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Enzymatic Changes in Phenylalanine Ammonia-lyase, Cinnamic-4-hydroxylase, Capsaicin Synthase, and Peroxidase Activities in *Capsicum* under Drought Stress

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ABSTRACT: Penylalanine ammonia-lyase (PAL), cinnamic-4-hydroxylase (C4H), capsaicin synthase (CS), and peroxidase (POD) are involved in the capsaicinoid biosynthesis pathway and may be altered in cultivars with different pungency levels. This study clarified the action of these enzymes under drought stress for hot *Capsicum* cultivars with low, medium,and high pungency levels. At the flowering stage, control plants were watered at field capacity, whereas drought-induced plants were subjected to gradual drought stress. Under drought stress, PAL, C4H, CS, and POD enzyme activities increased as compared to the non-drought-stressed plants. A novel discovery was that PAL was the critical enzyme in capsaicinoid biosynthesis under drought stress because its activities and capsaicinoid increased across the different pungency levels of hot pepper cultivars examined.

KEYWORDS: *Capsicum annuum, capsaicinoids biosynthesis, water stress, pungency*

INTRODUCTION

Pungency, or the sensation of heat when hot *Capsicum* (pepper) fruits are consumed, results from the capsaicinoid compounds in the placenta epidermis.[1] The accumulation of capsaicinoids is affected by genotype, environment, and the genotype by environment interaction.[2,3] Drought stress has been reported as a strong factor increasing capsaicinoid contents.[4−6] Different cultivars vary in the amount of increase of capsaicinoids under drought stress. Estrada et al.[4] reported that the Padrón cultivar when grown under drought stress had a 2.56-fold increase of capsaicinoids than when grown under optimal conditions at 28 days after flowering (DAF). In addition, Sung et al.[6] reported that the capsaicinoid content in drought-stressed plants differed between cultivars with 1.00−2.56-fold higher levels than the control plants.

A previous study of Pimchan et al.[7] showed that fruit yield and some physiological characteristics of two high-pungent cultivars, BGH 1719 and Perennial, did not decrease under drought stress, whereas those of three low-pungent cultivars, Keenoo-Sakonnakorn, Num Keaw Tong 80, and Yuyi, did decrease. They also reported that yield responses under drought stress of four medium-pungent cultivars, C 04872, Takanotsume, Huay-Siiton, and Keenoo-Pama, were varied and inconsistent with drought stress. Interestingly, the capsaicinoid content of those cultivars with different initial pungency levels showed similar trends with fruit yield under drought stress conditions.[7]

Capsaicinoids are products from the phenylpropanoid pathway and fatty acid synthesis pathway.[8,9] The phenylalanine ammonia-lyase (PAL), cinnamic-4-hydroxylase (C4H), and capsaicin synthase (CS) enzymes are involved in capsaicinoid biosynthesis, whereas peroxidase (POD) affects capsaicin degradation.[10] The effects of drought stress on phenylpropanoid metabolism and pungency have been studied.[6] These studies indicated that the PAL, C4H, and CS activities were higher in the drought-stressed plants as compared to the control plants, whereas POD activity was lower under drought stress as compared to the nonstressed condition.[6] However, the response of these enzymes to drought stress among hot pepper cultivars with different pungency levels is unclear. In particular, the relationship between capsaicinoids and each of the enzymes in capsaicinoid biosynthesis is unknown. Therefore, this study clarified the critical enzymes for capsaicinoid biosynthesis under drought stress among hot pepper cultivars with different initial pungency levels.

MATERIALS AND METHODS

Plant Materials and Field Experiments. Five hot pepper cultivars (Table 1) were selected on the basis of their various initial pungency levels and different capsaicinoid responses under drought stress.[7] The three cultivars that had increasing capsaicinoid content under drought stress were the low-pungent cultivar Yuyi (<50,000 Scoville heat units (SHU)) and two medium-pungent cultivars, Keenoo-Pama and Huay-Siiton (50,000−100,000 SHU). The two high-pungent cultivars with unchanged capsaicinoid content under drought stress were BGH 1719 and Perennial (>100,000 SHU). Plant management and drought stress treatments were the same as previously described in Phimchan et al.[7] A randomized complete block design with two treatments, nondrought (control) and drought stress treatments, with three replications of five plants per replication was used. From each plant, five ripe fruits were randomly harvested, totaling 25 fruits for each replication. The fruits were frozen in liquid nitrogen, and the 25 fruits were bulked and kept at −20 °C until analysis. Later, 100 g fresh weight per each replication was taken for enzyme analysis.

