Incidence of fungus-growing termites (Isoptera, Macrotermitinae) on the structure of soil microbial communities

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Abstract

The aim of this study was to investigate the impact of subterranean fungus-growing termites on the structure of soil microorganism communities. We tested whether termites significantly modify the abundance and structure of microbial communities within their below-ground nests (fungus-comb chambers) and whether these effects are species-specific.

The investigations were carried out in a humid savanna reserve with material collected from the fungus-comb chamber walls of two widespread species differing in the mode of nest construction. Ancistrotermes builds diffuse and ephemeral nests while chambers of Odontotermes are mostly concentrated and occupy the same area for a comparatively much longer period of time than creating lenticular mounds. The soil properties (pH, texture and C, N content) and the microbial biomass were analysed and automated rRNA intergenic spacer analysis (ARISA) was used to characterise bacterial (B-ARISA) and fungal (F-ARISA) communities. Our results illustrate that the nest structures created by termites offer a diverse range of physical and chemical environments that differ strongly from those present in the general soil mass. Odontotermes had strong effects on microbial properties at the scale of the fungus-comb chamber and at the scale of the lenticular mound. In the fungus-comb chambers, the microbial biomass is not affected by termites but the structure of microbial community is different from that in the control open savanna soil. In the lenticular mound, the microbial biomass is higher and the structure of bacterial community is distinct than that in the fungus-comb chambers. Ancistrotermes also strongly influenced the structure of soil bacterial and fungal communities in the open savanna. However, we did not find any significant modification of bacterial and fungal community structures in the lenticular mound. The impact of fungus-growing termites is, therefore, species-specific and varies depending on the study site (open savanna vs. lenticular mound).

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1. Introduction

Soil macrofauna, through their building and/or foraging activities, play major roles in the creation of environments exhibiting different physical and chemical properties than the bulk soil, the so-called ‘hot-spots’ (Brown et al., 2000; Lavelle and Spain, 2001). In modifying the properties of soil to a great extent, such species, usually called ecosystem engineers (sensu Jones et al., 1994), modulate the availability of resources (e.g. physical space and food) for other species. Although such functional group is one of the major factor regulating the quality and availability of resources to soil microbes (Lavelle and Spain, 2001), its effects on the abundance and diversity of soil bacterial and fungal communities has received few attention.

Amongst soil engineers, termites constitute a major component of savanna and forest ecosystems in tropical and subtropical Southeast Asia and Africa (Bignell and Eggleton, 2000) because of their strong impacts on soil physical and chemical properties (Holt and Lepage, 2000). To understand these impacts, species are usually considered among two functional (or feeding-) groups: mainly soil feeding and fungus-growers, according to similarities in
their food sources and in their action on soils (Bignell and Eggleton, 2000; Lavelle, 1997). Soil-feeding termites consume humus and build their nests with faecal matter mixed with coarse, inorganic soil particles. The relationships between their digestive mechanisms and the microbial compartment have been reviewed (Brauman et al., 2000) and an impact of this feeding group has recently been demonstrated on soil bacterial and fungal density and genetic structure (Roose-Amsaleg et al., 2004; Fall et al., 2004). Conversely, fungus-growing termites (Macrotermiteinae) are characterised by an exosymbiosis with a fungus (Termitomyces sp.) which completes the degradation of the litter on which they feed. These latter do not incorporate faeces into their nests but enrich their constructions with saliva, which contains easily degradable carbon (Wood, 1976), and in fine particles, especially clays (Holt and Lepage, 2000; Jouquet et al., 2002a,b). The effect of this feeding group on soil microbial communities is poorly documented. The few data available concern the free-living bacteria and fungi in epigeous mound soil (Arshad et al., 1982; Paul et al., 1985; Holt, 1998) and the typology and microbial communities related to the nitrogen cycle in above-ground soil sheetings (Mora et al., 2003; Ndiaye et al., 2004).

