



30 years of course particulate organic matter exports from tropical montane watersheds

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Abstract. Leaf litter is an important energy source for aquatic food webs and biogeochemical cycles. As leaf litter from the watershed enters streams it slowly starts to break down and transform into course particulate organic matter (CPOM). While this has been extensively explored in temperate regions, many questions remain in the tropics about patterns, timing, and magnitudes of CPOM inputs. Here we present 30 years of continuous CPOM data collected in two streams of the Bisley Experimental Watersheds (BEW) in the Luquillo Experimental Forest in northeastern Puerto Rico. We report CPOM as litterflow, which is all the plant and organic material that flows and accumulates from multiple sources (i.e., canopy, riparian zone, and upstream) and is collected at a fixed location in each stream. In this long-term dataset, temporal patterns (peaks and seasonality) can be observed in relation to various hurricanes and drought periods that occurred in Puerto Rico. The BEW litterflow data provides a view into the inherent connection between terrestrial and aquatic ecosystems to better understand how organic material can move through the landscape to be exported in streams and transported downriver to sustain the food webs of receiving bodies of water.

1 Introduction

Allochthonous organic matter (OM) in the form of leaf litter inputs are important energetic subsidies to sustain aquatic food webs and biogeochemical processes in streams and rivers (Vannote et al., 1980; Wallace et al., 2015). The strong connection between terrestrial and aquatic ecosystems modulates the timing and magnitude of leaf litter inputs to streams which can be influenced by forest type and species therein (Gonçalves & Callisto 2013). Leaf litter enters streams, starts to leach and breakdown due to biological and abiotic processes that form coarse particulate organic matter (CPOM) (Tank et al., 2010). As CPOM continues to travel downriver, it transforms and continues serving as an energy source along the aquatic continuum (Vannote et al., 1980; Crowl et al., 2001; Cross et al., 2008) fueling organisms and nutrient cycles.

Streams and rivers draining temperate forests usually receive a large pulse of leaf litter in the fall and have shorter growing seasons (Fischer and Likens, 1972; Tank et al., 2010). In tropical rainforests, leaf litter inputs can occur year-round (Tonin et al., 2017; Brandão et al., 2022) in part due to a near constant photoperiod (Zalamea and González 2008; Chave et al., 2010)



30 supporting greater forest productivity (Huston & Wolverton 2009). Leaf litter can arrive to streams via different pathways
such as wind, rain, and transported from surface flows (Wallace et al., 1997; Colón-Gaud et al., 2008; Heartsill-Scalley et al.,
2012; Gonçalves et al., 2014) where different regional and landscape characteristics can greatly influence the timing and
magnitude of leaf litter inputs to streams. For example, rain can be an important modulator for transport of leaf litter into
streams (Rodríguez-Cardona et al., 2026) and with tropical rainforests receiving between 2500-5000mm of rain annually
35 (McDowell et al., 2021) compared to an estimated 1500mm of annual precipitation in temperate regions (Campbell et al.,
2011), leaf litter dynamics can be quite different and seldomly evaluated long-term in the tropics.

Tropical rainforests, especially those in the Caribbean face landscape level disturbances in the form of hurricanes and
tropical storms that can alter forest structure and composition. For instance, the Luquillo Experimental Forest (LEF) in
40 Puerto Rico experienced severe defoliation after Hurricane Hugo in 1989 (Walker 1991) and was again severely defoliated
from Hurricanes Irma and María in 2017 (Liu et al., 2018). Over an 8-year study in headwater streams of the LEF, the
greatest peak in leaf litter inputs occurred after Hurricanes Irma and María (Rodríguez-Cardona et al., 2026). Besides
defoliation, hurricanes or tropical storms can break branches or remove enough leaves to cause changes in the structure of
the riparian zone that alters light, leaf litter inputs, and stream temperature. Surface runoff from intense rain can also
45 transport pulses of material that can change the streams morphology or flow paths (Walker 1991; Scatena and Larsen 1991;
Heartsill-Scalley et al., 2012; Gutiérrez-Fonseca et al., 2024). On the other hand, droughts can also greatly influence forests
and alter leaf litter inputs into streams. The effects of droughts will depend on forest type but can generally lead to increased
leaf litter inputs due to water stress in riparian zones that lead to leaf loss that accumulate on the forest floor (Larned et al.,
2000; Colón-Gaud et al., 2008; Heartsill-Scalley et al., 2012; Gutiérrez-Fonseca et al., 2020). The transition between
50 extended drought periods and the onset of rain events can lead to increased inputs of leaf litter to streams as rain transport
accrued materials both from upstream trapped in eddied and behind rocks/jams as well as all material on the ground
(Rodríguez-Cardona et al., 2026). Consecutive disturbances are difficult to predict and therefore their effects on leaf litter
dynamics are rarely studied as they can only be captured with long-term monitoring in place.

