Physiological Responses of Papaya (*Carica papaya* L.) Plants to Flooding

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Key words: *Carica papaya*, Flooding, Photosynthesis, Plant growth

Summary

Potted papaya (*Carica papaya* L.) plants of four cultivars, 'Damoc', 'Jampada', 'Philippines wild' and 'Tainung No.2', grown in sand culture were subjected to flooding for 3 days under green-house condition. Flooding caused a reduction in plant fresh and dry weight in all cultivars. Leaf wilting appeared earlier in 'Da Moc' and 'Jampada'. Total leaf chlorophyll decreased by flooding treatment. After one days of flooding there was no effect on leaf photosynthesis. However, photosynthesis rate was significantly reduced after three days of flooding. The photosynthesis rate reduced about 30-40 percent in 'Tainung No.2' and' Philippines wild' after three days of flooding. Furthermore, the leaves of 'Da moc' plants showed wilting symptom. The ethylene production was increased in all cultivars after one day of flooding and reduced on the following days. There were significant different in the activity of alcohol dehydrogenase in roots among cultivars during 3 days of flooding.

Introduction

Flooding from excessive rainfall or high level of water-table in lowland can compromise the growth and yield of flood intolerance crops. The initial eco- physiological response of most plants to flooding is wilting within a day or two days following root exposure. Tolerance ratings

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have been based on different criteria including growth responses of plants amount of injury sustained and survival (Kozloski, 1984). The reduction net photosynthesis is observed in many flooding plants (Backman *et al*., 1992; Schaffer and Ploetz, 1989; Vu and Yelenosky, 1991; Dias-Filho and De Canvalho, 2000). In flood-tolerant plants, flooding has been hypothesized to increase alcohol dehydrogenase (ADH) activity (Crawford and Baines, 1977). In contrast, McManmon and Crawford, 1971 indicated that flood tolerance was depended on low ADH activity (Brown *et al*., 1976; Marshall *et al*., 1974). Increasing ADH activity in response to flooding has been reported in crop and woody species (John and Greenway, 1976; Lin and Lin, 1992; Pezeshki *et al*., 1993, 1996). Flooding stimulates ethylene production in both herbaceous and woody plants (Tang Kozlowski, 1982; Vossenek *et al*., 1993; Yamamoto *et al*., 1995; Pezeshki *et al*., 1996; Chen *et al*., 2002). There was no significant different in levels of ethylene in wax-apple of flooding plant and control (Lin and Lin, 1992).

For these reasons, the objective of study evaluated effects of flooding on photosynthesis, growth response of 'Da moc', 'Jampada', 'Philippines wild' and 'Tainung No.2' cultivars in potted.

Materials and Methods

Plant materials

Seedlings of four papaya cultivars, 'Tainung No.2', 'Philppines wild', 'Jampada' and 'Da Moc' was planted in the plastic pot (10x10x9cm) containing the media compost perlite and washed sand (1:1). Plants were watered with fourth strength Hoangland solution two times a week. When seedlings about 20cm in height were transplanted into Wagner’s pot (1/2000a), 14 liters filled in washed sand. Plants were watered and fertilized two times a week with half strength Hoangland solution.

Flooding treatment

Tow month-old plants were subjected to flooding for 3 days. Water level in the pots was maintained 3cm above the sand surface. Effects of flooding on leaf yellowing percentage, leaf chlorophyll content, leaf photosynthesis, ethylene production and alcohol dehydrogenase activity in roots were examined.

Leaf yellowing and chlorophyll content

Leaf yellowing symptom was observed during the flooding treatment.

Chlorophyll extraction and determination: Freshly leaf samples were collected extracted with acetone 80% (v/v). The total leaf chlorophyll concentration was determined following the method of Arnon, 1949 and modified.

Leaf photosynthesis

Measurement of leaf gas exchange were made between 1100- 1200 hr. on single, fully developed and sun exposed leaf, leaf kept in the control chamber, using 1 liter chamber in the closed gas exchange mode of LI-6200 Portable Photosynthesis System (LI-COR, Lincol, NE) as previously reported (Vu *et al*., 1991). The rate of air flow into the leaf chamber was 990-1100 $\mu mols^{-1}$ and the leaf temperature was 34-36^oC at the measurement of leaf level. The leaves gas exchange was expressed on a leaf area basis, determined after measurement with LI-COR LI-3000 Portable Area Meter.

