Title: Litter decomposition in afrotropical streams: effects of land use, home-field advantages, and terrestrial herbivory

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Abstract

Land use can strongly affect litter decomposition, a key ecosystem function in low-order streams. Recent evidence suggests that additional drivers of decomposition rates could include 'home-field advantages', when litter decomposes faster at nearby than distant sites, and terrestrial herbivory, whereby inducible plant defenses triggered by herbivore damage can slow down leaf decomposition in streams. To assess the relative importance of these three drivers, we conducted a decomposition experiment in an afrotropical stream system, manipulating land use (farm vs. forest sites), home-field advantage (home vs. away from site of leaf collection), and terrestrial herbivory (using leaves varying in their extent of herbivore damage). We measured decomposition in both fine-mesh and coarse-mesh litter bags to compare drivers of microbial vs. invertebrate-mediated decomposition. Microbial decomposition in fine-mesh bags was unaffected by experimental treatments. In coarse-mesh bags, land use was the only significant (and a strong) driver of decomposition rate, most likely because invertebrate shredders are absent from farm sites. We conclude that home-field advantages and terrestrial herbivory are unimportant drivers of litter decomposition rates in afrotropical streams, at least relative to a major anthropogenic disturbance such as agricultural land use.

Intro

Leaf litter breakdown a key ecosystem function contributing x % of carbon cycling in streams. Natural factors driving rates of litter breakdown include x and x. Anthropogenic disturbances affecting one or several of these physico-chemical and biological parameters thus also influence decomposition rates; for example, agricultural land use often slows down litter breakdown considerably (). This response of litter breakdown to disturbance has led some authors to suggest that litter decomposition should be employed as an indicator of stream integrity ().

Recent experimental evidence has revealed hitherto under-appreciated influences on decomposition rates, namely the spatial variation in terrestrial herbivory and in local adaptation of stream communities to role of intraspecific trait variation in trees. These effects have yet to be tested in a variety of stream systems. Moreover, no study has yet quantified the relative importance of these drivers relative to classic natural or anthropogenic drivers.

Here we X. reciprocal transplant experiment. Compare effect sizes.

Methods

Study system

Fieldwork was conducted in and around Kibale National Park, a 795 km2 mid-altitude (1100-1600 m) rainforest located in southwestern Uganda (0°13' – 0°41' N, 30°19' – 30°32' E). We selected one forested and one agricultural (farm) stream in each of the two main watersheds draining the park (the Mpanga River and Dura River watersheds, both of which are subwatersheds of the Nile Basin). The two forest streams have a fully forested and protected watershed. The two farm sites have a watershed dominated by intensive agriculture of food and cash crops, pastures for goats and cows, and sparse exotic trees (pine and eucalyptus trees) planted for timber. The four study sites are small first-order streams (<1.5 m mean wetted width; < 10 cm mean depth) with a similar geomorphology and hydrology, but they vary greatly in water chemistry and community composition based on land use; these differences have been described extensively elsewhere (**FW BIOL**). Briefly, the two farm sites have a much lower canopy cover than the two forest sites, as well as higher water temperature, higher turbidity, lower specific conductance, lower nitrogen and phosphorus concentrations, and a much lower richness and biomass of benthic invertebrates. Invertebrate shredders dominate the composition of forested sites but are largely absent from farm sites (**ecosphere**).

Our litter decomposition experiment focused on the tree species *Neoboutonia macrocalyx* Pax (Euphorbiaceae), the only species of tree occuring within < 10 m of all four streams. This tree, abundant within the park (**ref**), is kept for shade outside of the park in pastures that are otherwise entirely cleared. N. macrocalyx leaves are readily consumed by both macroinvertebrate shredders in streams and by terrestrial herbivores. Other than *N. macrocalyx*, vegetation in the riparian zone of agricultural streams was composed exclusively of grasses and emergent macrophytes, while the riparian zone of forested streams included a high diversity of trees, shrubs and ferns, with a canopy height generally > 20 m.

Reciprocal transplant experiment

We conducted our decomposition experiment in June-August 2011. Fresh leaves varying in their extent of herbivore damage were hand-picked from 3-5 trees around each stream.