55 Here we present a continuous 30-year record of CPOM or litterflow data, which include all accumulated material from
multiple sources (i.e., canopy, riparian zone, and upstream) and is collected at a fixed location in the two headwater streams.
The long-term record includes several hurricanes and tropical storms as well as prolonged drought periods. To the best of our
knowledge, this may be the only long-term leaf litter collection data set in a tropical montane forest.



2 Methods

60 2.1 Study Site

The study took place in two streams within the Bisley Experimental Watersheds (BEW) in the Luquillo Experimental Forest also known as El Yunque National Forest in northeast Puerto Rico. The two sites, Bisley 1 (Q1) and Bisley 2 (Q2), are adjacent headwater streams of the Río Mameyes Watershed and are dominated by Tabonuco forest (*Dacryodes excelsa* Vahl.) and underlain by volcanoclastic lithology (Scatena 1989; McDowell et al., 2021). Both streams are similar in size, elevation, forest, geology and other characteristics (Scatena 1989; Heartsill-Scalley et al., 2012). Given their similarities, these streams can be used as replicates or averaged to increase number of observations.

2.2 Collection and processing of leaf litter

Litterflow was collected in a 12.7×12.7-mm metal mesh that was placed across the width of the channel in each of the study streams and captures both base and high flow conditions capturing all coarse material that travels downstream (Heartsill-Scalley et al., 2012). Material was collected from both mesh every 2 weeks, from 1987 up to 2018, dried at 65°C for at least 2 weeks, and sorted as leaves, small wood (<2.5cm diameter), large wood (>2.5cm diameter), and miscellaneous parts (flowers, fruits, and other plant parts or unidentifiable material). The different compartments were weighed using a calibrated top loading balance that provides at least three decimal places in the Chemistry Laboratory of the International Institute of Tropical Forestry. We report wood as the sum of small and large wood and total CPOM as the sum of leaves, wood, and miscellaneous parts for each sampling date per stream. Long-term records of stream discharge for both sites can be found in Denner et al., (2022) and long-term meteorological data can be found in Ramírez (2024).

2.3 Natural Disturbances

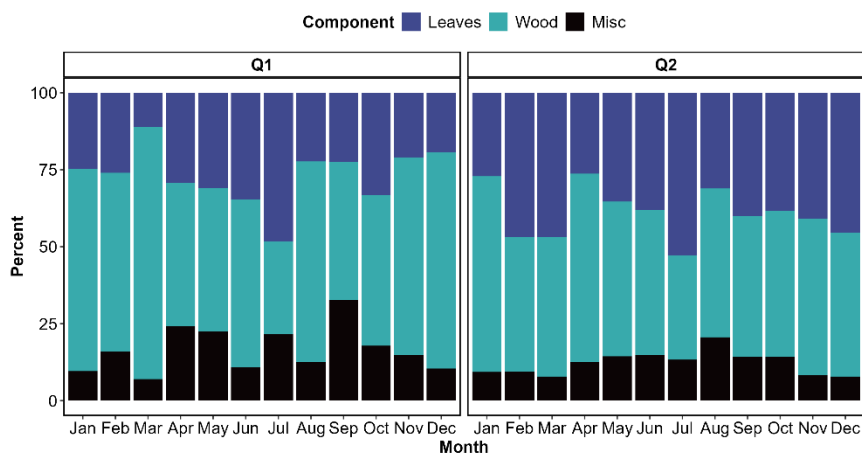
Throughout the study period, various largescale natural disturbances affected the region, from tropical storms and hurricanes to intense and prolonged droughts. Other disturbances that occur in this forest landscape are landslides, Saharan dust deposits, and frequent tree falls that collectively influence stream geomorphology, inputs and outputs of materials from the streams (Scatena and Lugo 1995; McDowell et al., 2021) although not presented here. We compiled date records for tropical storms and hurricanes (López Marrero & Rivera Castro 2018; López Marrero et al., 2019) that impacted the LEF and drought intensity classifications (<https://www.drought.gov/states/puerto-rico>) as examples of variables that may influence leaf litter inputs. For the purpose of data exploration, we categorized as “before and after the disturbances” for identified hurricanes, tropical storms, and droughts. We note that these classifications are subjective and researchers using this data set should consider their own criterion for setting classifications.