Ethylene production determination

For measurement of ethylene production the method described by Saltveit and Yang (1987) was followed. Whole root was enclosed in vessel and sealed with cap. After incubated for 1 hour, the ethylene production was assayed by withdrawing 1 ml gas sample using gas tight syringe from each vessel and injected into a gas chromatography (GC-8A, Shimadzu model, Tokyo, Japan) which used nitrogen as the carrier gas and was equipped with an active alumina column at 80^oC and flame ionization detector at 110^oC (Ververidid and Jonhn, 1991).

Alcohol dehydrogenase (ADH) determination

Alcohol dehydrogenase (ADH) extraction: The lateral roots were harvested and rinsed with distilled water, immediately frozen in liquid nitrogen and store at -70^oC until extraction. The frozen roots was placed in mortar containing liquid nitrogen and ground to fine powder using pestle. The powder was homogenized in 3ml g^{-1} of extraction buffer solution containing 0.1M HEPES (pH 7.4), 0.5mM $MgCl_2$, 0.1M 2-Mercaptoethanol, 1mM DTT, 12.5% (v/v) glycerol and 8% (w/v) PVPP. The homogenate was centrifuge at 10000 rpm for 30 minutes at 4^oC. The supernatant was assayed immediately for the alcohol dehydrogenase (Hanson *et al*. 1984 and Kato-Noguchi, 2001).

Alcohol dehydrogenase (ADH) assay following the method described by Kimmerer (1987).

$$CH_3CHO \text{ (alcohol)} + NADH + H^+ \rightarrow CH_3CH_2OH \text{ (acetaldehyde)} + NAD^+$$

The assay mixture consisted of 0.8 ml of reaction buffer containing 90 mM MES-KOH (pH 6.4), 1mM DTT, 3 mM $MgCl_2$, 0.2 mM NADH, 0.1ml of 29.7 mM acetaldehyde and 0.1ml enzyme extraction. The measurements were done at OD 340nm by using spectrophotometer (Thermo spectronic software version 3.2, UK). ADH activity is reported in U ($\mu molmin^{-1}$).

Results

Fresh weight and dry weight of the leaf, stem, root

The results indicated that there were significantly different in stem, root fresh and dry weight among cultivars (Table 1 and 2).

Flooding for 3 days were reduced in fresh and dry weight of leaf, stem and root in all cultivars. The result also revealed that there were significantly different in fresh and dry weight of leaf, stem and root in all cultivars (except for fresh and dry weight of stem in 'Tainung No.2' and dry weight of stem in 'Philippines wild') between control and flooding treatment by t-test (Table 1 and 2).

Effect of flooding on the percentage of leaf yellowing and leaf chlorophyll content

The percentage of leaf yellowing and total leaf chlorophyll in 'Da Moc', 'Jampada', 'Philippines wild' and 'Tainung No.2' during 3 days flooding was presented in Table 3. Before flooding treatment leaves displayed green in all cultivars. Leaf yellowing symptom was increased with continuous flooding for 2 to 3 days.

Table 1. Effects of flooding on fresh weight of leaf, stem and root in papaya plants.

Cultivars	Fresh weight (g)					
	Control			Flooding		
	Leaf	Stem	Root	Leaf	Stem	Root
Tainung No.2	98.3**	143.4ns	66.1**	79.4** (80.8)y	138.1ns (96.3)	33.6** (50.8)
Da Moc	74.1**	88.6**	48.3**	38.7** (52.2)	53.4** (60.2)	20.9** (43.3)
Jampada	77.2**	123.6**	44.7*	60.9** (78.9)	69.1** (55.9)	37.5* (83.9)
Philippines wild	88.3**	127.5*	78.3**	68.3** (77.3)	110.3* (86.5)	54.9** (70.1)
LSD(P=0.05)x	8.0	19.8	9.4	13.9	21.9	9.5

y: Data in parentheses are percentage of control (100 percent).

x: Least significant difference among cultivars at P=0.05.

*,**: Significant difference between control and flooding by t-test at P=0.05 and 0.01, respectively.

Table 2. Effects of flooding on dry weight of leaf, stem and root in papaya plants.

