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Differential interactions of *Phytophthora capsici* isolates with pepper genotypes at various plant growth stages

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Abstract

Pepper cultivars from diverse geographic origins were evaluated for resistance to different isolates of *Phytophthora capsici* under controlled environmental conditions. All accessions tested were susceptible at the four-leaf stage to the six isolates of *P. capsici*. Inoculation at the eight-leaf stage resulted in significantly different interactions among the accessions and *P. capsici* isolates. The Korean and U.S. cultivars tested were highly susceptible to the isolates of *P. capsici* at this stage. In contrast, PI 201234 and PI 201238 had a differential interaction with some *P. capsici* isolates. At the twelve-leaf stage, Phytophthora blight developed slowly in the Korean and U.S. cultivars that were highly susceptible at the eight-leaf stage. Furthermore, the accessions from the Asian Vegetable Research and Development Center (AVRDC) became highly resistant to *P. capsici* at this stage.

Introduction

Phytophthora capsici Leonian is one of the most widespread and destructive soilborne pathogens, and it has a wide host range. The fungus infects pepper (*Capsicum annuum* L.), tomato (*Lycopersicon esculentum* Mill.), eggplant (*Solanum melongena* L.), cucumber (*Cucumis sativus* L.), honeydew melon (*Cucumber melo* L.), pumpkin (*Cucurbita pepo* L.), squash (*Cucurbita maxima* Duc.), watermelon (*Citrullus vulgaris* Schrad.), and cocoa (*Theobroma cacao* L.) [Leonian, 1922; Tompkins and Tucker, 1937, 1941; Kreuzer et al., 1940; Wiant and Tucker, 1940; Satour and Butler, 1967; Kellam and Zentmyer, 1986; Hwang and Hwang, 1993]. In particular, Phytophthora blight, which occurs in all organs of pepper plants, including root, stem, leaf, and fruit, has been responsible for major losses of pepper production all over the world, especially in fields excessively wet during prolonged periods of rainy weather [Weber, 1932; Tompkins and Tucker, 1941; Kimble and Grogan, 1960; Barksdale et al., 1984; Palloix et al., 1988 A, B; Kim and Hwang, 1992]. To minimize the yield losses of pepper caused by Phytophthora blight, fungicides, crop rotation, and resistant cultivars have been employed widely during the cultivation of pepper plants [Hwang and Kim, 1995]. However, because of the difficulties in effectively controlling the disease with soil or foliar fungicides, the use of resistant pepper cultivars and crop rotation would be a valuable contribution to growers [Palloix et al., 1988 A, B; Sung and Hwang, 1988; Kim et al., 1989].

Resistance of pepper to *P. capsici* was first identified in pepper genotypes by Kimble and Grogan [1960]. This resistance was later reported to be governed by two, distinct, dominant genes that act independently without additive effects [Smith et al., 1967; Polach and Webster, 1972], or by a single, dominant gene with modifiers [Barksdale, 1984]. However, prolonged incubation periods or very high inoculum concentrations of *P. capsici* used in those studies could occasionally overcome resistance and result in symptoms on resistant plants. The use of resistance to effectively control Phytophthora blight in fields has been problematical, especially during prolonged periods of rainy weather [Yang et al., 1989]. Several studies have been done to identify a stable and durable type of resistance to *P. capsici* for use in breeding programs [Kimble and Grogan, 1960; Smith et al., 1967; Barksdale, 1984]. Recently, it has been suggested that age-related resistance that is expressed as pepper plants mature, may be very effective in reducing damage from this disease [Kim et al., 1989], when pepper seedlings are transplanted.

