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Fruiting of putative ectomycorrhizal fungi under blue gum (*Eucalyptus globulus*) plantations of different ages in Western Australia

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Abstract The species richness of putative ectomycorrhizal (EM) fungi fruiting in blue gum (*Eucalyptus globulus* Labill.) plantations in Western Australia was investigated in relation to plantation age. Eleven plantations, 1–8 years old, were selected for study and two native *Eucalyptus* forest sites in the same region were chosen for comparison. Sporocarps of 44 species of putative EM fungi were collected from the 13 sites. Of these, 30 species were found in blue gum plantations. The number of fungal species was highly positively correlated with plantation age and inversely correlated with soil pH. Young plantations (1–5 years) had 2–9 fungal species and were overwhelmingly dominated by species of *Laccaria* and *Scleroderma*. In older plantations (6–8 years), the relative abundance of sporocarps of each species within the fungal community decreased, accompanied by an increase in the number of fungal species (12–17 per site). A brief survey of the two native eucalypt forests in this region revealed a much higher number of fungal species than that observed in plantations. In plantations, species of *Descolea*, *Laccaria*, *Pisolithus* and *Scleroderma* typically fruited in young plantations. Species of epigeous fungi of the genera *Boletus*, *Cortinarius*, *Hydnum*, *Inocybe*, *Lactarius*, *Paxillus*, *Russula* and hypogeous fungi, including species of *Descomyces*, *Hysterangium* and *Mesophellia*, were found only in older plantations, or in native forests. Some of the fungi that fruit in young plantations are now being evaluated for use in commercial spore inoculation programs to increase the species diversity of EM fungi in exotic eucalypt plantations.

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Introduction

Blue gum (*Eucalyptus globulus* Labill.), a native of southeastern Australia, has been widely planted in Australia and many other countries because of its wood quality, wide range of adaptations to soil conditions, and rapid early growth in the field (Cromer 1996). Blue gum was first commercially introduced into Western Australia in the early 1970s, and has since become the major hard wood plantation species for timber production, wood chips and land rehabilitation there (National Forest Inventory 1997).

Eucalypts predominantly form ectomycorrhizal (EM) associations in native forests (Chilvers 1973; Malajczuk and Hingston 1981) and plantations (Chu-Chou and Grace 1982; Brundrett et al. 1996). In Australia, there is a wide range of EM fungi associated with eucalypts and many are endemic (Castellano and Bougher 1994). Bougher (1995) suggested that there are about 6500 species of EM fungi in Australia, with less than 10% of them named. Hilton (1982, 1988) listed more than 500 larger fungi in Western Australia, many of which are associated with indigenous eucalypts. Inoculation with selected EM fungi to promote seedling growth of blue gum has been intensively studied (Burgess et al. 1993; Thomson et al. 1994), but little is known about the diversity and ecology of such fungi fruiting in blue gum plantations, especially changes with tree age.

Some eucalypt EM fungi are more commonly observed to be associated with young stands of trees on disturbed sites and others with old stands (Chu-Chou and Grace 1982; Gardner and Malajczuk 1988). This results in a few pioneering fungi being gradually replaced or supplemented by increasing numbers of fungi in older habitats. Some workers have used the terms "early-

stage fungi" and "late-stage fungi" to describe those associated with different ages of host plants (e.g. Dighton and Mason 1985), but these terms are sometimes misleading and are not always sufficient to explain changes in fungal populations over time (Newton 1992; Keizer and Arnolds 1994).

The primary aim of this present study was to identify the putative EM fungi fruiting under blue gum plantations and provide information about changes in aboveground fungal species richness and composition over time.

Materials and methods

Site description

The 13 study sites were located in the southwestern forest region of Western Australia (Table 1). This region has a typical Mediterranean climate with winter rainfall. The annual precipitation at these sites, using the nearest town records, ranges from 800 to 1400 mm. Eleven plantation sites (first rotation), previously agricultural (maintained as pasture for at least 20 years) or native eucalypt forest lands were selected to form a chronosequence from 1 to 8 years old. In addition, two sites with native jarrah (*E. marginata* Donn ex Smith) or regrowth karri (*E. diversicolor* F. Muell.), representative of the two main types of native forests in this region, were included for comparison. Location, soil, and site history information for the study sites are given in Table 1 and Figure 1.