But few data—if any—are available on fungus-growing termite species that live in subterranean nests. Each nest is made of several hundreds of units, so-called fungus-comb chambers, where the exosymbiosis between termites and fungus takes place. It has been observed that the density of fungus-comb chambers in a Guinean savanna can reach a density of 10.2 U m$^{-2}$ (Josens, 1971). The chamber wall is thoroughly handled by termites and laboratory experiments evidenced higher microbial activity and N-mineral production in such structures (Abbadie and Lepage, 1989). Underground nest chambers also have a quite large impact on CO$_2$ emission at the point- and landscape-scales in savannas (Konaté et al., 1999). These structures probably play a significant role as hot-spots in tropical ecosystem functioning since clay and soil organic matter (SOM) influence strongly soil bacterial diversity at a microscale (Lavelle and Spain, 2001). However, it remains necessary to determine whether these hot-spots could also induce strong changes in soil bacterial and fungal community structures.

Understanding the role played by soil macrofauna on the diversity and dynamic of indigenous microbial populations represents one challenge of modern soil ecology. In this context, we undertook a study to determine if subterranean fungus-growing termites can influence the structure of soil bacterial and fungal communities in their below-ground structures. The following hypotheses were tested: (i) subterranean fungus-growing termites can significantly modify the microbial community structure within their nests (fungus-comb chambers) as related to the modification of soil properties and (ii) these alterations are species-specific.

2. Materials and methods

2.1. Study site and species studied

Field data were collected in January 2001 at the Lamto Research Station in Côte d’Ivoire (West Africa, 6°13’N, 5°02’W), at the edge of the rain forest domain (Menaut and César, 1979), in the Guinean bioclimatic zone (rainfall $\sim$1200 mm yr$^{-1}$). The study site is a shrubby humid savanna with main grasses from the Andropogoneae tribe. The two species, Ancistrotermes cavithorax (Sjöstedt) and Odontotermes nr pauperans (Silvestri) (Isoptera, Macrotermiteinae), are dominant in this ecosystem within the fungus-growing (Macrotermiteinae) trophic group and represent about 70% of the total trophic group biomass (Josens, unpublished thesis). Ancistrotermes builds diffuse and ephemeral nests (few months) while chambers of Odontotermes are mostly concentrated and last for a comparatively longer period of time (few years) (Josens, unpublished thesis). The accumulation of Odontotermes nests is strongly suspected to be responsible for the formation of huge termite lenticular mounds (scale 1–300 m$^2$) (Abbadie et al., 1992; Konaté, unpublished thesis; Konaté et al., 1999). Lenticular mounds formed by Odontotermes are scattered in the Lamto savanna ecosystem and range from 0.5 to 20.0 m in diameter and cover about 10% of the ecosystem (Abbadie et al., 1992; Konaté, unpublished thesis).

2.2. Data collection

The soils processed by both Ancistrotermes and Odontotermes and the soil surrounding their nests (considered as control because being without any visible activity of termites) were excavated to about 20 cm depth in the open savanna and the lenticular mounds, air dried and stored at $-20$ °C. In the laboratory, these materials were carefully processed, as to extract the finer reddish material covering the inner layer of the fungus-comb chamber walls (as described in Abbadie and Lepage (1989)). Nests of Ancistrotermes were found in the open savanna and in the lenticular mounds while nests of Odontotermes were only found in the lenticular mounds (Fig. 1). We randomly chose five lenticular mounds with approximately the same size (about 80 m$^2$) and their surrounding environment. For each site (open savanna or mound), five soil samples per species and five soil samples without termite activity (control) were excavated to about 20 cm depth.

2.3. Soil properties

The percentage of organic substrates in soils was assessed by total C, N content with an elemental analyser (NA 1500 Series 2, Fisons). Soil pH was measured in H$_2$O (soil:solution = 1.5) and soil texture was determined using...
termes cavithorax
and
and in the surrounding savanna (n
Odontotermes
each site, five nests per species were collected and afterwards mixed.

fumigated soil)/0.54 (Brookes et al., 1985).

After extraction in 0.5 M K$_2$SO$_4$ with vigorous shaking for
chloroform vapour. Control samples were not fumigated.

Briefly, 5 g soil samples were fumigated for 24 h with
form-fumigation–extraction method (Brookes et al., 1985).

2.4. Microbial biomass

Soil microbial biomass was estimated with the chloro-
form-fumigation–extraction method (Brookes et al., 1985).

Briefly, 5 g soil samples were fumigated for 24 h with
chloroform vapour. Control samples were not fumigated.

