

## EFFECTS ON HOST LEAF REDUCTION BY A NEOTROPICAL MISTLETOE

### REDUCCION DE LAS HOJAS HUESPEDES POR EFECTO DEL MUERDAGO NEOTROPICAL

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#### ABSTRACT

The effects of the mistletoe *Phoradendron racemosum* (Aubl.) Krug & Urb. on host trees *Psidium guajava* L. (guava) are reported from transition forest in Guatopo National Park, north-central Venezuela. The relation between stem diameters and number of leaves supported by the stem was established in guava trees unaffected by hemiparasitic mistletoes. When recalculated for stems that supported mistletoes proximally (toward the main trunk), significantly fewer leaves were found per stem diameter. On stems that supported (distally) both host and mistletoe leaves, comparable leaf areas were found to those on nonparasitized stems (taking into account the larger leaf areas of the mistletoes). Such leaf distributions can be explained by greater transpiration rates and more negative osmotic potentials in *Phoradendron racemosum* than *Psidium guajava*, with the possible consequence that water is shunted preferentially to their leaves rather than to those of the host. Mistletoes at Guatopo may grow and reproduce most effectively at the end of the dry season when they can maintain higher light levels (through leaf drop in the host) than are possible later in the rainy season when the host is less affected by the water and nutrient drain of the parasite.

KEY WORDS: Mistletoes, hemiparasites, epiphytes, competition, nutrients, transition forest, Guatopo, Venezuela.

#### RESUMEN

Se reportan los efectos del muérdago *Phoradendron racemosum* (Aubl.) Krug y Urb. en árboles huéspedes *Psidium guajava* L. (guayaba) del bosque de transición del Parque Nacional Guatopo, en la región norte-central de Venezuela. Se estableció la relación entre el diámetro de las ramas y el número de hojas presentes en árboles de guayaba libres de la hemiparásita. Cuando se recalculó la relación para ramas que presentan a la hemiparásita en posición proximal (hacia el tronco principal), se encontraron significativamente menos hojas por unidad de diámetro de la rama. En ramas que presentaban hojas del huésped y del muérdago distalmente, se encontraron áreas foliares comparables con aquellas de ramas no parasitadas (tomando en cuenta la mayor área foliar de la hemiparásita). Estas distribuciones de área foliar pueden ser explicadas por las mayores tasas transpiratorias y potenciales osmóticos más negativos en *Phoradendron racemosum* que en *Psidium guajava*, con la posible consecuencia de que el agua es preferencialmente desviada hacia las hojas de la hemiparásita. Los muérdagos en Guatopo pueden crecer y reproducirse más eficientemente al final de la estación seca cuando es posible mantener un mayor nivel de radiación solar (debido a la caída de las hojas del huésped) de lo que puede ser posible posteriormente en la estación de lluvia cuando el huésped es menos afectado por el drenaje de agua y nutrientes por parte de la hemiparásita.

PALABRAS CLAVE: Muérdago, hemiparásitas, epífitas, competencia, nutrientes, selva de transición, Guatopo, Venezuela.

## INTRODUCCION

Mistletoes are parasitic plants that comprise several closely-related families in the order Santalales. While parasitic, they retain chlorophyll and their photosynthetic ability, and are thus called "epiparasitic" or "hemiparasitic". They utilize the water and soluble nutrients of their host, but produce their own photosynthate. For the general biology of parasitic mistletoes, see Kuijt (1969) or Calder & Berhardt (1983). The nutrition of mistletoes and their effects upon host plants are understood only incompletely, and subject to some debate (Ehleringer et al. 1985). Current opinion (and the balance of evidence) favors the view that *Phoradendron* mistletoes tap the xylem system of their host but not the phloem (as do some *Arceuthobium* mistletoe species), and therefore do not receive photosynthate from hosts. However, the haustorium between host and parasite might permit such phloem exchange, and the fact that mistletoes are observed to live for some time on "dead" hosts, at least on host which have lost their own photosynthetic structures, suggests that mistletoes photosynthate might be redistributed to maintain the root system of the leafless host (Calder 1983).

