Armillaria on cacao in São Tomé

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Outbreaks of root disease caused by *Armillaria* generally originated from infection of shade trees, some species of which were very susceptible. Serious attacks often developed after shade trees had been felled or otherwise killed, even if they were resistant to *Armillaria* whilst living. The fungus spread rapidly, up to 5 m/year, in cacao growing in areas of high rainfall. Mortality had reached nine per cent locally, but was usually much lower; considerable financial loss often resulted. The absence of rhizomorphs in soil may partly be explained by high soil temperatures and adverse conditions of soil aeration, but other inhibitory effects were probably also involved. Suitably situated trenches generally prevented further spread of the fungus in cacao, but further losses sometimes occurred within trenched areas. Other possible control measures are discussed, and attention is drawn to the possibility of new foci arising through infection by air-borne spores.

INTRODUCTION

Cacao is often infected by *Armillaria* in Africa: Thorold (1975) for example listed reports of attacks in nine African countries, of which all but one are in the west. The earliest published record for this area is by Dade (1927) who investigated the disease, aptly termed collar crack, in the countries then known as Gold Coast and Togoland. Subsequent papers describe the damage caused to a variety of other important crops such as tea, coffee and oil palm, and Fox (1964) gave no fewer than 52 hosts of the fungus for Ghana and Congo alone. Although the great majority of authors refer to the pathogen as *Armillaria mellea* (Vahl ex Fr.) Kummer (*Armillariella mellea* (Vahl ex Fr.) Karst.), other species resembling this have recently been described. Thus Heim (1963) has recorded *Armillariella elegans* Heim in Cameroon and Ivory Coast. In September 1970 an opportunity arose to visit the island of S. Tomé, where cacao, and to a lesser extent coffee, are affected by root disease. A short visit was also made to Príncipe. The observations throw further light on the behaviour of *Armillaria* in tropical plantations. The authorities quoted for tree hosts are generally those of Exell (1944). Some laboratory experiments are described.

THE OUTBREAKS OF DISEASE

Economically, cacao is the most important crop in S. Tomé, and in 1970 plantations occupied about 30 000 ha. Root disease, which was present at

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least 60 years before this, occurred throughout the island to the maximum elevation at which cocoa was grown, about 800 m, and above that in coffee. Almost certainly *Armillaria* was present in the original forest and persisted wherever this was replaced, partially or completely, by woody crops. On cacao the fungus often spread rapidly, killing trees and creating large gaps. The rate at which symptoms appeared was variable. The roots and even the stem might be extensively invaded before obvious external symptoms appeared. These included leaf yellowing and premature fall, branch die-back, cracking of the stem base and sudden heavy cropping.

Estimates of losses, which are seldom recorded in the literature, were available from a few farms. At Java, for instance, over 3000 trees were being killed annually, amounting to about one per cent of the crop. The resulting loss of beans was of the order of 1500 kg, worth 22500 escudos (about £340). At Milagrossa over 17000 cacao trees had been killed in 1969, representing about 3·5 per cent of the crop and involving a financial loss of some 100000 escudos (£1500). Apparently root disease had been much more active there 12 to 15 years earlier, resulting in a mortality of about nine per cent and an annual loss of about 250000 escudos (£3750). These figures represent direct loss in yield and do not take into account the cost of removing dead trees and other treatments. Although the incidence of the disease at these places was probably above average, financial loss must often have been considerable elsewhere.

OBSERVATIONS

Isolation of fungi

In order to check the identity of fungi causing disease, root samples were collected from all the farms visited and were plated on three per cent malt agar amended with lactic acid and sodium *o*-phenyl phenate (Rishbeth, 1972). Plates were incubated at room temperature, about 25°C. Most of the roots sampled had thick, white mycelial sheets characteristic of *Armillaria* beneath the bark. This fungus was isolated from 11 out of 19 samples obtained from cacao and from eight out of 14 taken from other trees. Some of the failures were probably due to replacement of *Armillaria* by other micro-organisms. No fruit bodies of the fungus were seen. Other fungi were obtained from material not thought from general appearance to contain *Armillaria*. In only one case was it possible to identify such fungi: *Rigidoporus lignosus* (Klotzsch) Imaz. was isolated from cacao at Santa Catarina, the tree having characteristic fruit bodies at the base. Judging by its prevalence on a wide range of hosts in west Africa, *R. lignosus* probably caused some damage in the plantations, but *Armillaria* was certainly the most important cause of root disease on the two islands. Clear evidence was obtained during excavations that the fungus, as in other parts of the tropics, passes from root to root where these are in contact. No rhizomorphs of *Armillaria* were seen in soil or on root surfaces at sites up to an elevation of 1000 m. This accords with other observations in west Africa, though in Kenya, for example, rhizomorphs may be abundant above about 2000 m.

