

Genetic Structure of Races of *Heterodera glycines* and Inheritance of Ability to Reproduce on Resistant Soybeans¹

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Abstract: Four field populations of *Heterodera glycines* tested for ability to reproduce on three host differentials were each classified into one of the recognized races. A fifth population represented a new race. Genetic analysis indicated that the designated races are actually field populations that differ from each other primarily in the frequencies of three groups of genes (genes for parasitism) that act quantitatively and control the ability of the nematode to reproduce on resistant P.I. 88788, Pickett, and P.I. 90763 soybeans. Populations of race-3 have none of these genes for parasitism, or they have some in low frequency that results in an index of parasitism of less than 10 on any one of the resistant soybeans. Race-1 has a high frequency of one group of genes that enable it to reproduce on P.I. 88788. Race-2 has two groups of genes for parasitism in high frequency; one for P.I. 88788, and one for Pickett. Based on these findings, it was assumed that race-4 has three groups of genes for parasitism; one for P.I. 88788, one for Pickett, and one for P.I. 90763. Additional races may be recognized when new genes are identified, or when new gene combinations are discovered. The ability to reproduce on P.I. 88788 is inherited independently from the ability to reproduce on Pickett. Although the genetic structure of field populations does not provide a solid foundation for race designation, recognizing races under the present system may be useful when it clearly characterizes the behavior of field populations. Race designations, however, should be regarded as provisional since gene frequencies change with time in response to selection forces and, therefore, the race status of a population may change accordingly. **Key words:** index of parasitism, genes for parasitism, cyst nematodes.

Four races of the soybean cyst nematode, *Heterodera glycines* Ichinohe, have been recognized on the basis of ability to reproduce on three resistant soybean, *Glycine max* (L.)

Merr., cultivars or breeding lines (4). All four races reproduce freely on the susceptible cultivar Lee. Race-3 cannot reproduce on any of the resistant soybeans; race-1 reproduces only on P.I. 88788 resistant soybeans; race-2 on P.I. 88788 and Pickett, and race-4 on all three resistant soybeans, P.I. 88788, Pickett, and P.I. 90763. A fourth resistant cultivar, Peking, was also proposed as a host differential, but Peking and Pickett have a similar genetic background for resistance and,

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therefore, the use of one of them may be sufficient. Under this scheme, cyst development on a resistant host of less than 10% of that on Lee soybean results in a negative rating. Thus, race designation is based on a quantitative criterion.

Host-specific races, biotypes, pathotypes, or trophotypes have been recognized, or simply detected, in practically every nematode species for which host range or host specificity have been studied (13). Of particular importance are races that have been recognized on the basis of ability to develop and reproduce on a number of differential plant hosts used as sources of resistance in breeding programs. Information about the mode of inheritance of the ability of a nematode to overcome plant resistance could be very instructive. It could elucidate how fast genotypes capable of reproducing on resistant plants, normally present in low frequency in natural populations, would increase in frequency when resistant plant cultivars are grown in the field. This, in turn, would indicate how frequently a resistant cultivar could be grown in the same field without losing much of its effectiveness within a crop rotation system. Much of the genetic work in this area, however, has concerned the inheritance of plant resistance to nematodes, and very little has been done to understand the other side of the same problem; i.e., the inheritance of the ability of the nematode to overcome resistance.

Among the cyst nematodes, limited genetic studies have been conducted only with *Heterodera rostochiensis* Woll., *H. avenae* Woll. and *H. glycines*. Selection experiments with several populations of potato cyst nematodes on various resistant potatoes have indicated recessive inheritance of the ability to overcome resistance in some nematode-plant combinations, but different types of inheritance in others (7). It was later hypothesized that major genes for resistance to *H. rostochiensis* in potatoes bred from *Solanum tuberosum* ssp. *andigena* Juz. & Buk., from *S. multidissectum* Hawkes and from both are matched by recessive genes in the nematodes able to overcome resistance (6). More recent crosses between two populations of the British pathotype A of *H. rostochiensis* and a Bolivian population indicated that the ability of the Bolivian population to reproduce on the resistant potato cultivar Maris Piper is inherited as a

recessive trait which, in addition, may be influenced by the action of some modifying genes (12). Crosses between two races of *H. avenae* indicated that the ability of the nematode to overcome resistance of the barley cultivar Drost is conferred by two dominant genes (1). Similarly, crosses between two populations of *H. glycines*, one able to reproduce on the resistant soybean cultivars Pickett and Dyer and the other unable to do so, gave F₁ progeny that could reproduce on these resistant cultivars suggesting a nonrecessive type of inheritance of the ability to overcome resistance (8).

