New Legume Hosts of *Phakopsora pachyrhizi* Based on Greenhouse Evaluations

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ABSTRACT

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Phakopsora pachyrhizi, the causal organism of soybean rust, was first found in the continental United States in 2004 and has been found on soybean, kudzu, Florida beggarweed, and three *Phaseolus* species in the field. The pathogen has been reported to occur on more than 90 legume species worldwide and it is likely to infect native and introduced legume species in the United States. The objective of this study was to determine if 176 species representing 57 genera of legumes, the majority of which are either native or naturalized to soybean-growing areas of the United States, could be hosts of *P. pachyrhizi*. Between one and three accessions of each species, a total of 264 accessions, were inoculated with a mixture of four isolates of *P. pachyrhizi*. Severity and sporulation were rated on a 1-to-5 scale at 14 and 28 days after inoculation. *P. pachyrhizi* was confirmed by the presence of sporulating uredinia and/or immunological assay on 65 new species in 25 genera; 12 of these genera have not been reported previously as hosts. Many of the newly identified hosts grow in the southern United States, and like kudzu, could serve as overwintering hosts for *P. pachyrhizi*.

Additional keywords: host range, Papilionoideae

Soybean rust is caused by the obligate fungus *Phakopsora pachyrhizi* Syd. & P. Syd. and was first reported in Asia (10). It is a serious foliar disease on soybean in Africa, Asia, Australia, and South America (15), but its impact on soybean production in North America has been limited since its arrival in 2004 (22) to the southern United States (24).

There are 93 hosts of *P. pachyrhizi* reported from inoculated and noninoculated plants (12,17,21,23). All hosts belong to the legume family Fabaceae, which is one of the largest families of flowering plants containing over 650 genera and 18,000 species (18). The host range of *P. pachyrhizi* is restricted to the subfamily Papilionoideae, a monophyletic clade within Fabaceae (26). The subfamily contains an estimated 476 genera and 13,860 species (5). *P. pachyrhizi* is known to infect 42 genera of papilionoid legumes, but the limits of its host range are not known. Legume systematics might provide useful insight on the potential host range of *P. pachyrhizi* and its relationship with host plants.

In the United States, six species have been reported as hosts of *P. pachyrhizi*: soybean (22); kudzu, *Pueraria lobata* (Willd.) Ohwi (8); Florida beggarweed, *Desmodium tortuosum* (Sw) DC. (23); dry bean, *Phaseolus vulgaris* L.; lima bean, *P. lunatus* L.; and scarlet runner bean, *P. coccineus* L. (12).

With the appearance of soybean rust in the continental United States in 2004 (22), there are many new potential legume hosts of *P. pachyrhizi*. Many legume species in the United States were either not previously tested or were not in the same geographic region as the fungus. These leguminous species may aid in the overwintering of the fungus and provide a source of inoculum at the beginning of the soybean-growing season. The objective of this study is to identify leguminous hosts that are either native or naturalized to the southern United States or other major soybean-growing areas.

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MATERIALS AND METHODS

Species selection. All species tested belong to the legume subfamily Papilionoideae and all occur in the southern United States or in major soybean-producing states (25) with the exception of previously reported hosts and four unscreened species in *Teramnus*, the genus most closely related to *Glycine* (11). Seed was ordered from several repositories in the USDA-ARS National Plant Germplasm System (Table 1).

Experimental procedures. Between 2 and 20 seeds per entry per replication were planted into each 4-cm^2 cell in 6 × 12 flats containing soilless medium (Sunshine Mix, LC1; Sun Gro Horticulture Inc., Bellevue, WA) in a rust-free greenhouse. Seed number varied because of seed size, availability, germination, and plant size. Seeds of some species were scarified or pregerminated on water agar to improve the likelihood of survival. The experimental design was a randomized complete block with three replications. Two soybean cultivars, GC00138-29 and UG-5, were included in each replication as susceptible checks. The experimental unit was a cell containing 1 to 20 plants of a single entry, which represented a unique plant introduction (PI).