There are no pathogenic races of *P. capsici* on pepper plants, but several reports indicate varying degrees of virulence of isolates on different hosts. Polach and Webster [1972] defined 14 pathogenic strains of *P. capsici* based on pathogenicity to different hosts, but not to different pepper cultivars. In their study, recombination between pathogenicity and mating type occurred, based on 391 single-oospore progenies from crosses of A1 and A2 types. The ability of *P. capsici* to overcome resistance of pepper plants was controlled by at least two genes. In our earlier studies, we examined the pathogenic variation on Korean pepper cultivars of *P. capsici* isolates from diverse geographic origins [Yang et al., 1989; Kim and Hwang, 1992]. However, the Korean pepper genotypes did not differentiate any vertical pathotypes from the *P. capsici* isolates used. Other findings of genetic variation in these same isolates of *P. capsici* from Korea, Europe, and New Mexico based on restriction fragment length polymorphisms of mitochondrial DNA [Hwang et al., 1991] suggests the possible existence of variation in virulence of naturally occurring *P. capsici* isolates. Recently, Bowers and Mitchell [1991] also demonstrated that oospore progenies from pairings of pathogenic isolates of *P. capsici* differed in their ability to cause disease in pepper plants.

In the present study, the pathogenic reactions of different isolates of *P. capsici* along with diverse pepper accessions at different plant growth stages were determined.

Table 1. Analysis of variance for disease severities on 17 pepper cultivars stem-wound inoculated with each of six isolates of *Phytophthora capsici* at different leaf stages

Source of variation	df	Mean square	*F* value	*P*
4-leaf stage				
Cultivar	16	3.5	27.8	< 0.01
Isolate	5	10.4	82.3	< 0.01
Cultivar × isolate	80	0.9	7.0	< 0.01
8-leaf stage				
Cultivar	16	42.8	505.4	< 0.01
Isolate	5	42.0	496.5	< 0.01
Cultivar × isolate	80	10.3	122.6	< 0.01
12-leaf stage				
Cultivar	16	102.8	965.8	< 0.01
Isolate	5	49.0	460.8	< 0.01
Cultivar × isolate	80	6.1	57.5	< 0.01

Materials and methods

Plant and fungus

Seventeen pepper cultivars were used for evaluating resistance to Phytophthora blight : Hanbyul and Kingkun from Korea; Cayenne Cajun 1, Cayenne Cajun 1A, Cayenne Cajun 2, Cayenne Cajun 2A, Peto Seed Cayenne, Durkee Cayenne, Capritto Cayenne, Bruce Foods, and Tabasco (*Capsicum frutescens*) from the Department of Plant Pathology and Crop Physiology, Louisiana State University, U.S.A.; CO 0352 (PM 217, INRA-France in origin), CO 1176 (PI 201234, INRA-France), CO 2227 (PI 188478, Mexico), CO 2230 (PI 189550, Mexico), CO 2289 (PI 201238, Mexico) and CO 3289 (T.C. 3191, Mexico) provided by the Asian Vegetable Research and Development Center (AVRDC), Taiwan. Seeds of each cultivar were sown in a plastic tray (55 × 35 × 15 cm) containing a steam-sterilized soil mix of a commercial compost soil (peat moss, perlite, and vermiculite: 5 : 3 : 2, v/v/v), sand, and loam soil (1 : 1 : 1, v/v/v). Six seedlings (30 days old) were transplanted into each of plastic pot (15 × 5 × 10 cm) containing the soil mix. Pepper plants were raised in a growth room at 25±2 °C with 5,000 lux illumination for 16 h/day.

The isolates of *P. capsici* used were: 87E1, 87I33, 87K14, 87L19 from Korea; S197 from INRA-France, and CBS 178.26 from Italy [Kim and Hwang, 1992]. All isolates were grown on oatmeal (Difco) agar plates at 25±1 °C for 7 days. Zoospores were produced as described previously [Kim et al., 1989], and a zoospore suspension was used as inoculum. Zoospores in suspension were counted with a hemacytometer, and inoculum densities were adjusted with sterile tap water to give 1×10^5 zoospores per milliliter.

Inoculation and disease evaluation

Each cultivar was inoculated at four-, eight-, and twelve-leaf stages with a zoospore suspension (10^5/ml) on the wounded stems by using the stem-wound tech-

Table 2. Disease severity incited by six isolates of *Phytophthora capsici* on 17 pepper cultivars or accessions at the eight-leaf stage[a]