Cultivars	Dry weight (g)					
	Control			Flooding		
	Leaf	Stem	Root	Leaf	Stem	Root
Tainung No.2	15.1*	18.6^{ns}	6.1**	9.5* (62.9)	14.8^{ns} (79.6)	3.3** (54.1)
Da Moc	12.8**	12.5**	4.9**	7.6** (59.4)	6.8** (54.4)	1.8** (36.7)
Jampada	11.6*	19.7**	4.4*	8.8* (75.9)	8.9** (45.2)	2.9* (65.9)
Philippines wild	14.1*	15.9^{ns}	7.6**	11.1* (78.7)	13.9^{ns} (87.4)	4.4** (57.9)
LSD(P=0.05)^{x}	ns	5.1	1.6	ns	5.6	1.4

y: Data in parentheses are percentage of control (100 percent).

x: Least significant difference among cultivars at P=0.05, ns: not significant.

*,**: Significant difference between control and flooding by t-test at P=0.05 and 0.01, respectively.

The lowest in percentage of leaf yellowing was recorded in 'Philippines wild' (19.8%) followed by 'Tainung No.2' (30.3%). Whereas, the highly percentage of leaf yellowing was 'Da Moc' (38.6%) which were observed after 3 days of flooding.

The result indicated that leaf chlorophyll content was reduced during flooding. After 3 days of flooding the chlorophyll in 'Philippines wild' (1.23 mg gfw^{-1}) was significantly higher than 'Jampada', and 'Da Moc' (0.99 and 0.91 mg gfw^{-1}, respectively). Besides, leaf chlorophyll content in 'Da Moc', 'Jampada', 'Tainung No.2' and 'Philippines wild' were reduced (46.3, 51.0, 56.9 and 80.4 percent, respectively) and significant different when compared to before flooding (0 day) by t-test (Table 3).

Effect of flooding on leaf photosynthesis

Before flooding, photosynthesis rate in 'Philippines wild', 'Jampada' , 'Tainung No.2' and 'Da Moc' (11.6, 11.4, 10.9, 10.9 µmol m^{-2} s^{-1}, respectively) were not significantly different among cultivars (Fig.1).

The result indicated that under flooding 1 day, photosynthesis rate was reduced greatly in 'Da Moc' (5.7 µmol m^{-2}s^{-1}) while 'Philippines wild' (11.5 µmol m^{-2} s^{-1}) was unchanged when compared to before flooding. Photosynthesis of 'Tainung No.2' and 'Jampada' (9.5 and 8.7 µmol m^{-2}s^{-1}) was statistically on par. After flooding for 2 to 3 days, photosynthesis rate was reduced in all cultivars. The lowest photosynthesis was recorded in 'Da Moc' (4.2 and -1.9 µmol $m^{-2}s^{-1}$, respectively). Photosynthesis rate in 'Philippines wild' and 'Tainung No.2' were reduced 30 to 40 percent, respectively when compared to before flooding which was recorded after 3 days of flooding (Fig.1).

Effect of flooding on ethylene production rate in roots

Flooding had a marked effect on ethylene production in roots papaya plants (Table 4). Under flooding for 1 day the result showed that ethylene production rate in flooded roots were increased significantly when compared to control. The highly ethylene production rate were recorded in 'Tainung No.2' and 'Philippines wild' (12.8 and 11.6 µl $kgfw^{-1}hr^{-1}$, respectively) followed by 'Jampada' (8.5 µl $kgfw^{-1}hr^{-1}$) and lowest ethylene production in roots of 'Da Moc' (4.1µl $kgfw^{-1}hr^{-1}$). Flooding for 3 days, ethylene production rate in flooded roots continuously decreased in all cultivars. It also revealed that there was significantly different in ethylene production rate between control and flooding treatment by t-test (Table 4).

Table 3. Effects of flooding on leaf yellowing percentage and total leaf chlorophyll content of papaya plants.