Origin of the outbreaks

Before cacao was planted the forest has been opened up considerably by selective felling, leaving a wide variety of trees to provide shade. In addition, many species of shade tree had been introduced. Following the introduction of cacao varieties giving a greater yield with increased exposure to light, the number of shade trees had been much reduced. The significance of these operations is evident in that the great majority of root disease outbreaks originated from infection of shade trees. Occasionally the origin was obscure because, as a result of rapid decay, little or nothing remained of inoculum sources such as small roots two years after they had died. Here, purely for convenience, disease development is considered as being of three types, though in any particular outbreak they could be combined in various ways.

Infection around shade trees

Outbreaks of attack by *Armillaria* were commonly associated with the use of *Albizia falcata* Backer and *Erythrina velutina* Willd. as shade trees. Sporadically associated were *Ceiba pentandra* (L.) Gaertn., *Cedrela toona* Roxb. ex Willd., *Celtis soyauxii* Eng., *Chlorophora excelsa* (Welw.) Benth. and Hook., *Dacryodes edulis* (Don.) Lam., *Erythrina umbrosa* H.B. and K., *Ficus* sp. and *Persea americana* Mill. Shade trees very rarely associated with outbreaks of *Armillaria* in cacao were *Artocarpus communis* J.R. and G. Forst., *A. integer* Thunb., *Carapa procera* DC, *Musanga cecropioides* R. Br., *Pentaclethra macrophylla* Benth. and *Pseudospondias microcarpa* (A. Rich.) Engl.

Of the two species particularly susceptible to infection, *Albizia falcata* and *Erythrina velutina*, the former was probably more often attacked. On the mainland it is known to suffer serious damage from *Armillaria*, Gibson (1967) reporting that losses of up to 60 per cent occur in Gabon. The timing of attack on adjacent cacao, in relation to that on shade trees, was very variable. At one extreme, symptoms developed only when the shade tree had died. Again, as at Porto Alegre, trees with a partially dead crown were to be seen with diseased cacao around them. At another farm, cacao with recent symptoms was found 5 m from the base of an *Albizia* having a fairly healthy crown but some trunk rot; small lateral roots of the cacao were touching a rotted tree root containing *Armillaria*. Finally, by contrast, cacao sometimes became diseased near apparently healthy shade trees: thus at Plancas two trees were dying immediately beneath an *E. velutina* which had some infected roots.

Of special interest was the discovery on Príncipe of a diseased cacao tree about 4 m from the base of an *Artocarpus integer*. A lateral root of this tree, rotted by *Armillaria*, passed close to the base of the cacao and was almost certainly the source of infection. However, the furthest extent to which *Armillaria* had grown along the lateral root towards the tree was 2 m from the trunk, so that cacao may become infected from roots of shade trees even before the fungus reaches the main stem. Another example of an outbreak near a species normally resistant to *Armillaria* was seen at Colónia Açoreana: a large *Musanga cecropioides*, having a healthy crown but some root rot, was at the centre of a disease gap about 20 m in diameter. Intermediate conditions were also found, as in the case of an *Erythrina umbrosa* the crown of which had died four years earlier. A new stem had been regenerated on one side, and adjacent to this the crop had remained healthy, whereas on the other side it had been killed to a distance of 16 m. This suggests that sometimes *Armillaria* is able to invade only part of the root system of a shade tree.