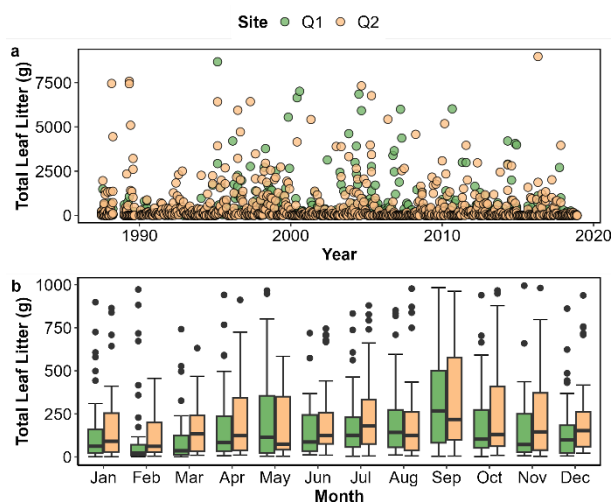
3 Results and Discussion

3.1 CPOM or Litterflow over time

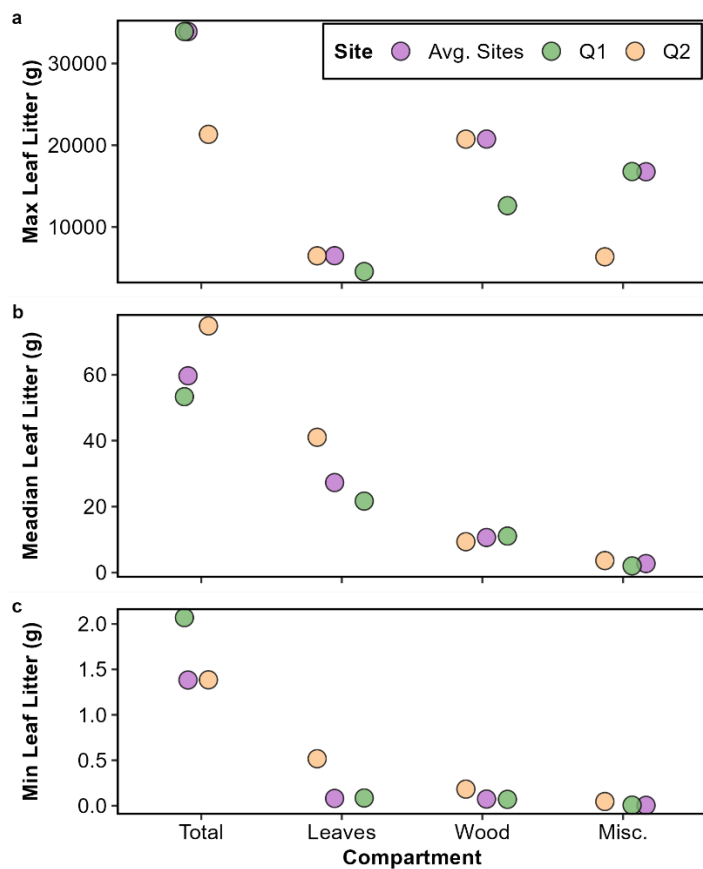
Of the litterflow, leaves, followed by wood compose most of the material regardless of site while miscellaneous materials makes up the smallest proportion (Fig. 1). Total CPOM shows a large variability over the 30-year time series (Fig. 2a) with values ranging between 4.9g to 33888.9g with a median value of 412g (± 156 g) across both sites while individual sites can reach higher and lower quantities of litterflow (Figure 3). Throughout the time series, there are several peaks in total leaf litter in both sites that could be attributed to hurricanes, tropical storms, or even droughts. For both Q1 and Q2, the months of May and September showed the greatest CPOM values (Fig. 2b) coinciding with rainy conditions and peak hurricane activity in September, consistent with the findings of Heartsill-Scalley et al. (2012). Generally, Q2 had greater CPOM than Q1 but they follow the same patterns.



