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From forest to fen: Microarthropod abundance and litter decomposition in a southern Appalachian floodplain/fen complex ☆

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Summary

Our study compared decomposition and litter microarthropod abundance among five plant communities in a mountain floodplain/fen complex located in the southern Appalachian Mountains, USA. We found that the least disturbed plant communities, red maple in particular, have the quickest decomposition, the greatest number of litter microarthropods, the highest soil organic carbon, and the lowest soil pH. Positive correlations were shown between soil organic carbon and total microarthropods; negative correlations were found between soil pH and total microarthropods. No correlations were found between soil moisture and decomposition or total microarthropod numbers. We conclude that soil characteristics related to disturbance, rather than to the presence of a closed canopy, are the main influences on decomposition and litter microarthropods.

Introduction

Decomposition is a primary ecosystem function in the recycling of nutrients (Swift et al., 1979; Seastedt, 1984), and is influenced by factors such as soil nutrients, temperature, composition of plant material, and composition and activity of soil fauna (Coleman, 1985). Although many studies have been carried out on decomposition in upland hardwood

communities in the southern Appalachians (Reynolds et al., 2003), and some research has been carried out on decomposition in cypress-gum wetlands (Battle and Golladay, 2001) and playa wetlands in the southern Great Plains (Anderson and Smith, 2002), little has been published about decomposition in wetlands of the southern Appalachians except for recent work by Neher et al. (2003).

The vital role of microarthropods in decomposition and nutrient cycling has been long established (Swift et al., 1979; Coleman, 1985). Soil and litter microarthropods feed upon soil microbes, the primary decomposers, thus affecting microbe community structure. Microarthropods also may transport microbial propagules and thus help to disperse these decomposers and catalyze the rate of decay (Petersen and Luxton, 1982; Wardle, 2002; Coleman et al., 2004). In addition, microarthropods fragment litter and excrete nutrient-rich frass (Petersen and Luxton, 1982; Coleman et al., 2004; Cole et al., 2006). Due to their importance in decomposition and distribution of soil organic matter (SOM), soil and litter microarthropods have been suggested as useful bioindicators of the effects of land management on nutrient dynamics (Bird et al., 2004).

Research specifically about microarthropods and decomposition in wetland systems appears to be minimal. Braccia and Batzer (2001) have examined invertebrates associated with woody debris in a southeastern-forested floodplain, but their study does not include decomposition or invertebrates associated with soil. They hypothesize that perennial inhabitants of wood in their system, including mites, probably make significant contributions to wood decomposition. Indeed, these authors emphasize that terrestrial wetland fauna have been overlooked, and they found that non-aquatic (including Acari and Collembola) rather than aquatic arthropods, were the most significant component of overall community structure. Batzer and Wissinger (1996) in a review article about insects in wetlands, point out that although forested floodplains are a common wetland type in southern latitudes, their invertebrate communities have been studied less than other wetlands. Tronstad et al. (2005) studied the response of floodplain invertebrates to receding water levels in a medium-sized river in Alabama and found that Collembola and Acari were among the most abundant invertebrates in floodplain soils. In particular, they found that Acari, including Oribatida, had significantly greater densities in inundated than exposed (non-inundated) soil. These findings indicate that there could very well be significant differences in numbers of soil microarthropods between wetland and upland soils, thus indicating possible differences in decomposition rates between these two systems. However, Tronstad et al. (2005) did not examine decomposition. Neher et al. (2003) compared decomposition of museum board (primarily cellulose) and balsa wood between disturbed and undisturbed areas and among agriculture, forest and wetland ecosystems in North Carolina. They found that decomposition of museum board in wetland soils was greater initially in disturbed than undisturbed sites, but later the regression lines for percentage of museum board substrates were parallel, suggesting similar magnitudes of decay. Balsa wood decomposition in all ecosystem types and both levels of disturbance was similar. Our objectives for this study were to compare decomposition and microarthropod community structure among five plant communities, representing differing levels of disturbance, at the Tulula Wetlands Mitigation Bank, a mountain floodplain/fen complex, and relate these data to soil pH, moisture, and organic carbon. We have found no other published studies that focus on decomposition and microarthropods in a wetland.