Infection around deliberately killed shade trees

Unwanted shade trees were occasionally felled but more often left standing and deeply ringed, or both ringed and then poisoned with sodium arsenite. Ringing carried out in S. Tomé, unlike the method advocated by LEACH (1937), generally involved cutting into the wood, thus limiting or preventing transfer of stored nutrients from roots to crown. The result of felling an *Artocarpus integer* was seen at Boa Entrada: although the body of the stump had been removed, lateral roots were left, and about two years later cacao nearby had started to die. At Diogo Vaz a disease gap more than 20 m in diameter was seen around the stump of a *Pseudospondias microcarpa* that had been killed by burning three years before. These were typical examples of resistant species that became sources of infection after deliberate killing. LEACH (1939) found that tree species whose roots were resistant to decay and died slowly were specially dangerous in promoting root disease at sites where the forest had been felled and tea then planted. The same principle probably applied in S. Tomé, although the situation differed in that often only a proportion of trees was removed and the susceptible crop, cacao, was already established.

Other examples of killing were seen around trees that had been ringed. At Água Izé, for instance, a large *Albizia falcata* had died nine months after this treatment, and after a further three months adjacent cacao had been attacked. Apparently root disease developed even more frequently around susceptible shade trees after deliberate killing than when they were left alone. Cacao similarly became diseased when shade trees were both ringed and poisoned, there being no clear difference in this respect from ringing alone.

Infection within cacao

Irrespective of the ways in which an outbreak started, a large proportion of disease cases developed as a result of *Armillaria* growing from root to root within the crop. This mode of spread predominated wherever disease gaps were extending in several or all directions, whereas transfer of the fungus from roots of shade trees was more likely to have been involved where disease cases were scattered. Cacao could also have provided a link for infection between shade trees too far apart to have had direct root contact. *Armillaria* invaded the root system of cacao extensively, sometimes penetrating to the full extent of the tap root: it was found in this position at a depth of 1·3 m. The fungus was also able to grow a considerable distance up the stem beneath the bark; for example it had reached a height of 2·3 m in one tree which had only recently shown leaf symptoms but had probably become infected more than eight months before. Symptoms often appeared quite suddenly in such cases, especially after changes of weather, as when rains followed a dry period.

Factors affecting severity of disease

There was a marked tendency for symptoms to develop more rapidly

Table 1. The rate of spread of Armillaria *in cacao and its relationship to annual rainfall*

Farm	*Annual rainfall** *(mm)*	*Rate of spread* *(m/year)*
Plancas	1400	0·9, 1·0
Milagrossa	1700	1·5
Colónia Açoreana	2800	3·0, 5·0
Água Izé	2900	3·5

* Mean for a ten year period, to the nearest 100 mm.

around infection foci in areas of high rainfall than in drier ones. The rate of spread was determined at several sites by measuring the distance between the probable inoculum source and the diseased cacao furthest from it, then dividing by the number of years that had elapsed since the first appearance of symptoms. Data obtained from one or more foci at four farms are given in *Table 1*. Small mistakes in dating the initiation of such foci may have led to considerable errors in calculating rate of spread, so that the figures given are necessarily tentative. However, they certainly suggest that *Armillaria* spread more rapidly in high rainfall areas and support earlier observations by FOX (1964) and others that outbreaks tend to be more severe in such places. This relationship also holds for at least one other root pathogen in the tropics: WIJEWANTHA (1964) found that the percentage of rubber holdings infected with *Rigidoporus lignosus* in Sri Lanka increased strikingly with the amount of annual rainfall.

It is by no means certain why some sites within high rainfall areas were worse for root disease than others. No adequate survey of soil types was possible in the time available, but it was noted that the structure of some soils would probably have led to poor aeration after heavy rains, and in other instances drainage was impeded. Such factors are known to predispose trees to attack by *Armillaria*. The balance between host and parasite is often delicate, and there is evidence to show that severe pruning may lower host resistance, for example in pines (REDFERN, 1966). A possible relationship between pruning and root disease was seen at one farm. In an area of scattered *Armillaria* attack three out of 20 cacao trees that had been heavily pruned by removing the main shoot within the last one to two years were dead or dying, while in an area of more intensive attack three out of seven pruned trees were affected. The proportion of unpruned cacao that was obviously infected was lower in each case. To possible factors influencing the severity of root disease, such as soil type and management practices, there might be added the relative abundance of susceptible shade trees.