Also of special importance is the nature of variation regarding the ability to overcome resistance among nematode populations of the same race. Thus, populations of pure pathotype A of *H. rostochiensis* are known to produce a few females on *Solanum tuberosum* ssp. *andigena* carrying the H₁ gene for resistance (2, 5, 14). These females appear not to be genetically different from the rest of the population, since their reproductive rate does not increase following continuous propagation on the resistant host. Still other populations of *H. rostochiensis* (Dutch pathotype C) show a strong response to selection on potatoes carrying the H₁ gene for resistance, indicating the presence of heritable variability within such populations (11). The genetic basis of this type of variation needs to be clarified.

The main objective of the present study was to gain understanding of the nature of races in the soybean cyst nematode from a genetic viewpoint. This could be accomplished by identifying the genetic factors that control the ability of the nematode to overcome resistance, and analyzing the structure of nematode populations of different races with regard to these genetic factors. Cross-matings between individual males and females of known phenotypes would probably be the proper way to initiate such a study. However, such crosses are technically difficult and testing of the few progeny of such individual crosses to identify the phenotypes of the F₁ and F₂ generations did not seem to be practical. For this reason, other indirect approaches were employed in this study. These involve: (i) Precise determination of the relative number of viable cysts developed by several field populations on each one of the three resistant soybeans used as host differentials in race designations and on the

TABLE 1. Parasitism of five field populations of *Heterodera glycines* on a susceptible (Lee) and three resistant (P.I. 88788, Pickett, and P.I. 90763) soybeans.

Nematode population	Average cyst production on soybean cultivar ^a				Index of parasitism ^b on:			Race designation
	Lee	P.I. 88788	Pickett	P.I. 90763	P.I. 88788	Pickett	P.I. 90763	
Johnston	118	40	0.5	0	34	0.4	0	race-1
Beaufort	216	34	0	0	15.7	0	0	race-1
Sampson	47	9.6	24.5	0	20.4	52.1	0	race-2
Gates	146	0	0	0	0	0	0	race-3
Camden	222	10.8	49	0	4.8	22	0	new race

^aAverage number of cysts recovered from six replicate plants inoculated with 500 larvae each. The coefficient of variation calculated separately for each "average number of cysts" in this table varied from 7 to 60% with most values being smaller than 35.

^bIndex of parasitism refers to the number of cysts developed on a resistant cultivar expressed as percent of those developed on the susceptible cultivar Lee.

TABLE 2. Change in degree of parasitism of the Johnston population of *Heterodera glycines* following continuous propagation for seven generations on resistant (Peking) soybeans.

	Field population propagated for seven generations on:					
	Field population originally checked on:		Lee and then checked on:		Peking and then checked on:	
	Lee	Peking	Lee	Peking	Lee	Peking
Number of cysts per plant ^a	108	3.0	120	4.0	103	76
Index of parasitism		2.8		3.3		74

^aAverage from six replicate plants inoculated with 500 larvae each. The coefficient of variation for the numbers of cysts varied from 13 to 33%.

susceptible cultivar Lee; (ii) determination of changes that may occur in the ability of the nematode to produce viable cysts following continuous selection on resistant hosts; and (iii) analysis of the F₁ and F₂ progeny of mass crosses between males and females of known phenotype, in an attempt to identify the genetic factors that enable the nematode to produce viable cysts on Pickett soybeans.

Although of a preliminary nature, these studies have paved the way for more effective approaches to the study of the genetics of parasitism and reproduction of the soybean cyst nematode now underway in our laboratory.