Inoculation. Four-week-old plants were inoculated with a mixture of four isolates of *P. pachyrhizi* at the USDA-ARS Foreign Disease-Weed Science Research Unit (FDWSRU) Biosafety Level 3 Plant Pathogen Containment Facility at Ft. Detrick, MD (13). The inoculum consisted of an equal mixture of isolates from Brazil (BZ 01-1), Paraguay (PG 01-2), Thailand (TH 01-1), and Zimbabwe (ZM 01-1) (14). Spores were removed from liquid nitrogen storage, heat shocked at 40°C for 5 min, and allowed to rehydrate by incubating over water in an enclosed petri plate for 12 h (14). Distilled water with 0.01% (v/v) Tween 20 (Sigma, St. Louis, MO) was added to the dry spores and the mixture was stirred with a glass rod. The spore suspension was then filtered through a 53-µm nylon screen into a beaker to remove debris and clumps of spores, and the spore concentration was determined with a hemacytometer. Distilled water was added to adjust the final spore concentration to 25,000 spores per ml. Each flat was inoculated with 25 ml of the spore suspension with an atomizer at 138 kPa. Flats were

placed in a dew chamber at 20 to 22°C for 16 h and then transferred to a greenhouse at 20 to 25°C with a 16-h photoperiod. Supplemental lighting was provided with 1,000-watt Metalarc high-intensity lamps (Sylvania, Danvers, MA). The plants were rated 14 days after inoculation (DAI) and reinoculated with the same procedure as described above. After incubation in the dew chamber, the plants were placed in a mist chamber in the greenhouse at 20 to 25°C with natural light. Mist was provided for 1 min at 20 min intervals for the duration of the experiment. The plants were rated as before at 14 DAI.

Table 1. List of legume hosts that were susceptible when inoculated with *Phakopsora pachyrhizi* in the greenhouse and the lesion type and severity ratings for each species

Scientific name	Accession[b]	Seed source[c]	New genus[d]	New species[d]	Lesion type[e]	No.[f]	Severity[a]		
							Mean	Range	Standard error
Alysicarpus rugosus	PI 286530	S9		x	RB	9	1.9	1–4	0.39
Astragalus canadensis	PI 232539	W6	x		RB	8	1.8	1–3	0.25
A. cicer	PI 362119[a], PI 452451[a], PI 576968[a]	W6			BL, RB	16	3.2	2–4	0.16
A. crassicarpus	DLEG 900280	DLEG			RB	4	1.3	1–2	0.25
A. glycyphyllos	PI 206882, PI 420665[a]	W6			RB	10	1.6	1–2	0.16
Baptisia alba var. macrophylla	Ames 27423[a], PI 636376	NC7	x	x	RB	10	2.0	1–3	0.26
B. australis	Ames 24958, PI 443123	NC7		x	BL, RB	11	1.5	1–3	0.21
B. bracteata var. *laevicaulis*	Ames 3095[a]	NC7		x	BL, RB	6	2.5	1–3	0.34
Cajanus cajan	NSL 73128, PI 520598[a]	NPGS			BL, RB	9	3.6	2–5	0.38
Calopogonium caeruleum	PI 362125[a]	S9			RB, TAN	5	4.0	3–5	0.45
Calopogonium mucunoides	PI 204364[a], PI 279595[a], PI 286288[a], PI 322302[a]	S9		x	RB, TAN	24	3.1	2–5	0.15
Caragana arborescens	PI 310390[a], PI 369217[a], PI 371524[a], PI 633648[a], PI 636378[a]	NC7	x	x	RB	27	1.9	1–3	0.14
Centrosema virginianum	PI 322350[a], PI 386281[a]	S9		x	BL, RB	8	1.9	1–4	0.35
Cologania angustifolia var. *angustifolia*	DLEG 900669[a], DLEG 990127[a]	DLEG	x	x	RB, RED	12	3.7	2–5	0.26
Cologania angustifolia var. *stricta*	DLEG 890367D[a], DLEG 990130[a]	DLEG		x	RB, TAN	11	3.1	2–4	0.21
Cologania lemmonii	DLEG 880053D[a]	DLEG		x	RB	1	4.0	4	.
Crotalaria incana	PI 263427[a], PI 336996[a]	S9		x	RB, TAN	14	1.8	1–3	0.19
C. lanceolata	PI 322408[a]	S9		x	TAN, NF	5	1.6	1–3	0.40
C. ochroleuca	PI 274767, PI 543869[a]	S9		x	RB, NF	14	1.7	1–3	0.19
C. pallida	PI 189272	S9		x	RB	6	1.2	1–2	0.17
C. sagittalis	DLEG 900645[a]	DLEG		x	RB	6	1.5	1–2	0.22
C. spectabilis	PI 240413, PI 407529	S9			BL, RB, NF	12	1.7	1–2	0.14
C. verrucosa	PI 209316[a]	S9		x	BL, RB	6	1.8	1–3	0.31
C. virgulata ssp. *grantiana*	PI 68849	S9		x	BL, RB	2	3.0	3	0.00
Desmodium canadense	PI 214108	S9		x	RB	3	1.7	1–3	0.67
D. cuspidatum	PI 214105[a]	S9		x	RB	4	2.0	1–3	0.41
D. obtusum	PI 316210[a]	S9		x	RB	6	3.0	2–4	0.45
D. perplexum	PI 322465[a]	S9		x	RB	6	2.7	2-4	0.33
Genista tinctoria	PI 325343, PI 502384	W6	x	x	RB	16	1.8	1–4	0.26
Glycine max	GC00138-29[a], UG-5[a]	UIUC			RB, TAN	12	3.3	2–5	0.25
Glycyrrhiza lepidota	PI 215212[a], PI 215213, PI 215215[a]	W6	x	x	BL, RB	18	2.3	1–3	0.20
Indigofera miniata	PI 477963	S9	x	x	RB	12	1.3	1–3	0.19
I. spicata	PI 257752[a]	S9		x	BL, RB	10	2.0	1–4	0.33
I. suffruticosa	PI 206323, PI 331110	S9		x	RB	10	2.1	1–3	0.28
I. tinctoria	PI 198005, PI 300006	S9		x	RB	12	1.5	1–3	0.23
Kummerowia stipulacea	PI 186584[a], PI 295943[a], PI 419958	S9			RB	18	2.6	1–5	0.22
K. striata	PI 419960	S9			BL, RB	14	3.4	1–5	0.33
Lablab purpureus ssp. *uncinatus*[g]	PI 532672	S9			BL, RB	5	2.6	2–3	0.24
Lathyrus aphaca	PI 227511[a], PI 283485[a], PI 358856[a]	W6	x	x	BL, RB	13	2.3	1–4	0.33
Lathyrus sylvestris	PI 383275	W6		x	RB	14	1.1	1–2	0.10