100 **Figure 1.** Proportion of litterflow or coarse particulate organic matter (CPOM) components across both sites in the Bisley Experimental Watersheds, Puerto Rico, based on monthly means across the entire time series with leaves in blue, wood in green, and miscellaneous (Misc) in black.

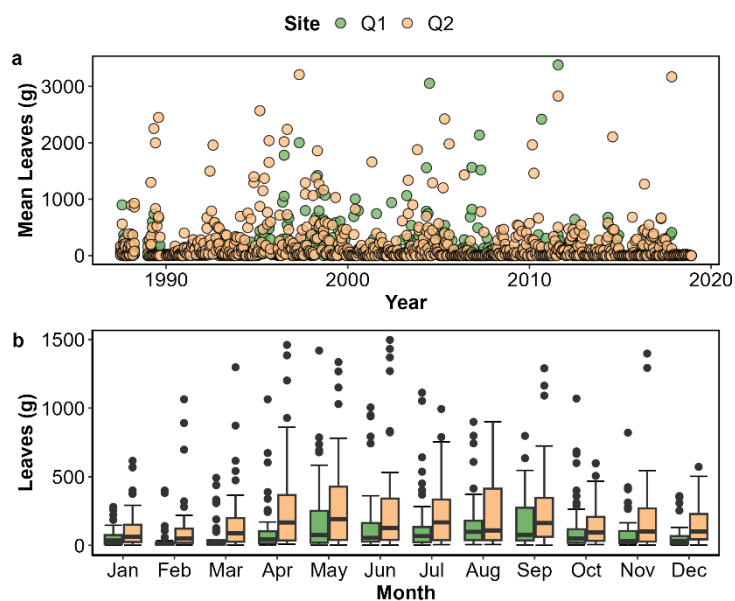


105 **Figure 2.** Course particulate organic matter (CPOM) from the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico presented as sum of all compartments for each site with Q1 in green and Q2 in orange presented as (a) monthly mean values over the 30-year time series and (b) monthly boxplots across all years where some high values were removed since they obscured the y-axis.



110 **Figure 3.** Maximum (max), median, and minimum (min) mass in grams (g) of total CPOM (sum of all compartments), leaves, wood, and miscellaneous materials as an average across both sites (purple), Bisley 1 (Q1, green), and Bisley 2 (Q2, orange) across all years (1987- 2018) in the Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico.

115 Leaves make up one of the largest portions of the litterflow material therefore, the peaks in leaves can also be attributed to the same factors (Figure 1) Leaves within CPOM also show a large range in mass over the time series (Fig. 4a) values ranging between 0.52g to 4505g with a median value of 118.5g (± 29.7 g) across both sites (Figure 3).. Similar to total CPOM (Figure 4b), May was one of the months with the highest leaf inputs followed by July and September (Fig. 4b).



120 **Figure 4.** Mass of leaves within the coarse particulate organic matter (CPOM) or litterflow for each site with Q1 in green
and Q2 in orange presented as (a) monthly mean values over the 31-year time series and (b) monthly boxplots across all
years where some high values were removed since they obscured the y-axis.