LABORATORY STUDIES

Armillaria was isolated from a variety of hosts growing at elevations between 10 m above sea level and about 1000 m. Isolates obtained from different hosts or localities were very similar, regardless of altitude. Ten isolates, including one from Príncipe, were grown in Petri dishes containing three per cent malt agar, and the rate of radial spread was determined at temperatures near the limit for growth of the fungus. Tests at such temperatures are more likely to reveal small differences in behaviour than those at temperatures nearer the optimum. For comparison, ten isolates of *Armillaria mellea* from Cambridge gardens were similarly tested. At 30°C the mean growth rate of the S. Tomé isolates was 2·3 mm/week and that of the Cambridge ones 2·0 mm/week: the means did not differ significantly. The S. Tomé isolates did not grow at temperatures above 30°C and were therefore unlikely to be *Armillaria tabescens* (Scop. ex Fr.) Bres., from which they also differed in other respects (Rishbeth, 1978a). At 5°C none of the S. Tomé isolates grew, whereas all the Cambridge ones did, the mean growth rate being 1·0 mm/week. The S. Tomé isolates produced abundant rhizomorphs in malt agar at temperatures between 5 and 30°C, which were often of the type described by Gibson (1961) for African isolates. Since the rhizomorphs were pointed at the apex and cultures were luminous, the fungus was probably not *Armillariella elegans*, as described by Dadant (1963). The fungus closely resembled *Armillaria mellea*, apart from its failure to grow at 5°C, but in the absence of fruit bodies more positive identification is uncertain.

Although not so convenient to determine, the growth rate of *Armillaria* through woody tissues seems more relevant to conditions in the plantations than the growth rate in agar culture. Two isolates from S. Tomé were grown, as described elsewhere (Rishbeth, 1968), in fresh stem lengths of sycamore, *Acer pseudoplatanus* L., held at 24°C. The extent of growth under the bark was easily seen from the swelling caused by the mycelial sheet: this facilitated measurement without disturbance to growth. The fungus took 10 to 14 days to become established in the lengths and then grew rapidly. Results obtained with the two isolates were similar, the maximum rates of growth in 16 lengths ranging from 11 to 21 mm/day: the mean value, 11 mm/day, corresponds to an annual extension of 5·8 m. This may be compared with a rate of 5 m/year recorded in a plantation where the mean soil temperature was probably about 24°C. Since *Armillaria*, in passing from root to root, would have grown further than direct measurement above ground indicated, cacao at this site must have offered very little resistance to spread of the fungus. Similar rapid spread of *Armillaria*, at about 5·2 m/year, has been reported by Swift (1968) on another susceptible species, *Pinus elliottii* Engelm., in Rhodesia.

The freedom with which S. Tomé isolates produced rhizomorphs in culture was in marked contrast to their absence in soil. One isolate was grown in woody inocula and these were then incubated at different temperatures in jars of soil (Rishbeth, 1978a). The mean dry weight of rhizomorphs produced was maximal, 75 mg at 20°C, falling off to 25 mg at 15°C and only 10 mg at 26°C. Neither this isolate nor one other, tested subsequently, produced any rhizomorphs in soil at temperatures above 26°C. Records taken throughout the year at three low-lying sites in S. Tomé show that the soil temperature at a depth of 20 cm seldom fell below 26°C and that the mean was about 27°C. In such situations high temperature alone could account for the absence of rhizomorphs. However, temperatures recorded during the visit at a similar soil depth but at higher elevations ranged from 24°C at 200 m to 21°C at 600 to 800 m, and these, if representative, were not high enough to have prevented rhizomorph growth.

Another factor to be considered is the gaseous composition of the soil atmosphere. An experiment was set up to determine the effect of varying the concentration of O_2 on the production of *Armillaria* rhizomorphs from woody inocula in jars of soil (Rishbeth, 1978a). With an isolate from S. Tomé the mean dry weight of rhizomorphs produced at 25°C with air was 99 mg, whereas with five per cent O_2 it was 27 mg, the difference being significant ($P < 0{\cdot}01$). Experiments with isolates from other parts of the world have shown that the dry weight of rhizomorphs produced declines as the concentration of CO_2 increases. Particularly in soils of heavy texture, the concentration of O_2 is likely to fall and that of CO_2 to increase after heavy rainfall, as also occurs after irrigation where the O_2 concentration at 15 cm depth may decline to five per cent (Furr and Aldrich, 1943). Where drainage is impeded, such changes in soil atmosphere are likely to be more persistent. There was no opportunity in S. Tomé to determine the composition of the atmosphere in different soils, but from observations made elsewhere it seems unlikely that concentrations of O_2 and CO_2 were often unfavourable enough to prevent rhizomorph growth altogether. However, other inhibitory effects may well have been involved, and the absence of rhizomorphs in soil at higher elevations in S. Tomé was almost certainly due to a combination of factors.