Materials and methods

Tulula Wetlands Mitigation Bank is an 83 ha research area located in the floodplain of Tulula Creek in Graham County, North Carolina, USA, with an elevation of 800 m. The floodplain consists of a mosaic of open and wooded wetlands which include a mature red maple forest, a weakly minerotrophic fen, and early successional communities (Moorhead and Rossell, 1998; Warren et al., 2004). The site has been classified as a Swamp Forest–Bog Complex and defined by the North Carolina Natural Heritage program as poorly drained bottomlands with soils of alluvial origin but not currently being flooded regularly (Schafale and Weakley, 1990). Soils in the floodplain at Tulula are classified as Cumulic Humaquept (Moorhead et al., 2000). In the late 1980s, developers cleared parts of the fen and floodplain and channelized Tulula Creek (Rossell et al., 1999; Moorhead et al., 2001). In 1994, the N.C. Department of Transportation purchased this wetland site for restoration as a wetland mitigation bank.

Six plots were established in each of five plant community types at Tulula. Plant communities used were red maple (RM) forest, open fen (OF) and closed fen (CF), early successional floodplain (FP), and a former golf fairway – a disturbed alluvial (DA) bottomland. The RM forest is approximately 50

years old and grows in a floodplain approximately 1000 m downstream from the two fen, FP, and DA sites. The CF was logged about 34 years ago (Warren et al., 2004). The OF and FP were cleared in the mid-1980s, and the floodplain bushhogged in 1994, as part of the development. Thus, the five study sites not only present a variety of vegetation types, but represent a gradient in terms of age since disturbance. The fen sites receive a steady input of ground-water flow; the floodplain sites are drier (Rossell et al., 1999; Moorhead et al., 2001). Red maple is the dominant canopy species in RM and CF, and is a dominant sapling in the OF and FP. The FP and DA were cleared for a golf course in the mid-1980s and the DA bulldozed back into a "floodplain" type area in late 1999, as a series of golf ponds were partially backfilled. Drier areas of the DA, where we sampled, are dominated by blackberry (*Rubus argutus* Link), groundnut (*Apios americana* Medik.), goldenrod (*Solidago* spp.), common rush (*Juncus effusus* L.) and witch grass (*Dicanthelium* spp.) (I. Rossell, University of North Carolina at Asheville, pers. comm.).

Twelve fiber-glass screen litter bags, 15 × 15 cm with mesh size 1.5 mm, containing known weights of air-dried red maple (*Acer rubrum*) leaves were placed in each plot in a 4 × 3 grid. The fresh-fallen leaves were collected in October, 2002, and the litter bags placed in the field in January 2003. Each litterbag was anchored with a survey flag and lightly covered with surrounding litter. One litter-bag was removed from each plot every other month, beginning in March, 2003 and continuing through May of 2004. Individual litterbags were placed in zip-loc bags, all bags were then transported in a cooler to the lab, and the litter content weighed (dry weight) after microarthropod extraction. Percent mass remaining of litter was calculated.

Soil moisture measurements were made in the field with a Campbell Scientific Hydrosense (Campbell Scientific Inc. Logan, Utah) beginning in May 2004 within each litterbag plot. Since August 2004, triplicate measurements were taken in each plot and the values averaged for statistical analyses. Measurements from 20 May 2004 through 16 April 2005, the same period included in soil pH and organic carbon measurements, were used for Tukey's studentized range (HSD) test and for Spearman's correlation test.

Microarthropods were extracted from litterbags using a modified Tullgren funnel apparatus (Mallow and Crossley, 1984). Litterbags were left on the funnels for 3–4 days; the extracted microarthropods were preserved in 70% ethanole. Microarthropods were sorted under a stereomicroscope into the following categories: oribatid, prostigmatid, and mesostigmatid mites, Collembola, and others. Micro-arthropod abundances were determined as the mean number of animals/g dry litter.

Soil analyses were conducted on individual cores (5 cm deep, 4 cm diameter volume of 62.83 cm) taken through the litter layer from each plot in May 2004 and April 2005. Percent organic carbon content was determined by the Walkley–Black method (Nelson and Sommers, 1982); pH was measured on a 1:1 slurry of soil:distilled water using a Fisher Accumet pH meter and a standard electrode. Average values of pH and organic carbon were calculated for each plant community, combining the 2 years.