MATERIALS AND METHODS

The ability of five field populations to develop viable cysts was determined on a susceptible (Lee) and three resistant (P.I. 88788, Pickett, and P.I. 90763) soybean cultivars or breeding lines. Cysts extracted from field soil were propagated for one

generation on Lee soybean to increase the inoculum. About 500 cysts from each population were crushed and then placed on tissue paper supported by a plastic screen inside a petri dish in order to obtain infective second-stage larvae. Eight 15-day-old seedlings from each soybean cultivar growing in 10-cm diameter clay pots were each inoculated with 500 freshly hatched second-stage larvae, individually picked with a pipet. Inoculated plants were kept in a greenhouse at 25-30 C. About 33-38 days after inoculation, cysts were extracted from each pot and counted. This procedure was followed in all subsequent tests when the "index of parasitism" of a population was to be determined on a given resistant host. "Index of parasitism" is defined here as the number of cysts developing on a resistant soybean cultivar expressed as percent of those developing on the susceptible cultivar, Lee. It is a measure of the ability of larvae of a nematode population to successfully parasitize a resistant host and develop into reproductive females or viable cysts.

Procedural difficulties early in these studies did not allow the use of a more comprehensive measure, such as the "index of reproduction," which is defined as the number of eggs and larvae produced on a resistant host expressed as percent or ratio of those produced on a susceptible host.

To study any changes in the degree of parasitism through selection on a resistant host, the index of parasitism of the Johnston population was originally determined on the resistant cultivar Peking. Following this test, about 50 cysts obtained from the susceptible cultivar Lee were used to inoculate each of three Lee seedlings. All the cysts obtained from the resistant cultivar were used to inoculate three Peking seedlings. This was repeated every 40 days for seven generations. Larvae obtained from cysts of the seventh generation were used as inoculum to determine the index of parasitism of the two subpopulations on Peking.

In a third test, progressive changes in the degree of parasitism through selection on a resistant host were studied. The index of parasitism of the Beaufort population was determined on the resistant line P.I. 88788 during six consecutive generations. Larvae obtained from cysts that had developed during each generation on P.I. 88788 were used each time as inoculum to determine the index of parasitism in the following generation.

Changes in the degree of parasitism through selection on two resistant hosts were studied in the Camden population which produced cysts on both P.I. 88788 and Pickett soybeans. The original field population was propagated for five consecutive generations on either Pickett or P.I. 88788 soybeans. Larvae obtained from cysts produced on each resistant host, in each generation, were used to establish the next generation, on the same host. After the fifth generation the index of parasitism of the selected subpopulations was determined on both Pickett and P.I. 88788.

Reciprocal crosses were conducted between the Camden population which reproduces on Pickett, and the Gates population which cannot reproduce on Pickett. The Camden population had an index of parasitism of about 90 on Pickett because it had been previously propagated on Pickett for 18 consecutive generations. Seven Lee soybean seedlings each were inoculated with 500 larvae of the Camden population, and another seven

TABLE 3. Progressive change in degree of parasitism of the Beaufort population of *Heterodera glycines* following propagation for six successive generations on resistant, P.I. 88788, soybeans.

	Field population propagated on P.I. 88788 for:													
	Field population originally checked on:		One generation and then checked on:		Two generations and then checked on:		Three generations and then checked on:		Four generations and then checked on:		Five generations and then checked on:		Six generations and then checked on:	
	Lee	P.I. 88788	Lee	P.I. 88788	Lee	P.I. 88788	Lee	P.I. 88788	Lee	P.I. 88788	Lee	P.I. 88788	Lee	P.I. 88788
Number of cysts per plant ^a	216	34	204	68	119	49	114	60	123	80	158	134	204	135
Index of parasitism		16		33		41		53		65		85		66

^a Average from six replicate plants inoculated with 500 larvae each. The coefficient of variation for the numbers of cysts varied from 12 to 58% with most values being smaller than 30%.

TABLE 4. Changes in degree of parasitism of the Camden population of *Heterodera glycines* following selection on two resistant soybean cultivars.

	Field population originally checked on:			Field population propagated for five generations on:					
	Lee	Pickett	P.I. 88788	Pickett and then checked on:			P.I. 88788 and then checked on:		
				Lee	Pickett	P.I. 88788	Lee	Pickett	P.I. 88788
Number of cysts per plant ^a	222	49	10.7	138	101	4.4	147	31	58
Index of parasitism		22	4.8		73	3.2		21	40

^aAverage from eight replicate plants inoculated with 500 larvae each. The coefficient of variation of the numbers of cysts varied from 7 to 65%.