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Table 1. Descriptors of the Five Hot Pepper Cultivars Used in This Experiment

cultivar	*Capsicum* species	pungency category[a]	leaf characteristics	fruit characteristics	growth habit[b]	source
Yuyi	*annuum*	low	big leaf, ovate shape	bell, campanulate, blunt end	annual	Japan
Keenoo-Pama	*annuum*	medium	small leaf, lanceolate shape	short, slim, elongated, pointed end	perennial	Myanmar
Huay-Siiton	*annuum*	medium	small leaf, lanceolate shape	Thai chilli, elongated, pointed end	perennial	KKU, Thailand
BGH 1719	*chinense*	high	small leaf, deltoid shape	short, slim, elongated, pointed end	perennial	USDA, Brazil
Perennial	*annuum*	high	small leaf, deltoid shape	short, slim, campanulate, blunt end	perennial	USDA, Mexico

[a]High = >100,000 Scoville heat units (SHU); medium = 50,000−100,000 SHU; low = <50,000 SHU. [b]All cultivars were grown and harvested within one season. (Plant growth habits of these cultivars are typically perennial type, but actually grown and harvested as annual type.).

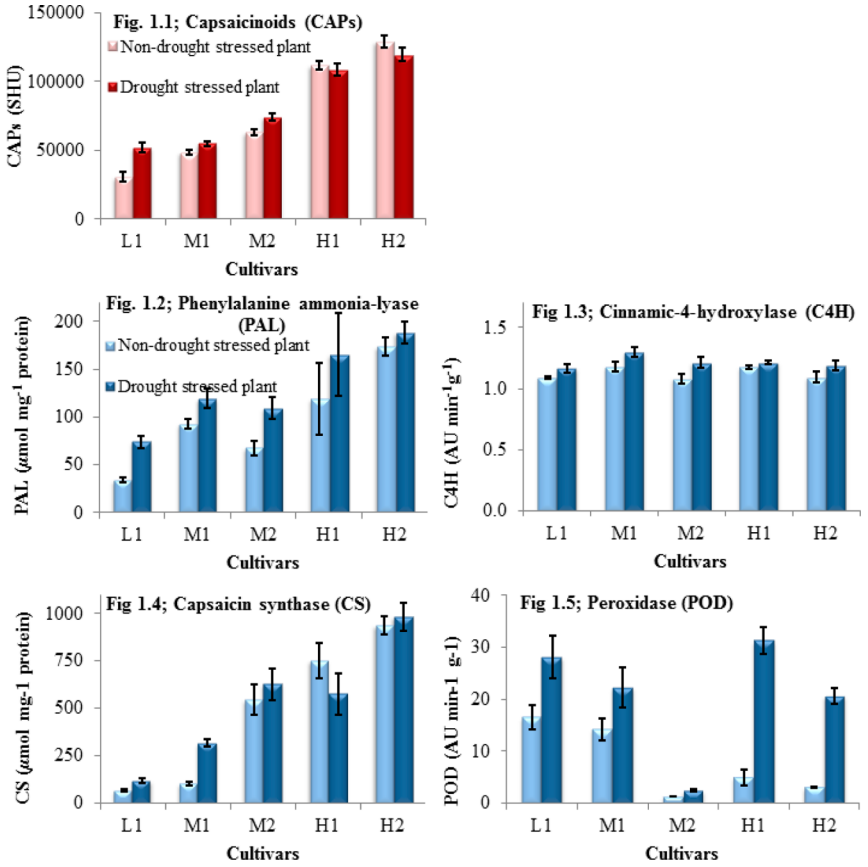

Figure 1. Sum of capsaicin and dihydrocapsaicin (CAPs) (redrawn from Phimchan et al.[7] (with permission from *HortScience*)) and activities of PAL, C4H, CS, and POD between non-drought-stressed and drought-stressed plants in the fruits of five hot pepper cultivars: one low pungent cultivar (L1, Yuyi), two medium pungent cultivars (M1, Huay-Siiton; M2, Keenoo-Pama), and two high pungent cultivars (H1, BGH 1719; H2, Perennial).