(*continued on next page*)

[a] Severity was based on a 1-to-5 scale, in which 1 = no reaction and 5 = a severe response.
[b] Accessions observed with uredinia and urediniospores.
[c] DLEG = Desert Legume Program, Tucson, AZ; NC7 = North Central Regional Plant Introduction Station, Ames, IA; NPGS = National Center for Genecic Resources Preservation; S9 = Plant Genetic Resources Conservation Unit, Griffin, GA; W6 = Western Regional Plant Introduction Station, Pullman, WA; and UIUC = University of Illinois, Urbana, IL.
[d] An "x" indicates that this is the first report of the genus and/or species as compared with Ono et al. (17).
[e] Lesion types observed on one or more entries and often observed in combination on a single entry. BL = black; BR = brown; NF = light-colored necrotic flecks; RB = reddish brown; RED = red; and TAN = tan.
[f] Number of entries evaluated.
[g] This is the first report of the subspecies as compared with a previous report (17).

Evaluation. Lesion type, disease severity, and sporulation were assessed for each entry. Lesions were rated as either tan (TAN), reddish brown (RB), or a mixture of both (mixed) (1,2). Lesion types that differed from the standard TAN or RB were noted. Disease severity was based on a 1-to-5 scale, in which 1 = no visible lesions, 2 = few scattered lesions, 3 = moderate number of lesions on at least part of the leaf, 4 = abundant number of lesions on at least part of the leaf, and 5 = prolific lesion development over most of the leaf (14). Sporulation within lesions was evaluated as none, some, or abundant. Abundant

Table 1. (*continued from preceding page*)

