, but involves a comprehensive evaluation of multiple indexes. Previous studies have identified many indicators related to high-temperature stress, and these include the heat damage index, relative electrolyte leakage, and chlorophyll *a* fluorescence (ZHENG *et al*. 2002, GULEN and ERIS 2004, KALAJI *et al.* 2016). In the present study, we examined the heat damage index, relative electrolyte leakage, and F_v/F_m in 68 grapevine varieties exposed to 50 °C. These indexes were well correlated and could be effectively used to evaluate the heat tolerance.

Owing to genetic diversity, we determined significant differences in response to heat stress between the investigated grapevine varieties. 'Hong Yuli', 'At Suma', 'Red Seedless', 'Hupei 3#', and 'Tamina' varieties were resistant to high-temperature stress; however, 'Brazil', 'Shenfeng', 'Gold Finger', 'Heimeixiang', 'Kaiji', and 'Zizhenxiang' varieties were highly sensitive to high-temperature stress and died after exposure to 50 °C. The heat-stress tolerance varied markedly within each of the four grapevine categories - VL, VD, VV, and R; hence, we were unable to classify these categories as heat resistant or heat sensitive. However, classification based on clustering grouped the five heat-resistant varieties into two classes - class I and class V (Tab. 2), verifying the reliability of our evaluation methods.

In summary, our research into the differences in physiological and biochemical indexes of high-temperature stress provides a valuable insight into heat resistance for grapevine. This was consistence with XU *et al.* (2014). Our result not only enriched the grapevine varieties numbers, but also enriched the analytical method when compared with the former study. Besides that, further research about heat tolerance of fruits, roots, stems, and flowers in grapevine would be needed.

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