Variants of Barley Yellow Dwarf Virus Collected in New York and Illinois

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Cooperative Investigation, Crops Research Division, ARS, USDA; Cornell University Agricultural Experiment Station; and Illinois Agricultural Experiment Station. Supported in part by Public Health Service Research Grant AI-02540 from the National Institute of Allergy and Infectious Diseases and by Federal Regional Research funds from Project NE-23.

We are grateful for the technical assistance of Irmgard Muller and Frances Slovik.

Accepted for publication 2 February 1970.

ABSTRACT

All 367 isolates of barley yellow dwarf virus recovered from 372 samples collected in the field during 1967 and 1968 could be grouped among the four major variants previously encountered. These are RPV, RMV, and MAV transmitted specifically by *Rhopalosiphum padi*, *R. maidis*, and *Macrosiphum avenae*, respectively, and PAV transmitted nonspecifically by *R. padi* and *M. avenae*. Parallel tests on samples of spring oats from New York and Illinois showed that all four variants occurred in both areas, but their prevalence was different. For 148 isolates from Illinois, the distribution of variants was the same in both seasons. About 75% of the isolates were like PAV, about 20% like RPV, a single one each year was like RMV, and a single isolate (in 1967) like MAV. The 76 isolates recovered from New York samples in 1967 were distributed about as follows: 46% PAV, 36% MAV, 10% RPV, and 8% RMV. The 54 New York isolates identified in 1968 were 28% PAV, 61% MAV, 6% RPV, and 6% RMV. Five of 16 winter wheat plants and 15 of 55 winter barley plants collected in New York were found to be infected by more than one of the variants. The distribution patterns of the isolates at the two locations and the mixed infections in winter cereals are considered relevant to epidemiology of the disease. Phytopathology 60:1030-1035.

Previous observations have suggested some important differences in barley yellow dwarf of oats in New York and Illinois (12). Differences include the aphid species considered to be the most common vector, the pattern of distribution of infected plants within oat fields, the type of barley yellow dwarf virus (BYDV) isolates that predominate, and the severity of the disease. Since further study of such differences appeared to be useful in understanding some aspects of epidemiology of barley yellow dwarf, we studied field-collected samples and evaluated the variation among BYDV isolates from the two states. This paper reports results of parallel tests on samples from New York and Illinois collected in 1967 and 1968, and shows how we believe results of such tests contribute to an understanding of this complex disease.

MATERIALS AND METHODS.—Plants with symptoms of barley yellow dwarf were collected in Illinois on each of seven consecutive Monday mornings in 1967 beginning on 8 May, and at six similar intervals in 1968 beginning on 20 May. Entire plants were packed to maintain turgidity, and sent (airmail, special delivery) to Ithaca, New York. The Illinois samples were used each Wednesday in Ithaca, together with New York samples collected that morning, to provide parallel tests on samples from each area within each experiment. The 1967 samples from Illinois were obtained from either of two fields each of about 20 acres of Holden oats on the farm of J. P. Smith, about 5 miles south of Urbana. The 1968 samples from Illinois originated from the same area, but some were from a field of Tyler oats and others were from a field of Jaycee oats. All New York samples were collected at the Cornell Tailby Farm near Ithaca, New York, from plots that contained bulk plantings of early generations of oat hybrids developed by N. F. Jensen.

Two or more leaves were detached from each plant to be tested and used in comparative transmission tests with four aphid species as described previously (6, 9). Acquisition feeding was for 2 days at 15 C; inoculation test feeding was on seedlings of Coast Black oats (*Avena byzantina* K. Koch) for 5 days at the rate of about 10 aphids/plant in a growth chamber providing about 1,000 ft-c of light at 21 C for a 16-hr day. The four aphid species used were *Rhopalosiphum padi* (Linnaeus), the oat bird-cherry aphid; *R. maidis* (Fitch), the corn leaf aphid; *Macrosiphum avenae* (Fabricius), the English grain aphid; and *Schizaphis graminum* (Rondani), the greenbug. The clone of each species was the same as that used in all previous studies (9). At least 30 aphids of each species from every group used in an experiment were always tested as controls. Since *S. graminum* had not aided characterization of virus isolates in previous tests in New York, this species was omitted in most of the 1967 tests. Because Gill (3, 4) has encountered isolates of BYDV transmitted specifically by *S. graminum*, however, the species was used in most 1968 tests.