CONTROL

Various methods were used in attempting to control root disease. The commonest procedure was to cut off the stem of a diseased cacao near soil level and apply lime around the stump. Sometimes most of the roots were removed by digging, and in other cases the cacao was pulled out by tractor. Such methods were not always effective. To try and prevent further spread of the fungus, systematic trenching was also sometimes carried out. Trenches about 40 cm wide and 50 cm deep were dug about 5 m beyond obviously affected cacao, any large excavated roots being stacked at the centre. Lime was applied to the sides and bottom of trenches, and to the surface of the enclosed area, at 10 t/ha. After this treatment *Armillaria* seldom if ever killed cacao outside the area, although in some localities trees left inside often succumbed. Young cacao replanted within the area was not attacked if a year or more had elapsed since the treatment was given; with an intervening period of six months, infection might still be only rare. At one farm cacao was replanted almost immediately after removal of dead trees, in positions between the original ones, apparently without serious loss. In this locality *Armillaria* seemed to be replaced rapidly by other fungi in infected roots. Since a wide range of conditions existed in S. Tomé, it was not surprising that experience with control varied. In some cases the measures taken were said to be justified on economic grounds, and at one farm losses from root disease had diminished despite considerable reduction in the number of shade trees.

DISCUSSION

Relatively harmless associations between *Armillaria* and indigenous trees are likely to have been common in the original forests of S. Tomé and Príncipe, as with the situation in Kenya described by GIBSON and GOODCHILD (1961). These authors suggested that outbreaks following removal of shade trees might be due to disturbance of the balanced state, and this would certainly apply to the attacks described here. Indeed in all continents it is possible to find examples of severe damage by *Armillaria* after large trees have been felled, especially on the introduction of a susceptible crop. In S. Tomé, as in other tropical countries, the ability of *Armillaria* to spread is not impeded by absence of rhizoomrphs.

Although most authors correctly put major emphasis on existing centres of infection for initiation of root disease, the possibility that new foci may arise from spore infection should not be overlooked. WIEHE (1952) drew attention to this when commenting upon outbreaks of *Armillaria* in orchards of tung planted on former arable in Nyasaland. The fields had been under cultivation of annual crops for an estimated period of 20 years. The distribution of diseased trees in one such plantation bears a remarkable resemblance to that in a first-rotation crop of oak in eastern England, described by RISHBETH (1978b). In the tung, which occupied about 2·8 ha, there were five foci around the edges of the plantation and two within; in the oak, of similar area, seven foci were located around the margin and two inside. The tendency for many of the first root infections in a first-rotation crop to appear near the edges has also been noted for *Fomes annosus* Fr. in British plantations (Low and GLADMAN, 1962). It probably arises from cumulative trapping of air-borne spores by foliage of the outermost trees; these are then washed off by rain on to suitable infection courts such as freshly cut stumps (RISHBETH and MEREDITH, 1957). Whereas the *Armillaria* foci in oak were commonly associated with thinning stumps infected by the fungus, no observations were available to indicate the means of primary infection in tung. Fruit bodies of *Armillaria* that might have provided inoculum for such infection were seen on tung by WIEHE (1952), and occur on cocoa in west Africa, as recorded for example by DADE (1927).

Judging by experience in S. Tomé and elsewhere, attempts to control root disease in cacao need to be undertaken chiefly in high-rainfall areas. Unfortunately no opportunity arose to set up experiments in the island. Experience derived from other crops can sometimes be valuable, but the types of method that are realistic depend very much on local conditions. One measure that does not seem to have received much consideration is avoiding the use of shade trees that are susceptible to *Armillaria*. For example in S. Tomé serious attacks often developed around *Albizia falcata* and *Erythrina velutina*, and in such cases it seems advisable to employ other species.