Sampling procedure

The time of sampling was chosen on the basis of the authors' previous experience. During the fungal fruiting seasons (June to October) in 1995 and 1996, sporocarps of putative EM fungi were collected from a sampling area of approximately 5 ha at each site. Each site was visited at least four times, at the same time during the peak fruiting season. Five random locations (approximately 5 m^2) within each site were dug to a depth of 20 cm in search of hypogeous sporocarps. Visual estimation of the relative sporocarp abundance of each fungus was made at the time of collection and was categorised into three levels (rare, common, abundant) relative to all sites. Fresh sporocarps of each fungus were gently brushed free of soil, photographed in the laboratory and identified to genus or species using names in Bougher and Syme (1998) whenever possible. All sporocarps were then air-dried at 35 °C for 24–48 h and voucher specimens and fungal cultures deposited in the Mycology Herbarium of CSIRO, Forestry and Forest Products in Perth, Western Australia.

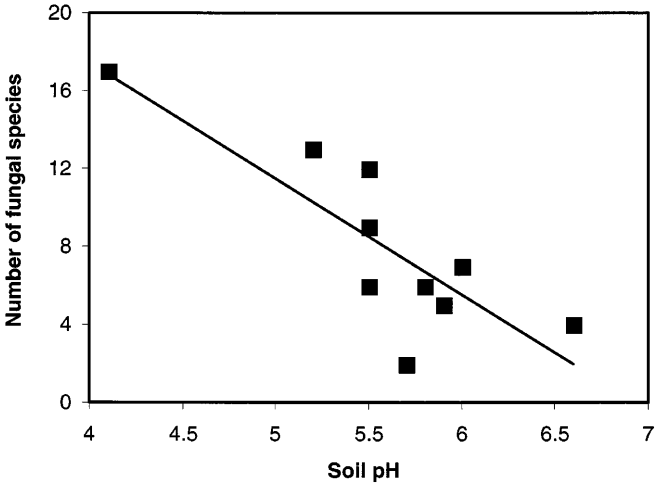

Fig. 1 Relationship between soil pH and the number of putative ectomycorrhizal (EM) fungal species fruiting in *Eucalyptus globulus* plantations

Results

Information about soil properties and site histories are summarised in Table 1. Soil pH (1:5, H_2O), which

Table 1 Details of the 13 sites in Western Australia including site name, site location, tree age, soil type, and site history. *Farm* refers to plantings on agricultural land: *forest* refers to recently-cleared forest (*NF* native forest)

Site	Tree age	Name	Lat (S)	Long (E)	Soil type	Site history
1	1	Landells Farm	34°15′	115°09′	Sandy loam	Farm
2	3	Keiths Block	34°03′	116°14′	Sandy loam	Farm
3	3	Carpenters Treefarm	34°20′	116°00′	Sandy loam	Forest
4	3	Payton Treefarm	33°10′	115°43′	Grey sand	Farm
5	3	Dunnets Farm	34°15′	115°21′	Grey sand over clay	Farm
6	4	Parkes Treefarm	34°27′	116°45′	Sandy loam over clay	Farm
7	5	Stretches Treefarm	34°08′	116°44′	Sandy loam	Farm
8	5	Boorara Treefarm	34°41′	116°11′	Sandy loam with gravel	Forest
9	6	Beebes Treefarm	34°40′	116°12′	Black acid sand	Forest
10	8	Wrens Rd Treefarm	34°11′	116°03′	Sandy loam with gravel	Farm
11	8	Boorara Treefarm	34°41′	116°11′	Sandy loam with gravel	Farm
12	NF	Amphion Block	32°46′	116°12′	Lateritic gravel	Jarrah forest
13	NF	Boranup Forest	34°06′	115°02′	Sandy loam	Karri forest 100-year-old regrowth after clear-felling

ranged from 4.1 to 6.6, was not highly correlated with plantation age, but was inversely correlated with the number of fungal species as shown in Figure 1 (correlation coefficient = –0.644, $P < 0.05$). Soil P varied considerably between the sites, ranging from 2.4 to 108 mg P kg^{-1}. Soil organic carbon contents ranged from 1.1 to 7.6%. Neither soil P nor organic carbon was correlated with EM fungal species richness.