HSD test, (SAS version 9.1, 2005) was used for statistical analysis of percent litter mass remaining and soil characteristics. Since the abundance values of soil microarthropods were not normally distributed, the data were analyzed using a generalized linear model (PROC Genmod SAS version 9.1., 2005; Littell et al., 2002). However, since the numbers of collembola were so low, the date × site term was not used due to overfitting of the data. The model without date × site term was suitable for over-dispersion of these collembolan data (Allison, 2001). Standard errors and Tukey lines in microarthropod graphs are provided for comparison purposes, but are not statistically rigorous because the data break the assumptions of normality. PROC CORR, with Spearman correlation coefficients, (SAS version 9.1, 2005) was used for correlation analysis among percent litter remaining, total number of microarthropods, soil pH, soil moisture, and soil organic carbon.

Results

After 17 months in the field, the percent mass of litter remaining averaged 50% for RM to 54.8% for FP (Fig. 1). The percent mass remaining in RM, CF, and OF was not significantly different among the three sites, nor was there a significant difference in percent mass remaining among FP, DA, OF, and CF. However, decomposition was significantly greater in RM than in DA and FP. After 2 years, the close of the experiment, the difference in decomposition between RM and all other sites was more apparent, as decomposition in RM was significantly greater than the other sites, although there was no significant difference in decomposition among the other four sites (Fig. 2).

Microarthropod numbers varied significantly with date (Table 1). We also found significant differences in litter microarthropod numbers by site for total
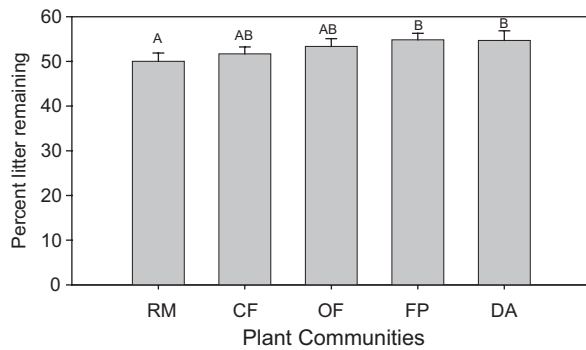
Figure 1. Percent litter remaining in litterbags after 17 months in the field. Plant communities are RM = red maple, CF = closed fen, OF = open fen, FP = flood plain, and DA = disturbed alluvial bottomland forest. Each bar is the average of 37–48 litterbags. Bars with the same letter are not significantly different; error bars are ±1 SE.
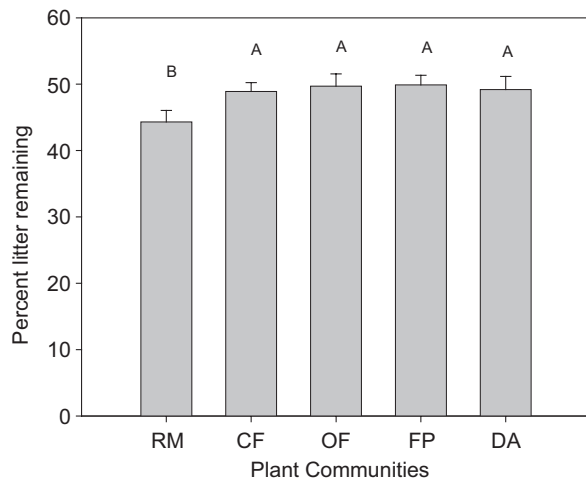

Figure 2. Percent litter remaining in litterbags after 24 months in the field. Plant communities are RM = red maple, CF = closed fen, OF = open fen, FP = flood plain, and DA = disturbed alluvial bottomland forest. Each bar is the average of 52–72 litterbags. Bars with the same letter are not significantly different; error bars are ±1 SE.

microarthropods and all individual taxa except for Prostigmatida, which were not abundant enough for statistical analysis (Table 1, Fig. 3). The average number of Prostigmatida per gram dry litter ranged from 3.0 at CF to 1.2 in OF and FP.

In all sites, oribatid mites were by far the most common microarthropod (Fig. 3) and they were most abundant in the RM community. Abundances of oribatids (and total microarthropods) appear to be significantly lower in FP and DA.