Intractable problems arise when shade trees or cacao adjacent to them start to die from attack by *Armillaria*. If the shade tree is a species generally resistant to the fungus, then it may be prudent to take no action other than remove infected cacao. If, however, the shade tree is known to be susceptible, there is a case for killing it at once. If such a tree is allowed to die from infection, *Armillaria* will probably invade all the roots, whereas if it is killed rapidly the fungus may be confined to part of the root system. The methods of killing unwanted trees used in S. Tomé were not very satisfactory. To kill standing trees involves the hazard of falling branches to people working below, and felling would often be more acceptable. In Britain it has been

found that applying a 40 per cent aqueous solution of ammonium sulphamate to stumps of broad-leaved trees directly after felling generally kills them rapidly and favours their colonization by decay fungi, some of which compete well with *Armillaria* (RISHBETH, 1976). This and other methods for rapidly killing stumps might well be tested in tropical plantations where *Armillaria* is prevalent. However, despite any such treatment, tree-to-tree spread of the fungus in adjacent cacao is unlikely to be prevented in all cases.

If a shade tree is no longer required and no attack by *Armillaria* is apparent, ring-barking (LEACH, 1937) seems the obvious choice. Good evidence of the effectiveness of this method in tung was provided by WIEHE (1952). In areas where ring-barking had been carried out, two trees/ha were killed by *Armillaria* up to 10 years after planting, whilst in untreated areas 30 trees/ha were killed. GIBSON and GOODCHILD (1961) found in Kenya that forest trees having natural root associations with *Armillaria* were not invaded by the fungus after ring-barking, although they were if directly felled.

It is rather surprising that trenching checked further spread of *Armillaria* in S. Tomé because the method has often been relatively ineffective elsewhere. The absence of rhizomorphs would have reduced the ability of *Armillaria* to extend beyond trenches, but it seems likely that this was not the only factor involved. Probably by the time new roots grew into trenched areas from outside, *Armillaria* had been replaced by other fungi in the infected roots. This suggestion is supported by the fact that young cacao trees planted within trenched areas were not attacked if a year or more had passed since the removal of diseased cacao, despite the likelihood that some infected roots remained in the soil. The method often fails because trenches are dug too near affected trees: a distance less than 5 m might well be unsafe, especially since appearance of symptoms is often delayed. LEACH (1939) pointed out that trenching is only likely to succeed where large tree roots no longer act as sources of infection and *Armillaria* is spreading within the crop.

The fact that *Armillaria* sometimes killed more of the residual cacao within trenched areas suggests that the treatments given did not always prevent root-to-root spread of the fungus. Merely cutting off the stem would have had little or no effect, while extraction by tractor, though removing the bulk of the food base for the fungus, would have left many lateral roots in the soil. Liming the soil for control of root disease was suggested many years ago, for example by PETCH (1921) in the case of rubber: the reduced acidity was said to be less favourable for fungus growth. Since *Armillaria* does not grow through the soil in S. Tomé, liming probably had little direct effect on spread of the fungus. However, since cacao is thought to grow better at about pH 6·5 than on more acidic soils, and values at several sites in S. Tomé ranged from pH 4·5 to 5·5, some of the young replanted trees might have resisted *Armillaria* more effectively after application of lime.

In the hope of avoiding the labour of trenching and procedures of dubious value, it would be interesting to try other ways of preventing root-to-root transfer of *Armillaria*. Because the fungus is less likely to spread over dead root systems than living ones, cacao adjacent to a diseased one could be cut down and the stumps killed at once, for instance with 40 per cent ammonium sulphamate. Depending on the conditions at the site, four or eight immediately adjacent trees might need to be removed. The method would involve a sharp decline in yield but would probably be economic if further spread of the fungus was prevented. If the method seemed promising, it might be improved by also inoculating cacao stumps with a suitable competitive fungus.

Several other suggestions have been made about control or alleviation of root disease in tropical crops. Attention is often drawn to the value of improving drainage, especially at sites where it is impeded. The establishment of suitable cover crops has sometimes given good results with rubber (Fox, 1965), but they are unlikely to be so useful with cacao owing to the relatively dense shade cast by its canopy. Encouragement of adventitious rooting is suggested as a possible procedure by Thorold (1975). Finally, the incidence of *Armillaria* on heavily pruned cacao might be noted: if it proves to be appreciably higher than average, some restriction of pruning is needed.

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