Changes in cation concentrations in red spruce wood decayed by brown rot and white rot fungi[1]

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Abstract: Red spruce (*Picea rubens* Sarg.) wood blocks were incubated in modified soil block jars and inoculated with one of nine white rot or brown rot basidiomycetes. Concentrations of calcium, magnesium, potassium, iron, and aluminum were determined using inductively coupled plasma emission spectroscopy in wood incubated 0, 1.5, 4, and 8 months after inoculation. Concentrations of calcium and magnesium tended to increase with time in a linear fashion in wood inoculated with fungi. Patterns of change in potassium concentrations varied. Concentrations of iron and aluminum were high in wood decayed by some of the fungi, particularly *Postia placenta* (Fr.) M. Larsen & Lombard. Temporal trends in wood cation concentration varied among decay fungi tested, indicating that species of decay fungus should be considered when examining the role of wood decay in nutrient cycling in the forest.

Résumé : Des éprouvettes de bois d'épinette rouge (*Picea rubens* Sarg.) ont été incubées selon la méthode modifiée d'essais sur sol et inoculés avec l'un ou l'autre de neuf basidiomycètes de carie blanche ou brune. La concentration de calcium, de magnésium, de potassium, de fer et d'aluminium dans les éprouvettes a été mesurée par spectroscopie d'émission atomique au plasma 0, 1,5, 4 et 8 mois après l'inoculation. La concentration de calcium et de magnésium avait tendance à augmenter de façon linéaire en fonction du temps dans le bois inoculé avec les champignons. Les patrons de changement dans la concentration du potassium étaient variables. La concentration de fer et d'aluminium était élevée dans le bois carié par certains des champignons, particulièrement *Postia placenta* (Fr.) M Larsen & Lombard. Les changements temporels dans la concentration des cations du bois variaient selon le champignon de carie testé suggérant qu'on devrait considérer l'espèce de champignon de carie lorsqu'on étudie le rôle de la carie du bois dans le recyclage des éléments nutritifs en forêt.
[Traduit par la Rédaction]

Introduction

Basidiomycete fungi decay wood in service, on the forest floor, and in living trees (Zabel and Morrell 1992). In addition to causing economic losses, these fungi play an important role in recycling elements in the forest (Boddy 1991; Boddy and Watkinson 1995).

Our understanding of the decay process is not complete. Theories attempting to elucidate the initial degradative steps in decay by brown rot fungi have included the possible role of the iron-based Fenton's reaction, biochelators, and oxalate, the last of which can complex with calcium to form calcium oxalate. In a preliminary laboratory study involving two fungi, Jellison et al. (1992) found that red spruce (*Picea rubens* Sarg.) wood decayed by the brown rot fungus *Postia placenta* (Fr.) M. Larsen & Lombard (≡*Oligoporus placentus* (Fr.) Gilbertson & Ryvarden) increased in concentrations of calcium, magnesium, and iron and that wood decayed by the white rot fungus *Phanerochaete chrysosporium* Burdsall increased in concentrations of calcium and magnesium.

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Decay of wood in living trees, as well as decay of wood in the laboratory, may result in increases in ion concentrations (Ellis 1965; Safford et al. 1974; Shortle 1982; Shortle and Smith 1987). Shortle (1982) found decreased electrical resistance in water extracts of decaying Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) wood in decay chambers. Decreased electrical resistance was associated with increased potassium ion or hydrogen ion concentration in decayed wood. Characterizing the cation environment associated with decay may provide insight into the decay process.

Many researchers have examined the cation content of decaying conifer wood on the forest floor (Grier 1978; Lambert et al. 1980; Foster and Lang 1982; Edmonds 1987; Sollins et al. 1987; Edmonds and Eglitis 1989; Arthur and Fahey 1990; Harmon 1992; Means et al. 1992; Busse 1994). These studies, which include decay class, chronosequence, and time series approaches, have not revealed a consistent pattern of cation changes in decaying wood. Foster and Lang (1982) determined nutrient content of wood in a chronosequence of red spruce and balsam fir logs left on the forest floor after logging in New Hampshire's White Mountains and found a net accumulation of nitrogen, phosphorus, calcium, and magnesium with time. Sodium and potassium loss was concomitant with loss of mass in spruce wood, and potassium was lost at a rate faster than that of mass in fir. Lambert et al. (1980) found a decrease in calcium in decaying balsam fir logs.