Cultivar or accession	Disease severity[b] incited by isolates						
	S197	87E1	CBS 178.26	87K14	87I33	87L19	Average
Hanbyul	5.0 (S)[c]	5.0 (S)	5.0 (S)	5.0 (S)	5.0 (S)	5.0 (S)	5.0
Cayenne Cajun 1	5.0 (S)	4.7 (S)	5.0 (S)	5.0 (S)	5.0 (S)	5.0 (S)	4.9
Cayenne Cajun 2A	4.3 (S)	4.4 (S)	4.5 (S)	4.0 (S)	4.8 (S)	5.0 (S)	4.5
Cayenne Cajun 1A	4.3 (S)	4.5 (S)	4.5 (S)	4.2 (S)	4.5 (S)	5.0 (S)	4.5
Cayenne Cajun 2	4.4 (S)	4.4 (S)	4.2 (S)	4.4 (S)	4.1 (S)	5.0 (S)	4.4
Peto Seed Cayenne	4.6 (S)	4.4 (S)	4.3 (S)	5.0 (S)	3.5 (S)	5.0 (S)	4.4
Tabasco	4.9 (S)	4.0 (S)	5.0 (S)	5.0 (S)	4.6 (S)	3.4 (S)	4.4
Bruce Foods	4.6 (S)	4.4 (S)	4.3 (S)	4.8 (S)	3.4 (S)	5.0 (S)	4.4
Durkee Cayenne	3.5 (S)	4.3 (S)	3.5 (S)	5.0 (S)	3.0 (S)	5.0 (S)	4.0
Kingkun	4.1 (S)	5.0 (S)	4.8 (S)	4.6 (S)	4.3 (S)	1.3 (R)	4.0
Capritto Cayenne	4.8 (S)	4.3 (S)	5.0 (S)	3.6 (S)	3.8 (S)	1.3 (R)	3.8
T.C. 3191	5.0 (S)	5.0 (S)	5.0 (S)	0.3 (R)	4.5 (S)	0.0 (R)	3.2
PI 189550	5.0 (S)	4.5 (S)	5.0 (S)	3.0 (S)	1.5 (R)	0.5 (R)	3.2
PI 201234	4.8 (S)	4.6 (S)	0.0 (R)	0.0 (R)	1.3 (R)	0.0 (R)	2.0
PI 188478	4.8 (S)	4.5 (S)	4.3 (S)	0.5 (R)	0.5 (R)	0.3 (R)	2.0
PM 217	5.0 (S)	3.0 (S)	0.0 (R)	1.0 (R)	4.0 (S)	0.0 (R)	2.0
PI 211238	2.0 (R)	0.0 (R)	5.0 (S)	3.0 (S)	0.0 (R)	0.0 (R)	2.0
Average	4.5	4.2	4.1	3.5	3.4	2.8	

[a] Plants were inoculated with a zoospore suspension (10^5/ml) at the eight-leaf stage by the stem-wound technique.
[b] Disease severity based on a 0–5 scale, where 0 = immune or highly resistant, no visible symptoms and 5 = highly susceptible, plant dead.
[c] S = susceptible (D.S. = 2.1–5.0), R = resistant (D.S. = 0.0–2.0).

nique previously developed by Kim et al. [1989]. The stems of pepper plants were wounded by cutting a 1-cm longitudinal slit 1 cm from the soil surface. A small quantity of sterile cotton dipped in a suspension of 1×10^5 zoospores per milliliter was placed on the wounded stem slits that were then covered with plastic tape. To evaluate resistance, disease severity was rated daily after inoculation based on a 0–5 scale: 0 = no visible disease symptoms, 1 = hypersensitive dark brown girdling on the stems or leaves slightly wilted with brownish lesions beginning to appear on stems, 2 = brownish lesion slowly progressing on the stem, or 30–50% of entire plant diseased, 3 = stem lesion progression up to half of the plant height, or 50–70% of entire plant diseased, 4 = stem lesion progressing toward the shoot apex, or 70–90% of entire plant diseased, 5 = plant dead.

All data are the means of 10 plants inoculated with each of six isolates. All experiments were repeated with similar results. Data are presented from one experiment only. Disease severities from one experiment were analyzed statistically by the analysis of variance procedures.

