

Litter Processing in Tropical Headwater Streams: Potential Importance of Palm Fruit Fall and Frond Fall

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ABSTRACT: Different phenological patterns of leaf and fruit fall among native and non-native riparian species provide a spatially and temporally heterogeneous series of alternative food resources for detritivores. Relatively little is known about qualitative differences among these different riparian species. Rates of litter inputs, decomposition, and retention for different sources of riparian litter require long-term documentation. Species of freshwater shrimps, crabs, insects, and gastropods are known to consume a wide range of litter inputs but how these dynamic food webs function under changing climatic and land-use conditions is unknown, especially in tropical streams. On-going studies in the Luquillo Experimental Forest, Puerto Rico provide an example of how inputs of fronds and fruits from palms (*Prestoea montana*) serve as important foods and microhabitat for species of freshwater crabs and shrimp. Native riparian species such as *Prestoea montana* are commonly distributed in the Luquillo Mountains especially along steep slopes and stream banks. After tropical storms with high winds, the large fronds from these native riparian trees provide important inputs of leaf litter to the stream food web. In some streams, the input of ripe fruit from non-native trees such as Java plum (*Syzigium jambos*) also provides a major source of detrital food resources, especially during periods when fruit fall from native species of palms may be limited.

Key Words: Litter Processing, Luquillo Experimental Forest, Riparian tree species, Tropical streams.

INTRODUCTION

The consequences of changes in riparian tree species distributions are often due to complex food-web connections between numerous sediment-dwelling species and the flow of energy from detrital inputs (Gregory *et al.* 1991, Dudgeon 1994, Lester *et al.* 1994, Friberg and Winterbourn 1997, Naiman and Decamps 1997). The context-dependent function of native riparian species is also influenced by the invasion of non-native species that alter freshwater ecosystem functions (Covich 1993, Covich *et al.* 1999).

Invasions by non-native riparian species can sometimes short circuit the energy flow through detrital-based food webs. A disconnect between the rates of leaf-litter and fruit production and the rates of consumption and processing by native freshwater species can greatly alter energy flow. For example, if the sources of riparian detritus change because of a shift in tree species, then there may be an accumulation of organic detritus. This buildup of organic debris will result in a decline in dissolved oxygen during drought periods when slow stream flows lower export of riparian leaf litter and fruit fall. As another illustration, shade from riparian trees is an important influence on water temperatures so that displacement of evergreen species by

seasonally deciduous species can increase stream water temperatures. Similarly, removal of an intact riparian tree canopy and replacement by low-growing herbaceous species can greatly increase water temperatures and alter detrital inputs of woody debris, leaf litter, fruit fall, and terrestrial insects.

Benthic invertebrates are known to be functionally important in many ecosystems (Hutchinson 1993, Wallace and Webster 1996, Covich *et al.* 1999). These bottom-dwelling species are often diverse and abundant in freshwater sediments. They consume a wide variety of food resources from both internally produced plants (algae and macrophytes) and externally produced organic matter (leaf litter, fruit fall, woody debris, and terrestrial insects) from the overhanging riparian canopy. Certain species of aquatic insects and decapod crustaceans use specialized mouthparts or feeding appendages to break up large pieces of organic detritus such as leaf litter into smaller fragments. In the process of feeding, some shredded and suspended fragments are transported downstream (along with fecal pellets) in small, headwater tributaries. Other species are specialized to filter out variously sized particles and are often located downstream of the shredders (Wallace and Webster 1996, Wallace *et al.* 1997). Such linkages suggest that loss of some pivotal riparian

species would alter ecosystem processing of detrital carbon.

While it is clear that fruit fall is important to many vertebrate species in neotropical streams and rivers (Kubitzki and Ziburski 1994, Moll and Jansen 1995, Goulding *et al.* 1995, Araujo-Lima and Goulding 1997, Horn 1997) and in Asian rivers (Dudgeon 1999), little is known about how benthic invertebrates consume fallen fruit from riparian trees. Streams on oceanic islands are thought to derive a large portion of their energy from fruit fall (Resh and DeSzalay 1995). Chemical studies document that certain riparian trees have secondary compounds that alter fish consumers and may have similar effects on invertebrates. For example, the "mad fish" (*Leptobarbus hoevenii*), native to the Mekong River, is known to consume fruit from *Hydnocarpus* trees. In doing so the fish's flesh becomes inedible to its predators while it becomes intoxicated with compounds from this fruit (Banarescu and Coad 1991).

A TROPICAL CASE STUDY

Luquillo Experimental Forest, Puerto Rico

Long-term data at landscape scales are needed in different locations to evaluate riparian detrital inputs and to determine phenological patterns of different energy sources for detrital-based food webs. Networks of sites can evaluate how natural communities respond over time to different sets of conditions in temperate and tropical ecosystems. Some existing sites have spatially specific data on litter production in forest plots where comparisons among tree species can be made along well-mapped riparian zones.

