Does leaf chemistry differentially affect breakdown in tropical vs temperate streams? Importance of standardized analytical techniques to measure leaf chemistry

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Abstract. Comparisons of the effects of leaf litter chemistry on leaf breakdown rates in tropical vs temperate streams are hindered by incompatibility among studies and across sites of analytical methods used to measure leaf chemistry. We used standardized analytical techniques to measure chemistry and breakdown rate of leaves from common riparian tree species at 2 sites, 1 tropical and 1 temperate, where a relatively large amount of information is available on litter chemistry and breakdown rates in streams (La Selva Biological Station, Costa Rica, and Coweeta Hydrologic Laboratory, North Carolina, USA). We selected 8 common riparian tree species from La Selva and 7 from Coweeta that spanned the range of chemistries of leaf litter naturally entering streams at each site. We predicted that concentrations of secondary compounds would be higher in the tropical species than in the temperate species and that high concentrations of condensed tannins would decrease breakdown rates in both sites. Contrary to our predictions, mean concentration of condensed tannins was significantly greater (2.6×, $p < 0.001$) for species at Coweeta than for species at La Selva. Concentration of condensed tannins was negatively correlated with breakdown rate among Coweeta species ($r = -0.80$), not among La Selva species, and negatively correlated when the 2 sites were combined ($r = -0.53$). Concentrations of structural compounds were strongly correlated with breakdown rate at both sites (Coweeta species, lignin $r = -0.94$, cellulose $r = -0.77$; La Selva species, cellulose $r = -0.78$, C $r = -0.73$). The chemistries of 8 riparian species from La Selva and 7 riparian species from Coweeta were not as different as expected. Our results underline the importance of standardized analytical techniques when making cross-site comparisons of leaf chemistry.

Key words: organic matter, decomposition, tannins, phenolics, lignin, nitrogen, carbon.

Leaf litter is an important energy source for organisms in forested streams (Wallace et al. 1999). The chemistry of leaf litter affects its decomposition rate, persistence, and availability to consumers (Webster and Benfield 1986). Leaf chemical characteristics known to decrease breakdown rate include: 1) high concentrations of lignin (Gessner and Chauvet 1994),

2) low N content (Melillo et al. 1983), 3) high lignin:N and C:N ratios (Enriquez et al. 1993), and 4) high concentrations of tannins (Ostrofsky 1997, Driebe and Whitham 2000). The effect of leaf litter chemistry on breakdown has been studied extensively in temperate streams, but leaf litter in tropical streams has not received as much attention. The physical and biological differences between tropical and temperate streams (Covich 1988) provide good reason to expect that the factors controlling leaf litter breakdown might differ between these 2 regions.

Leaves of many tropical plant species tend to have higher concentrations of secondary compounds and more recalcitrant compounds than do leaves of temperate species (Levin 1976, Coley and Aide 1991). Previous researchers hypothesized that high concen-

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trations of secondary compounds (e.g., tannins) in many tropical species inhibit leaf breakdown rates in tropical streams (Stout 1989, Irons et al. 1994). Stout (1989), using primarily published data, hypothesized that high concentrations of condensed tannins in tropical species decrease leaf breakdown rate in tropical streams. Most studies that have examined this hypothesis have incubated tropical leaves in temperate streams (but see Wantzen and Wagner 2006). In a temperate Australian stream, condensed tannin content was negatively correlated with breakdown rates of 6 species of *Eucalyptus,* but not with breakdown rates of 12 other tropical and temperate species (Campbell and Fuchshuber 1995). Leaf litter from tropical species with higher concentrations of tannins was processed more slowly by shredders in a German stream than was leaf litter from temperate species with lower concentrations of tannins (Wantzen et al. 2002).

Results from these previous studies might not be an accurate reflection of differences in leaf litter chemistry and leaf breakdown dynamics between tropical and temperate streams for 3 reasons: 1) literature reviews are hindered by the use of different analytical techniques to measure secondary compounds across studies (Stout 1989), 2) chemical changes in leaves during decomposition occur faster in tropical than in temperate streams (Ardón and Pringle 2008), and 3) the microbial and invertebrate fauna of temperate streams (i.e., where tropical leaves were incubated) might not have been adapted to the chemical characteristics of tropical leaves. The effects of secondary compounds (measured with standard analytical techniques) on breakdown rate of native species decomposing in their natural habitats at both a tropical and temperate site remain to be explored.