Phenylalanine Ammonia-lyase Activity. PAL activity was measured following the method of Koç et al.[11] with some modification from Ochoa-Alejo and Gómez-Peralta.[12] In this procedure, 0.5 g of fresh frozen fruit tissue was ground under 4 °C with 1.5 mL of 50 mM Tris-HCl buffer (pH 8.8) containing 1 mM EDTA, 15 mM β-mercaptoethanol, and 50 mM ascorbic acid. Then the mixture was centrifuged at 15,000 rpm for 30 min by using a Hettich Zentrifugen Universal 30RF model (Hettich GmbH & Co. KG, Kirchlengern, Germany), and after that, the supernatant was collected. The amount of protein was calculated by comparing the sample to the calibration curve obtained with bovine serum albumin (BSA) following the method of Bradford.[13] The absorbance at 595 nm was determined with a spectrophotometer using a Spectro SC-model (LaboMed, Inc., Los Angeles, CA, USA).

The assay mixture contained 0.1 mL of the enzyme extract, 1 mL of 100 mM Tris-HCl buffer (pH 8.8), 0.5 mL of 10 mM L-phenylalanine, and 0.4 mL of deionized water. The mixture was incubated for 1 h at 37 °C, and the reaction was terminated by adding 0.5 mL of 6 M HCl. Then the sample absorbance was measured at 290 nm with a spectrophotometer by using a GENESYS 10S UV−vis model (Thermo Scientific, Waltham, MA, USA). The calibration curve was constructed using cinnamic acid. The blank had the same constituent mixture as the sample.

Cinnamic-4-hydroxylase Activity. C4H activity was measured according to the method of Ochoa-Alejo and Gómez-Peralta[12] with some modification. One gram of fresh frozen fruit tissue was ground under 4 °C with 6 mL of 100 mM Tris-HCl buffer (pH 7.5). The extract was centrifuged at 15,000 rpm for 30 min at 4 °C, and the supernatant was collected as the enzyme extract.

The reaction mixture consisted of 1.5 mL of 100 mM Tris-HCl buffer (pH 7.5), 0.05 mL each of 20 mM glucose-6-phosphate, 12 mM β-mercaptoethanol, 8 mM cinnamic acid, and 8 mM NADP, 1000 units per 12.5 mL of G6P dehydrogenase, and 1 mL of the extract solution. The absorbance of the extracted solution at 340 nm was measured for 5 min by using an Agilent 8453 UV−visible model (Agilent Technologies, Inc., Santa Clara, CA, USA) with the time course method.

Capsaicin Synthase Activity. The procedure for the measurement of CS activity followed that of Ochoa-Alejo and Gómez-Peralta[12] with some modification. The extract was prepared by grinding 0.5 g of

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Table 2. Phenylalanine Ammonia-lyase (PAL), Cinnamic-4-hydroxylase (C4H), Capsaicin Synthase (CS), and Peroxidase (POD) Activities under Control (C) and Drought Stress (D) Treatments