Different species of wood decay fungi may play similar or different roles in various biogeochemical processes, but this is difficult to determine in the forest. Decay fungi are identified infrequently, if at all, in field studies of cation changes in decaying conifer wood. Blanchette (1984), however, compared

cation concentrations in sound hemlock (*Tsuga canadensis* (L.) Carrière) wood, in *Ganoderma tsugae* Murr. sporophores, and in associated decaying hemlock wood. Calcium concentrations were greater in decaying hemlock than in the sporophores or in sound wood. Potassium concentration was greatest in the sporophores. Harmon et al. (1994) focused on fungal sporocarps as an avenue for nutrient loss from conifer logs. Cation concentrations in sporocarps varied with the species of fungus. Observations on cation changes in wood decayed by different fungi may help clarify the role of fungi in biogeochemical cycles in the forest and suggest whether differences in the species of fungus decaying wood could be responsible for some of the variation in patterns of cation concentrations in the forest ecosystem.

The purpose of this laboratory study was to determine whether (1) changes in cation concentrations occurred in decaying wood of red spruce, (2) changes were progressive, and (3) changes varied with the species of fungus causing the decay.

Materials and methods

The effects of nine decay fungi on the cation concentrations of red spruce wood in modified ASTM soil block jars incubated for up to 8 months was examined (American Society for Testing and Materials 1994). Fifty grams of a soil mix (potting soil – sphagnum peat moss – vermiculite, 4:5:5) was placed in each of one hundred and eight 1-qt (1.101-dm^3) Mason jars. Deionized distilled water (120 mL) was added to each jar and allowed to absorb overnight. Two pieces of birch tongue depressor were placed on the soil surface in each jar to serve as feeder strips. Lids were inverted to prevent sealing and were screwed on with rings. Jars were autoclaved for 30 min.

The brown rot fungi *Postia placenta* and *Fomitopsis pinicola* (Swartz:Fr.) Karst. and the white rot fungi *Trametes versicolor* (L.:Fr.) Pilat, *Phanerochaete chrysosporium* Burdsall, *Armillaria* sp., *Amylostereum chailletii* (Pers.:Fr.) Boidin, *Resinicium bicolor* (Albertini & Schwein.:Fr.) Parmasto, *Scytinostroma galactinum* (Fr.) Donk., and *Irpex lacteus* (Fr.:Fr.) Fr. were used in this study.

Feeder strips in each of three replicate jars for each of three sampling times were inoculated with squares (approximately 0.5 cm^2) cut from malt extract agar cultures of one of the decay fungi. One culture square was placed at each end of each of the two feeder strips in each jar. Squares of sterile malt extract agar were placed on feeder strips in control jars. Jars were incubated at room temperature (approximately 25°C) for approximately 3 months to allow colonization of feeder strips.

Radial sections of red spruce heartwood (1 × 1 × 0.25 in. (1 in. = 25.4 mm)) cut from the same tree were oven-dried, weighed, and placed, one per jar, on top of inoculated feeder strips. Jars were incubated at room temperature until harvest after approximately 1.5, 4, and 8 months of incubation with decay fungi. Three wood blocks per treatment were harvested at each incubation time, but only two control blocks were harvested at 8 months. Blocks were wrapped in foil, placed in a plastic bag, and frozen until further processed.

Surface mycelium was removed from blocks with a clean razorblade. Fresh weights of colonized wood blocks were measured and blocks were oven-dried for 23 h at 104°C. Dry weights were measured and the percentage of dry weight lost was calculated. Oven-dried blocks were ground in a Wiley mill through a 40-mesh screen in preparation for cation analysis.

Samples of ground wood (0.5 g) were weighed into silica crucibles and ashed in a muffle furnace at 550°C for 6 h. The ash in each cooled crucible was wetted with deionized distilled water and digested with 5 mL of 50% HCl and 2 mL of concentrated HNO_3. Samples were gently heated to just below boiling. Another 5 mL of 50% HCl was added and samples were brought to volume in 50-mL volumetric flasks. Concentrations of calcium, potassium, magnesium, aluminum, and iron were determined with inductively coupled plasma emission spectroscopy (ICP) (Jarrell-Ash model 975).