TABLE 5. Parasitism on Pickett soybeans of the F₁ and F₂ progeny of crosses between a selected Camden and the Gates population of *Heterodera glycines*.

Crosses (females × males)	Number of cysts recovered per plant ^a on:		Index of parasitism on:
	Lee	Pickett	Pickett
Parental populations			
Camden	70	63	90
Gates	48	0	0
F ₁ generation			
Camden × Gates	54	22	40
Gates × Camden	63	26	41
F ₂ generation			
Camden × Gates	61	22	36
Gates × Camden	53	28	53

^aAverage from eight replicate plants inoculated with 200 larvae each. The coefficient of variation of the numbers of cysts in each one of the tests was smaller than 28%.

with 500 larvae of the Gates population. Eight days later, the plants were washed free of soil. Each plant was transferred to an aluminum paint-coated glass container with its roots suspended in continuously aerated half-strength Hoagland's solution and maintained at 30 C-day and 25 C-night temperature. Every 5 days the solution was changed and at the same time males that had emerged from the roots were discarded. After the fifth change (i.e., 33 days from the time of inoculation) the plants were transplanted to 10-cm diameter clay pots filled with fine sand. About 200-300 young males of a given population were then added to each of the five plants of each cross. No males were added to the remaining two plants of each cross. Twenty-five days later cysts were extracted from all the plants. Only noninseminated females, without eggs, were found on the two plants where no males had been added. Cysts

with many eggs were found on the five plants to which males had been added. The index of parasitism of larvae obtained from these cysts (F₁ larvae) was determined on Pickett. Eight Lee and eight Pickett seedlings growing in 10-cm diameter clay pots were inoculated each with 200 F₁ larvae for this test. The F₂ generation was established by propagating F₁ larvae on Lee soybeans. Forty days after inoculation, the index of parasitism of larvae of the F₂ generation was determined on Pickett.

RESULTS

Parasitism of field populations of Heterodera glycines on resistant soybeans: The various nematode populations produced considerably different numbers of cysts on the susceptible cultivar, Lee (Table 1). The Sampson population, which produced the smallest number of cysts, was tested for a second time on all host differentials with practically the same results.

The indices of parasitism of field populations on the resistant soybeans (Table 1) indicated that four of the five populations can be classified into one of the recognized races of *H. glycines* (4). The Johnston and Beaufort populations are typical of race-1, since they have an index of parasitism of more than 10 on P.I. 88788 and less than 10 on Pickett and P.I. 90763. The Sampson population which produced many cysts on both Pickett and P.I. 88788 is typical of race-2. The Gates population is a typical representative of race-3, since it failed to produce cysts on any of the resistant soybeans. The Camden population, however, is a new combination, not represented among the presently recognized races. It had an index

of parasitism of 22 on Pickett, but less than 10 on P.I. 88788.

The two populations of race-1 had different indices of parasitism on P.I. 88788 and, although the Johnston population produced some cysts on Pickett, the Beaufort population failed to produce a single cyst on Pickett even in another two repetitions of the same test. This demonstrates that qualitative and quantitative differences exist among populations of the same race.

Change in degree of parasitism of Heterodera glycines through selection on a resistant host: The index of parasitism of the Johnston population on Peking soybeans remained unchanged following propagation of the field population for seven consecutive generations on Lee soybeans (Table 2). In contrast to this, the index of parasitism of the same population on Peking increased from 2.8 to 74 following propagation for seven generations on Peking soybeans.

Progressive changes in degree of parasitism of Heterodera glycines on soybeans through selection on a resistant host: The index of parasitism of the Beaufort population increased progressively from 16 to 85 during five generations of selection on P.I. 88788 soybean (Table 3). The index of parasitism was 66 in the sixth generation, probably indicating that a plateau was reached at a level below 85.

Changes in degree of parasitism of Heterodera glycines through selection on two resistant hosts: Propagation of the Camden population for five consecutive generations on Pickett increased the index of parasitism of the population from 22 to 73.1, but did not affect its index of parasitism on P.I. 88788 (Table 4). Conversely, propagation of the same population for five generations on P.I. 88788 increased the index of parasitism of the population on P.I. 88788 from 4.8 to 40.0, but did not alter its index of parasitism on Pickett.