This study documents the effects of the mistletoe *Phoradendron racemosum* on the host tree *Psidium guajava* in neotropical forest vegetation in Venezuela. In Guatopo National Park in the northern coastal cordillera at 400 m. elevation, this mistletoe is widespread on many host species including the guava (*P. guajava*), which may support zero, a few or many clumps of the parasite. Subjective observations showed that

guava trees with extremely heavy mistletoe infestations were virtually devoid of host leaves, while those with light or no parasite loads were fully verdant. We quantify this relation by measuring the effects of the mistletoe on its host, relating loss of host leaves per stem diameter to the parasite load, discuss some possibilities for cause and effect, and the potential limiting factors in the mistletoe's life history.

## METHODS

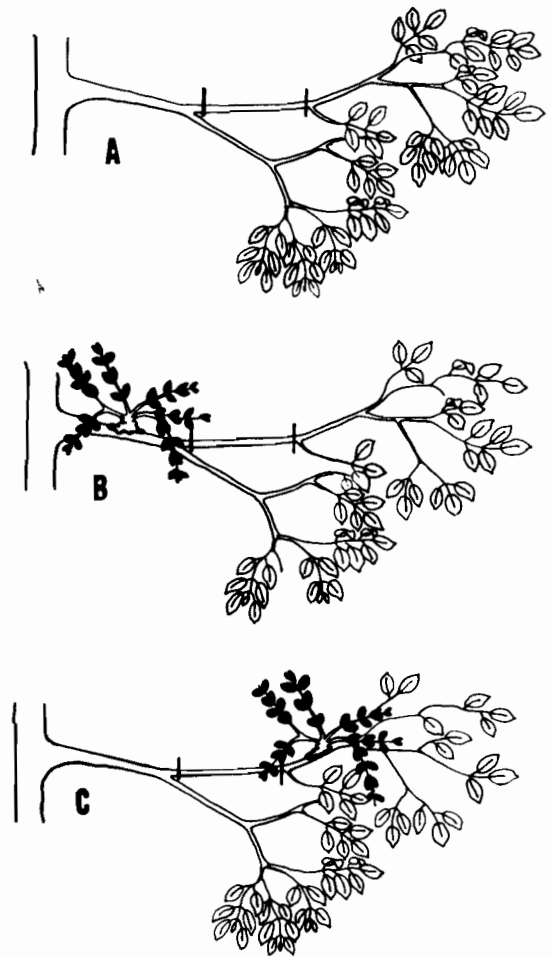
The study was conducted at the end of the dry season in April, 1987 at Aguas Blancas, a field station in Guatopo National Park, Miranda State, north-central Venezuela. The project centered on two adjacent trees of the evergreen *Psidium guajava* in the immediate vicinity of the station, on the fringes of the clearing in the transitional forest. Subject trees were selected to satisfy two conditions: a) they grew close together (3.5 m apart, and therefore subject to very similar environmental conditions), and yet b) bore quite different mistletoe loads. One tree was lightly infested (several small,  $\pm 0.01$  m<sup>3</sup>, and inconspicuous clumps), 5 m in height and single-trunked; the other was more heavily infested (with conspicuous mistletoe clumps up to 0.2 m<sup>3</sup> in volume), 6.5 m in height, and three-trunked. Compared to other guava trees in the vicinity, the two subjects were of average height and supported intermediate levels of the parasite.

Terminal stems were selected haphazardly in the subject trees, and the number of leaves supported by each terminal stem were counted. The stem

diameters of the terminal stems were measured with an electronic caliper at two points, one most distal from the main trunk, and the other most proximal to the main trunk, with the proviso that no other leaf-bearing twigs occur between the two points of measurement (see Fig. 1). Stem measurements avoided the swollen part of the stem close to the attachment of mistletoes. Three classes of stems were chosen: 1) stems bearing no mistletoe, only guava leaves, and with no mistletoe back along the path of successive branches to the base of the trunk (Fig. 1a); 2) stems bearing only guava leaves distally from the points of stem measurement, but bearing mistletoe clusters proximally, between the terminal branch and the main trunk (Fig. 1b); 3) stems bearing both guava leaves and mistletoe leaves distally from the points of measurement, in various relative abundance (Fig. 1c). The relations between stem diameters and numbers of leaves, both of guava and of the parasite, were investigated with linear regression analysis on log-transformed variables.