Cation concentrations of ground spruce wood from the same tree that had not been placed in soil block jars were also determined. Cation concentrations were corrected for weight loss to eliminate increases in cation concentrations due soley to the decreased carbon content of decayed wood using the following formulae:

$$\%\ \text{wt. loss} = \left(1 - \frac{\text{final dry wt.}}{\text{initial dry wt.}}\right) \times 100$$

$$\text{corrected value} = \text{cation concn.} \left(\frac{100 - \%\ \text{wt. loss}}{100}\right)$$

A two-way analysis of variance (ANOVA), 10 × 3 factorial design, was used to evaluate the effect of fungal species and incubation time on concentrations of calcium, magnesium, potassium, iron, and aluminum. If a significant effect was found due to time, then a planned polynomial contrast was performed to determine if the changes with time were linear. A metric adjustment was made to compensate for the unequal spacing of sampling times.

If the interaction between species and months of incubation was significant, and the planned polynomial contrast revealed a significant linear trend in cation concentration, linear regression analysis including time 0 values was performed. Regession analyses were conducted with Statistica/Mac, Stat Soft Inc.

One-way ANOVA were used to evaluate the effect of species on the concentration of each cation after approximately 8 months of incubation. If the effect due to species was significant, a protected least significant difference test (LSD) was used to compare cation concentrations between treatments. All ANOVA and LSDs were conducted on $\log_{10}$ values in order to satisfy the need for constant variance. ANOVA and LSDs were performed with SYSTAT for the Macintosh (version 5.2, SYSTAT, Inc., Evanston, Ill.).

Results

After approximately 8 months of incubation with decay fungi, the greatest weight loss occurred in wood decayed by the brown rot fungus *Postia placenta* and the white rot fungus *T. versicolor.* The percentage of wood dry weight lost was as follows: *Postia placenta*, 69%; *T. versicolor*, 61%; *P. chrysosporium*, 47%; *I. lacteus*, 34%, *A. chailletii*, 27%; *R. bicolor*, 7%; *S. galactinum*, 4%; *F. pinicola*, 2%; *Armillaria* sp., 2%.

Calcium concentrations in decaying wood were significantly related to fungal species and to months of incubation (Tables 1 and 2; Fig. 1). Cation concentrations shown in Fig. 1 are corrected for weight loss but are not expressed as $\log_{10}$ values. Within the time limits of this study, calcium concentrations in inoculated wood tended to increase with time. A significant interaction between species and months occurred, indicating that not all of the fungi had the same effect on calcium concentrations over time. The nature of this interaction is revealed by linear regression analyses of wood calcium concentration as a function of time for the controls and for wood incubated with each of the fungi (Table 3; Fig. 2). Figure 2 illustrates the range in slopes obtained when wood calcium content as a function of incubation time is depicted.

After 8 months of incubation, calcium concentrations in wood inoculated with *S. galactinum*, *Armillaria* sp., *T. versicolor*, *I. lacteus*, *P. chrysosporium*, and *Postia placenta* were greater than those in incubated control wood. After 8 months, wood incubated with *S. galactinum* had significantly higher

Table 1. ANOVA tables for cation concentrations (μmol/g original wood dry weight) in wood incubated for approximately 1.5, 4, and 8 months in modified ASTM soil block jars with various decay fungi.

Cation	Source of variation	df	Mean squares	*F* ratio	*p* value
Ca	Species	9	0.071	6.56	0.000
	Months	2	0.289	26.60	0.000
	Linear	1	0.571	52.48	0.000
	Species × months	18	0.021	1.93	0.031
	Error	59	0.011		
Mg	Species	9	0.289	9.94	0.000
	Months	2	0.736	25.25	0.000
	Linear	1	1.442	49.51	0.000
	Species × months	18	0.039	1.34	0.197
	Error	59	0.029		
K	Species	9	0.844	18.63	0.000
	Months	2	0.051	1.12	0.333
	Linear	1	0.079	1.75	0.191
	Species × months	18	0.103	2.27	0.010
	Error	59	0.045		
Fe	Species	9	7.651	9.84	0.000
	Months	2	8.395	10.80	0.000
	Linear	1	16.660	21.43	0.000
	Species × months	18	0.920	1.18	0.304
	Error	59	0.777		
Al	Species	9	2.622	5.66	0.000
	Months	2	1.635	3.53	0.036
	Linear	1	3.060	6.60	0.013
	Species × months	18	0.196	0.42	0.977
	Error	59	0.463		

Note: ANOVA were conducted on $\log_{10}$ values.

concentrations of calcium than wood incubated with any of the other fungi except *Armillaria* sp.