125 On occasion, wood can make up a large portion of the CPOM, for example in February and December while July typically
has the lowest wood content (Fig 1). Wood in CPOM had similar patterns across years (Fig 5a) with ranges between 0.07g
and 20735g with a median of 10.5g (± 23 g) (Figure 3). Monthly patterns were relatively consistent (Fig 5b) with no clear
peaks although wood tended to increase in May (Fig. 5b), consistent with Heartsill-Scalley et al., (2012). The consistency in
wood proportion of litterflow suggests that this is a regular source of CPOM to the streams despite adverse effects and
130 influences that natural disasters can have on the landscape and inputs to streams.

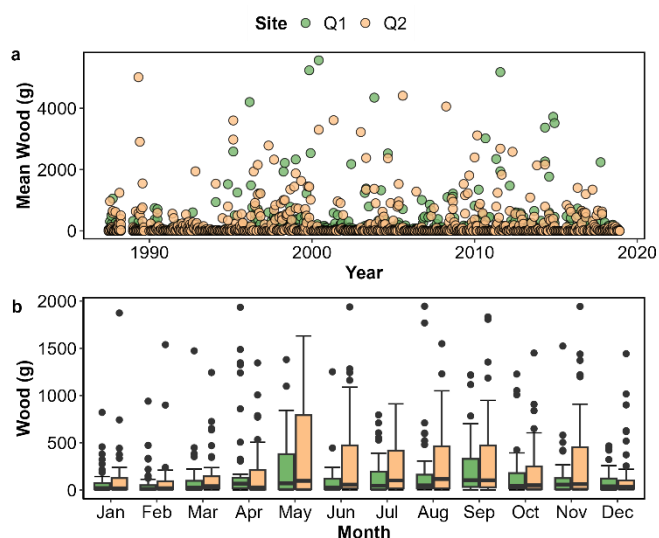
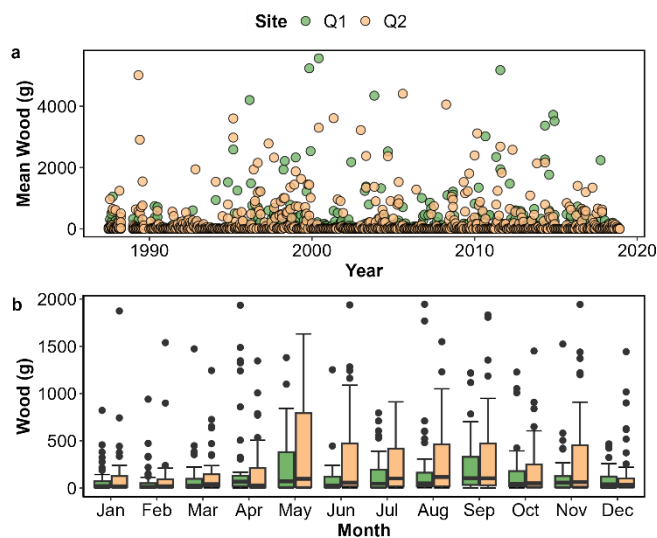


Figure 5. Mass of wood within the coarse particulate organic matter (CPOM) or litterflow for each site of the Bisley Experimental Watersheds in Puerto Rico, with Q1 in green and Q2 in orange presented as (a) monthly mean values over the 135 31-year time series and (b) monthly boxplots across all years where some high values were removed since they obscured the y-axis.

Miscellaneous material (flowers, fruits, and other plant parts or unidentifiable plant material) made up the smallest contribution of litterflow (Fig. 1). Miscellaneous parts in CPOM were also similar across the time series for both sites (Fig. 140 6a) and over months (Fig 6b). Although there is no clear pattern of inputs across months, August and September had the greatest variance suggesting that during this time the proportion of miscellaneous CPOM can drastically vary, potentially due to hurricanes or storms that are common during that part of the year. Miscellaneous inputs ranged between 0.23g and 16,758g with a median of 39.7g ($\pm 62.3g$) (Figure 3).