The objectives of our study were to: 1) directly compare initial leaf litter chemistry of common native riparian tree species spanning a wide range of quality from a tropical site (La Selva Biological Station, Costa Rica) and a temperate site (Coweeta Hydrologic Laboratory, North Carolina, USA) using standardized analytical techniques and 2) examine the importance of leaf secondary compounds on leaf breakdown at these 2 sites, where a relatively large amount of information exists on plant chemistry and breakdown dynamics in streams (Hartshorn 1983, Swank and Crossley 1988, Rosemond et al. 1998, Webster et al. 1999). We predicted that concentrations of secondary compounds (total phenolics, condensed and hydrolyzable tannins) would be higher among species from the tropical site than among species from the temperate site, and that secondary compounds would inhibit breakdown rates in both sites.

Methods

Site descriptions

La Selva Biological Station (lat 10°26′N, long 84°01′W; 1536 ha) is in the Caribbean lowlands of Costa Rica, at the lowland end of the last protected unbroken biological corridor spanning altitudinal extremes in Central America. La Selva receives 4000 mm of rain annually, with >400 mm/mo from May to December (Sanford et al. 1994). Mean annual stream water temperature ranges from 24 to 26°C. Streams at La Selva display a wide range of variation in solute concentrations and pH because of geothermally modified groundwater inputs (Pringle and Triska 1991). Algal assemblages in streams at La Selva are light limited by dense canopy cover (>90%). Thus, food webs are detritus based (Pringle et al. 1993). Most trees in La Selva are nondeciduous, and leaf fall is continuous throughout the year (Hartshorn 1983).

Coweeta Hydrologic Laboratory (lat 35°00′N, long 83°30′W; 2185 ha watershed) is a US Department of Agriculture Forest Service research facility and Long Term Ecological Research site in the Blue Ridge Province of the Southern Appalachian Mountains (North Carolina). Coweeta Hydrologic Laboratory has 50+ y of hydrologic and climate monitoring data. Coweeta receives ~1700 mm of rain annually, and stream temperatures range from 4 to 17°C (Swank and Crossley 1988). Dissolved concentrations of N and P are usually low (<10 µg/L), and pH averages ~6.6 to 6.8 (Wallace et al. 1986). Streams in Coweeta drain mixed-hardwood forests dominated by oaks and hickories and are heavily shaded by riparian rhododendron (Wallace et al. 1982). Thus, food webs are detritus based (Wallace et al. 1999).

Selection of tree species for chemical analyses and breakdown experiments

At least 2015 native plant species exist at La Selva, but the exact number that can be considered riparian is unclear (C. Taylor, Missouri Botanical Garden, personal communication). Up to 116 plant species have been reported near streams and wetlands in vegetation studies at La Selva (Lieberman et al. 1985). A list of trees and shrubs species that commonly occur along streams in La Selva was compiled based on the literature (Hartshorn 1983, Lieberman et al. 1985, Hartshorn and Hammel 1994) and consultation with experts on the La Selva flora (B. Hammel and M. Grayum, Missouri Botanical Garden; O. Vargas and N. Zamora, Organization for Tropical Studies and Costa Rica's Instituto Nacional de Biodiversidad; Appendix). Species selected from this list for inclusion in the litter

breakdown experiment were chosen to span the range of litter chemical quality of leaves that naturally enter La Selva streams. These species had high (*Zygia longifolia* [Fabaceae, sotacaballo], *Carapa nicaraguensis* [Meliaceae, caobilla]), intermediate (*Castilla elastica* [Moraceae, hule], *Luehea seemannii* [Malvaceae, guácimo colorado], *Simira maxonii* [Rubiaceae, guatil colorado], *Terminalia oblonga* [Combretaceae, sura]), and low (*Trema integerrima* [Ulmaceae, capulín], *Ficus insipida* [Moraceae, chilamate]) concentrations of secondary compounds (Janzen and Waterman 1984, Stout 1989).