	PAL (μmol mg^{-1} protein)						C4H (AU min^{-1} g^{-1})					
	C[a]		D[a,b]				C[a]		D[a,b]			
cultivar	mean	SD	mean	SD	*t* test	% increase[c]	mean	SD	mean	SD	*t* test	% increase[c]
Yuyi	33.99 d	2.73	74.02 e	6.49	**	117.75	1.092 b	0.012	1.167 c	0.036	*	6.90
Huay-Siiton	92.59 bc	5.03	135.59 b	10.21	*	28.44	1.181 a	0.042	1.298 a	0.040	*	9.90
Keenoo-Pama	67.68 c	7.69	109.16 bc	11.12	*	61.26	1.084 b	0.040	1.215 b	0.047	*	12.02
BGH 1719	148.91 b	37.85	165.23 ab	43.51	ns	38.95	1.177 a	0.013	1.214 b	0.018	*	3.20
Perennial	173.54 a	9.54	188.32 a	11.79	ns	8.52	1.093 b	0.043	1.191 b	0.043	*	9.00
F test	**		**				*		**			
CV (%)	11.65		10.46				12.92		11.72			
	CS (μmol mg^{-1} protein)						POD (AU min^{-1} g^{-1})					
	C[a]		D[a,b]				C[a]		D[a,b]			
cultivar	mean	SD	mean	SD	*t* test	% increase[c]	mean	SD	mean	SD	*t* test	% increase[c]
Yuyi	67.60 f	5.34	119.60 g	11.23	*	76.90	16.50 a	2.310	28.13 ab	4.157	*	70.48
Huay-Siiton	104.90 ef	10.78	316.70 de	19.39	**	201.96	14.25 ab	2.116	22.26 bc	3.924	*	56.21
Keenoo-Pama	546.80 c	81.77	628.50 bc	83.85	ns	14.96	1.26 f	0.051	2.46 g	0.214	**	95.24
BGH 1719	752.40 ab	92.14	578.30 c	109.48	ns	−23.14	5.06 d	1.524	31.31 a	2.504	**	518.77
Perennial	936.40 a	47.09	982.70 a	76.22	ns	4.94	3.13 de	0.115	20.63 c	1.504	**	559.11
F test	**		**				**		**			
CV (%)	13.64		15.00				19.78		12.72			

[a]Means followed by different letters in the same column are significantly different ($P < 0.01$). [b]ns, *, ** nonsignificant, significant difference between control and drought within cultivar at $P < 0.05$ and 0.01 probability levels by *t* test, respectively. [c]Percentage increase was calculated with the equation [(drought − control)/control] × 100.

fresh fruit tissue with 6 mL of 100 mM Tris-HCl buffer (pH 6.8). The homogenate was centrifuged at 15,000 rpm for 30 min at 4 °C and the supernatant collected for enzyme source.

The reaction mixture contained 0.1 mL of 0.4 M Tris-HCl (pH 6.8), 10 μL of 0.2 M vanillylamine, 5 μL each of 40 mM ATP, 40 mM $MgCl_2$, and 40 mM 8-methyl-6-nonenoic acid, and 0.3 mL of extracted enzyme. The reaction was performed at 37 °C for 1 h and terminated with 0.1 mL of 1 M HCl. The assay mixture was extracted with 0.5 mL of chloroform and evaporated to dryness at 50 °C in vacuo. Then, 1 mL of acetone was added, and the mixture was placed on a shaker for 1 h. The mixture was filtered with 0.45 μm PVDF Millipore; 10 μL of filtered solution was used for each HPLC assay using a Shimadzu VP series model (Shimadzu Co., Kyoto, Japan).

Peroxidase Activity. POD activity was measured through adaptation of the method of Arnnok et al.[14] All steps of enzyme extraction were carried out at 4 °C. A total of 1 g of homogenized hot pepper tissue was extracted with 0.1 M phosphate buffer (pH 7) containing 5 g of polyvinylpyrolidone using a magnetic stirrer for 15 min. The homogenate was filtered through Whatman no. 41 filter paper and then centrifuged at 2500 rpm for 20 min. The supernatant was filtered through Whatman no. 42 filter paper and collected as an enzyme extract. The activity of POD was assayed at 470 nm. The reaction mixture contained 0.15 mL of 40% (v/v) guaiacol, 0.15 mL of 1% (v/v) H_2O_2, 2.66 mL of 0.1 M phosphate buffer (pH 7), and 40 μL of the enzyme extract. The blank sample contained the same mixture solution without the enzyme extract.