After extraction in 0.5 M K$_2$SO$_4$ with vigorous shaking for
30 min, total N in the extracts were measured by dry
combustion. Nitrogen in the soil microbial biomass was
calculated as [(total N in fumigated soil) – (total N in non-
fumigated soil)]/0.54 (Brookes et al., 1985).

2.5. ARISA fingerprint of bacterial and fungal communities

The genetic community structure was assessed by using
automated ribosomal intergenic spacer analysis (ARISA)
which exploits the variability in the length of the
intergenic spacer (IGS) between the small (16S for bacteria and 18S
for fungi) and the large (23S for bacteria and 28S for fungi)
subunit rRNA genes in the rrn operon. ARISA was
previously demonstrated to be a reproducible and robust
method for discriminating between microbial communities
of different soil types and plots within a site (Ranjard et al.,
2001). However, in some case the between plots variability
can hamper the analyses of DNA fingerprint. To eliminate
the impact of plot-to-plot variation from the analyses,
Tom-Petersen et al. (2003) analysed a ‘consensus finger-
print’ profiles’ including only the dominant peaks of each
profiles of plots. In this study, we pooled and mixed soil
samples of the same species collected in the same site in
order to determine the general profiles of the bacterial and
fungal communities and to compare communities between
treatments. The variability was tested by four replications of
the mix-treatments.

The DNA extraction procedure used followed the
method described by Ranjard et al. (2003). Briefly, this
procedure involved sample homogenization and cell
disruption by grinding in liquid nitrogen followed by
enzymatic lysis (lysozyme and protease K). This method
was shown to allow the recovery of at least 60% of the DNA
from the various samples. The bacterial and fungal
ribosomal IGS were amplified with the following primers:
S-D-Bact-1522-b-S-20/L-D-Bact-132-a-A-18 and 2234C/
3126T, respectively, and PCR conditions were as described
by Ranjard et al. (2001). Automated ribosomal intergenic
spacer analysis (ARISA) involves the use of a fluorescent-
labelled primer for the PCR which is the IRD800 dye
fluorochrome (MWG SA Biotech, Ebersberg, Deutschland)
for the LiCor® DNA sequencer (ScienceTec, Les Ulis,
France). The concentration of labelled PCR products was
estimated, and 2 µl of the product was added to deionised
formamide (1 µl) and denatured at 90 °C for 3 min. ARISA
fragments were resolved on 3.7% polyacrilamide gels and
run under denaturing conditions for 12 h at 1500 V/80 W on
an LiCor® DNA sequencer (ScienceTec). The data were
analysed using the 1D-Scan software (ScienceTec). The
software converted fluorescence data into electrophore-
grams where peaks represented PCR fragments. The height
of the peaks was calculated in conjunction with the median
filter option and the Gaussian integration in 1D-Scan, and
represented the relative proportion of the fragments in the
total products. Lengths (in base pairs) were calculated by
using a size standard with bands ranging from 200 to
1206 bp. The standard was made by PCR amplification of
different fragment sizes of phage M13 mp18 (Promega,
Charbonnières, France).

2.6. Statistical analysis

Homogeneity of variances was tested using Levene’s
test. The effects of termites on soil pH, texture, C and N
content, and microbial biomass were tested by means of
one-way ANOVA and differences between means were
tested with the LSD test. Correlation analyses were tested to
investigate the effects of clay and organic matter content on
the microbial biomass by means of Pearson’s correlation
coefficient. All statistical calculations were carried out using
Statistica for Windows.

Data obtained from the 1D-Scan software were con-
verted into a table summarizing the band presence (i.e.
peak) and intensity (i.e. height or area of peak) using the
PrepRISA program (Ranjard et al., 2001). The analysis was
performed with a resolution of 2 bp and the 100 more
dominant peaks were considered. Principal component
analysis (PCA) on a B-ARISA and F-ARISA covariance
matrix was performed to evaluate similarities between
communities using ADE-4 software (Ranjard et al., 2001;
Thiouloise et al., 1997).
3. Results

3.1. Soil physical and chemical properties

The results did not show any significant effect of termites on soil pH, either directly through the building of fungus-comb chambers or indirectly through the creation of the lenticular mounds (Table 1; mean value: pH 6.79, SE 0.17; \( P > 0.05 \) in all cases).