Reciprocal crosses between a population of Heterodera glycines selected on Pickett and a population of race-3: The parent populations of these crosses behaved as expected (Table 5). Thus, Camden had an index of parasitism of 90 on Pickett, whereas Gates failed to produce viable cysts on Pickett. The F₁ generation in the reciprocal crosses showed an index of parasitism intermediate between the two parents. Larvae of the F₂ generation showed again intermediate index of parasitism, with some deviation from the F₁ generation.

DISCUSSION AND CONCLUSIONS

The average number of cysts produced by each nematode population on Lee soybeans varied considerably (Table 1). No effort was made to determine the cause of this variation. It is possible that this was due to differences in viability and infectivity of the larvae in the inoculum from the various populations. It is also possible that Lee, which is commonly regarded as a susceptible cultivar, may possess some resistance against some nematode populations. Miller (10) also found that single-cyst isolates of *H. glycines* produced significantly different numbers of cysts on Lee soybeans, but as in the present test, this may be due to differences in viability of inoculum. Further clarification of this important question is needed.

Data about the index of parasitism of the Johnston and Beaufort populations on the resistant Pickett and P.I. 88788 soybeans demonstrate that populations of the same nematode race may differ qualitatively and quantitatively with regard to their ability to produce viable cysts on resistant soybeans (Table 1). This suggests that the populations may also differ with regard to the genetic factors controlling parasitism, and with regard to the frequency of such factors in each population. To explain the observed differences on a genetic basis, one needs to assume only that there may be one gene which conferred ability to parasitize Pickett, and another which conferred ability to parasitize P.I. 88788. Quantitative differences between the populations can then be attributed to differences in gene frequency. A third gene which confers ability to parasitize P.I. 90763 soybean could be assumed for populations of race-4 described from other states. In its simplest form, therefore, the hypothesis about the genetic basis of successful parasitism leading to reproduction on a resistant cultivar, which is the basis for race designation (4), would be as follows: Race-3 has no genes for parasitism of resistant cultivars, or it has some in low frequency which results in an index of parasitism of less than 10 on any one of the three resistant soybeans.

Race-1 has in high frequency one gene for parasitism that enables it to overcome resistance of P.I. 88788.

Race-2 has two genes for parasitism in high frequency; one for P.I. 88788, and one for Pickett.

Race-4 has three genes for parasitism in high frequency; one for P.I. 88788, one for Pickett, and one for P.I. 90763.

Under this scheme, populations with different gene combinations could possibly be found in the future, and this would necessitate the recognition of additional races. The Camden population appears to represent such a new combination that can be characterized as a new race, since it has a high index of parasitism on Pickett and a low index of parasitism on P.I. 88788. A population with similar behavior was actually known to the committee that originally designated the races (4). That population (Va. 2) reproduced well on Pickett, but very little on P.I. 88788 and, therefore, should have not been classified as race-2, but as a separate race. It should be understood that many more genes for parasitism are likely to be detected in the future if nematode populations are checked for ability to develop and reproduce on soybeans with other sources of resistance, or on other resistant plant species. The race situation, therefore, can soon become chaotic unless designation of new races is made with wisdom, and only when it serves a useful purpose.

The above hypothesis concerning the genetic basis of races of *H. glycines* formulated early in this study was subsequently tested through an analysis of the genetic behavior of various field populations. Thus, in a second test (Table 2) it was found that propagation of the Johnston population for seven consecutive generations on Peking increased the index of parasitism of the population on Peking from 2.8 to 74. This clearly demonstrated that parasitism (i.e., the ability of a population to produce viable cysts on a resistant host) is indeed a heritable character which responds to selection. Continuous propagation on Peking selected the genotypes possessing the gene or genes which conferred the ability to parasitize Peking soybean and decreased the frequency of genotypes that lacked these genes.

The increase of the index of parasitism of the Beaufort population during five generations of selection on P.I. 88788 was progressive (Table 3). This information is not conclusive evidence about the genetic factors involved in the selection scheme. If only one gene is involved, this gene must exhibit a certain degree of dominance and, as a result, must be subject to progressive selection.

Selection would be completed in one generation if this gene was completely recessive. If more than one gene is responsible for parasitism of P.I. 88788, selection of genotypes capable of parasitizing P.I. 88788 would most likely be progressive. The latter interpretation, implicating more than one gene, is strongly supported by the observation that the index of parasitism reached a plateau at a level below 85. Such a plateau would not be expected if a single gene was involved.