Notes on growth and reproductive activity were taken in the field. Several leaves of both guava and mistletoe were used in the laboratory to record leaf area (electronically), to calculate leaf weight/unit area, and also to measure stomatal sizes and record stomatal densities as reported below. Portions from the middle regions of several leaves of each species were treated by soaking in  $\text{NH}_4\text{OH}$  overnight and cleared in Chlorox bleach. Lower and upper epidermal layers were separated and mounted in lactophenol. Guard cell length and stomatal density were measured using a light microscope;

because actual size of stomatal opening can not be determined from fixed leaves, guard cell lengths are used as indicators of the potential maximum opening of the stoma.



**FIGURE 1.** Stem diameters are made where indicated by the bars, and leaf counts made distally. Class 1 stems (Fig. 1a) are nonparasitized, class 2 stems (Fig. 1b) have mistletoe clumps proximally on the stem, while class 3 stems (Fig. 1c) support mistletoe distally.

## RESULTS

The relation between log (stem diameter) and log (number of leaves) in the mistletoe-free guava stems, Class (1) see above, is linear (see Fig. 2), and given by the relation:  $\text{Log}(\# \text{ lvs}) = 2.097 + 1.837 \text{ Log}(\text{stem diam})$ . Thus stems support leaves in proportion to their circumference, as might be predicted from the peripheral vascularization of stems and branches. The relation is highly significant ( $n = 56$ ,  $r = 0.918$ ;  $F_{1,54} = 261.1$ ,  $p < 0.001$ ), and 84.3 % of the variation in leaf number is accounted for by variation in stem diameter. When

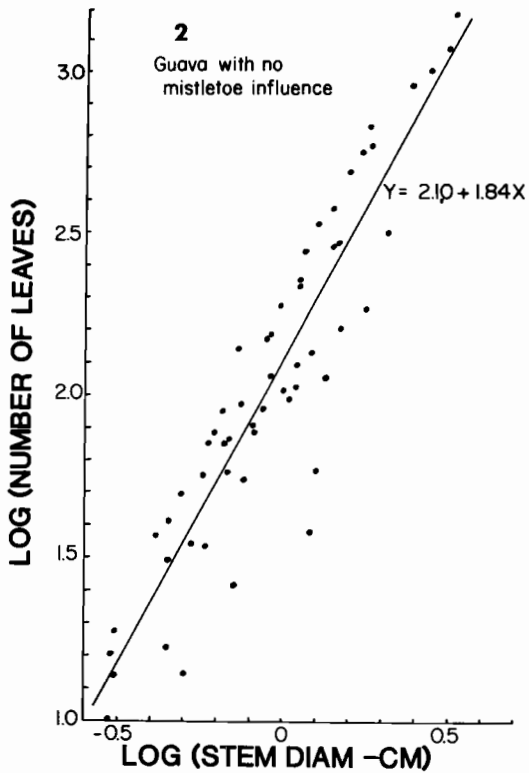


FIGURE 2. Linear relationship (on logarithmic scales) between stem diameter and leaf number on Class 1 guava stems unaffected by mistletoe.

Class (2) stems are considered, those with mistletoe growing proximally on the same branch but with no mistletoe distally, the regression line becomes:  $\text{Log}(\# \text{ lvs}) = 1.872 + 1500 \text{ Log}(\text{stem diam})$ , with  $r^2 = 43.2 \%$ . This relation is shown in Fig. 3; note that, while the regression is still significant ( $n = 16$ ;  $F_{1,14} = 10.65$ ,  $P < 0.01$ ), only about half as much of the variation in leaf number is accounted for by variation in stem diameter relative to Class (1) stems. This figure illustrates the deleterious effects of the mistletoe on the host, since the number of leaves supported per stem diameter is significantly reduced (e.g. for 1 cm. stems from 125 to 74, a reduction of  $>40 \%$ ).

Next consider Class (3) stems which support both mistletoe and guava leaves distally. For these data (Fig. 4) the regression line falls between the first two, and the slope is not significantly different from those of Class (1) and Class (2) stems. For 1 cm stems with both guava and mistletoe leaves, leaf numbers are intermediate, averaging 87 (vs 125 for nonparasitized stems), a 30 % reduction. For Class (3) data,  $r^2 = 64.4 \%$ , also an intermediate value (with  $n = 26$ ,  $F_{1,24} = 43.49$ ;  $p < 0.001$ ).