Average organic carbon varied from 30.26% to 4.17%, and was highest in soils from RM (30.26%), with organic carbon decreasing in this order: CF

(25.44%) > OF (20.24%) > FP (14.29%) > DA (4.17%) (Fig. 4). Organic carbon in the FP and DA was significantly lower than in RM and CF.

Average soil pH values ranged from 3.44 to 4.23, with the DA having the highest pH (4.23), followed by FP (4.02), OF (3.78), CF (3.70), and RM (3.44) (Fig. 5). pH was significantly lower for RM compared to all other sites.

Soil moisture was significantly lower for RM and DA (52.6% and 48.1%, respectively) than the other sites, which increased in the order FP (60.7%), CF (84.9%), and OF (95.4%). These last three sites were significantly different from RM and DA (which were not significantly different) and significantly different among themselves. Spearman's Correlation procedure found no significant correlation between soil moisture and percent litter remaining, or between soil moisture and total microarthropods.

A comparison of litter microarthropods was made in March 2003 before canopy closure to determine if presence/absence of the canopy affected numbers of microarthropods. We found that even before canopy closure there were fewer microarthropods in the DA and FP sites (Fig. 6).

Discussion

After 17 months in the field, percent litter remaining in RM was less than all other sites and after 24 months this difference was significant. The RM site is the least disturbed site at Tulula, and also has the highest percent soil organic carbon and the lowest soil pH. Although Spearman correlation analyses did not indicate any strong relation between percent litter remaining and these two soil characteristics (0.009 and 0.001, respectively), we suspect an indirect relation, at least, because litter total microarthropods had a strong negative correlation with soil pH and a strong positive correlation with soil percent organic carbon (−0.634 and 0.603, respectively). It is widely accepted that soil microarthropods play an important, though often indirect, role in decomposition (Swift et al., 1979; Coleman, 1985; Wardle, 2002). Neher et al. (2003) did find a negative correlation between soil pH and percent of substrate remaining (museum board and balsa wood in their study) but no correlation between percent substrate remaining and percent SOM. In comparing disturbed and undisturbed wetland sites for decomposition, Neher et al. (2003) found similar magnitudes of decay for museum board after the initial incubation period. This contrasts with our data which indicate greater rates of decay in our least disturbed wetland area compared to more disturbed sites.

Table 1. Microarthropod responses to date and site: data analyzed were average numbers of microarthropods per gram of red maple litter from litterbags in the field for 17 months (January 2003–May 2004)

Organism	Log-likelihood	Terms	χ^2	df	P
Total	1213.55	Date	43.30	7	<0.0001
		Site	52.38	4	<0.0001
		Date × Site	38.28	28	0.0932
Oribatida	946.16	Date	36.62	7	<0.0001
		Site	43.42	4	<0.0001
		Date × Site	39.85	28	0.0682
Mesostigmatida	357.81	Date	61.37	7	<0.0001
		Site	39.95	4	<0.0001
		Date × Site	44.93	28	0.0224
Collembola	119.02	Date	51.30	7	<0.0001
		Site[a]	47.26	4	<0.0001

[a]No values are presented for Collembola date × site due to over-fitting of the data with that term in the model.
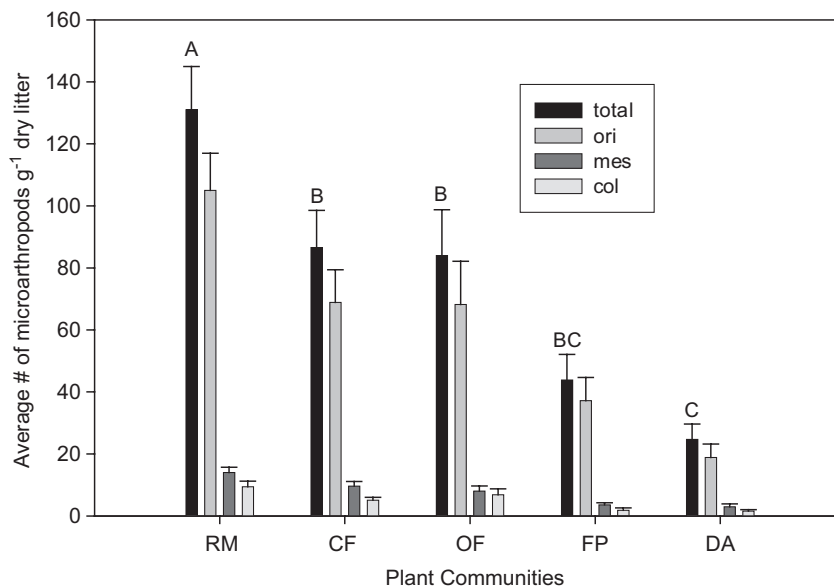
Figure 3. Average number of microarthropods/g dry red maple litter for 17 months. Plant communities are RM = red maple, CF = closed fen, OF = open fen, FP = flood plain, and DA = disturbed alluvial bottomland forest. Each bar is the average of 38–46 litterbags; error bars are ±1 SE. Means with the same letter are not significantly different; but see text.