Statistical Analyses. Statistical analyses were conducted following the procedure of Gomez and Gomez.[15] Analysis of variances (ANOVA) in a randomized complete block design was used with LSD to compare the significant differences among cultivars within treatment, and a *t* test compared the significant differences between control and drought stress treatments within a cultivar. A percentage increase of enzyme activities was calculated by using the equation [(drought − control)/control] × 100. In addition, the sum of capsaicin and dihydrocapsaicin (CAPs) of the five hot peppers cultivars used in this experiment was redrawn from a previous experiment[7] to estimate the relationship between the responses of enzyme activities and capsaicinoid content to drought stress (Figure 1).

RESULTS

All enzyme activities, PAL, C4H, CS, and POD, differed significantly among cultivars within a treatment (Table 2). The cultivars grown under the control treatment gave enzyme activities significantly lower than those under drought stress, except for PAL within cv. BGH 1719 and Perennial and CS within cv. Keenoo-Pama, BGH 1719, and Perennial.

Phenylalanine Ammonia-lyase Activity. For both control and drought-stressed plants, the activities of PAL differed significantly among cultivars (Table 2). As expected, the values of PAL activity under both treatments of the high-pungent cultivars were high, followed by medium-pungent ones, and PAL activity was low in the low-pungent cultivar. The high-pungent cv. Perennial exhibited the highest value of PAL activity under drought stress and control treatments (188.32 and 173.54 μmol mg^{-1} protein, respectively). Even though the PAL activity of cv. BGH 1719 under control treatment (148.91 μmol mg^{-1} protein) was significantly lower than that of cv. Perennial, its value under drought stress (165.23 μmol mg^{-1} protein) was not significantly different from that of cv. Perennial. The PAL activities of the medium-pungent cv. Huay-Siiton under control and drought stress treatments (92.59 and 135.59 μmol mg^{-1} protein, respectively) were not significantly different from those of cv. Keenoo-Pama (67.68 and 109.16 μmol mg^{-1} protein, respectively) within treatment. Yuyi, the low-pungent cultivar, showed the lowest values of PAL activities under control and drought stress treatments (33.99 and 74.02 μmol mg^{-1} protein, respectively). Moreover, the increase percentages of this enzyme activity in the drought-stressed plants related to control ones were large and highly significant for the low-pungent cv. Yuyi (117.75%), followed by those of the medium-pungent cv. Keenoo-Pama (61.26%) and Huay-Siiton (28.44%). However, they were small and not significantly different for the high-pungent cv. BGH 1719 (39.0%) and Perennial (8.52%).

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Cinnamic-4-hydroxylase Activity. Under control and drought stress treatments, the activities of C4H differed significantly among cultivars (Table 2). The significant difference of this enzyme's activity between the control and the treatment were found in all cultivars studied. For the control treatment, the value of medium-pungent cv. Huay-Siiton and the high-pungent cv. BGH 1719 exhibited high values of 1.181 and 1.177 AU min^{-1} g^{-1}, respectively. Under drought stress treatment, cv. Huay-Siiton presented the highest C4H value (1.298 AU min^{-1} g^{-1}), which was significantly higher than those of the other cultivars (1.167−1.215 AU min^{-1} g^{-1}). The low-pungent cv. Yuyi gave a low C4H value. Although the increase percentages of the drought-stressed plants related to the controls were not as large as those of PAL activities, a significant difference between control and drought-stressed plants was observed in all cultivars studied.

Capsaicin Synthase Activity. The activity of the CS enzyme was significantly different among cultivars under both the control and drought stress treatments (Table 2). Similarly to PAL activity, the responses of CS activities in cultivars with different pungency levels were elevated in the high-pungent cultivars, followed by medium-pungent, and lowest in the low-pungent cultivars under both treatments. However, the responses among cultivars were different within a treatment. The high-pungent cv. Perennial presented the highest values of CS under control and drought stress treatments (936.4 and 982.7 μmol mg^{-1} protein, respectively). The value of CS activity in the other high-pungent cultivar, cv. BGH 1719, in the control treatment (752.4 μmol mg^{-1} protein) was not significantly lower than that in cv. Perennial. However, its value in stress conditions (578.3 μmol mg^{-1} protein) was not as high as that of cv. Perennial. Of the medium-pungent cultivars, cv. Keenoo-Pama gave higher CS values under control and stress treatments (546.8 and 628.5 μmol mg^{-1} protein, respectively) compared to cv. Huay-Siiton (104.9 and 316.7 μmol mg^{-1} protein, respectively). As expected, the low-pungent cv. Yuyi had the lowest values of CS activities under control and drought stress treatments (67.6 and 119.6 μmol mg^{-1} protein, respectively). In addition, the increase in this enzyme's activity in the drought-stressed plants related to the control was large (201.96%). In addition, it was significantly different in the medium-pungent cv. Huay-Siiton and the low-pungent cv. Yuyi (76.90%), whereas it was not different for the other cultivars.