Species of fungus and months of incubation had significant effects on wood magnesium concentrations (Tables 1 and 2; Fig. 1). No significant interaction occurred between species and months of incubation. Magnesium concentrations in wood decayed by most of the fungi examined tended to increase with time within the time limits of this study. After 8 months of incubation, the magnesium concentration in control wood was less than that in wood inoculated with *Postia placenta*, *S. galactinum*, *P. chrysosporium*, *T. versicolor*, *Armillaria* sp., *I. lacteus*, *R. bicolor*, and *F. pinicola*.

Significant effects due to fungal species occurred in wood potassium concentrations (Tables 1 and 2; Fig. 1). There was no overall significant effect due to months of incubation, but the interaction between months and species was significant, indicating that not all fungi had the same effect on potassium concentrations in wood over time. When potassium concentrations in wood incubated for 1.5, 4, and 8 months with various fungi were examined, a variety of trends occurred that would account for the significant interaction (Fig. 1). For example, potassium concentration increased with incubation time in wood inoculated with *Armillaria* sp., but decreased in wood decayed by *T. versicolor* and stayed about the same in wood inoculated with some of the other fungi (Fig. 1).

Table 2. ANOVA tables for cation concentrations (μmol/g original wood dry weight) in wood incubated for approximately 8 months in modified ASTM soil block jars with various decay fungi.

Cation	Source of variation	df	Mean squares	*F* ratio	*p* value
Ca	Species	9	0.061	5.319	0.001
	Error	19	0.011		
Mg	Species	9	0.103	7.935	0.000
	Error	19	0.013		
K	Species	9	0.469	14.036	0.000
	Error	19	0.033		
Fe	Species	9	4.154	10.355	0.000
	Error	19	0.401		
Al	Species	9	1.270	5.731	0.001
	Error	19	0.222		

Note: ANOVA were conducted on $\log_{10}$ values.

The concentration of iron in wood varied with respect to fungal species and incubation time (Tables 1 and 2; Fig. 1). Iron concentrations in wood tended to increase with time. There was no significant interaction between species and months of incubation. After 8 months of incubation, iron concentrations in wood inoculated with *Postia placenta*, *I. lacteus*, *P. chrysosporium*, *T. versicolor*, *R. bicolor*, *S. galactinum*, and *Armillaria* sp. were greater than the that in control wood. After 8 months of incubation, iron concentration in wood decayed by *Postia placenta* was significantly greater than that in all other wood except wood inoculated with *I. lacteus*, *P. chrysosporium*, and *T. versicolor*.