However, the pH of our RM, the least disturbed site, was much lower than the site investigated by Neher et al. (3.44 and 4.7, respectively), and organic carbon in RM was much higher than at the site of Neher et al. (30.26% vs. 8.4%). Using one standard conversion factor for OC to SOM, 1.74 (Nelson and Sommers, 1982), the contrast between RM (53% SOM) and Neher et al. (8.4% SOM) is more pronounced. It must be noted, however, that soil samples for Neher et al. went to a depth of 20 cm and probably did not include the surface litter layer.

As expected, litter microarthropod numbers varied significantly with date. Similar seasonal variations in microarthropod numbers have been reported for upland hardwood forests in the southern Appalachians (Reynolds et al., 2003; Brennan, pers. comm.). Date × site interactions were not significant for total microarthropods nor the most abundant taxon, Oribatida. Although there were significant date × site interactions for the Mesostigmatida, thus confounding interpretation of significance by site, the low numbers of Mesostigmatida, similar to even lower numbers for Collem-
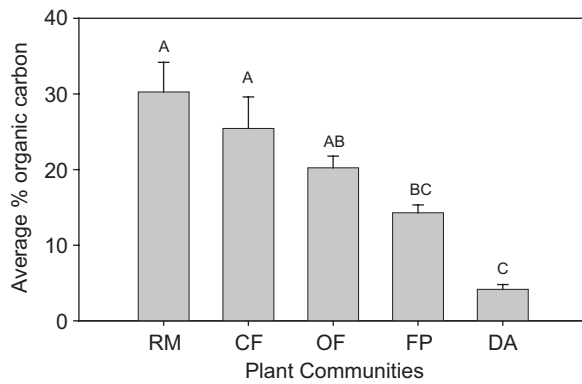
Figure 4. Average percent organic carbon for soil from five plant communities: RM = red maple, CF = closed fen, OF = open fen, FP = flood plain, DA = disturbed alluvial bottomland forest. Each bar is the average of 11–12 soil core samples. Bars with the same letter are not significantly different; error bars are ±1 SE.
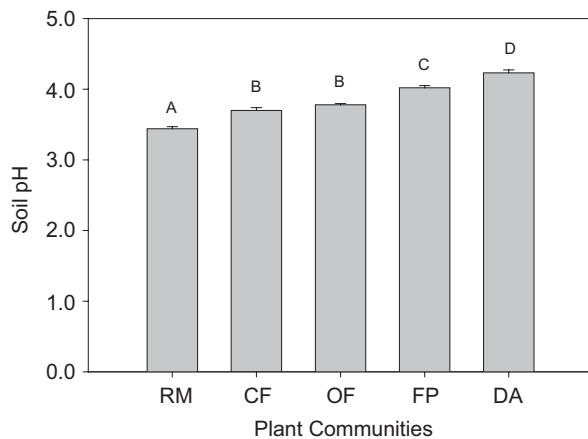

Figure 5. Average pH for soil from five plant communities: RM = red maple, CF = closed fen, OF = open fen, FP = flood plain, and DA = disturbed alluvial bottomland forest. Each bar is the average of 11–12 soil core samples. Bars with the same letter are not significantly different; error bars are ±1 SE.