Cultivars	Leaf yellowing (%)			Total leaf chlorophyll (mg gfw^{-1})			
	1	2	3	0	1	2	3
TainungNo.2	6.8	9.8	30.3	1.74	1.65	1.51	0.99*
				(100)	(94.8)[y]	(86.8)	(56.9)
Da Moc	9.2	19.7	38.6	1.75	1.41	1.39	0.81*
				(100)	(80.6)	(79.4)	(46.5)
Jampada	5.3	11.1	32.1	2.04	1.84	1.44	1.04*
				(100)	(90.2)	(70.6)	(51.0)
Philippines wild	6.2	11.2	19.8	1.53	1.54	1.49	1.23*
				(100)	(100)	(97.4)	(80.4)
LSD(P=0.05)[x]	ns	7.1	10.6	ns	ns	ns	0.26

y: Data in parentheses are percentage of before flooding (100 percent).

x: Least significant difference among cultivars at P= 0.05, ns: not significant.

*: Significant difference between flooding and before flooding (0 day) by t-test.

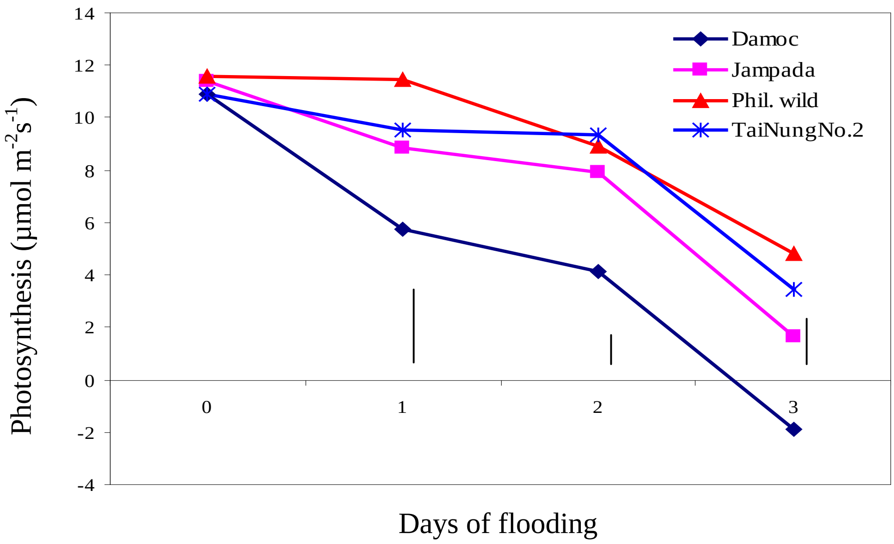

Fig.1. The effect of flooding on photosynthesis of papaya plants. Vertical bar is LSD (P=0.05)

Table 4. Effect of flooding on ethylene production (µl kgfw-1 h-1) in papaya roots.

Cultivars	Days of flooding					
	1		2		3	
	Control	Flooding	Control	Flooding	Control	Flooding
TainungNo.2	8.8^{*}	12.8^{*}	8.9^{ns}	7.8^{ns}	8.9^{**}	3.4^{**}
Da Moc	3.2^{*}	4.1^{*}	3.3^{ns}	3.0^{ns}	3.5^{**}	2.2^{**}
Jampada	7.4^{*}	8.5^{*}	7.8^{ns}	6.3^{ns}	7.8^{*}	3.5^{*}
Philippines wild	8.5^{*}	11.6^{*}	8.8^{*}	10.3^{*}	8.8^{**}	4.4^{**}
LSD(P=0.05) [y]	0.9	2.7	2.0	1.5	2.2	ns

y: Least significant difference among cultivars at P=0.05.

*,**: Significant difference between control and flooding by t-test at P=0.05 and 0.01, respectively.

ns: Not significant.

Effect of flooding on alcohol dehydrogenase (ADH) activity in roots

The results revealed that there were significant different in ADH activity among cultivars during treatments (Table 5). In addition, ADH activity in 'Philippines wild', 'Tainung No.2', 'Jampada' and 'Da Moc' (1.29, 1.20, 0.22 and 0.15 $Ugfw^{-1}$, respectively) were increased but not significant different when compared to control which was recorded after 1 day of flooding. Flooding for 3 days showed that ADH activity in 'Tainung No.2' and 'Philippines wild' were reduced and significantly different when compared to control. ADH activity in roots of 'Philippines wild' (0.86 U gfw^{-1}) was 1.3, 9.5 and 10.7 folds higher than 'Tainung No.2' (0.64$Ugfw^{-1}$), 'Jampada' (0.09 U gfw^{-1}) and 'Da Moc' (0.08 U gfw^{-1}), respectively (Table 5).