Scientific name	Accession[a]	Seed source[b]	New genus[c]	New species[c]	Lesion type[d]	No.[e]	Severity[f]		
							Mean	Range	Standard error
Lespedeza bicolor	PI 561142	S9			RB	4	2.0	1–3	0.41
L. capitata	PI 215225[a], PI 287114[a], PI 340795	S9		x	RB	18	2.8	1–5	0.24
L. cuneata	PI 286451[a], PI 419955[a], PI 597489[a]	S9		x	BL, RB, RED	18	2.3	1–3	0.16
L. cyrtobotrya	PI 295323[a], PI 360903[a]	S9		x	BL, RB, RED	16	2.3	1–3	0.17
L. thunbergii	PI 360908[a]	S9		x	BL, RB	10	1.7	1–2	0.15
L. virgata	PI 218004[a], PI 349428	S9		x	RB	8	1.8	1–3	0.25
Lotus corniculatus	PI 568200	W6			RB	18	1.2	1–2	0.09
Lotus glaber (synonym = *L. tenuis*)	PI 246737	W6		x	RB	12	1.2	1–2	0.11
Lotus pedunculatus	PI 631960[a]	W6		x	RB	6	1.3	1–3	0.33
Lotus unifoliolatus	PI 215235, PI 631744	W6			RB, RED	10	1.7	1–4	0.30
Lupinus albus	PI 381322, PI 481554[a], PI 502651	W6			RB	13	1.9	1–3	0.18
Lupinus angustifolius	PI 168527[a], PI 383249[a], PI 384551, PI 615400	W6			RB	23	1.9	1–2	0.06
Lupinus luteus	PI 168544[a], PI 224493, PI 505850[a], PI 533713[a]	W6			RB	22	1.7	1–2	0.10
Lupinus perennis	DLEG 920280[a]	DLEG		x	RB, TAN	2	2.0	2	0.00
Lupinus texensis	DLEG 910497[a]	DLEG		x	RB	4	2.8	2–4	0.48
Macroptilium atropurpureum	PI 311515[a], PI 543380[a]	S9			RB	8	3.4	2–4	0.32
Macroptilium lathyroides	PI 276183[a], PI 292360[a], PI 330353[a]	S9			RB, RED, TAN	10	3.2	2–4	0.20
Medicago laciniata	PI 516674[a]	W6		x	RB	15	1.2	1–3	0.14
M. lupulina	PI 631966[a], W6 19435	W6		x	RB	16	1.2	1–2	0.10
M. minima	PI 498935, PI 499137, PI 537253	W6		x	RB	15	1.3	1–2	0.13
M. orbicularis	PI 249918[a], PI 287236, PI 535517[a], PI 535518	W6		x	BL, RB	29	1.9	1–4	0.16
M. polymorpha	PI 535528, W6 4234, W6 5380	W6		x	BL, RB	18	1.9	1–4	0.21
M. sativa ssp. *falcata*	PI 440539[a]	W6		x	RB	17	1.2	1–2	0.10
M. sativa ssp. *sativa*	PI 247790, PI 536536	W6		x	BL	36	1.1	1–2	0.05
Neonotonia wightii	PI 284804, PI 339895[a]	S9			RB, TAN	12	2.7	1–4	0.28
Pseudovigna argentea	PI 365594[a]	S9	x	x	RB, TAN	3	4.0	3–5	0.58
Robinia pseudoacacia	DLEG 910265	DLEG	x	x	RB	7	2.4	1–5	0.57
R. viscosa var. *hartwegii*	PI 560156[a]	NC7		x	RB	5	2.4	1–3	0.24
Senna sophera	DLEG 900003[a]	DLEG		x	RB	6	2.3	1–3	0.21
Sesbania punicea	DLEG 940172	DLEG		x	BL, RB, NF	7	1.4	1–3	0.30
S. virgata	PI 175007	S9		x	BL, RB	6	1.8	1–2	0.17
Tephrosia cinerea	PI 296078[a]	S9	x	x	RB	2	2.5	1–3	0.50
Tephrosia purpurea	PI 200238[a], PI 219855, PI 270391[a], PI 318815[a]	S9		x	RB	15	2.5	1–3	0.19
Teramnus labialis	PI 200233, PI 365056[a], PI 517204[a]	S9	x	x	BR, RB	21	2.4	1–4	0.18
Teramnus labialis	CU-383	UIUC			RB, RED	21	2.4	1–4	0.18
Teramnus micans	CU-414-2[a]	UIUC		x	RB	4	2.3	1–3	0.25
Teramnus repens	CU-220	UIUC		x	RED	2	2.0	1–3	1.00
Teramnus uncinatus	PI 241837, PI 296583, PI 316041, PI 321388[a]	S9		x	BL, RB	22	2.4	1–4	0.14
Trifolium aureum	PI 440721[a]	S9		x	RB	6	1.3	1–2	0.21
T. cernuum	PI 196307[a]	S9		x	BL, RB	6	2.2	1–3	0.31
T. incarnatum	PI 613044[a]	S9			RB	17	1.6	1–5	0.32
T. lappaceum	PI 254917[a], PI 517114	S9		x	RB	17	2.4	1–5	0.32
T. reflexum	PI 291825	S9		x	RB	11	1.3	1–3	0.19
T. resupinatum	PI 445907, PI 517144	S9		x	RB	16	1.2	1–3	0.14
T. striatum	PI 502625	S9		x	RB	6	1.5	1–3	0.34
T. tomentosum	PI 422494	S9		x	RB	9	1.1	1–2	0.11
Vigna adenantha	PI 312898, PI 430216[a]	S9		x	RB, NF	10	2.1	1–3	0.28
V. luteola	PI 196813[a], PI 355920[a], PI 406347[a]	S9			BR, RB, RED	18	3.1	2–4	0.14
V. unguiculata	PI 352832[a], PI 578893[a], PI 612519	S9			BL, RB, RED	16	2.9	1–5	0.20