Selection tests on two resistant cultivars (Table 4) indicated that the genetic factors which controlled parasitism of the Camden population on Pickett were inherited independently from those controlling parasitism on P.I. 88788. Thus, selection in favor of increased parasitism on Pickett does not affect the index of parasitism on P.I. 88788 and vice versa. This suggests that there are two different genes or groups of genes, one which confers to the nematode the ability to parasitize Pickett, and another which controls ability of the nematode to parasitize P.I. 88788.

Data from the mass cross-matings of females and males of differing phenotypes (Table 5) are not easy to interpret. The intermediate index of parasitism of the F_1 generation of reciprocal crosses suggests that parasitism is not controlled by a single dominant or recessive gene, and that the trait is not sex linked. Incomplete dominance in a single locus can explain the intermediate index of parasitism of the F_1 and F_2 generations. However, the kind of responses to selection and the plateau reached through continuous selection in various tests tend to weaken the "single locus-incomplete dominance" hypothesis. It is more likely that parasitism is controlled by two or more genes which exhibit a quantitative type of inheritance. The Gates population has no alleles for parasitism at all and completely lacks the ability to produce viable cysts on Pickett. The Camden population, following intensive selection, has accumulated most of the alleles for parasitism in a homozygous condition and shows a high index of parasitism. The F_1 hybrids became heterozygous for all the loci involved, and show intermediate index of parasitism. In the F_2 generation, segregation probably occurred to classes of varying degrees of parasitism, but in the absence of any selection pressure, the gene frequency remained approximately the same.

Findings about the genetic factors which controlled parasitism do not substantially modify the assumptions made early in this discussion about the genetic structure of *H. glycines* races. They tend to support the idea that the ability of a nematode to parasitize a resistant soybean cultivar is conferred by a group of genes rather than the single gene which had been assumed earlier. This interpretation is compatible with previous knowledge that soybean resistance to *H. glycines* is controlled by three independently inherited recessive genes and one dominant gene (3, 9). The findings also elucidate that the designated races of *H. glycines* are actually local populations which differ from each other primarily with regard to the frequencies of the genes that control parasitism. The presence in a population of a certain allele responsible for parasitism is also important, but it is not the key criterion for race designation. The following example may illustrate more explicitly the genetic structure of a *H. glycines* population as visualized by the author. A given field population may include nematodes which have no genes for parasitism of resistant cultivars (i.e., nematodes that would be characterized as members of race-3). The same population may include also individuals which have some or all the alleles for parasitism of P.I. 88788 and, therefore, could be classified as race-1. If the race-1 nematodes within the population are more than 10 percent of the total, this field population would be identified as race-1. If not, it would be identified as race-3. The same concept can be extended to characterize race-2 and probably race-4. Under this interpretation, most field populations of *H. glycines* are mixtures of genotypes, representing different races. The kinds of genotypes which are present, and particularly their frequency, specify the race to which the population is classified. Extensive physiological variation detected earlier within a field population of race-2 of *H. glycines* (10) exemplifies the genotypic complexity of such field populations, and supports the previous interpretation.

This genetic interpretation tends to diminish the significance of race designations in *H. glycines*. Since gene frequencies change with time in response to selection forces, the race status of a nematode population may change following certain crop rotations involving resistant soybeans. Still, changes

under field conditions are not likely to be very rapid even following repeated cultivation of resistant soybeans. In our tests, selection of genotypes for parasitism was intensive, because old cysts were eliminated in each generation and only the latest, host-selected cysts were used to establish each next generation. Under field conditions, nonselected cysts of several previous generations contribute to the reproduction of the nematode, thus diminishing the effect of selection on a resistant host. This is possible primarily because males of previous generations with no genes for parasitism of resistant cultivars are usually capable of developing on resistant soybeans and mating with selected females. As a result of this, the selection pressure of a resistant cultivar is minimized and the build-up of nematodes with genes for parasitism is rather slow. Designation of a race therefore, under the present scheme, can be useful, when it clearly characterizes a population and predicts its short-term future behavior against the major cultivars of host plants, or major sources of resistance.

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