Table 5. Effect of flooding on alcohol dehydrogenase activity (U gfw-1) in papaya roots.

Cultivars	Days of flooding					
	1		2		3	
	Control	Flooding	Control	Flooding	Control	Flooding
TainungNo.2	0.98 ^{ns}	1.20 ^{ns}	1.49 ^{ns}	1.09 ^{ns}	1.51 **	0.64 **
Da Moc	0.12 ^{ns}	0.15 ^{ns}	0.13 ^{ns}	0.12 ^{ns}	0.12 ^{ns}	0.08 ^{ns}
Jampada	0.15 ^{ns}	0.22 ^{ns}	0.14 ^{ns}	0.15 ^{ns}	0.15 ^{ns}	0.09 ^{ns}
Philippines wild	0.84 ^{ns}	1.29 ^{ns}	1.55 ^{ns}	1.23 ^{ns}	1.59 **	0.86 **
LSD(P=0.05) ^{y}	0.53	0.72	0.16	0.64	0.18	0.12

y: Least significant difference among papaya cultivars at P= 0.05.

*,**: Significant difference between control and flooding by t-test at P=0.05 and 0.01, respectively.

ns: Not significant difference.

Discussion

The data indicated that there were significantly different in the leaves, stem and roots fresh and dry weight among cultivars. It is also resulted that flooding reduced significantly in fresh and dry weight of leaf and root when compared to control. The common responses for a plant under flooding stress are reduction in growth of leaves, shoots and roots (Kozlowski, 1984).

Summer flooded of apple also decreased leaf and root dry weight (Olien, 1987). Joyner and Schaffer (1989) observed that leaf, stem and root dry weight of carambola decreased with increased flood duration. Vu and Yelenosky (1991) reported that prolonged flooding also reduced the biomass of fibrous roots in both rootstocks rough lemon and sour orange.

Flooding for 1 day was not significantly different in the percentage of leaf yellowing among papaya cultivars. The percentage of leaf yellowing was increased when plants exposed to flood for 2 and 3 days. Chen *et al*. (2002) reported that adaptive responses of *Lepidium latifolium* to soil flooding, leaves exhibited chlorosis, an increasingly reddish green color after 3 days of flooding.

The present study shown that within 3 days of flooding total leaf chlorophyll content was reduced and significant different when compared to before flooding which was recorded after flooding for 3 days. Total leaf chlorophyll content in 'Philippines wild', 'Tainung No.2', 'Jampada' and 'Da Moc' were reduced about 80.4, 56.9, 51.0 and 56.9 percent, respectively when compared to before flooding. Vu and Yelenosky (1991) study on sweet orange 'Hamlin' grafted onto rootstocks as sour orange and rough lemon flooded for 24 days were reduced 38 and 18% of leaf chlorophyll content, respectively.

Leaf gas exchange parameters have been used to study photosynthesis capacity of plants during flooding treatments. An early response of fruit crops to water-logging is a reduced of net CO_2 assimilation. Flooding for 1 days, photosynthesis rate was reduced great in 'Da Moc' while 'Philippines wild' was unchanged when compared to before flooding. Under flooding for 3 days photosynthesis rate in 'Da Moc' was reached to negative and plants displayed wilting, photosynthesis rate in 'Philippines wild' and 'Tainung No.2' were reduced about 30-40 percent, respectively when compared to before flooding treatment. Flooding on container grown of mango reduced net CO_2 assimilation after 2 to 3 days (Larson *et al*., 1989). Malik *et al*. (2001) reported that net light-saturated rates of photosynthesis in leaves of wheat growing in soils water-logged at the surface were slightly reduced after 1 day and severely reduced after 2 days or more days of water-logging. The decline in net CO_2 assimilation by fruit crops associated with flooding is affect by flood duration as well as environment factors (Crane and Davies, 1989). The flooding reduced in leaves photosynthesis have been reported on grape, mango, carambola, ‘Tahiti’ lime, rough lemon and orange (Larson *et al*., 1989; Joyner and Schaffer, 1989; Vu and Yelenoski, 1991).