To measure litter decomposition rates, we conducted a litterbag experiment (Graça, Bärlocher, & Gessner, 2005) using leaves from
We also chose this tree species because shredders were often associated with N. macrocalyx

leaves in benthic samples, and because feeding observations in laboratory aquaria confirmed that two common shredder taxa (Calamoceratidae and Lepidostomatidae) readily consumed N. macrocalyx leaves (V. Fugère, unpublished data). Leaves were collected near trees located close to each study reach by gently shaking branches and gathering fallen leaves, which were then brought to the laboratory and air-dried in a food dehydrator. A subset of air-dried leaves was weighed, then oven-dried to constant mass at 60 °C for 48 hrs and then weighed again to obtain an air-dried to oven-dried (i.e., DM) conversion equation (DM = -0.0118 + 0.86 × air-dried mass; R^2 = 0.9988). A subsample of these dried leaves was combusted at 550 °C to estimate mean ash content (10.2 %) and to convert DM to AFDM. Another subset of air-dried leaves was immersed in water for 72 hrs, and then oven-dried and weighed to estimate a correction factor for leaching (leaching-corrected AFDM = -0.008 + 0.8 × AFDM; R^2 = 0.9769). The remainder of air-dried leaves was weighed, rehydrated, and placed in either fine- or coarse-mesh litterbags (mesh sizes = 0.5 and 10 mm). Fine-mesh and coarse-mesh bags, respectively, prevent and allow macroinvertebrate shredders from accessing the leaves that they contain, and can thus be used to compare rates of microbial decomposition (fine-mesh bags) vs. microbial + shredder-mediated decomposition (coarse-mesh bags).

A total of 320 bags were constructed (160 fine-mesh bags and 160 coarse-mesh bags), allowing 40 bags of each type to be deployed in each of the four focal streams. Sites of leaf collection were standardized, such that an equal number of leaves from all four collection sites were used for each stream. Before deployment, the leaching-corrected AFDM of each litterbag was calculated (AFDMt0). Bags were then anchored to the stream bottom across each study reach using stones and twist ties. Ten bags of each type were subsequently retrieved from all streams at weekly intervals over four weeks. The litter content remaining in each bag was dried to constant mass, weighed, and combusted to calculate AFDM of litter retrieved from the stream (AFDMt1). Proportion of leaf litter remaining in each bag after stream exposure was then calculated as AFDMt1 / AFDMt0. We estimated decomposition rate for each site and mesh type combination by fitting a linear regression between ln-transformed proportion AFDM remaining and days of stream exposure; the slope of this regression gives the exponential leaf decay rate (-k / day). Land use effects on decomposition rates in fine and coarse mesh bags were tested by using separate LMMs and LRTs for each mesh type, using as replicates arcsine-transformed values of proportion AFDM remaining in litter bags collected on week 4, the last time point of the experiment.

Statistical analyses

beta regression

Results

dcsdcs

Discussion

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Acknowledgements

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Figure legends

Figure 1. Measurement of herbivore damage. The photograph shows a N. macrocalyx leaf fragment with some herbivore damage. The solid black line depicts leaf area assuming no damage while dashed lines encircle areas eaten by herbivores. Leaf damage was quantified as the total number of pixels inside polygons with dashed lines divided by the number of pixels within the polygon with a solid line.

Figure 2. Decomposition rates in fine-mesh (a) and coarse-mesh (b) bags as a function of land use (left panels), home-field advantage (middle panels), and terrestrial herbivory (right panels). Lines and shaded polygons indicate means +/- 95% confidence intervals of the mean. For terrestrial herbivory, data are shown for the final time point of the experiment.

Figure 3. Results of GLMMs quantifying the influence of five variables on the proportion of leaf litter decomposed by the end of the experiment. Separate models were fitted for fine-mesh bags (a) and coarse-mesh bags (b). Symbols and error bars indicate parameter estimates +/- 95 % confidence intervals; statistically-significant effects with confidence intervals that do not overlap zero are shown in solid colour, while non-significant effects are shown in transparent colour. Models were fitted using data from the final time point of the experiment.