Sporocarps of 44 species, in 29 genera, of putative EM fungi were collected from the 13 study sites (Table 2). Among them, 30 species from 22 genera were observed to fruit in blue gum plantations and 35 species from 28 genera were found in nearby native jarrah or karri forests. Comparison of the fungal collections between plantations and native forests revealed that 21 of the 29 genera were common in both types of stands. The genus *Thelephora* was only found in plantation stands, whereas the 7 genera *Austrogautieria*, *Hydnotrya*, *Leucopaxillus*, *Martellia*, *Mesophellia*, *Tricholoma* and *Zelleromyces* were observed in native eucalypt stands, but not in plantations.

There was a strong positive linear correlation (correlation coefficient = 0.818, $P < 0.01$) between plantation age and the number of fungal species (Fig. 2). In plantations, species number increased from 2 in 1-year-old, to 4–9 in 3- to 5-year-old, to 12–17 in 6- to 8-year-old stands (Table 2). The number of putative EM fungi collected at the two native forest sites (21, 23 species) was much higher than in the plantation sites surveyed. There were no consistent differences in species richness between sites where plantations were established on forest or pasture lands (Fig. 2).

The species composition of putative EM fungi fruiting on each site also changed with stand age (Table 2). The most common EM fungi fruiting in young plantations (1–5 years) were *Laccaria lateritia*, *Scleroderma cepa*, *S. areolatum* and a *Laccaria* sp. Other species, such as *Amanita umbrinella*, *Descolea maculata* and *Pisolithus* sp., were common at this stage. In addition to those found in young plantations, species of *Boletus*, *Cortinarius*, *Hydnum*, *Inocybe*, *Lactarius*, *Paxillus* and *Russula* were observed fruiting in older plantations (6–8 years). In the native forests, fungi that dominated in young plantations, such as species of *Scleroderma* and *Laccaria*, were rarely encountered. Instead, more hypogeous fungi were found, including species of *Descomyces*, *Hydnangium*, *Hysterangium*, *Hydnotrya*, *Martellia*, *Labyrinthomyces*, *Mesophellia*, *Zelleromyces* and *Scleroderma*. Some of these hypogeous fungus genera (e.g. *Descomyces* and *Hydnangium*) were also found in 8-year-old blue gum plantations, but were not observed in younger stands. Difference in fungal fruiting with plantation age was also observed among species within the same genus. For example, *Amanita umbrinella* was generally associated with 5-year-old or younger plantations, whereas *A. xanthocephala* was more frequently found to fruit in older plantations and native forests (Table 2). A hypogeous *Scleroderma* species fruited abundantly in an 8-year-old blue gum plantation (Site 10), but was not found in the other plantations.

Site 9 had a higher number of fungal species fruiting than the other plantation sites, with 17 fungi collected from this site (see Figure 2 and Table 2). The species at this site were more similar to those found in native forests than those collected in the other plantations. For example, *Hydnum repandum*, *Lactarius eucalypti* and *Russula* spp. were all commonly observed to fruit in native eucalypt forests but were not collected from young blue gum plantations. This latter site was on recently cleared forest and was the only plantation site with a substantial accumulation of leaf litter on the forest floor.

There were marked differences in the estimated relative abundance of sporocarps produced by different species of EM fungi between young and old plantations, and between plantations and native forests (Table 2). For example, sporocarps of *Scleroderma* spp. and *Laccaria* spp. were very abundant in the first few years after planting, but fruiting by these fungi declined with increasing plantation age. We have also observed that fungi in the genera *Pisolithus, Scleroderma* and *Laccaria* rarely produce sporocarps in undisturbed natural eucalyptus forests. These observations provide evidence that these fungi prefer young stands or disturbed habitats, in contrast with other fungi that were only observed in older stands of eucalypts.