Identification of the virus isolates recovered from the field-collected samples was based on the pattern of transmission by the four aphid species and on the relative severity of symptoms. In addition, many subsequent comparative transmission tests were carried out, especially in cases where the original data did not clearly differentiate among the possibilities. The subsequent comparative tests were carried out with the

same four aphid species in a manner similar to that used for the original tests on the field-collected samples, although all four species were not always used in every experiment. Data for *S. graminum* are not tabulated because this species transmitted the same isolates as did *R. padi* in all subsequent tests.

RESULTS.—All BYDV isolates recovered were similar, but not necessarily identical, to the four major variants previously encountered (6, 9). In tests on New York samples, BYDV was recovered from 76 of 78 samples in 1967 and from 54 of 61 samples in 1968 (Table 1). Isolates similar to PAV predominated in 1967, as they did in 1965 and 1966 (6). Of the 76 isolates recovered in 1967, 35 were similar to PAV, 27 were MAV, 8 were RPV, and 6 were RMV. In 1968, however, MAV was the most common type (33 of 54 isolates recovered), and PAV was identified in only 15 of the 54 samples. Three isolates of RPV and 3 of RMV were identified in the 1968 New York collections.

Collections in 1967 were made separately for the borders of the plot and for the middle, but results of all collections are combined in Table 1. For samples collected in New York from the middle, 47% were MAV and 37% were PAV. From the border of the plot, 55% of the isolates were PAV and 24% were MAV. Although the significance of such differences is doubtful, the trend agrees with previous observations that MAV-infected plants often are scattered at random throughout fields, whereas PAV-infected plants often are concentrated along borders (8, 12).

During both seasons, *M. avenae* was the most common aphid species on oats at the Tailby Farm in New York, but populations were low. On several occasions aphids were collected in the field, allowed to feed singly for 5 days on test plants in the greenhouse, and then removed by fumigation. Five of 64 such *M. avenae* transmitted BYDV in 1967; two of 41 field-collected *M. avenae* transmitted BYDV in 1968. Subsequent tests on the seven infected plants showed that in one case each year an aphid had transmitted PAV; the other five plants were infected by MAV isolates.

Although the same four types of BYDV were also encountered in samples from Illinois, PAV predominated (Table 1). BYDV was recovered from 75 of the 87 Illinois samples tested in 1967, and from 73 of 75 samples in 1968. Fifty-six isolates were similar to PAV, 17 were RPV, one was RMV, and one was MAV in 1967. Fifty-seven samples were PAV, 15 were RPV, one was RMV, and no MAV was detected in 1968. PAV and RPV were distributed about equally between samples collected from the borders and middle of fields in 1967. The RMV isolate in 1967 came from a plant collected in the border; the MAV isolate came from a plant collected in the middle of the field.

Rhopalosiphum padi was the predominating aphid species on Illinois oats in 1967, as in most previous

TABLE 1. Recovery and identification of barley yellow dwarf virus (BYDV) isolates in comparative tests with *Rhopalosiphum padi* (RP), *R. maidis* (RM), and *Macrosiphum avenae* (MA) from samples of spring oats collected in New York or Illinois during the summer of 1967[a]

Source of samples	No. of samples identified as BYDV isolate shown	Distribution of samples according to transmission (+) or nontransmission (−) by each of 4 aphid species in original test of field-collected sample[b]				Subsequent tests on plants that became infected by transmission from original field-collected sample			
		No. samples in group	Transmission pattern			No. samples tested from group at left	Transmission by aphid species shown[c]		
			RP	RM	MA		RP	RM	MA
New York	27 MAV	23	−	−	+	9	5/36	0/36	35/35
		4	+	−	+	4	1/27	0/27	27/27
	35 PAV	4	+	+	+	4	48/48	2/48	39/48
		18	+	−	+	3	15/15	0/15	3/15
		7	+	−	−	5	20/21	0/21	4/21
		4	−	−	+	4	18/18	0/18	13/18
		1	−	+	−	1	3/3	0/3	0/3
		1	−	+	+	1	9/9	0/9	6/8
	8 RPV	8	+	−	−	8	27/27	0/27	1/27
	6 RMV	4	−	+	−	4	2/21	13/21	0/21
		2	+	+	−	2	1/30	21/30	0/30
Illinois	56 PAV	5	+	+	+	4	36/36	0/36	28/36
		35	+	−	+	14	120/120	1/120	71/120
		11	+	−	−	4	18/18	0/18	1/18
		5	−	−	+	5	48/48	1/48	30/48
	17 RPV	17	+	−	−	13	84/84	0/84	0/84
	1 MAV	1	−	−	+	1	8/48	2/48	48/48
	1 RMV	1	−	+	+	1	1/27	26/27	0/27