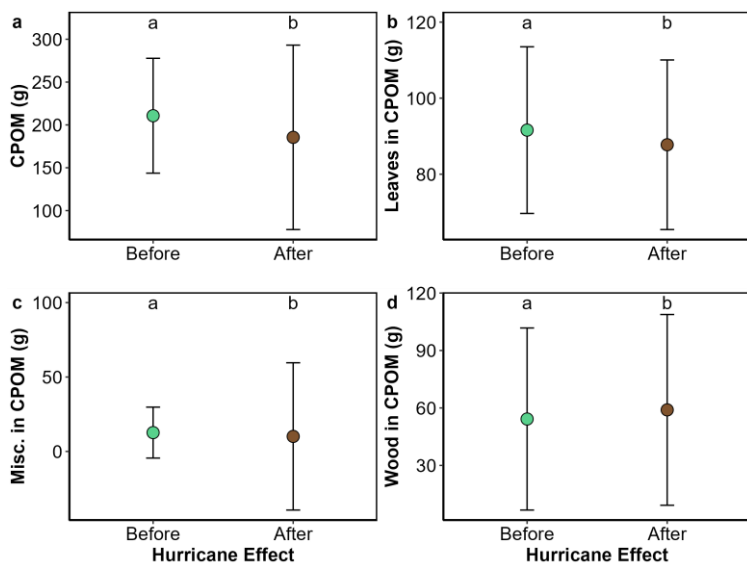


145 **Figure 6.** Mass of miscellaneous material (flowers, fruits, and other plant parts or unidentifiable material) within the course
particulate organic matter (CPOM) or litterflow from Bisley Experimental Watersheds, Puerto Rico for each site with Q1 in
green and Q2 in orange presented as (a) monthly mean values over the 31-year time series and (b) monthly boxplots across
all years where some high values were removed since they obscured the y-axis.

150 3.2 Influence of Disturbances

3.2.1 Hurricanes

Natural disturbances such as hurricanes and droughts can shape the structure and influence the functioning of a tropical forest (Gutiérrez-Fonseca et al., 2025) which can have direct impacts of leaf litter inputs into adjacent streams. As wind can damage trees and rains can cause high surface runoff that transports materials into streams, increases in leaf litter may be observed. Hurricanes have a clear impact on leaf litter inputs where generally the periods after hurricanes show lower median values of CPOM but have a wide range in variance compared to before hurricanes (Fig. 7). Similarly, others have found that hurricanes and tropical storms can enhance leaf litter inputs to streams or litterflow (Heartsill-Scalley et al., 2012; Benson & Pearson 2020; Gutiérrez-Fonseca et al., 2024; Gutiérrez-Fonseca et al., 2025). This is due to the initial pulse and export of leaf litter transported with surface runoff and winds from the storm or hurricane (Rodríguez-Cardona et al., 2026).
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160 Consequently, stocks or sources of materials can be drastically depleted, leading to declined inputs. As the forest starts to regenerate and regular leaf senescence patterns are reinstated, leaf litter inputs start to gradually increase but export rates take longer to recover and will depend on the condition of the forest previous to and the severity of the disturbance (Heartsill-Scalley et al., 2012; Gutiérrez-Fonseca et al., 2024).



165 **Figure 7.** Median mass (g) values with error bars representing the standard error of course particulate organic matter
(CPOM) or litterflow and its compartments before (green) and after (brown) hurricanes across the 31-year time series for
Bisley Experimental Watersheds, Puerto Rico (a) CPOM (sum of all compartments), (b) leaves in CPOM, (c) miscellaneous
parts in CPOM, and (d) wood in CPOM. Lowercase letters denote statistically significant differences determined by
Kruskal-Wallis rank sum test ($\alpha=0.05$); CPOM chi-squared = 11.3, $p = 0.0008$; leaves chi-squared = 15.4, $p = 0.0009$; misc
170 chi-squared = 11.2, $p = 0.0008$; wood chi-squared = 16.7, $p = 0.00004$.