Approximately 610 plant species exist at Coweeta. An estimated 27 tree species and 4 shrub species commonly occur alongside streams (mesic, hemlock–poplar community; Elliott et al. 1999). Species selected for the breakdown experiment were chosen to represent the main categories of leaf breakdown rates in Coweeta streams (Wallace et al. 1982, Webster et al. 1999). These species had slow (*Pinus strobus* [Pinaceae, white pine], *Quercus rubra* [Fagaceae, northern red oak], *Rhododendron maximum* [Ericaceae, rhododendron]), medium (*Acer rubrum* [Aceraceae, red maple], *Liquidambar styraciflua* [Hamamelidaceae, sweetgum]), or fast (*Cornus florida* [Cornaceae, dogwood], *Liriodendron tulipifera* [Magnoliaceae, tulip poplar]) breakdown rates.

Freshly fallen leaves from La Selva were collected in January and February 2003 and 2004. Recently senesced leaves were collected from the ground (leaves that had begun to decompose or showed signs of herbivory were avoided), brought to the laboratory, and stored in an air conditioned room until used. Freshly fallen leaves from Coweeta were collected in October 2003 and 2004 as described for leaves from La Selva.

Leaf litter chemical analyses

Standardized analytical methods were used to measure the chemistry of leaves from La Selva and Coweeta. Structural compounds (i.e., cellulose, hemicellulose, and lignin) were estimated with sequential neutral detergent/acid detergent digestion on an Ankom 2000 fiber analyzer (ANKOM Fiber Technologies, Fairport, New York; Goering and Van Soest 1970). Three separate analyses were conducted for secondary compounds: condensed tannins (acid-butanol assay; Rossiter et al. 1988), hydrolyzable tannins (potassium-iodate technique; Schultz and Baldwin 1982), and total phenolics (Folin–Denis assay; Swain 1979). Samples were extracted in 70% acetone with 1 mM ascorbic acid and evaporated under reduced pressure to provide aqueous extracts. Condensed

tannins and hydrolyzable tannins can be higher than total phenolics in our assays because they are measured with different reactions (Schultz and Baldwin 1982). All samples were compared to standards prepared from pooled litter samples from each site to avoid problems associated with use of commercial standards (Appel et al. 2001). Leaf C and N content were determined using a Carlo Erba NA 1500 CHN analyzer (Carlo Erba, Milan, Italy). For P analysis, ground leaf material was weighed into acid-washed and precombusted ceramic crucibles, combusted at 500°C, acid-digested, and analyzed spectrophotometrically (ascorbic acid method; APHA 1998).

Measurements of leaf breakdown rate

Breakdown rates at La Selva were measured in the Sabalo, a 3rd-order stream on the east border of the reserve. Water temperature in the Sabalo is fairly constant (diel range = 24–26°C, annual range = 24–27°C; Rosemond et al. 1998). Daily maximum and minimum temperatures were recorded with a maximum–minimum thermometer during the breakdown experiment. Plastic mesh bags (20 cm × 36 cm) were filled with 5 g of dried leaf litter. The bags had a coarse mesh (5 mm) so that stream invertebrates could access the litter (Benfield 1996). Five grams of litter was used to approximate the average mass of naturally occurring leaf packs in streams at La Selva (5.3 ± 3 g; M. Ardón, unpublished data), and this mass of litter was used in previous studies at La Selva (Rosemond et al. 1998, 2001, 2002, Ardón et al. 2006, Stallcup et al. 2006). Litter bags were anchored to the stream bed with metal stakes. Litter bags were placed in the stream in February 2003 and 2004 and were collected over 7 dates for each species (the dates for each species depended on their breakdown rate) over a period of 4 mo. Data reported for *F. insipida* and *Z. longifolia*, which were used both years, are from the 2003 experiment. On each collection date, 4 litter bags were brought to the laboratory. Litter was washed to remove insects and sediments, oven dried (40°C, 24–48 h), weighed, combusted (500°C, 1 h), and reweighed to obtain ash-free dry mass (AFDM) remaining. Chemical changes in the leaves during breakdown and microbial and insect colonization of these leaves are reported elsewhere (Ardón and Pringle 2008).