In the open savanna, there was a slight, but significant increase of soil carbon in Ancistrotermes nest structures (\( P = 0.048 \)), while no difference occurred in N content (\( P = 0.287 \)) (Table 1). Lenticular mounds build by Odontotermes contained much larger quantities of soil carbon and nitrogen than the control soil in the open savanna (\( P = 0.08 \) and 0.01 for the C and N content, respectively). The carbon content was significantly less in soil recently worked by Odontotermes than in the bulk of the lenticular mound (\( P = 0.016 \)), while no difference occurred with the soil worked by Ancistrotermes (\( P = 0.095 \)). Whatever the soil structures (control vs. termite nests), the nitrogen content did not vary in the lenticular mound (\( P = 0.383 \) and 0.130 for Ancistrotermes and Odontotermes nest structures, respectively).

The soil texture was clearly different in the soil processed by both termite species (Table 1). The control soil in the open savanna was very sandy, with a greater proportion of fine and coarse sands than the soil in the bulk of the lenticular mound (\( P = 0.015 \) and 0.001 for the fine and coarse sand fractions, respectively). In the open savanna, Ancistrotermes enriched its nest structure in clay and fine silt to the detriment of coarse sand (\( P = 0.015, 0.005 \) and 0.001 for the clay silt and coarse sand fractions, respectively). Within the lenticular mound, soil processed by Ancistrotermes and Odontotermes were similar to the surrounding soil without visible activity of termites (control mound soil) (\( P > 0.05 \) for all the fractions).

3.2. Soil microbial properties

Analysis of soil microbial N showed the influence of fungus-growing termite species on microbial biomass (Fig. 2). We did not find any significant difference between soil microbial N in the open savanna and that in the fungus-comb chamber wall of Ancistrotermes, when collected in the open savanna, and Odontotermes in the mounds (\( P > 0.05 \) in each cases). However, we observed that soil microbial N was greater in mound soil for the control and Ancistrotermes nest treatments (without significant difference between them) than in control open savanna soil (\( P < 0.05 \)).

Fingerprinting of bacterial (B-ARISA) and fungal community (F-ARISA) structure provided complex profiles with peaks ranging from 200 to 1026 bp (Fig. 3a and b). Because, of the high sensitivity of the automated sequencer and its high resolution power, about 100 bands per profile were detected with a resolution of 2 bp. Independent comparison of the B- and F-ARISA profiles showed that each soil was characterized by a specific pattern suggesting a particular genetic structure of the bacterial and fungal communities. Differences in bacterial community structures between soils were analysed by principal component analysis (PCA) of the profiles (Fig. 4a). Soils collected in the open savanna and those from the mound were easily separated on the first axis, which explained 42.0% of the total variability. In the open savanna, PCA also discriminated the bacterial communities between the control soil and the Ancistrotermes nest structure. In the lenticular mounds, soils handled by Odontotermes were separated from the control soil and from the soil handled by Ancistrotermes on the second axis (22.3% of the total variability). However, PCA did not discriminate any effect of Ancistrotermes on bacterial community structure in the mound. PCA analysis was also performed on F-ARISA fingerprints and led to a good distinction of each soil type (Fig. 4b), confirming the overall effect of termites on microbial communities in the open savanna. The control soil

### Table 1

Soil organic matter content (C% and N%), pH and texture (%clay, fine and coarse silts, fine and coarse sands) for the control savanna soil, the control lenticular mound soil, the soil worked by Ancistrotermes cavithorax either in the open savanna or in the lenticular mound, and the soil worked by Odontotermes nr pauperans in the lenticular mound.