sporulation was similar to that of the susceptible soybean cultivars used as checks.

Immunoassay. Leaf samples with lesions were excised from each entry at 28 DAI and stored at –80°C. At least one sample from each entry was tested for the presence of *P. pachyrhizi* by enzyme-linked immunosorbent assay (ELISA) with the Envirologix QualiPlate Kit for Soybean Rust (Envirologix, Portland, ME) and recommended protocol. Tissue samples were prepared by grinding the leaf section with a plastic pestle attached to a power rotary tool in a microcentrifuge tube containing 500 µl of QualiPlate Kit extraction buffer. Several negative controls were utilized in the immunoassay. To control for error in the sensitivity of the test kit, 15 entries without visible lesions were randomized among the positive samples. To control for cross-contamination and error in technique, two each of noninoculated soybean leaf samples and plain extraction buffer controls were randomized within each plate. ELISA plates were visually evaluated for a color change to blue, which indicated a positive reaction.

RESULTS

One hundred fifty-nine entries representing 89 species in 31 genera were visually confirmed to have soybean rust lesions and/or uredinia on at least one of the two rating dates (Table 1). Sixty-five new host species and one new host subspecies were identified, representing 25 genera; 12 genera have not been previously reported. Of the 65 new host species, 39 species had visible uredinia and urediniospores and the remaining had nonsporulating lesions.

Lesion type. The majority of the entries had RB lesions. Only 11 species had TAN lesions: *Calopogonium caeruleum*, *C. mucunoides*, *Cologania angustifolia* var. *stricta*, *Crotalaria incana*, *Crotalaria lanceolata*, *Lupinus perennis*, *Macroptilium lathyroides*, *Neonotonia wightii*, *Pseudovigna argentea*, *Vigna adenantha*, and the soybean inoculated controls. Several lesion types that differed from RB or TAN were also observed. These ranged from black, brown, and red to lightly colored necrotic flecks and often occurred in conjunction with the RB lesion type (Table 1).

Sporulation. Sporulation was abundant on all entries that had TAN lesions. Low-to-moderate sporulation was observed on entries with other lesion types with the exception of *Caragana arborescens*, *Cologania lemmonii*, *Crotalaria incana*, *Lathyrus aphaca*, *Lupinus perennis*, *Medicago lupulina*, and *Vigna adenantha*, which had abundant sporulation on non-TAN lesion types. There was a strong differential sporulation response for several species. For example, on *V. adenantha*, PI 312898 had no sporulation on either rating date while PI 430216 had a high level of sporulation on both dates.

ELISA. Thirty-two species had lesions with no visible sporulation but were ELISA positive for *P. pachyrhizi*. Of the 176 species tested, 87 did not develop lesions for the duration of the trial. Those asymptomatic entries and the negative controls were negative for *P. pachyrhizi* by ELISA.