[a] Similar data for 1968 from both states allowed identification of 72 isolates of PAV, 33 of MAV, 18 of RPV, and 4 of RMV. Subsequent comparisons, involving a total of 2,426 test plants in 1968, allowed confirmation of 28 isolates of PAV, 20 of MAV, 18 of RPV, and 4 of RMV.

[b] One of 273 plants infested as controls in these experiments became infected.

[c] Numerator is no. plants that became infected; denominator is no. infested with about 10 aphids of species shown for a 5-day inoculation test feeding following a 2-day acquisition feeding on detached leaves. One of 561 plants infested as controls became infected.

seasons, but *M. avenae* was the most common species in 1968. The unusual occurrence of *M. avenae* in 1968 was associated with a lower percentage of infected plants than in many previous seasons, and with a more random distribution of infected plants within fields than was previously encountered in Illinois.

Since vector specificity of most virus isolates is relative, more than one comparative test is often needed to identify an isolate. Subsequent comparative tests were made on 157 of the 278 isolates recovered from oats (Table 1). Emphasis was given to cases where the original pattern of transmission and severity of symptoms made identification of an isolate difficult. For example, it is hard to distinguish between PAV and RPV without subsequent comparative tests because both are transmitted efficiently by *R. padi,* but PAV causes more severe symptoms and is more readily transmitted by *M. avenae* than is RPV. Identification of 39 of the 43 RPV isolates was based on several subsequent comparative transmissions in which virus was transmitted essentially only by *R. padi,* and symptoms of infected plants were relatively mild (Table 1).

Nineteen of the subsequent tests for MAV confirmed the original pattern in which only *M. avenae* had recovered virus from the field sample (Table 1). In other cases, one or two plants also became infected in original tests with one of the other aphid species. Subsequent tests of 15 such plants enabled identification of MAV, and showed that the original transmissions by *R. padi* or *R. maidis* were merely examples of occasional transmissions of MAV by "nonvectors" (9).

The greatest variation in original transmission patterns occurred for PAV (Table 1). Usually all 3 plants infested with *R. padi* became infected in a test on a field-collected plant infected by PAV, but in 16 cases *R. padi* did not transmit PAV in the original tests. Often one or two plants became infected following feeding by *R. maidis* in the original tests, but subsequent comparisons on leaves from 18 such plants showed that PAV (not RMV) was involved. The importance of such subsequent tests is shown most clearly by the nine cases in which only *M. avenae* recovered PAV in the initial test on the field sample. In the absence of subsequent tests, six of the 1967 Illinois isolates might have been identified as MAV because only *M. avenae* recovered virus from six field-collected samples. Further tests showed, however, that five of the six isolates were PAV because they were transmitted most efficiently by *R. padi,* were transmitted fairly efficiently also by *M. avenae,* and caused relatively severe symptoms.

Subsequent tests allowed identification of 11 RMV isolates. Most of them proved to be similar to the RMV previously described (9) because they caused mild symptoms in Coast Black oats, were transmitted efficiently by *R. maidis,* and were transmitted rarely by the other aphid species. A few of the isolates were studied in more detail because they were transmitted more readily by *R. padi* than were most RMV isolates. These cases are discussed later.

Tests were also made on samples of winter wheat and winter barley collected near Ithaca, New York, in May and June of each year before spring oat samples became available. The same four kinds of BYDV isolates were detected in these tests, which included 184 subsequent comparative tests of 38 isolates. Virus was recovered from 15 of 16 wheat samples and from 53 of 55 barley samples tested (Table 2). In both years, winter grains infected by more than one variant of BYDV were common. More than one type of BYDV was isolated from five of the wheat samples and from 15 of the barley samples (Table 2).