Breakdown rates at Coweeta were measured in a 1st-order stream (catchment 53). Daily mean, maximum, and minimum temperatures were recorded using Ryan temp-mentors (Ryan Instruments Inc., Washington). Plastic mesh bags (20 cm × 36 cm, 5-mm mesh; Eggert and Wallace 2003) were filled with 15 g of dried leaves. The average mass of naturally occurring leaf packs at

Coweeta is 15 g (J. B. Wallace, University of Georgia, personal communication) and has been widely used in previous studies at this site (Webster et al. 1999). Litterbags were placed in the stream on 1 December 2003 and 2004, and 3 to 7 replicates were collected on 9 to 11 collection dates (Eggert and Wallace 2003). Litter bags were placed on ice and transported back to the laboratory for processing. Litter was washed to remove invertebrates and sediments, oven dried (60°C, 7 d), weighed, combusted (500°C, 12 h), and reweighed to obtain AFDM remaining.

Data analyses

Breakdown rate, k, was estimated by linear regression of $\ln(x)$-transformed % AFDM remaining vs day (d) and vs degree day (dd) for both sites (negative exponential model; Benfield 1996). Relationships between breakdown rate (per d and per dd) and concentrations of leaf litter chemical constituents were examined in species from both sites with Pearson correlation coefficients (Proc Corr; SAS; Version 9.1, SAS Institute, Cary, North Carolina). Principal component analysis (PCA; SAS) on untransformed leaf chemistry data was used to examine overall variation in leaf chemistry between the 2 sites (SAS). Mean concentrations of chemical constituents were compared with analysis of variance (ANOVA on $\ln(x + 1)$-transformed data to meet assumptions of normality; SAS).

Results

Leaf litter chemistry

Leaf chemistry varied widely among species from the 2 sites (Table 1). Mean concentration of condensed tannins was higher for Coweeta than for La Selva species ($F_{1,58} = 24.3$, $p < 0.001$; Fig. 1A). Both total phenolics and hydrolyzable tannins were slightly higher for Coweeta than for La Selva species (Fig. 1B, C). Lignin was higher for Coweeta than for La Selva species ($F_{1,58} = 4.27$, $p < 0.05$; Fig. 1D). Cellulose concentrations were similar between both sites, whereas hemicellulose was higher for La Selva than for Coweeta species ($F_{1,58} = 4.19$, $p < 0.05$; Fig. 1E, F). P and N concentrations were higher in La Selva than in Coweeta species ($F_{1,58} = 13.5$, $p < 0.001$; $F_{1,58} = 102.5$, $p < 0.0001$; respectively; Fig. 1G, H). C concentration was higher for Coweeta than for La Selva species ($F_{1,58} = 45.1$, $p < 0.0001$; Fig. 1I).

PCA of leaf chemistry data did not show a clear separation of species from the 2 sites (Fig. 2). PC axis 1 explained 40% of the variation and was positively correlated with condensed tannins ($r = 0.41$) and

TABLE 1. Mean (SE) concentrations (% dry mass) of chemical constituents of leaves from 7 common riparian species in Coweeta Hydrologic Laboratory, North Carolina, and 8 common riparian species from La Selva Biological Station, Costa Rica.