DISCUSSION

The host range of *P. pachyrhizi* was summarized in 1992 and consisted of 91 species in Papilionoideae (17). With the introduction of *P. pachyrhizi* to geographical areas outside of the eastern hemisphere, it was likely that the pathogen would encounter and potentially infect additional host species in this same subfamily.

The 65 newly reported host species varied in their response to *P. pachyrhizi* from those with nonsporulating lesions to those with fully sporulating uredinia. The sporulation data suggest some hosts may not be as epidemiologically important as others. Although some plant species had no sporulating uredinia, they are considered hosts because they had become infected by *P. pachyrhizi* and confirmed by ELISA. Sporulation may have been restricted by a number of factors in the trial, including isolate, environmental conditions, duration of experiment, and host genotype and age. On the basis of other studies, the presence of sporulating uredinia may not be a good criterion for identifying a host. For example, accessions in the same host species respond differently when exposed to the same isolate of *P. pachyrhizi* (3,4,9,16). If a host is capable of becoming infected, sporulation may occur under different environmental conditions. Differences in sporulation might serve as an indication of the strength of the host in the epidemiology of the disease. Hosts with lesions that produce urediniospores increase the likelihood for secondary infection or subsequent infection on soybean.

Polymerase chain reaction (PCR) has been used to identify and distinguish between the two very similar soybean rust pathogens, *P. pachyrhizi* and *P. meibomiae* (7). The discovery of *P. pachyrhizi* in South Africa, Argentina, and the United States was confirmed by PCR (19,20,22). When PCR was initially tested with nonsusceptible plants in this trial, it resulted in false positives. The PCR results were also positive for multiple entries showing no symptoms or signs of infection, indicating that the PCR assay was detecting urediniospores on the surface of the leaf. Recently, antibodies have been generated to *P. pachyrhizi*, and an ELISA kit has been developed (Envirologix, Inc.). The ELISA kit was used in this study to confirm infection by *P. pachyrhizi* because it did not react with the urediniospores on the leaf surface of the nonsusceptible host plants.

The exact limits of *P. pachyrhizi*'s host range are still uncertain. The host range lies within the monophyletic Papilionoideae subfamily of Fabaceae, but it is unclear if the host range is limited within the subfamily. A more exhaustive screening of papilionoid legumes is needed to determine the host range restrictions. Additionally, while a genus may contain one or more host species, not all the species in that genus may be hosts.

The canavanine-accumulating clade within Papilionoideae is a monophyletic group (26) and includes the majority of known hosts of *P. pachyrhizi*. The exceptions are three genera, *Baptisia*, *Crotalaria*, and *Lupinus*, which belong to the genistoid clade. Legume phylogeny by using Bayesian analysis of the MATK gene showed the genistoid clade as a sister group to the dalbergioid clade, as well as the remaining papilionoids (25). However, parsimony analysis revealed a slightly different phylogenic relationship with the dalbergioid clade branching before the genistoid clade (26). Other host range studies have been used for legume systematics (6), and the host range of *P. pachyrhizi* may be useful in clarifying some relationships in Papilionoideae. If the exception of the genistoid clade is the only other host group outside the canavanine-accumulating clade, it may lend more support to the phylogeny based on parsimony analysis. It can be expected that additional species in the aforementioned genistoid and canavanine-accumulating clades will be susceptible to infection by *P. pachyrhizi*, and closely related groups may also contain hosts.

Of the 65 newly identified species, 62 occur in Alabama, Florida, Louisiana, Mississippi, and Texas, where they may be important for overwintering of the soybean rust pathogen. These include *Caragana arborescens*, a perennial tree; *Crotalaria incana*, a perennial forb/subshrub; and *Crotalaria lanceolata*, an annual forb. Although none of these species is known to overwinter the pathogen, it is known that kudzu in southern Florida can stay infected year round (8). Knowledge of the host range will help to predict potential overwintering sites and the level of primary inoculum from these sites that might be available to infect soybean fields at the start of the growing season. It will also help define species and prioritize areas to be scouted. Scouting the newly defined host species will result in a greater understanding of their natural infection as well as increased knowledge of their importance in the overwintering of soybean rust in the United States.

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