Doubly infected samples were identified both by severity of symptoms of test plants in the original transmission from the field-collected sample and by subsequent comparative tests of such plants. In most cases, the original plants infected by means of *R. maidis* developed milder symptoms than those infected by means of the other aphid species in the same test. For example, seven cases of double infection by RMV and MAV were confirmed by the fact that virus recovered initially by *R. maidis* (and in one case also by *R. padi*) caused mild symptoms and was subsequently transmitted specifically by *R. maidis.* In contrast, that recovered initially from the same seven samples by *M. avenae* subsequently was transmissible only by *M. avenae* (Table 3). Similar tests identified seven samples as doubly infected by RMV and PAV because virus recovered initially by *R. maidis* was subsequently transmitted specifically by *R. maidis,* while that recovered initially by both *R. padi* and *M. avenae* was subsequently transmitted most efficiently by *R. padi,* less efficiently by *M. avenae,* and produced the severe symptoms characteristic of PAV. Similar tests indicated that one of the field plants was doubly infected by RMV and RPV (Table 3). One sample proved to be infected by three variants. Virus recovered initially by *R. padi* subsequently was identified as PAV because of efficient transmission by *R. padi* and severe symptoms; that recovered initially by *M. avenae* was MAV because it was subsequently transmitted specifically by *M. avenae*; and that recovered initially by *R. maidis* proved to be RMV because of specific transmission by *R. maidis* (Table 3).

Although there is much variation within each group of BYDV variants, those similar to RMV are probably the most variable. For example, isolates similar to RMV range from those never (or rarely) transmitted also by *R. padi* to those that are transmitted fairly often by *R. padi* (Table 1). Since an isolate transmitted regularly by both *R. padi* and *R. maidis* has not yet been encountered in our tests in New York, special emphasis was given to some of the RMV isolates that appeared to be transmitted fairly regularly by *R. padi.* Many tests over a period of about 10 months compared transmission of the isolates by *R. maidis* and *R. padi.* Tests were done so that data could be summarized on the basis of whether a source leaf was from a plant that had been infected by means of *R. padi* or *R. maidis.* We tried to determine whether continued transmission of such RMV isolates by means of *R. padi* resulted in any change in the isolate in comparison with parallel transmissions by means of *R. maidis.*

Results of tests with five isolates showed that *R.*

TABLE 2. Recovery and identification of barley yellow dwarf virus (BYDV) isolates in comparative tests with *Rhopalosiphum padi* (RP), *Macrosiphum avenae* (MA), and *R. maidis* (RM) from samples of winter grains collected in New York during the summers of 1967 and 1968

Sample	No. samples infected by BYDV variant shown	No. of samples in group	Distribution of samples according to transmission (+) or nontransmission (—) by each of 3 aphid species in original test of field-collected sample[a]		
			Transmission pattern		
			RP	RM	MA
Winter winter	5 PAV	1	+	+	+
		4	+	—	+
	3 RPV	3	+	—	—
	1 MAV	1	—	—	+
	1 RMV	1	—	+	—
	2 RMV + MAV	2	—	+	+
	2 RMV + PAV	1	+	+	+
	1 RMV + MAV + PAV	1	+	+	+
	1 None	1	—	—	—
Winter barley	17 PAV	13	+	—	+
		3	+	+	+
		1	+	—	—
	8 MAV	7	—	—	+
		1	+	—	+
	11 RMV	9	—	+	—
		2	+	+	—
	2 RPV	2	+	—	—
	9 RMV + MAV	8	—	+	+
		1	+	+	+
	5 RMV + PAV	5	+	+	+
	1 RMV + RPV	1	+	+	—
	2 None	2	—	—	—

[a] None of about 60 plants infested as controls in these experiments became infected.

maidis was the better vector regardless of whether a previous transmission had been by means of *R. padi* or *R. maidis* (Table 4). Moreover, a previous transmission by *R. padi* did not consistently raise the probability of *R. padi* transmitting an isolate in a subsequent test (Table 4). Although some of the isolates were transmitted by both of these aphid species, the isolates were considered to be similar to RMV, because *R. maidis* was the only consistent vector in tests made over a period of time.