Peroxidase Activity. POD activities in all cultivars studied under drought stress treatment were significantly different among cultivars within a treatment and higher than those under the control treatment. The POD activity in the control treatment was contradictory to the other three enzyme activities (Table 2 and Figure 1). The POD enzyme activities were low in both of the high-pungent cultivars, BGH 1719 and Perennial, under control treatment (5.06 and 3.13 AU min^{-1} g^{-1}, respectively), but they were high under drought stress treatment (31.31 and 20.63 AU min^{-1} g^{-1}, respectively) and highly significantly different from those of the controls. For the medium-pungent cultivars, their POD activities in both treatments were not consistent. For example, cv. Huay-Siiton gave high values of POD activity under both control and drought stress treatments (14.25 and 22.26 AU min^{-1} g^{-1}, respectively), which were significantly higher than those of cv. Keenoo-Pama (1.26 and 2.46 AU min^{-1} g^{-1}, respectively). Moreover, the low-pungent cv. Yuyi gave high POD activity (16.50 and 28.13 AU min^{-1} g^{-1}, respectively); however, these values were not significantly different from those of cv. Huay-Siiton within a treatment. The increase of this enzyme's activity in the drought-stressed plants related to the control plants was large and highly significantly different for the high-pungent cv. BGH 1719 and Perennial (518.8 and 559.1%, respectively). A small increase of this enzyme activity was observed for the medium-pungent cv. Huay-Siiton and Keenoo-Pama and for the low-pungent cv. Yuyi (56.21, 95.24, and 70.48%, respectively), but they were all significantly different.

Relationship between Enzyme Activities and Capsaicinoid Responses to Drought Stress. The low- and medium-pungent cultivars under drought stress produced significantly higher amounts of capsaicin and dihydrocapsaicin (CAPs) than the control plants. The high-pungent cultivars did not significantly differ in capsaicinoid amount when subjected to drought stress conditions (Figure 1.1). The responses of PAL activity showed a trend similar to the responses of the capsaicinoid amounts under both treatments, with the values for PAL activities and capsaicinoid content low in the low- and medium-pungent cultivars and high in the high-pungent cultivars under both treatments (Figure 1.2). Moreover, the significant increase of PAL values in the low- and medium-pungent cultivars and the nonsignificant increase in the high-pungent cultivars were exactly the same responses of CAPs of those cultivars with different pungency levels under drought stress. The enzyme C4H activities did not show any association with the capsaicinoid responses, where C4H values in all cultivars with different pungency levels were all significantly increased compared to their control ones (Figure 1.3). The responses of CS activities and capsaicinoid amount in the low- and high-pungent cultivars showed a similar trend under drought stress; that is, both traits were increased for the low-pungent cultivar and not increased for the high-pungent ones (Figure 1.4). However, those values of both traits in the medium-pungent cultivars were inconsistent and not associated with capsaicinoid responses. Meanwhile, values of both traits in cv. Huay-Siiton were increased, but they were not for cv. Keenoo-Pama. In contrast to the other enzyme activities, POD values showed a negative trend for capsaicinoid amount under control treatment, where POD value was high in the low-pungent cultivar and low in the high-pungent cultivars (Figure 1.5). Nevertheless, these enzyme activities in all cultivars with different pungency levels were all significantly increased compared to their control plants.