Adding in the mistletoe leaves to count of guava leaves brings Class (3) stems into closer accord with leaf counts on nonparasitized stems, although the combined counts still fall short of the latter. But mistletoe leaves average 3.31 times larger in area (mean area  $40.28 \pm 13.14 \text{ cm}^2$ ,  $n = 10$ ) than guava leaves (mean area  $12.17 \pm 3.68 \text{ cm}^2$ ,  $n = 16$ ). Thus, considering Class (3) stems again but now with leaf counts computed by

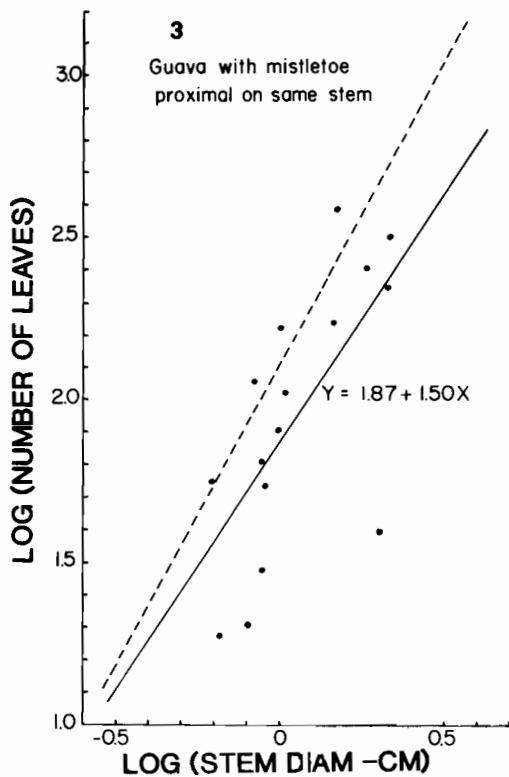


FIGURE 3. On Class 2 stems, which support mistletoe clumps proximally but not distally, numbers of guava leaves are reduced (by >40 % on 1 cm stems). The lower intercept relative to the nonparasitized stems (long-dashed line from Fig. 2), but not the lower slope, is statistically significant.

adding 3.31 times the number of the mistletoe leaves to the guava leaves, a new regression analysis shows a very close concordance with leaf counts on nonparasitized stems (results shown in Fig. 5). For 1 cm stems, area-weighted leaf counts average 126.6, and are virtually identical to the mean of 125.1 leaves on nonparasitized 1 cm stems. In the area-weighted Class (3) regression for nonparasitized stems, but still highly significant ( $n = 26$ ;  $F_{1,24} = 66.2$ ,  $p < 0.001$ );

the slope does not differ significantly from that in Fig. 2.

Although the area-adjusted leaf areas of parasite and host combined are similar in parasitized and nonparasitized stems, the mistletoe leaves do effect a reduction in host leaves (see Fig. 3), and possibly achieve their deleterious effects by greater transpiration rates than host