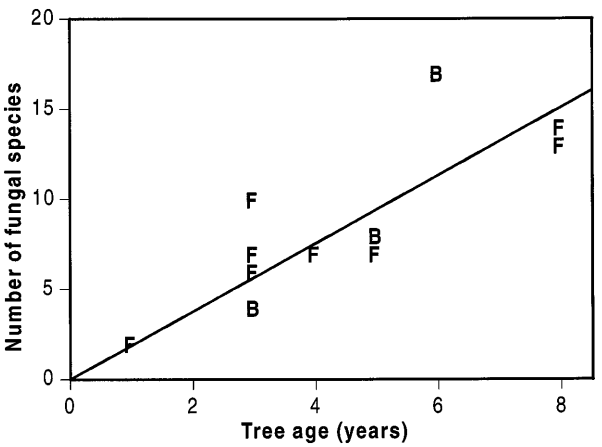

Fig. 2 Relationship between tree age and the number of putative EM fungal species fruiting in *E. globulus* plantations (*F* farm sites, *B* forest sites)

Discussion

This survey identified sporocarps of 30 fungal species, representing 22 genera, of putative EM fungi associated with blue gum plantations in Western Australia. Most of these fungi have been experimentally confirmed to form ectomycorrhizas with *E. globulus* and other eucalypt species (Malajczuk et al. 1982; Burgess et al. 1993; Thomson et al. 1994). As our primary focus was on the plantation sites, the number of fungi fruiting on the two

Table 2 Putative ectomycorrhizal (EM) fungi and relative sporocarp abundance in 11 blue gum plantation stands of different ages (site 1–11) and 2 *Eucalyptus* native stands (site 12 and 13) in Western Australia. Relative abundance of sporocarps was scaled as: +, rare; ++, common; +++, abundant (* hypogeous fungi)

Site	1	2	3	4	5	6	7	8	9	10	11	12	13
Amanitaceae													
Amanita umbrinella Gilbert & Cleland			+	+		++	+			+			
Amanita xanthocephala (Berkeley) Reid & Hilton								+	+	+		++	+
Boletaceae													
Austroboletus cookei (Saccardo & Sydow) Wolfe									+		+		
Boletus multicolor Cleland											+		
Boletus sp.									+		+	+	
Tylopilus sp.									+		+		
Clavariaceae													
Clavaria sp.									+		+		+
Ramaria sp.								+		+		+	+
Cortinariaceae													
Cortinarius austro-venetus Cleland												+	
Cortinarius basirubescens Cleland & Harris						+			+				
Cortinarius radicatus Cleland												+	
Cortinarius sp.									++	+	+	+	+
Descolea maculata Bougher					+				++				
**Descomyces albellus* (Massee & Rodway) Bougher & Castellano											++		+
**Descomyces* sp.													+
Inocybe sp.									+	+		+	+
Gautieriaceae													
**Austrogautieria manjimupana* Trappe & Stewart												+	
Hydnaceae													
Hydnum repandum L. ex Fr.									++			+	
Hydnangiaceae													
**Hydnangium carneum* Wallroth											++		+
Hysterangiaceae													
**Hysterangium* sp.											+	+	+
Mesophelliaceae													
**Mesophellia* sp. 1													++
**Mesophellia* sp. 2													++
Paxillaceae													
Paxillus muelleri (Berkeley) Saccardo								+			++		+
Paxillus sp.												+	
Russulaceae													
Lactarius eucalypti Miller & Hilton									+			+	
**Martellia* sp.												++	+
Russula sp. 1													+
Russula sp. 2									+				
Russula sp. 3									+				
Russula sp. 4										+		+	
**Zelleromyces* sp.													+
Sclerodermataceae													
Pisolithus albus (Cooke & Massee) Priest *nom. prov.*		+	+	++	++	++	++			++		++	
Pisolithus sp.					++				++		+		++
Scleroderma areolatum Ehrenberg		+++		++	+++	++	+	+		+	+		
Scleroderma cepa Persoon	+	+++	++	+++	+++	+++	++	+	++	++	++		
**Scleroderma* sp.										+++			+
Thelephoraceae													
Thelephora sp.					+++				++				
Tricholomataceae													
Laccaria lateritia Malencon	+++	+++	++	++	+++	+++	++	++	++	+++	++	+	
Laccaria sp.		++		++	+++	++	+	+		+	+		
Leucopaxillus lilacinus Bougher												+	
Tricholoma sp.												+	
Discinaceae													
**Hydnotrya* sp.												+	+
Pezizaccae													
Peziza sp.										+		+	++
Tuberaceae													
**Labyrinthomyces* sp.											+		+
Total fungal species: 44	2	5	4	6	9	6	6	7	17	13	12	23	21

native forest sites is undoubtedly an underestimation. Such habitats require more intensive sampling (Vogt et al. 1992) than plantation sites, where additional time spent searching for fungi rarely revealed new species.