Results

When inoculated by stem-wounding with different isolates of *P. capsici*, susceptible pepper plants had a brownish stem-discoloration rapidly extending upward from the wound-inoculated stem site accompanied by a sudden wilt of the entire plant, leaf defoliation, or damping-off in juvenile plants. The light brownish lesions extended rapidly into the upper part of the stem. Leaf lesions also rapidly expanded to form round or irregularly shaped, dark green, water-soaked areas that later dried and became a light tan. In contrast, resistant plants were symptomless or had a hypersensitive, dark brown girdling rot that developed very slowly on the stems. No leaf defoliation and wilting occurred in the resistant plants, although there were dark brown lesions on the stems.

Table 3. Disease severity incited by six isolates of *Phytophthora capsici* on 17 pepper (*Capsicum* spp.) accessions at the twelve-leaf stage[a]

Cultivar	Disease severity[b] incited by isolates						
or accession	S197	87E1	CBS 178.26	87K14	87I33	87L19	Average
Hanbyul	5.0 (S)[c]	5.0 (S)	2.6 (S)	5.0 (S)	5.0 (S)	5.0 (S)	4.6
Cayenne Cajun 1	5.0 (S)	4.5 (S)	5.0 (S)	4.4 (S)	4.0 (S)	3.5 (S)	4.2
Cayenne Cajun 2A	3.5 (S)	4.2 (S)	4.6 (S)	5.0 (S)	3.0 (S)	4.5 (S)	4.1
Cayenne Cajun 1A	4.5 (S)	4.0 (S)	5.0 (S)	3.0 (S)	4.0 (S)	3.5 (S)	4.0
Cayenne Cajun 2	5.0 (S)	4.3 (S)	4.7 (S)	3.3 (S)	4.0 (S)	4.5 (S)	3.8
Peto Seed Cayenne	5.0 (S)	3.7 (S)	0.0 (R)	3.2 (S)	2.8 (S)	4.6 (S)	3.1
Tabasco	5.0 (S)	1.5 (R)	0.0 (R)	3.5 (S)	3.0 (S)	0.0 (R)	2.1
Bruce Foods	5.0 (S)	2.0 (R)	0.0 (R)	3.5 (S)	3.5 (S)	0.0 (R)	2.3
Durkee Cayenne	5.0 (S)	4.2 (S)	4.0 (S)	3.5 (S)	3.5 (S)	3.7 (S)	3.9
Kingkun	3.7 (S)	3.7 (S)	0.0 (R)	2.9 (S)	3.8 (S)	1.0 (R)	2.5
Capritto Cayenne	5.0 (S)	3.6 (S)	0.0 (R)	3.5 (S)	2.8 (S)	1.0 (R)	2.6
T.C. 3191	1.6 (R)	1.6 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	1.1
PI 189550	0.8 (R)	1.1 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.3
PI 201234	0.2 (R)	1.7 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.3
PI 188478	3.2 (S)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.5
PM 217	1.0 (R)	2.3 (S)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.6
PI 211238	0.6 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.0 (R)	0.1
Average	3.5	2.7	1.6	2.4	2.3	2.0	

[a] Plants were inoculated at the twelve-leaf stage with a zoospore suspension (10^5/ml) by the stem-wound technique.
[b] Disease severity based on a 0–5 scale, where 0 = immune or highly resistant, no visible symptoms and 5 = highly susceptible, plant dead.
[c] S = susceptible (D.S. = 2.1–5.0), R = resistant (D.S. = 0.0–2.0).

The analyses of variance for the disease severities on pepper cultivars inoculated with *P. capsici* at different leaf stages showed highly significant differences among cultivars, isolates, and cultivar × isolate interactions (Table 1). There was in general a differential interaction between the pepper cultivars and *P. capsici* isolates.

At the four-leaf stage, significant differences in disease severity were observed among the 17 pepper cultivars tested, although these differences were quantitative rather than qualitative (no data presented). In general, all cultivars were highly susceptible to all the tested isolates of *P. capsici* at the four-leaf stage. However, the pepper accessions, T.C. 3191, PI 189550, PI 201234, PI 188478, PM 217, and PI 201238, from the AVRDC had slower infection, as compared to the other cultivars tested.