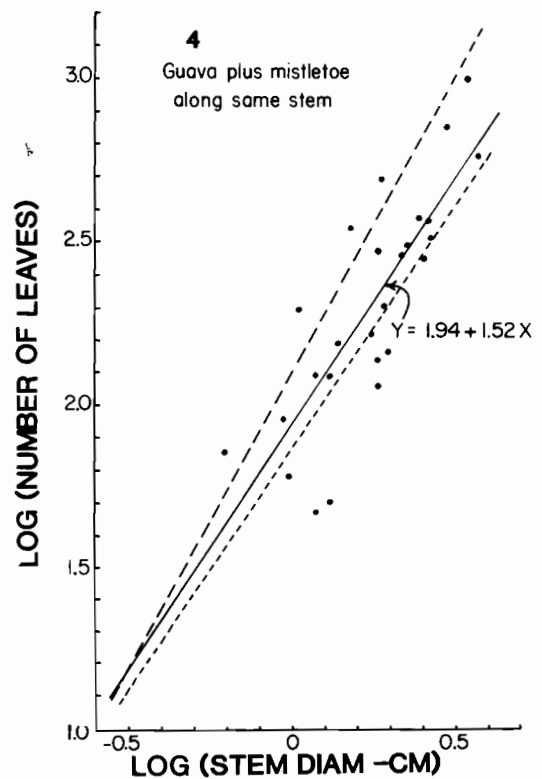


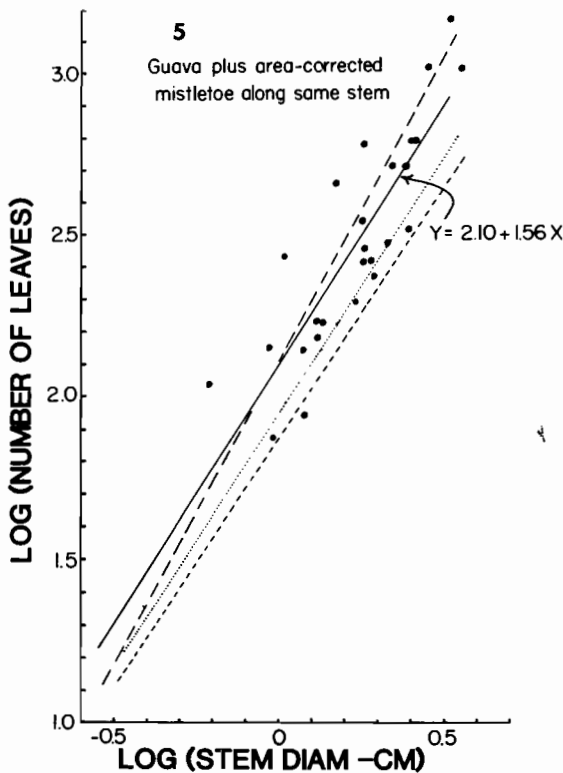
FIGURE 4. Class 3 stems, which support both mistletoe and guava leaves, are intermediate in leaf count between nonparasitized stems (long-dashed line from Fig. 2) and stems located distally from the parasites (short-dashed line from Fig. 3). The intercept is intermediate (indicating a 30 % reduction in leaf count on 1 cm stems relative to nonparasitized stems), and the slope is not significantly different from those of Fig. 2 and 3.

leaves. Analysis of stomatal densities was conducted using several leaves of each species. In guava, stomata were small (guard cell length averaging 0.19 mm;  $n=30$ ), located exclusively on leaf undersides, and densely crowded (average 889  $\text{mm}^{-2}$ ; area sampled 8.3  $\text{mm}^2$ ). In the mistletoe, stomata are much larger (mean guard cell length 0.59 mm;  $n=30$ ), but with stomatal densities averaging much lower (mean 45  $\text{mm}^{-2}$  on

lower epidermis; 51  $\text{mm}^2$  sampled), and 29  $\text{mm}^2$  on the upper surface (46  $\text{mm}^2$  sampled). Leaf weight/unit area averages much higher in mistletoe (mean  $0.0253 \pm 0.00487$  (S.E.)  $\text{g cm}^{-2}$ ), versus only  $0.0133 \pm 0.00150$  (S.E.)  $\text{g cm}^{-2}$  in guava, significantly lower by a factor of almost 2. When the larger stomatal areas in mistletoe and their presence over both leaf surfaces are taken into account, mistletoe pore area per (whole) leaf surface is similar to that of the host. Yet, because a) only the mistletoe has stomata on the upper leaf surface facing direct solar radiation, b) mistletoe leaves, because of their adverse effects on the host, are relatively unshaded, c) mistletoe has larger leaf capacitance by dint of larger leaf area and thicker leaves, and d) only guava leaves have pubescence on their lower surfaces, reducing heat loads, increasing the boundary layer and likely reducing transpiration, we expect transpiration rates to be greater in the parasite than in the host.

## DISCUSSION

Our results demonstrate that *Phoradendron racemosum* reduces leaf number on host stems distally from their point of attachment. The degree of this reduction is proportional to mistletoe leaf numbers, with a nearly equal substitution of parasite for host leaf area. Anatomy and morphology of both host and parasite demonstrate that the parasite has a much higher capacitance, and suggest that higher transpiration rates could occur in the mistletoe. Assuming that transpiration rates are indeed higher and osmotic potentials are more negative in the parasite, its higher



**FIGURE 5.** Stems supporting both mistletoe and host leaves are plotted here, but mistletoe leaves are weighted by 3.31, the factor by which they are larger in area than host leaves. This brings the regression line for the parasitized stems into close conformity with nonparasitized stems (long-dashed line; nonsignificant differences in both intercept and slope).

water demand could affect a reduction of leaves in the host as seen in Fig. 3.