3.2.2 Droughts

Droughts can lead to an accumulation leaf litter and materials on the forest floor or accumulated in eddies or disconnected
pool that are subsequently transported into the stream or downstream when the dry period is broken (Larned 2000;
175 Rodríguez-Cardona et al., 2026). In the Bisley Experimental Watersheds, during and after drought periods, total CPOM and
wood in CPOM tended to increase (Figure 8). Leaves and miscellaneous materials in CPOM show no statistically significant
differences during droughts. Trees within the riparian zone can undergo hydric stress leading to increased leaf fall or
increased standing stocks of materials in tropical forests (França et al., 2009; Gonçalves & Callisto 2013; Benson & Pearson
2020; Cortés Guzmán et al., 2022). In other tropical regions increased leaf litter inputs during droughts have also been
180 observed (Selva et al., 2007; Gonçalves et al., 2014). Leaf litter inputs may still remain elevated compared to before drought
conditions because rain events that break droughts can transport leaves and materials that have been on the forest floor.
Exploratory analyses between drought categories (D1 is moderate drought, D2 is severe drought, and D3 is extreme drought)
resulted in no statistically significant differences, although mass of the different compartments tended to decline in D2 and
D3 conditions (Figure 9).



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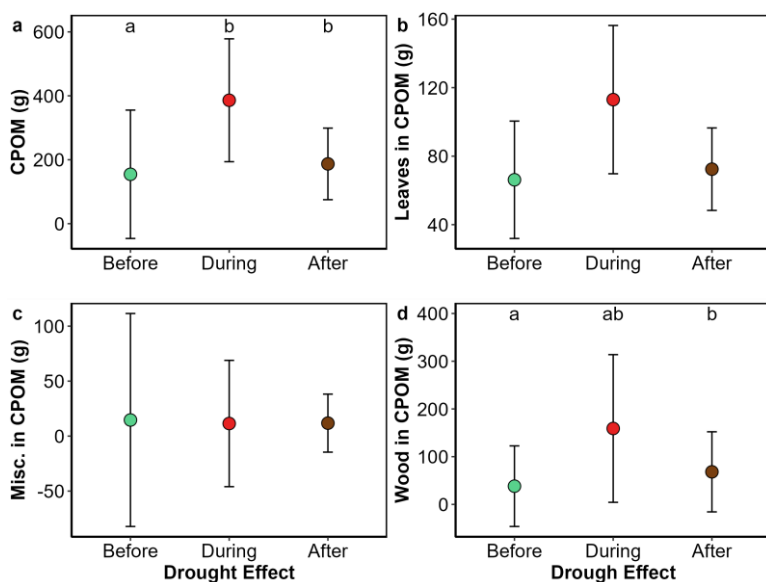
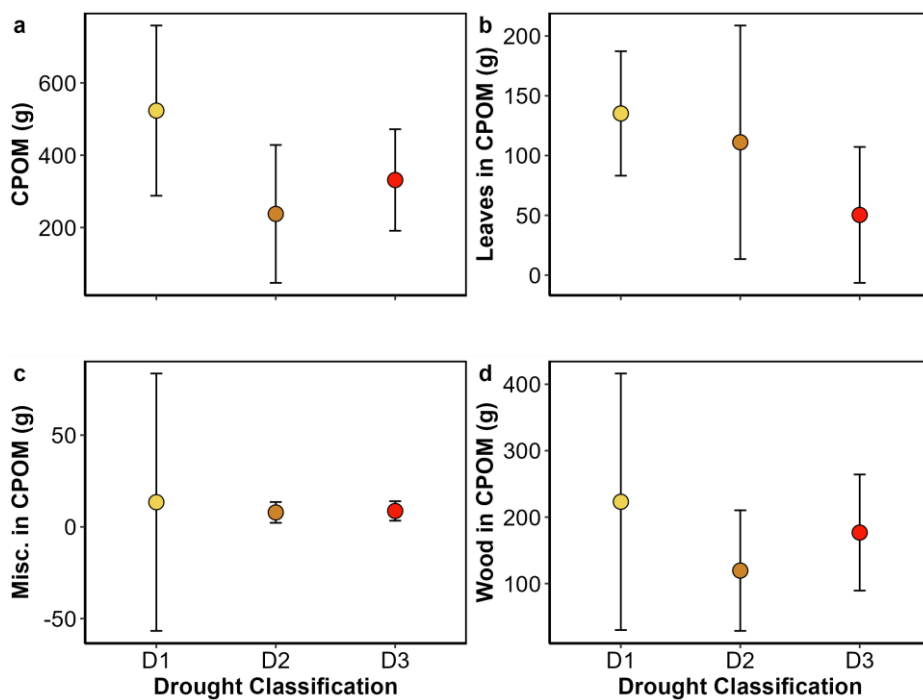