At the eight-leaf stage, hypersensitive resistant responses to *P. capsici* were observed in some of the pepper cultivars tested (Table 2). When disease severity ratings were 0, 1, and 2, we classified the pepper accessions as resistant. The pepper accessions,

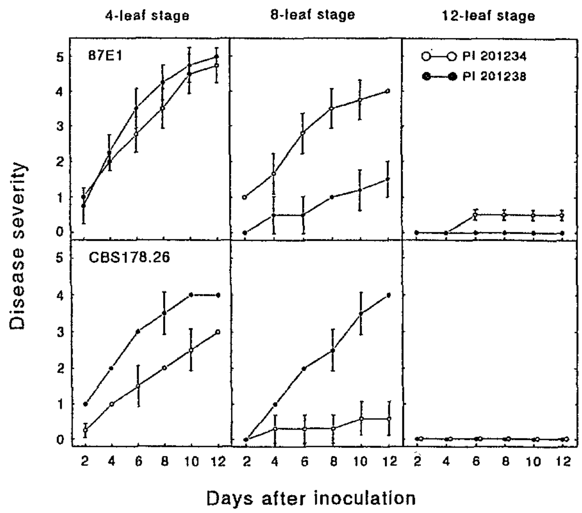

Figure 1. Disease severity curves for two pepper accessions PI 201234 and PI 201238 inoculated with each of two isolates of *Phytophthora capsici* (87E1 and CBS 178.26) by using the stem-wound inoculation method at the different leaf stages. Disease severity rating based on a 0–5 scale, where 0 = no visible symptoms and 5 = plant dead. Each value represents a mean ± standard deviation of 10 plants.

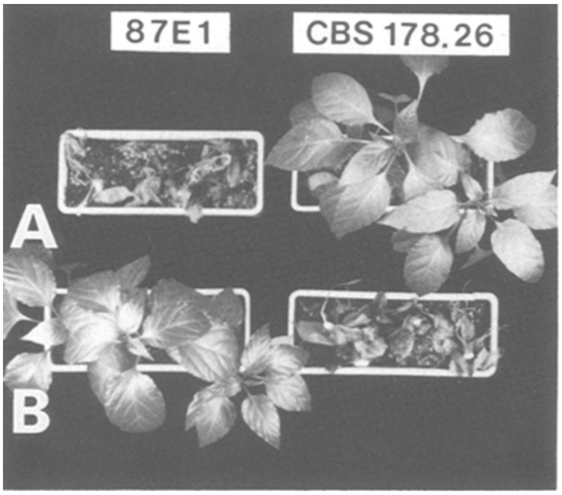

Figure 2. Differential interactions of the pepper accessions (A) PI 201234 and (B) PI 201238 after inoculation by the stem-wound technique with each of *Phytophthora capsici* isolates 87E1 and CBS 178.26 at eight-leaf stage.

PI 201234, PI 188478, PM 217, T.C. 3191, and PI 201238, were highly resistant at this stage to some isolates of *P. capsici* from different geographic origins. However, the other 11 pepper cultivars at the eight-leaf stage were highly susceptible. The isolates tested appeared to be different in virulence. For instance, the French isolate S197 was highly virulent to most of the cultivars tested, except PI 201238. There were differential interactions between some pepper cultivars and *P. capsici* isolates.

At the twelve-leaf stage, the cultivars, Hanbyul, Cayenne Cajun 1, Cayenne Cajun 2A, Cayenne Cajun 1A, and Cayenne Cajun 2 were highly susceptible to all of the isolates of *P. capsici* tested (Table 3). The cultivars, Peto Seed Cayenne, Tabasco, Bruce Foods, Durkee Cayenne, Kingkun, and Capritto Cayenne, were moderately susceptible. The pepper accessions, T.C. 3191, PI 189550, PI 201234, PI 188478, PM 217, and PI 201238, from the AVRDC were highly resistant. The French isolate S197 was highly virulent to most of the cultivars tested, whereas the four Korean isolates were moderately virulent. Most importantly, there were differential interactions between pepper cultivars and *P. capsici* isolates. For example, the pepper accession, PI 188478, was moderately susceptible to isolate S197, but highly resistant to all other isolates tested. In contrast, the pepper accession, PM 217, was moderately resistant to isolate S197, but moderately susceptible to isolate 87E1. In general, most cultivars became less susceptible to *P. capsici* as pepper plants aged (Tables 2 and 3). In particular, the expression of resistance to Phytophthora blight at the later growth stages were more apparent in the AVRDC pepper accessions than the Korean and U.S. pepper cultivars.