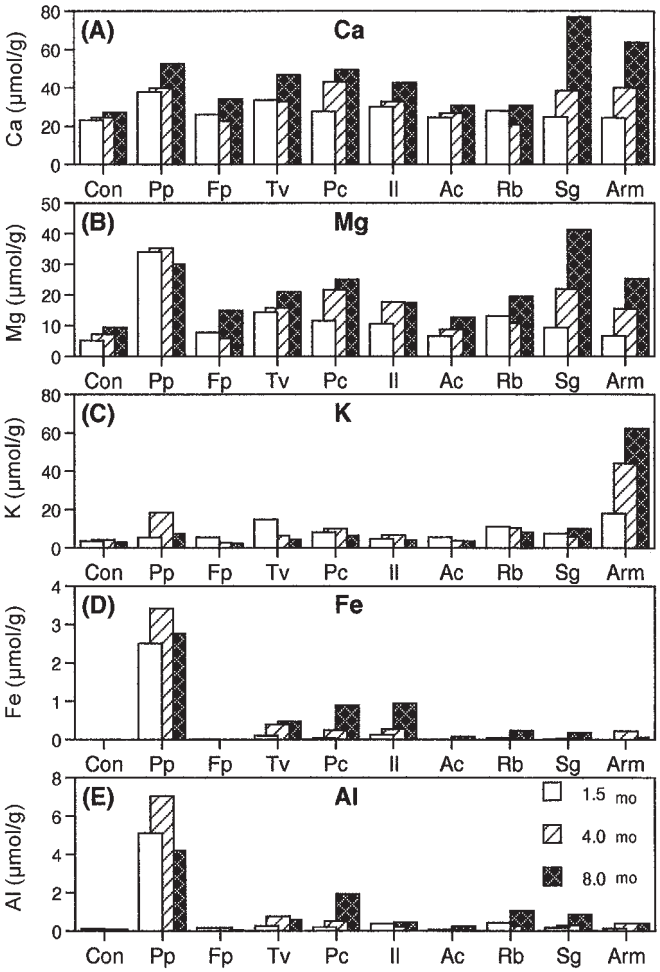
There were significant effects of fungal species and months of incubation on aluminum concentrations (Tables 1 and 2; Fig. 1). No significant interaction beween species and months of incubation occurred. aluminum concentrations tended to increase with time. After 8 months of incubation, aluminum concentrations in wood inoculated with *Postia placenta*, *P. chrysosporium*, *R. bicolor*, *S. galactinum*, *T. versicolor*, *I. lacteus*, and *Armillaria* sp. were greater than those in control wood. After 8 months of incubation, aluminum concentrations in wood inoculated with *Postia placenta* were significantly greater than those in all other wood except wood inoculated with *P. chrysosporium*, *R. bicolor*, and *S. galactinum*.

Iron and aluminum concentrations in wood decayed by *Postia placenta* were also examined in relation to weight loss (data not shown). Wood sampled early in the decay process and showing comparatively minor weight loss (<15%) had low concentrations of iron (<0.02 μmol/g) and aluminum (<0.3 μmol/g). Wood sampled later in the decay process and showing a substantial loss in dry weight (>60%) had high concentrations of iron (>2.0 μmol/g) and aluminum (>3.0 μmol/g).

Discussion

Cation concentrations changed during the wood decay process. These changes were sometimes progressive and related to the species of decay fungus. Concentrations of calcium and magnesium increased with time in wood decayed by most of the basidiomycetes studied. Increases in cation concentration sometimes occurred before large weight loss was observed.

Fig. 1. Cation concentrations (µmol/g original wood dry weight) in wood incubated for approximately 1.5, 4, and 8 months in modified ASTM soil block jars with decay fungi. Con, control; Pp, *Postia placenta*; Fp, *Fomitopsis pinicola*; Tv, *Trametes versicolor*; Pc, *Phanerochaete chrysosporium*; Il, *Irpex lacteus*; Ac, *Amylostereum chailletii*; Rb, *Resinicium bicolor*; Sg, *Scytinostroma galactinum*; Arm, *Armillaria* sp. Values are means of three replicates. Cation concentrations (µmol/g wood dry weight) in uninoculated, unincubated wood were as follows: Ca, 21.2; Mg, 2.87; K, 1.91; Fe, 0.191; Al, 0.168. See Table 1 for statistical analyses (ANOVA).



The isolate of *F. pinicola* (KTS 028) used in this study was not an aggressive one compared with other isolates in this laboratory (J.H. Connolly, personal communication). This suggests that with some fungi, strain differences as well as species differences may be important. Weight loss in wood blocks inoculated with *R. bicolor* and *S. galactinum* was also low, but is less in red spruce heartwood than in red spruce sapwood (unpublished data). Fungal biomass in wood leads to underestimation of mass loss in wood decayed by fungi (Jones and Worral 1995). Visual examination of red spruce blocks decayed by *Armillaria* sp. revealed that fungal tissue occupied much of the space previously occupied by wood tissue. In *Armillaria* sp., percent weight loss values were not a good indication of fungal activity.

For most fungi, changes in potassium concentrations were not progressive, perhaps reflecting potassium's high solubility in water. Studies of cation binding in wood indicate that calcium plays a dominant role in displacing other cations from wood exchange sites (Momoshima and Bondietti 1990). In competition experiments between calcium and potassium in red spruce wood, calcium accumulated preferentially to potassium at various pH levels and calcium concentrations. In field studies, where rainfall is a factor, potassium was lost from decayed balsam fir wood at a rate faster than that of mass (Foster and Lang 1982). In our study, potassium concentrations did increase with time in wood decayed by *Armillaria* sp.