<table>
<thead>
<tr>
<th>Soil properties</th>
<th>Control (open savanna)</th>
<th>Ancistrotermes (open savanna)</th>
<th>Control (mound)</th>
<th>Ancistrotermes (mound)</th>
<th>Odontotermes (mound)</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH (H₂O)</td>
<td>6.53 (0.32)</td>
<td>6.64 (0.20)</td>
<td>6.82 (0.30)</td>
<td>7.06 (0.64)</td>
<td>6.92 (0.39)</td>
</tr>
<tr>
<td>C (%)</td>
<td>0.67 (0.07)</td>
<td>0.82 (0.06)</td>
<td>1.31 (0.11)</td>
<td>1.14 (0.07)</td>
<td>1.02 (0.06)</td>
</tr>
<tr>
<td>N (%)</td>
<td>0.05 (0.01)</td>
<td>0.06 (0.01)</td>
<td>0.09 (0.01)</td>
<td>0.08 (0.01)</td>
<td>0.09 (0.01)</td>
</tr>
<tr>
<td>Clay (%)</td>
<td>9.57 (0.55)</td>
<td>12.70 (0.98)</td>
<td>14.45 (1.14)</td>
<td>15.91 (0.81)</td>
<td>16.67 (2.14)</td>
</tr>
<tr>
<td>Fine silt (%)</td>
<td>8.76 (1.08)</td>
<td>11.61 (0.96)</td>
<td>15.25 (0.76)</td>
<td>15.05 (0.78)</td>
<td>15.46 (1.25)</td>
</tr>
<tr>
<td>Coarse silt (%)</td>
<td>24.34 (1.09)</td>
<td>23.71 (2.53)</td>
<td>34.63 (0.74)</td>
<td>34.02 (1.50)</td>
<td>34.89 (2.42)</td>
</tr>
<tr>
<td>Fine sand (%)</td>
<td>27.76 (2.15)</td>
<td>28.06 (1.55)</td>
<td>24.73 (0.73)</td>
<td>25.40 (0.88)</td>
<td>22.51 (3.89)</td>
</tr>
<tr>
<td>Coarse sand (%)</td>
<td>30.21 (2.59)</td>
<td>20.45 (3.52)</td>
<td>8.98 (0.96)</td>
<td>10.26 (2.07)</td>
<td>9.58 (1.39)</td>
</tr>
</tbody>
</table>

The effects of termites on soil properties were tested by means of one-way ANOVA and differences between means were tested with the LSD test (\( n = 5 \), standard errors are in parentheses).
and the soil handled by *Ancistrotermes* in the open savanna were clearly separated on the first axis while the control soil in the open savanna and the soils influenced by *Odontotermes* (control mound and fungus-comb chambers of both termite species in the mound) were separated on both the first and second axis (26 and 23% of the total variability, for the first and the second axis, respectively).

4. Discussion

4.1. Soil properties and microbial biomass

The impact of Macrotermitinae epigeous nests on soil physical and chemical properties in tropical ecosystems has well been studied (see Holt and Lepage, 2000 for a review). In the present field study, analysis of fungus-comb chamber wall revealed that subterranean Macrotermitinae termites could also have strong impacts on soil properties, and as a consequence on soil microbial properties.

The influence of fungus-growing termite species on soil properties was first studied through their influence on soil pH, because it is a strong factor regulating soil microbial abundance and diversity. However, our results did not show any significant effect. Other important parameters were soil organic matter (SOM) and texture, which influence the habitat and the quantity and quality of available food for microbes. Our results showed that...
nest structures of both termite species are enriched in SOM (that is one of the primary determinants of soil microbial growth) and in fine particles. One consequence should be a greater proportion of microhabitats (< 50 µm) where bacterial cells are usually concentrated (Ranjard and Richaume, 2001). Effectively, these particular habitats are suspected to be more favourable for the development and persistence of bacterial communities because of (i) less extreme wetting and drying cycles, (ii) less leaching of nutrients necessary for growth and (iii) enhancement of the protection from predators (Numan et al., 2003; Young and Ritz, 1998). The lack of significant impact of Ancistrotermes on soil microbial biomass in the open savanna and that of Odontotermes in fresh structures (fungus-comb chambers) were therefore surprising and could be explained by different mechanisms: we suggest that (i) termites could compact the soil through the creation of their nest (Lavelle and Spain, 2001), thus limiting the availability of SOM to microbes, and consequently their growth; (ii) and/or that they could inhibit the development of bacterial and fungal growth through the secretion of antibacterial and antifungal peptides from their saliva (Batra and Batra, 1979; Thomas, 1987; Rosengaus et al., 2000; Lamberty et al., 2001).