The pepper accessions PI 201234 and PI 201238, showed significantly different interactions with the two isolates, 87E1 and CBS 178.26 (Table 2). They were reevaluated (Figure 1) and isolate 87E1 was more virulent than the isolate CBS 178.26 on both accessions at the four-leaf stage. At the eight-leaf stage, there was a significant differential interaction: plants of PI 201234 were dead 18 days after inoculation with the isolate 87E1, while PI 201238 remained healthy, and conversely with CBS 178.26 (Figure 2). Such a differential interaction occurred distinctly at this stage. It was not observed at the twelve-leaf stage, because both pepper accessions, PI 201234 and PI 20138, became resistant to isolates 87E1 and CBS 178.26 (Figure 1).

Discussion

Resistance of pepper cultivars from diverse geographic origins to different isolates of *P. capsici* could be effectively evaluated under controlled environmental conditions. When inoculated on juvenile pepper plants at the four-leaf stage, all tested cultivars or accessions showed typical symptoms on the stems by 2 days after inoculation and were dead after 13 to 15 days, 'pepper plants of all the tested accessions were dead', indicating that they were susceptible to the six isolates at this stage. However, the levels of susceptibility of the pepper cultivars varied quantitatively. The two PI and T.C. 3191 accessions from the AVRDC showed the retardation of symptom development, but no hypersensitive symptoms were observed in any case. These data suggest strongly that the hypersensitive type of resistance to Phytophthora blight may not be expressed in the juvenile pepper plants. Similarly, lack of resistance in juvenile plants has been demonstrated in previous screening studies of Korean pepper cultivars [Kim et al., 1989; Kim and Hwang, 1992].

At the eight-leaf stage, inoculation of *P. capsici* on pepper plants resulted in the induction of significantly different interactions between the pepper cultivars and *P. capsici* isolates (Tables 1 and 2, Figs. 1 and 2). The Korean and U.S. cultivars tested were in general highly susceptible to the diverse isolates of *P. capsici*. In contrast, some PI accessions, such as PI 201234 and PI 201238, interacted differentially with some *P. capsici* isolates. Considerable variation in virulence was observed in the tested isolates of *P. capsici*. The existence of variation in virulence of naturally occurring *P. capsici* isolates was supported by our earlier findings of genetic variation in these same isolates by examining restriction fragment length polymorphisms of mitochondrial DNA [Hwang et al., 1991]. Resistance of specific pepper genotypes to Phytophthora blight may be distinctly expressed at late growth stages rather than early growth stages. Accordingly, such age-related resistance in pepper plants appears to play a significant role in the detection of the avirulence in some *P. capsici* isolates.

At the twelve-leaf stage of pepper plants, Phytophthora blight developed slowly in the Korean and U.S. cultivars that had been highly susceptible at the eight-leaf stage. In particular, the AVRDC-pepper accessions became highly resistant to the disease at this stage. Although all pepper cultivars became increasingly resistant as plants grew older [Kim et al., 1989], expression of the age-related resistance may be more apparent in the pepper genotypes carrying some resistance genes capable of reducing the development of Phytophthora blight. Furthermore, the expression of resistance genes at a particular plant growth stage may accompany the expression of the corresponding avirulence genes in some *P. capsici* isolates. Virulence of *P. capsici* isolates appeared at different levels in the pepper plants depending on the inoculation methods.

The Korean cultivar, Hanbyul, U.S. local cultivars Cayenne Cajun 1, 2A, 1A, 2, and Durkee Cayenne, do not have resistance genes against the tested isolates of *P. capsici*. However, the differential susceptibilty to the isolates CBS 178.26 and 87L19 of the cultivars, Kingkun and Capritto Cayenne, suggests that they may have specific resistance genes. The AVRDC-pepper accessions contain useful resistance genes against the tested isolates of *P. capsici*.

In conclusion, our data suggest that there are differential interactions between *P. capsici* isolates and some pepper genotypes at late plant growth stages.

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