Results from on-going, long-term studies of riparian tree species and stream food webs in the Luquillo Experimental Forest (Caribbean National Forest), Puerto Rico provide an example of forest-stream connections in a tropical montane ecosystems (Covich and McDowell 1996, Covich *et al.* 1996). The forest contains 225 tree species and covers steep terrain consisting of volcanoclastic sandstones with a network of five rivers draining 11,000 ha. Near the El Verde Field Station, a 16 ha forest grid has two streams flowing through the mapped grid (400 20 m × 20 m plots with 5 m × 5 m subplots). The grid was surveyed in 1990 (after Hurricane Hugo) and has 91 tree species with over 4,400 identified and mapped trees (Zimmerman *et al.* 1995). This grid and its riparian zones are being compared with several other riparian areas outside the grid to evaluate the functional roles of native and nonnative riparian tree species and their effects on benthic

food webs.

Leaf fall, especially of the palms, is often episodic and associated with wind winds and storms (Vogt *et al.* 1996, Reed 1998). These fronds provide protective cover from predators and a source of detrital food. Much less is known about the importance of fruit fall in detrital energy budgets. For example, in the Luquillo Experimental Forest, Puerto Rico, fruit fall is a major source of energy that varies with elevation and forest type. On average 600 kg ha⁻¹ yr⁻¹ is reported for the entire forest with a large proportion derived from palm fruits (Lugo and Frangi 1993). Palms (*Prestoea montana* = *Euterpe globosa*) are a dominant component of the riparian forest (Reed 1998). Phenological patterns of fruit production include seasonal and inter-annual variation (Bannister 1970, Wunderle 1999). Palms often synchronize the months of peak fruit production and produce many more fruits in some years than other years. The significance of these palm fruit mast years for stream consumers, such as the freshwater crab (*Epilobocera sinuatifrons*), is currently under study.

LITTER INPUTS

Recent studies in The Luquillo Experimental Forest have also tracked the spread of non-native bamboo (*Bambusa vulgaris*) and Java plum (*Syzigium jambos*) along headwater streams (O'Connor 1998). The dominant native riparian species such as palms (*Prestoea montana*) and tabonuco (*Dacryodes excelsa*) have relatively slow rates of decomposition (Vogt *et al.* 1996). Unlike native species, bamboo forms large clumps along montane streams in the Luquillo Experimental Forest. Leaf-fall rates for bamboo in this forest averaged 1.61 g m⁻² day⁻¹ compared to 1.10 g m⁻² day⁻¹ for native tree species. Leaf litter accumulates in pools that appeared to indicate a low rate of decomposition or relatively high rate of production. In these same montane streams, another non-native species, Java plum (*Syzigium jambos*), forms dense mono-specific stands.

Leaf litter-bags (with 4 g of dry leaves in fine-mesh bags to prevent access by macroinvertebrate consumers) were placed in stream pools in three headwater streams (water temperatures averaged 21°C). Replicate samples were removed over a six week period. Both bamboo and Java plum leaves had similar and rapid rates of decomposition. Rates of dry-mass loss followed a negative linear pattern with daily weight losses being 0.052 grams per day for bamboo and 0.051 grams per day for *S. jambos*. In a second study, tethered leaf packs were exposed to detritivores (freshwater

shrimp). These results were different from the first study's results. There was an increased rate of loss only for *S. jambos* (0.075 grams per day) while the loss rate observed for bamboo when it was exposed to detritivores remained the same low rate as when it was placed in litter bags (O'Connor 1998). This difference led to the hypothesis that shrimp would avoid pools with bamboo because of its apparently lower value as detrital food (slow rate of leaf breakdown).

A field survey was conducted in the Luquillo Experimental Forest to determine the distributions of freshwater shrimp in 24 pools distributed in two watersheds. Shrimp were sampled using baited wire-mesh traps (overnight for four nights) in 12 pools with bamboo and in 12 pools with native riparian species. Unexpectedly, more freshwater shrimp (both *Atya* and *Macrobrachium*) were found in pools with riparian bamboo when compared to adjacent pools of similar size but where bamboo was absent. Additional two-choice studies indicated a marked preference for non-native bamboo leaves when shrimp were offered either bamboo or native leaves as cover (O'Connor 1998). These results indicate that native detritivores distribute themselves in ways that suggest bamboo serves not only as a substitute for native leaf litter but as a preferred resource. The microhabitat created by bamboo litter in streams appears very well suited for use by these shrimp. It is still to be determined if the shrimp use the bamboo leaves only cover (as suggested thus far) or if they do provide an abundant supply of leaf litter. Nor is it yet determined if Java plum leaves and fruit are both used by shrimp as detrital foods.

CONCLUSIONS

Non-native riparian species may provide alternative detrital resources that substitute or complement inputs from native riparian species. Use of additional new resources by stream detritivores may include food supplies during periods of time when inputs from native species would be reduced or absent. However, the complete displacement of native riparian species by non-native species will likely limit the diversity of resource supplies over time and space. Thus, long-term monitoring of the spread of non-native riparian species and their ecological impacts are essential if the ecological integrity of stream food webs is to be preserved.

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