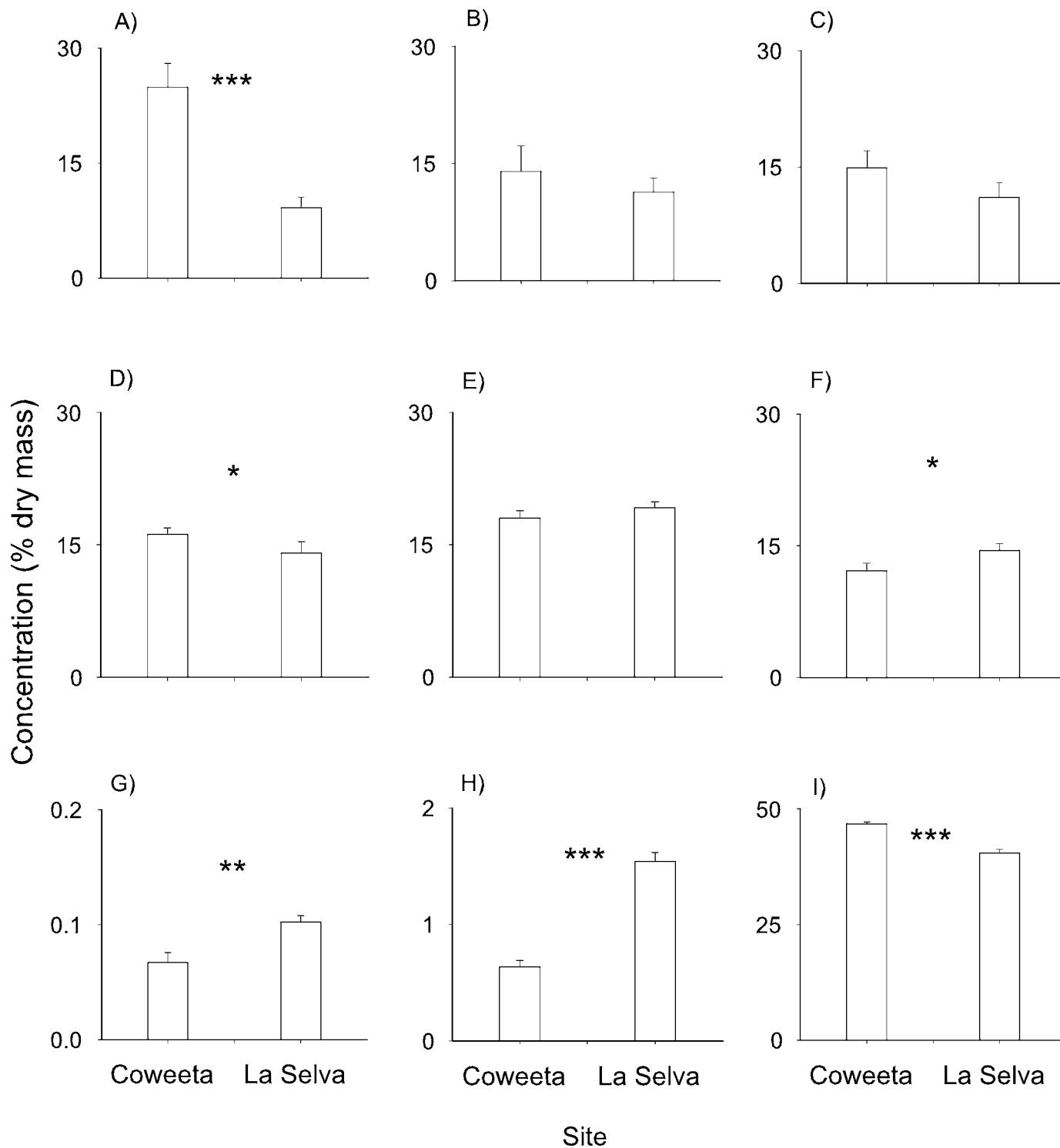| Species	Condensed tannins	Total phenolics	Hydrolyzable tannins	Lignin	Cellulose	Hemicellulose	P	N	C
Coweeta									
Acer rubrum	26.8 (1.10)	35.3 (15.20)	39.7 (1.68)	16.5 (0.46)	14.8 (0.24)	9.5 (0.21)	0.032 (0.00001)	0.41 (0.002)	47.6 (0.06)
Cornus florida	9.3 (0.48)	12.7 (0.97)	14.7 (0.33)	8.4 (0.15)	12.4 (0.07)	9.0 (0.09)	0.161 (0.002)	0.80 (0.010)	44.9 (0.44)
Liquidambar styraciflua	22.3 (1.63)	6.8 (0.19)	9.6 (0.43)	14.9 (0.29)	13.0 (0.09)	9.3 (0.24)	0.069 (0.0008)	0.58 (0.002)	44.4 (0.06)
Liriodendron tulipifera	5.5 (0.27)	4.4 (0.41)	3.9 (0.09)	15.9 (0.96)	18.6 (0.31)	15.8 (0.54)	0.095 (0.0008)	1.24 (0.010)	45.5 (0.09)
Pinus strobus	57.7 (4.88)	5.6 (0.41)	10.2 (1.37)	19.2 (1.79)	22.3 (0.66)	15.6 (0.15)	0.041 (0.0002)	0.40 (0.002)	50.3 (0.09)
Quercus rubra	35.9 (3.50)	7.7 (1.64)	13.1 (1.68)	16.9 (0.21)	21.3 (0.34)	16.0 (0.67)	0.036 (0.0001)	0.68 (0.003)	47.3 (0.01)
Rhododendron maximum	24.8 (2.31)	25.3 (12.60)	17.2 (1.88)	21.1 (0.40)	23.6 (0.25)	9.8 (0.70)	0.032 (0.001)	0.32 (0.004)	47.3 (0.10)
Range	5.5–57.7	4.4–35.3	3.9–39.7	8.4–21.1	12.4–3.6	9.0–16	0.032–0.161	0.32–1.24	44.4–50.3
La Selva									
Carapa nicaraguensis	23.2 (2.82)	32.3 (5.94)	34.9 (5.32)	18.3 (2.36)	18.0 (1.41)	7.5 (1.09)	0.08 (0.0002)	0.91 (0.13)	41.7 (0.23)