Figure 6. Average number of total microarthropods/g dry red maple litter for March, 2003. Plant communities are RM = red maple, CF = closed fen, OF = open fen, FP = flood plain, and DA = disturbed alluvial bottomland forest. Each bar is the average of six litterbags; error bars are ±1 SE.

relatively wetter soils at Tulula have a dampening effect on collembolan populations. Braccia and Batzer (2001) found collembolan numbers to be roughly one-quarter those of all acarina in a study of arthropods associated with woody debris in a forested wetland in the southeastern US; collembola numbers in our samples were approximately one-tenth those of acarina. Although soil pH was relatively low for all sites, many species of collembolans are reported to be acid-tolerant (Cassagne et al., 2003). Thus, although differences in soil pH may have influenced the distribution of collembolans among our sites, we do not believe that their relatively low numbers compared to other areas are due to low soil pH.

Since no correlation was found between soil moisture and percent litter remaining or between soil moisture and total microarthropods, and the sites with highest (RM) and lowest (DA) decomposition had similar soil moisture, we conclude that soil moisture was adequate in all sites to support decomposition and microarthropod communities and that it did not contribute to differences we found among the sites.

In comparing different vegetation communities, we found significantly higher numbers of total microarthropods, comprised mostly of Oribatida, in the RM site compared to all other sites. In addition, we found a strong negative correlation with soil pH (−0.63) and a strong positive correlation with soil organic carbon (0.60) for total microarthropods. Soil organic carbon was highest in RM and soil pH was significantly lower in RM. Neher et al. (2003) also found a lower pH in

bola and Prostigmatida, call into question the significance of these taxa for the present study, especially when compared to the abundance of the Oribatida.

The proportion of Collembola to Oribatida is much lower in Tulula samples than what has been reported for upland hardwood forests in the southern Appalachians (Reynolds et al., 2003; Knoepp et al., 2005), although numbers for total microarthropods are far greater at Tulula than in upland forests. Similar relations between collembolan and oribatid numbers are found in soil cores from the same vegetation sites at Tulula (Hamel and Reynolds, unpublished data). We assume that the
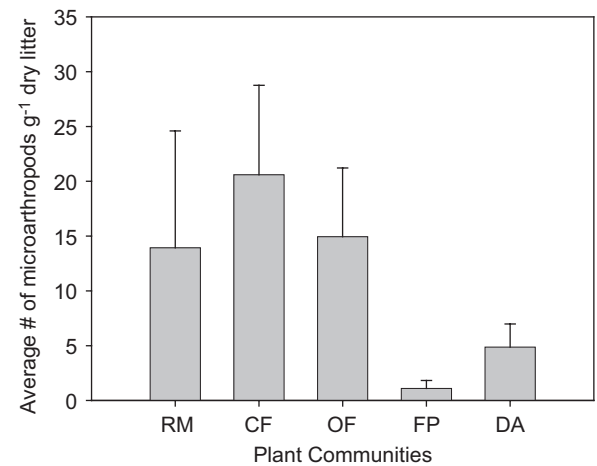
wetland soils from an undisturbed site compared to a disturbed area.

The significantly lower OC for DA is probably the result of mixing soil horizons after bulldozing the area for a fairway and then back again to recreate floodplain. In addition, the DA site has had less addition of carbon from leaf litter compared to the RM. Sites with the least disturbance, and thus the more mature plant communities – the fens and red maple forest – have the highest OC in the soil. In addition, the OC data are probably strongly influenced by the amount of litter in the cores taken for soil analyses. Since SOM is known to be strongly influenced by soil fauna (Coleman et al., 2004), these results appear to be correlated with the distribution of microarthropod abundances, especially for RM and OF. Spearman's correlation coefficients substantiate this positive correlation, with a value of 0.60 for the relation between litter total microarthropods and soil organic carbon.

What characteristic of the RM site could explain the differences we measured in percent litter remaining, total microarthropod numbers, highest organic carbon and lowest pH? We conclude that these measurements are all indicators of an undisturbed soil, and that the high rate of decomposition and high total microarthropod numbers are functions of an older, least disturbed, ecosystem.

These findings could be related to the presence of a canopy in RM and CF, protecting litter-dwelling arthropods from extremes in temperature and from desiccation when exposed to solar radiation. However, the low numbers of total microarthropods in DA and FP, compared to sites with more canopy (RM, CF, and OF), even before leaves are present in March 2003 indicates that other factors are involved. We posit that soil disturbance, once again, plays a major role in a critical ecosystem factor – the abundance of litter microarthropods.

Acknowledgments

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