Records from several brief surveys reported in the CSIRO fungal herbarium list at least 60 species of putative EM fungi fruiting in native blue gum plantations and forests in Tasmania (CSIRO Mycology Herbarium Database, Perth, Western Australia). According to the present study, the number of putative EM fungi in exotic blue gum plantations in Western Australia is much lower than in its natural habitats in Tasmania. In addition, many of those fungi found in native plantations in Tasmania are different from those observed in Western Australia. For example, some hypogeous *Cortinarius* are associated with young blue gum plantations in Tasmania (N. Malajczuk unpublished data), but have not been observed in Western Australia. These discrepancies may largely be the reflection of evolution of fungal flora with different habitats and vegetation types in different parts of Australia.

Previous reports have shown a low number of EM fungi associated with young eucalypt plantations in exotic locations (Table 3). From Table 3, it can be seen that many of the EM fungi reported to associate with eucalypts in exotic locations belong to genera common in young blue gum plantations in Western Australia, such as *Laccaria, Pisolithus* and *Scleroderma*. The proportion of fungi listed in Table 3 indigenous to these regions outside Australia or introduced with eucalypts from Australia remains unclear. Most genera are common throughout the world, but some of the fungi listed are different from those found in Australia. Regarding *Pisolithus*, there is now molecular evidence that some isolates of this fungus associated with eucalypts outside their natural range have been introduced from Australia (B. Dell et al. unpublished data).

There is some evidence for primary succession of sporocarps of EM fungi in blue gum plantations in Western Australia. Species of fungi in the genera *Descolea*, *Laccaria*, *Pisolithus* and *Scleroderma* were dominant under young trees, but were rare or absent under older plantations. The species that gradually became more important in older plantations belonged to the genera *Boletus*, *Cortinarius*, *Descomyces*, *Hydnum*, *Hysterangium*, *Inocybe*, *Lactarius*, *Paxillus* and *Russula.* These fungi only fruited in older plantations or forests, but we do not know how long it takes for these

Table 3 Diversity of putative EM fungal genera associated with young eucalypt plantations in selected exotic locations

Region	Country	Number of fungal genera	Genera	Eucalypt species and age	Reference
Asia					
	China	6	*Amanita, Boletus, Cantharellus, Laccaria, Hysterangium, Pisolithus, Russula, Scleroderma*	6 Eucalypt species (under 7 years)	Gong and Chen 1991, B. Dell and N. Malajczuk unpublished data
	Indonesia	7	*Amanita, Boletus, Descomyces, Laccaria, Lactarius, Russula, Scleroderma*	*E. urophylla, E. grandis* (3–7 years)	Dr. Supriyanto personal communication
	New Zealand	6	*Hydnangium, Hymenogaster, Hysterangium, Laccaria, Paxillus, Scleroderma*	5 Eucalypt species (2–5 years)	Chu-Chou and Grace 1982
		9	*Cortinarius, Hydnangium, Hysterangium, Inocybe, Laccaria, Mesophellia, Paxillus, Scleroderma, Tricholoma*	5 Eucalypt species (6–10 years)	Chu-Chou and Grace 1982
	Philippines	6	*Boletus, Cortinarius, Pisolithus, Russula, Scleroderma, Thelephora*	*E. urophylla, E. deglupta, E. camaldulensis* 2–3 years	N. Pampolina personal communication
	Thailand	6	*Amanita, Pisolithus, Russula, Thelephora, Tylopilus, Scleroderma*	*E. camaldulensis* (under 5 years)	Chalermpongse 1995
Africa					
	Kenya	2	*Pisolithus, Scleroderma*	*E. camaldulensis* (age unknown)	Ivory et al. 1996
South America					
	Brazil	6	*Chondrogaster, Descomyces, Laccaria, Pisolithus, Scleroderma, Thelephora*	*E. dunnii, E. grandis* (under 9 years)	Giachini and De Oliveira 1996, B. Dell unpublished data
	Chile	5	*Amanita, Hydnangium, Laccaria, Scleroderma, Setchelliogaster*	*Eucalyptus* spp. (age unknown)	Garrido 1986
Europe					
	Portugal	7	*Amanita, Cenococcum, Laccaria, Pisolithus, Scleroderma, Thelephora, Tricholoma*	*E. globulus* (under 8 years)	Neves Machado 1995

fungi to initiate sporocarps after establishment in new habitats. It would be interesting to determine at what plantation age the late-fruiting fungi first appear as mycorrhizas.