Additional observations in this study indicate that the species of the fungus decaying wood may affect changes in wood cation concentrations. No trends were characteristic of all brown rots or all white rots, but some changes were characteristic of decay by a given fungus. Levels of iron and aluminum, for example, were high in wood decayed by *Postia placenta*. This is consistent with preliminary observations (Jellison et al. 1992). Many brown rot fungi produce organic

Fig. 2. Examples of regressions of calcium concentrations (µmol/g initial wood dry weight) in decaying red spruce wood to days of incubation in modified ASTM soil block jars. Examples were chosen to show a range of slopes. See Table 2 for R^2 and p values. Con, control; Tv, *Trametes versicolor*; Rb, *Resinicium bicolor*; Sg, *Scytinostroma galactinum*.

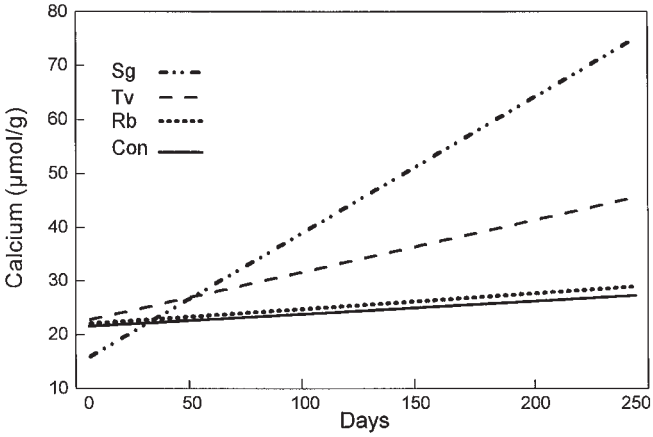


Table 3. R^2 values and slopes from linear regression analyses of calcium concentrations (µmol/g original wood dry weight) in wood decayed by various fungi as a function of time.

Fungus	R^2	Slope
Control	0.12	0.023
Postia placenta	0.61*	0.135
Fomitopsis pinicola	0.60*	0.047
Trametes versicolor	0.85*	0.091
Phanerochaete chrysosporium	0.60*	0.119
Irpex lacteus	0.60*	0.083
Amylostereum chailletii	0.89*	0.037
Resinicium bicolor	0.23	0.027
Scytinostroma galactinum	0.93*	0.237
Armillaria sp.	0.85*	0.184

*$p < 0.01$.

acids (Takao 1965) that, by lowering the pH or through chelation activity, may increase iron solubility.

Although concentrations of calcium in wood decayed by most basidiomycetes in this study increased at rates greater than in incubated control wood, this was not the case for *R. bicolor*. Connolly and Jellison (1995) found that *R. bicolor* translocated calcium several centimetres away from blocks of red spruce and soil to sites on mycelial cords growing up the inside of glass jars in modified ASTM soil block assays. While the activity of other fungi in this study increased calcium concentrations within wood blocks, *R. bicolor* may have transported calcium to parts of its mycelium outside the wood block. In order to determine whether the patterns of ion accumulation seen in this study are species specific or characteristic of given isolates, numerous isolates of various species would need to be compared.

Armillaria sp., *R. bicolor*, and *S. galactinum* have been found on roots and (or) butts of balsam fir and red spruce in New Hampshire's White Mountains, but the prevalence of a given species varied with elevation (Rizzo and Harrington 1988). These same species can inhabit logs and slash on the forest floor (Ginns and Lefebvre 1993). In our laboratory study, wood decayed by these fungi showed different trends of change in cation concentrations.

Field studies of decaying wood address a complex and dynamic situation in which many factors may affect the fate of wood over a long time period. These factors include variability within and between tree species, infection status of wood, arthropod activity, weather, site characteristics, environmental dynamics, and microorganism activity. If the differences in wood cation concentrations found in the laboratory reflect differences in the physiology of fungi, the species of decay fungi involved may contribute to some of the variability found in the field. Our results confirm the importance of considering the species of the fungus when examining cation changes in decaying wood and describing nutrient cycling in the forest.

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