A preliminary study was made of the serological relationship among some of the isolates recovered in

TABLE 3. Summary of comparative transmission tests with *Rhopalosiphum padi* (RP), *R. maidis* (RM), and *Macrosiphum avenae* (MA) that enabled identification of mixed infections by more than one variant of barley yellow dwarf virus (BYDV) in field-collected samples of winter grains

BYDV variants identified	No. cases from Table 2 tested	Aphid species that transmitted BYDV in original test on field sample	Transmission by aphid species shown in subsequent tests on plants infected by means of aphid species shown at left in original test on field sample[a]		
			RP	MA	RM
RMV + MAV	7	RP	0/3	0/3	2/3
		MA	0/21	21/21	0/21
		RM	3/21	0/21	14/21
RMV + PAV	7	RP	21/21	13/21	0/21
		MA	15/15	7/15	0/15
		RM	42/162	2/162	140/162
RMV + RPV	1	RP	6/6	0/6	0/3
		RM	0/3	0/3	3/3
RMV + MAV + PAV	1	RP	9/9	0/9	0/9
		MA	0/9	9/9	0/9
		RM	4/12	0/12	10/12

[a] Numerator is no. plants that became infected; denominator is no. infested with about 10 aphids for a 5-day inoculation test feeding following a 2-day acquisition feeding on detached leaves. None of about 140 plants infested as controls became infected.

TABLE 4. Relative transmission of isolates of barley yellow dwarf virus (BYDV) similar to RMV following a previous transmission by *Rhopalosiphum padi* or *R. maidis*

1968 BYDV isolate source	Previous transmission by	No. test plants infested	% Test plants that became infected in tests with aphid species shown[a]	
			R. padi	*R. maidis*
N. Y. Barley	*R. padi*	18	17	89
	R. maidis	39	33	85
N. Y. Barley	*R. padi*	21	24	90
	R. maidis	30	30	97
N. Y. Barley	*R. padi*	42	48	90
	R. maidis	57	46	96
N. Y. Oats	*R. padi*	27	59	81
	R. maidis	42	43	86
Ill. Oats	*R. padi*	12	25	58
	R. maidis	39	8	89

[a] None of about 185 plants infested as controls became infected.

1967. The three plants that became infected in the original test of the field-collected sample were harvested and stored in a freezer. Samples included the MAV isolate from Illinois, an MAV isolate from New York, and an isolate similar to RPV from each state. The total tissue for each sample varied from 55 to 84 g. Each of the samples was thawed, ground thoroughly, and used to make a clarified preparation which was not concentrated (11). Identity of the four isolates was confirmed in a test based on serological blocking of aphid transmission (10). Transmission of both RPV samples was prevented by incubation with an antiserum for RPV, but not by incubation with antiserum for MAV, or with antiserum prepared against a preparation of healthy oats. Both MAV isolates were transmitted from preparations incubated with the RPV-serum and the healthy-oat serum, but not from preparations incubated with the antiserum for MAV. Thus, the four isolates appeared to be similar to the RPV and MAV previously described (1, 2, 9).

DISCUSSION.—Although the same four variants of BYDV were recovered from samples collected in New York and Illinois, the big differences in their prevalence in the two areas is in agreement with previous observations of differences in some features of the disease (12). Since samples from the two areas were studied in the same tests with the same aphid clones under the same conditions, the parallel comparisons of virus isolates now have a reasonably sound basis. PAV was the most prevalent variant in Illinois during both seasons, just as it was in all previous years when tests were made (12). The picture in New York was more complicated than for Illinois because PAV dominated in 1967, but MAV was the most common isolate in 1968. Together with previous results (6), the data suggest a gradual change in prevalence of the BYDV variants at the Tailby Farm in New York. MAV had been the predominating type of BYDV from 1957 to 1963, although the relative proportion of samples from which MAV was isolated declined each year from 1957 through 1966. A simultaneous increase in PAV isolates occurred during those years. The generally cyclic pattern of change observed in New York is in contrast to the stable picture for Illinois and the abrupt changes observed by Gill from year to year in Manitoba (3, 4). The three different patterns of changes in the predominating types of BYDV may reflect important differences in epidemiology of the disease in the three areas. In contrast to the situation in Manitoba, the stability of the predominating variant in Illinois and the gradual change in variants predominating in New York suggest a local source of virus and differences in population dynamics of the vector species in the different regions. The presence of winter grains in both New York and Illinois may be a major factor in the epidemiology of barley yellow dwarf for spring oats, but little is known about the role of susceptible grasses.