When plants treated to flooding for 1 day ethylene production rate was increased in all cultivars but there were not significant different when compared to control. The highly ethylene production rate were recorded in 'Tainung No.2' and 'Philippines wild' followed by 'Jampada' and lowest ethylene production rate in roots of 'Da Moc'. Flooding for 3 days resulted decreased in root ethylene production of all cultivars. The biosynthesis of ethylene is inhibited under anoxic conditions because the conversion of ACC to ethylene by ACC oxidase requires oxygen (Peng *et al*., 2001). Sine oxidation to ethylene can not proceed in the absence of oxygen. In many woody and herbaceous species, ethylene concentrations in both root and shoots increase in response to soil flooding (Vossenek *et al*., 1993, Chen *et al*., 2002) whereas the ethylene production in root of wax-apple was no significant different in both flooded and control plants during 7 days of flooding (Lin and Lin, 1992). Flooding resulted in increased root ethylene production in highly flood-tolerant *Taxodium distchum* L. species but had no effect on root ethylene production in the oak species as flood-tolerant *Quercus lyrata* and flood- sensitive *Quercus falcata* species (Pezeshki *et al*., 1996).

In flood-tolerant plants, flooding has been hypothesized to increase alcohol dehydrogenase (ADH) activity (Crawford and Baines, 1977). The present study indicated that the ADH activity in root of control plants as 'Philippines wild' and 'Tainung No.2' were higher than 'Jampada' and 'Da Moc'. Johnson *et al*. (1989) reported that pre-exposure to hypoxic conditions resulted in increased ADH activity, adenylate charge ratio and survival of corn root. Many investigators have studied the relationship of ADH activity and flood tolerance. The present study indicated that there were significantly different in ADH activity among cultivars during flooding. Besides, after flooding for 1 day ADH activity in root of 'Philippines wild', 'Tainung No.2', 'Jampada', Da Moc' were increased but not significant different when compared to control. However, on ADH activity was reduced in all cultivars after flooding for 2 and 3 days. ADH activity was highly in 'Philippines wild' followed by 'Tainung No.2'. Van Toai *et al*. (1985) found that there was no correlation between ADH activity and flooding tolerance of maize seeds. The significance of induction of high levels of ADH activity in maze root tip is therefore obscure. Whereas, Jackson *et al*. (1982), Tripepi and Mitchell (1984) indicated that many flood-tolerant species have been shown to exhibit increased ADH activity when exposed to root hypoxia. Induction of ADH during low oxygen conditions has been observed in many plant species (Kennedy *et al*., 1992; Ricard *et al*., 1994; Tadege *et al*., 1998). During 7 days of flooding treatment, the wax-apple roots increased in ADH activity (Lin and Lin, 1992). Plants judged to be flood-intolerant had a high ADH activity under flood conditions (Crawford and Baines, 1977).

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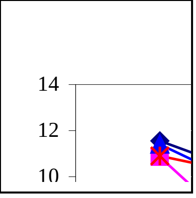

番木瓜植株在淹水逆境下之生理反應

阮一月[1)]楊耀祥[2)]

關鍵字：番木瓜、淹水、光合成作用、植株生長

摘要：'Da moc'、'Jampada'、'Philippines Wild'及'台農 2 號'四種番木瓜栽培種之砂耕盆栽植株，在溫室內以淹水處理 3 天，全部的供試植株之鮮重及乾重均呈下降。'Da moc'及'Jampada'兩栽培種之葉片較早發生凋萎現象。在淹水處理 3 天後，葉片的總葉綠素含量呈下降，且與淹水處理前有顯著差異。淹水處理 1 天後葉片光合成作用未受影響。但是，淹水處理 3 天後，其葉片的光合成速率迅速下降。'Philippines Wild'及'台農 2 號'約為淹水處理前的 30-40%，'Jampada'及'Da moc'幾乎無光合成能力。在淹水處理後 1 天，各栽培種根部之乙烯生成量皆呈上升，處理後 3 天則降低至一半左右。在淹水處理 3 天的期間內，栽培種之間的根部酒精去氫酵素活性有顯著差異，耐水較強的'Philippines Wild'及台農 2 號有較高的活性。顯示不同栽培種對淹水逆境有不同的生理反應。

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