DISCUSSION

PAL, C4H, CS, and POD are reported as the important enzymes in capsaicinoid biosynthesis.[9,16] In addition, they are the key enzymes involved for capsaicinoid changes under drought stress.[6] In this study, PAL activity showed an obvious trend associated with the capsaicinoids among hot pepper cultivars with different pungency levels. The three other enzyme activities, C4H, CS, and POD, had an inconsistent relationship to capsaicinoid content.

The different levels of enzyme activity among cultivars within a treatment and between treatments within a cultivar illustrated the significant interaction of the environments on the enzymes. These observations confirm previous studies that different pepper cultivars vary in their enzymatic responses.[10,14,18] Hot pepper cultivars with high capsaicinoid levels were less sensitive to drought stress as compared to the low- and medium-pungent cultivars. This indicates the stability of high-pungent cultivars under stress conditions to produce capsaicinoids. Our results concur with the finding by Gurung et al.[19] that capsaicinoid

amounts in high-pungent cultivars do not fluctuate as compared to low-pungent cultivars in the different environmental conditions. On the other hand, genotype by environment interaction does affect capsaicinoid production;[3] however, a genotype is the major factor compared to the environmental effect.[19]

It has been reported that capsaicinoid content increases under drought stress,[4] and the increase is related to four key enzymes of the capsaicinoid biosynthesis pathway.[6] The changes of these enzyme activities under drought imply that these enzymes were strongly influenced by the drought stress effects.[7] The enzymatic activities in the phenylpropanoid pathway starting from lignin and free phenolic compounds,[20] which are the products of the shikimate pathway, were increased by stress. Subsequently, they resulted in the increase of phenylalanine, the precursor of the capsaicinoid.[21] Thereafter, phenylalanine enters and converts to cinnamic acid, thus increasing this precursor under drought stress, which affects further enzyme activity in the capsaicinoid synsthesis pathway, including C4H, CS, and POD.[16] Our results showed increases of activity for the four enzymes for all of the cultivars under drought stress. Among these four enzymes, PAL changes under drought stress showed a complete association with capsaicinoids, in all five hot pepper cultivars examined. The changes of PAL and CAPs between the control and drought-stressed plants in the low- and medium-pungent cultivars were all significantly different, but they were not for the high-pungent cultivars. Moreover, the responses of PAL in the five cultivars concur with the results of Estrada et al.,[4] in which the PAL activities increased with water stress.

It is important to note that the C4H activities were significantly increased under drought stress, but those changes were not associated with an increase of capsaicinoids among the cultivars. CS activities showed a similar trend to PAL in that there was an unchanging amount in the stressed plants of high-pungent cultivars. PAL activity between the two medium-pungent cultivars was not associated with the capsaicinoid responses. The increase of CS activity was found in cv. Huay-Siiton and was not found in cv. Keenoo-Pama, whereas capsaicinoids in these two cultivars did increase. Furthermore, POD activity had a negative association with capsaicinoid amounts, which is similar to the observations reported by Contreras-Padilla and Yahia[22] and Di et al.[23] This adverse relationship might be attributed to the fact that POD activity is closely related to the oxidization of the capsaicinoid metabolism,[17] resulting in a decrease in POD activity, with an increase in the capsaicinoid amount. The significant increase in POD activity under drought stress observed for all cultivars studied was not associated with their capsaicinoid content. The increase in POD activity under drought stress in all cultivars studied clearly indicated a negative relationship between the evolution of capsaicinoids and POD activities due to its involvement in capsaicinoid degradation.[22,23] The increase in POD activity in our results contradicted the results of Sung et al.,[6] who found a decrease in POD activity under drought stress. The difference could be attributed to the fact that our stressed plants received a level of stress to alter the physiological metabolism,[24] for example, capsaicinoid biosynthesis, and resulted in an increase of this enzyme under the stress.

In conclusion, PAL, C4H, CS, and POD activities were found to differ due to drought stress induction. Under drought stress, the activities of the enzymes increased as compared to the optimum water application treatment. A novel discovery was that under drought stress the PAL enzyme was the only one to affect the capsaicinoid biosynthesis.

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Notes

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