The prevalence of PAV in Illinois appears to be associated with *R. padi,* usually the most common aphid species on spring oats. In 1968, however, *M. avenae,* not *R. padi,* appeared to be the most common aphid species near Urbana, Illinois. This change in the most common aphid species is probably responsible for the fact that infected plants were scattered at random throughout many Illinois oat fields in 1968, in contrast to previous seasons when many infected plants were concentrated along borders of fields. Thus, the distribution of infected plants and the most common aphid species in Illinois in 1968 were similar to the pattern often observed in New York (12). It seems plausible that a relatively low incidence of barley yellow dwarf occurred in spring oats in Illinois in 1968 because the most common aphid species (*M. avenae*) is a relatively inefficient vector of PAV as compared with *R. padi* (9, 12). It may be important to learn whether the abundance of *M. avenae* in 1968 results in any change in prevalent virus variants in 1969.

It is somewhat surprising that all 367 isolates identified during this 2-year period fell into one of the four main types of BYDV previously encountered. Although there was a spectrum of variation among isolates within any one of the four groups, none was found that did not fit into one of the groups. It should be emphasized that factors other than variation among the virus isolates can influence such tests. For example, the clone of each aphid species used, the test plant, and the temp for feeding of aphids are important factors that can influence any attempt to identify variation among virus isolates (8, 9). The preliminary serological information for isolates of MAV and RPV from both states suggests that our attempts to standardize the factors that might affect identification of virus isolates were successful.

BYDV was not recovered from 26 of the 372 field samples tested. Over half the failures were from samples shipped from Illinois; in most cases they were from plants in the later stages of growth when diagnosis and testing is more difficult. There are many possible reasons for failure to recover BYDV from this small proportion of plants tested. The samples may have been from plants affected by other diseases, such as aster yellows (5). The plants may have been in-

fected with isolates of BYDV not regularly transmitted by one of the four aphid species used. For example, virus transmitted specifically by *S. graminum* would not have been detected in most of the 1967 tests in which *S. graminum* was not included (4). Virus actually may have been recovered from some of the "negative" samples, but not recognized, because high greenhouse temp could have obscured symptoms of avirulent vector-specific isolates; retesting of some plants gave no support for this possibility. The negative samples may have reflected poor virus distribution within source plants; i.e., some of the negative samples may simply reflect the probability of using some virus-free or low titer tissue from the field-collected plant. It might be significant that both negative samples in 1968 from Illinois were from the tolerant variety Jaycee, and that BYDV was recovered from all samples of the intolerant Tyler variety.

The importance of variation among isolates of BYDV should be considered in the light of two recent developments. Although the four main types of BYDV were originally considered strains by most workers, it is now thought that some of them are actually distinct viruses. Thus, RPV and MAV are unrelated on the basis of available data on serological properties and their interactions in vivo (1, 2), a distinction that is not merely an academic matter. Such great variation between virus isolates will require that an even greater awareness be focused on practical questions related to control of BYDV by resistant varieties. Such varieties, characterized by their ability to tolerate virus infection, will remain useful only so long as there are no major shifts in differential reaction to different variants of BYDV most prevalent in the field. With tolerant varieties, there is also always a potential danger of synergism when mixed infections by more than one virus occur. Information about virus isolates in an area helps to identify the most important vector species, and could lead to new approaches for disease control through the reduction of aphid populations.

Another recent development is the evidence for phenotypic mixing in the interaction of RPV and MAV (7). Although *R. padi* is normally unable to transmit MAV, *R. padi* can transmit MAV from plants doubly infected by both MAV and RPV, apparently because the simultaneous synthesis of the two viruses results in some MAV nucleic acid becoming coated with protein of RPV. Such phenotypically mixed particles appear to function in *R. padi* as does RPV, and thus are transmitted; in the plant, however, the infection is controlled by the MAV nucleic acid and thus results in plants infected by MAV. This mechanism suggests a possible basis for much variation encountered among the isolates of BYDV and emphasizes the potential practical importance of mixed virus infections in nature. Since mixed infections were especially common in winter grains, these crops could play an important role in epidemiology. This might be especially true in areas such as New York, where all the virus variants often are present.

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