Conversely, the greater carbon content and microbial biomass found in the lenticular mound (control and Ancistrotermes nest structures) suggest that a greater SOM content has became available to microbes in these soils. This hypothesis is supported by the correlation found between the microbial biomass and the carbon content (r = 0.67, P < 0.05) while we did not find any correlation with the proportion of clay in soil (r = 0.37, P > 0.05) (data not shown). These enrichments in available substrates for microbes could be explained by two ways. First, as suggested by Konaté (unpublished thesis) Ancistrotermes has probably utilized the soil previously worked by Odontotermes for the creation of their fungus-comb chambers. Since it did not modify the soil texture, we assume that there was probably no need to enrich the soil in clay in the lenticular mound where the clay content is already higher enough, owing to previous actions of Odontotermes. However, in building its nest structures, Ancistrotermes incorporated saliva which constituted substrates for microbes. Second, lenticular mounds are covered by grasses (Konaté, unpublished thesis; Jouquet et al., 2004) which produce litter, roots and root exudates that constitute as substrates for microbes. Therefore, these results suggest that major processes such as the enhancement of soil microbial activity mainly occur in soil, but not in soil which are currently processed by Odontotermes.

4.2. Soil microbial community structure

The application of the B- and F-ARISA methods has also demonstrated that through the modification of soil physical and chemical properties, subterranean fungus-growing termites are important regulators of the structure of soil bacterial and fungal communities. PCA analysis showed that Ancistrotermes and Odontotermes had strong effects on both bacterial and fungal communities which might be due to their effect on soil physical and chemical properties, and that the impact of Ancistrotermes on soil microbial communities varies depending on the study site (open savanna vs. lenticular mound). The effects of termites on soil organic matter and soil texture suggest that their impacts on the structure of microbial communities were
rather attributable to modifications of complex ecological features than to alterations of individual parameters of soil conditions. Therefore, the influence of termites on the microbial community structures could mainly be explained by changes in nutrient availability, together with concomitant differences in microenvironments due to changes in soil porosity. Given that soils worked by termites were derived from chambers replete with Termitomyces sp. fungi, it is also possible that both Termitomyces were detected from position 600 to 630 bp (ITS length compiled in the GenBank database for the different group of Termitomyces sp) in F-ARISA profiles and consequently might contribute significantly to discrimination of fungal communities.

The effects of Odontotermes on the bacterial community were two-fold: they create fungus-comb chambers (scale of months and 1–100 cm²; Josens, unpublished thesis; Abbadie and Lepage, 1989) where the structure of microbial community was different from that in control open savanna and, at a greater scale of time and space, they also create mounds (scale of years and 1–100 m²; Abbadie et al., 1992; and, at a greater scale of time and space, they also create mounds (scale of years and 1–100 m²; Abbadie et al., 1992; Konate et al., 1999) where the structure of bacterial community was distinct than that in the fungus-comb chambers (no significant difference occurring with fungi). The difference between the structure of the bacterial community in the wall of the fungus-comb chambers (considered as soil freshly worked by Odontotermes) and that in the lenticular mounds without visible activity of termites (control soil considered as previously worked) could be explained by the higher SOM content and by a change in soil structure which could occur when termites ceased to work it. These results show that the lifespan of nest structures is an important parameter for appreciating the influence of Odontotermes on bacterial communities. Ancistrotermes also strongly influenced the structure of soil bacterial and fungal communities in the open savanna through its nest building. However, we did not find any significant modification of bacterial and fungal community structures in the lenticular mound, suggesting that Ancistrotermes did not drastically modify the environment of soil microbes in such structures.

5. Conclusions

Macrotermiteinae termites are usually considered as belonging to the same functional group when considering their influence on the ecosystem functioning (Lavelle, 1997; Bignell and Eggleton, 2000). However, this study also shows that although fungus-growing termite species (Ancistrotermes vs. Odontotermes) have approximately the same impact on soil aggregate properties (enrichment in SOM and fine particles), they could have both general and species-specific effects on soil bacterial and fungal biomass and community structure. When applied to fungus-growing termites, the biological attributes of each species (pattern and lifespan of the termite built structures) should therefore be taken into account to assess their relative importance in the biological functioning of soil, and especially their impact on the abundance and diversity of soil microbes. Finally, we suggest that future objectives in studying the impacts of fungus-growing termite species on microbial populations should be to establish the link between the diversity of fungus-growing termites, the microbial community structure and their functions, such as those responsible for the nitrogen cycle.

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