EM fungus succession is a complex phenomenon, involving three-way interactions between fungus, host plant and their habitats. A number of factors, including tree age (Dighton and Mason 1985), root age (Gibson and Deacon 1988), soil microbes (Last et al. 1983), litter accumulation (Last et al. 1987; Gardner and Malajczuk 1988) and inoculum availability (Newton 1992), have been proposed to be involved in determining mycorrhizal succession. Gardner and Malajczuk (1988) suggested that litter development was a key factor influencing fungal succession as they found the first appearance of late-stage fungi was accompanied by the build-up of leaf litter under trees. In blue gum plantations in Western Australia, canopy closure normally occurs about 5 years after planting and leaf litter starts to accumulate. The decomposition of leaf litter may change the quality and quantity of organic matter in soil (Aggangan et al. 1998) and this may influence the development of fungal communities; many early-stage fungi are thought to be characteristic of mineral soils (Danielson 1985). In this regard, it is interesting that species richness was inversely correlated with soil acidity in our study, reflecting the influence of soil organic matter and leaching processes on the acidification of weakly buffered sandy soils.

Recent studies have suggested that above-ground fungal fruiting does not always reflect the occurrence of mycorrhizas below ground (Gardes and Bruns 1996; Pritsch et al. 1997). Using molecular analysis, Gardes and Bruns (1996) observed that correlation between above- and below-ground fungal occurrence varied between fungal species in natural stands of bishop pine (*Pinus muricata*). Some species were present as both fruiting bodies and mycorrhizas, while other species were recorded either as fruiting bodies or mycorrhizas. However, discrepancies between fruiting and mycorrhizal formation by fungi are likely to be much greater in complex forest systems than in plantations recently established on soil initially devoid of these fungi. We have also observed low diversity of mycorrhizal types (identified by morphology) on young *E. globulus* roots in Western Australian plantations (M.C. Brundrett, N. Pampolina unpublished data). Confirmation of the relationship between fungal fruiting and mycorrhizal occurrence in soils in blue gum plantations will require detailed molecular identification.

There is some question as to how EM fungi colonised the plantation sites used in the present study. In Western Australia, blue gum seedlings are raised as container-grown seedlings in nurseries, where natural colonisation by EM fungi is rare. In natural ecosystems, potential propagules of EM fungi include basidiospores, vegetative hyphae, sclerotia and mycorrhizal root tips (Brundrett 1991). Basidiospores are mainly dispersed by wind. Some mycophagous animals provide another means for dispersal of hypogeous fungi by consuming fruiting bodies of these fungi (Claridge et al. 1996). All of the propagules mentioned above are likely to be important in the EM colonisation of the forest sites, where they could persist in soil or litter (Brundrett and Abbott 1995). However, in the case of farm sites where agricultural crops or pasture have grown for many years, there are unlikely to be many EM propagules. We, therefore, assume that recolonisation of these farm sites is primarily by means of spore dispersal via wind from adjacent forests (most sites were within 1 km of established eucalypts in forests, shelter-belts, or road verges).

That fact that the number of fungal species under trees planted on recently cleared forest sites was similar to that on farm sites of a similar age suggests that (i) propagules of fungi in forest soils lost viability before trees became established, or (ii) the majority of surviving fungi were not compatible with blue gum saplings, or (iii) forest fungi persisted under trees but were unable to fruit. More research is required to determine which of the above factors limit the occurrence of fungi in young blue gum plantations.

The information from the present study will be useful for the selection of appropriate EM fungi for commercial nursery inoculation programmes using spore inoculum, since (i) growth promotion of young seedlings after inoculation with EM fungi collected from young plantations has been demonstrated (Grove et al. 1991), and (ii) the availability of large amounts of spores in the field is an important criterion for the selection of fungi for spore inoculation.

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