Our assumptions are consistent with what has been reported in the literature. It is known that in general mistletoes maintain lower water potentials (Scholander et al. 1965; Fisher 1983), and higher transpiration rates (Ehleringer et al. 1985) than their hosts. Stomatal openings and transpiration rates have also been found to be larger for *Phoradendron* species on *Richeria* (Euphorbiaceae) and *Gaiadendron* (Loranthaceae, itself a root parasite--Kuijt 1963) in Venezuela (Vareschi & Pannier 1953). Our interpretations also conform to Glatzel's (1983) host-parasite model for water system relations.

Such high rates of water use in the parasite presumably are required to accumulate dissolved nutrients, especially but not exclusively nitrogen (Ehleringer et al. 1985), which is stored in leaves in the form of arginine to balance reproduction costs. Schulze & Ehleringer (1984) found that mistletoe growth rates are much faster (>7X) on nitrogen-fixing hosts such as *Acacia* species than on non-nitrogen fixing hosts under otherwise comparable conditions. This picture of mistletoes as nutrient parasites and as wasteful water-sinks to acquire dissolved nutrients is broadly confirmed (Lamont & Southall 1982; Glatzel, 1983; Schulze et al. 1984; Ehleringer & Schulze 1985). Their effects on hosts are deleterious to the extent that they reduce the foliage on infected branches of *Acacia wrightii* (Kibota 1986), kill distal parts of infected branches in *Juniperus osteospermum* after 5-8 years (Ehleringer et al. 1986), and become serious pests in plantations

(Hawksworth 1983). In Guatopo, it seems that water and nutrients that would otherwise have supported host leaves are diverted to an equivalent leaf area in the parasite, with host leaves distal to the mistletoe in turn receiving significantly reduced resources.

Most mistletoe-host systems have been studied in deserts where water is limiting and climate dictates a largely overlapping growing season for parasite and host. At the Aguas Blancas study site, however, the dry season may be more suitable for mistletoe growth and reproduction than the wet season. Here the dry season is very marked, with <10% of the average 1479 mm of annual precipitation falling in the months February-April. In 1987 the dry season was particularly severe (only two light showers in the six weeks before the first week of May), and the onset of the rainy season was unusually late. At the end of the dry season during the period of this study, the mistletoes appeared to be growing vigorously and fruiting copiously. The host guavas studied (on open slopes) were relatively dormant, with some leaf production just beginning and very few flowers and fruits present; on the other hand, streamside guavas were in full leaf with more flowers, and parasite infection rates were very low in these shadier and wetter sites.

In view of the results on parasite leaf substitutability, the low values of stomatal density we measured in *Phoradendron racemosum* relative to the host guavas seem somewhat anomalous. Yet, given that the parasite has very much larger stomata, and if it is geared specifically for dry-season water budgets,

this anomaly is less remarkable. Moreover, this mistletoe has large, heavier leaves of higher capacitance than the host, and such leaves appear ideally suited for drawing water and its dissolved nutrients preferentially into the parasite and away from the host (e.g. Glatzel 1983). Conceivably the best use of the limited dry-season water availability is made by mistletoe leaves that are still relatively water-efficient. It appears that, if water and nutrients are shunted largely into the mistletoes at the end of the dry season, when the host is maximally water-stressed, the parasites will effect a maximal reduction in the leaf densities of their hosts and thereby maintain higher light levels within the canopy of the hosts where the parasites are located. In contrast, later on in the rainy season when water is less limiting and the effects of the mistletoes on the hosts less severe, the mistletoes might not be able to have much effect on host leaf density. At that time the host could conceivably place the parasite in a light-limited environment.

The notion of light-limitation has not been discussed in the mistletoe literature, but this factor would seem to be a reasonable possibility as the rainy season advances and canopy densities increase in the transitional forest. Reduced light levels might be the selective force that has pushed these mistletoes into late dry season growth and reproduction, away from the season of higher water and therefore higher nutrient availability. Further speculation on potential light-limitation of mistletoes living on largely evergreen hosts in seasonal environments must wait until more data on growth and transpiration

rates are collected over the full annual cycle.

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