Figure 8. Median mass (g) values with error bars representing the standard error of leaf litter components before (green), during (red), and after (brown) droughts from 2000-2018 for Bisley Experimental Watersheds, Puerto Rico (a) course particulate organic matter (CPOM) or litterflow (sum of all compartments), (b) leaves, (c) miscellaneous parts, and (d) wood. Lowercase letters denote statistically significant differences determined by Kruskal-Wallis rank sum test ($\alpha=0.05$); CPOM chi-squared = 17.7, $p = 0.0001$; leaves chi-squared = 4.7, $p = 0.09$; misc chi-squared = 5.1, $p = 0.08$; wood chi-squared = 9.7, $p = 0.008$.

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195 **Figure 9.** Median mass (g) values with error bars representing the standard error of leaf litter compartments from Bisley
Experimental Watersheds, Puerto Rico by drought severity category, where D1 is moderate drought, D2 is severe drought, and
D3 is extreme drought, from 2000-2018 for (a) course particulate organic matter (CPOM) or litterflow (sum of all
compartments), (b) leaves, (c) miscellaneous parts, and (d) wood. There were no statistically significant differences between
drought classifications determined by Kruskal-Wallis rank sum test ($\alpha=0.05$); CPOM chi-squared = 2.0, $p = 0.37$; leaves chi-
200 squared = 3.2, $p = 0.20$; misc chi-squared = 2.9, $p = 0.23$; wood chi-squared = 0.7, $p = 0.72$.

4 Conclusion

The 30-year record of litterflow at the Bisley Experimental Watersheds presents an ideal data set to study temporal patterns
of leaf litter exports both as CPOM and by type of component or proportion. This long-term record has captured various
205 disturbances that otherwise would have been missed with sporadic sampling or short-term monitoring. Previous studies in
tropical forests have monitored inputs for 8 years or less (Rodríguez-Cardona et al., 2026) and rarely capture the effects of
natural disturbances. We have combined the efforts of various technicians and staff from IITF that continuously maintained
and collected data despite droughts, hurricanes, and the disruptive events to BEW infrastructure. Once leaf litter mass was
entered into a spreadsheet, they were vetted and double checked through a screening process of the Chemistry Laboratory at
210 IITF. The field technicians also made many notes when they collected leaf litter to get a better sense of stream conditions on
the date of collection.. The long-term data presented here can also be analyzed in parallel to long-term records of stream



215 chemistry for both streams (McDowell and IITF 2024) to fully understand the terrestrial aquatic connection of these sites including carbon and nutrient cycling in streams. This unique data set of stream leaf litter as CPOM exports from a tropical montane forest contributes to developing knowledge from aquatic ecosystems which are often overlooked in broad to global carbon modelling.

Data Availability

The data are published (Rodríguez-Cardona & Heartsill Scalley, 2026) and will be openly available through Zenodo once article is accepted. For review process, the data can be viewed with the following link:

220 <https://zenodo.org/records/18207792?token=eyJhbGciOiJIUzUxMiJ9.eyJpZCI6IjgyZmYzZWU5LTlwNGMtNDIzNy1hZTAyLTMyNTQ3Mjg4N2I2NyIsImRhdGEiOnt9LCJyYW5kb20iOiJkMzQyZWQ3NjcwNWQ3Zjk0ZWVvMDg2NDE4OGIxY2U3ZiJ9.j4Typ9xBtiS28P-7mickQqlcyInHXb2avH4MzFMhUtsz2tWJZJaFbZgtvR49BCdJH5gK1Q8RZD46IbjDOS7tVw>

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Competing Interests

The authors declare that they have no conflict of interest.

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