Castilla elastica	11.3 (2.34)	12.3 (3.72)	9.4 (1.51)	13.4 (0.72)	19.5 (0.83)	22.0 (1.37)	0.16 (0.01)	2.03 (0.10)	40.4 (0.52)
Ficus insipida	0.5 (0.11)	11.8 (2.62)	2.7 (0.15)	8.3 (0.78)	19.1 (0.67)	14.7 (0.65)	0.08 (0.0002)	1.27 (0.02)	35.0 (0.32)
Luehea seemannii	13.6 (1.75)	7.4 (1.41)	14.0 (2.30)	16.3 (0.41)	19.9 (0.35)	15.5 (0.65)	0.11 (0.01)	1.27 (0.07)	44.2 (0.05)
Simira maxonii	2.8 (0.27)	4.3 (0.34)	6.6 (0.55)	15.3 (1.56)	23.0 (0.30)	14.6 (0.20)	0.11 (0.01)	2.05 (0.07)	44.9 (0.41)
Terminalia oblonga	12.8 (3.76)	11.5 (1.35)	11.4 (1.00)	6.9 (0.81)	17.5 (0.20)	13.9 (0.64)	0.12 (0.01)	1.36 (0.07)	39.2 (0.23)
Trema integerrima	0.8 (0.06)	0.9 (0.14)	3.0 (0.12)	5.5 (0.68)	12.2 (0.35)	10.1 (0.61)	0.10 (0.01)	1.61 (0.06)	34.1 (0.27)
Zygia longifolia	8.1 (0.25)	10.0 (0.65)	7.8 (0.42)	28.3 (0.55)	24.6 (0.80)	17.5 (0.41)	0.06 (0.001)	1.87 (0.04)	46.4 (0.27)
Range	0.4–23.1	0.9–32.3	2.8–34.8	5.5–28.3	12.2–24.6	7.5–22.0	0.058–0.160	0.91–2.05	34.1–46.4

Fig. 1. Mean (±1 SE) concentrations of (A) condensed tannins, (B) total phenolics, (C) hydrolyzable tannins, (D) lignin, (E) cellulose, (F) hemicellulose, (G) P, (H) N, and (I) C of leaves from 7 riparian species from Coweeta Hydrologic Laboratory, North Carolina, and 8 riparian species from La Selva Biological Station, Costa Rica. Significant differences are from analysis of variance. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.
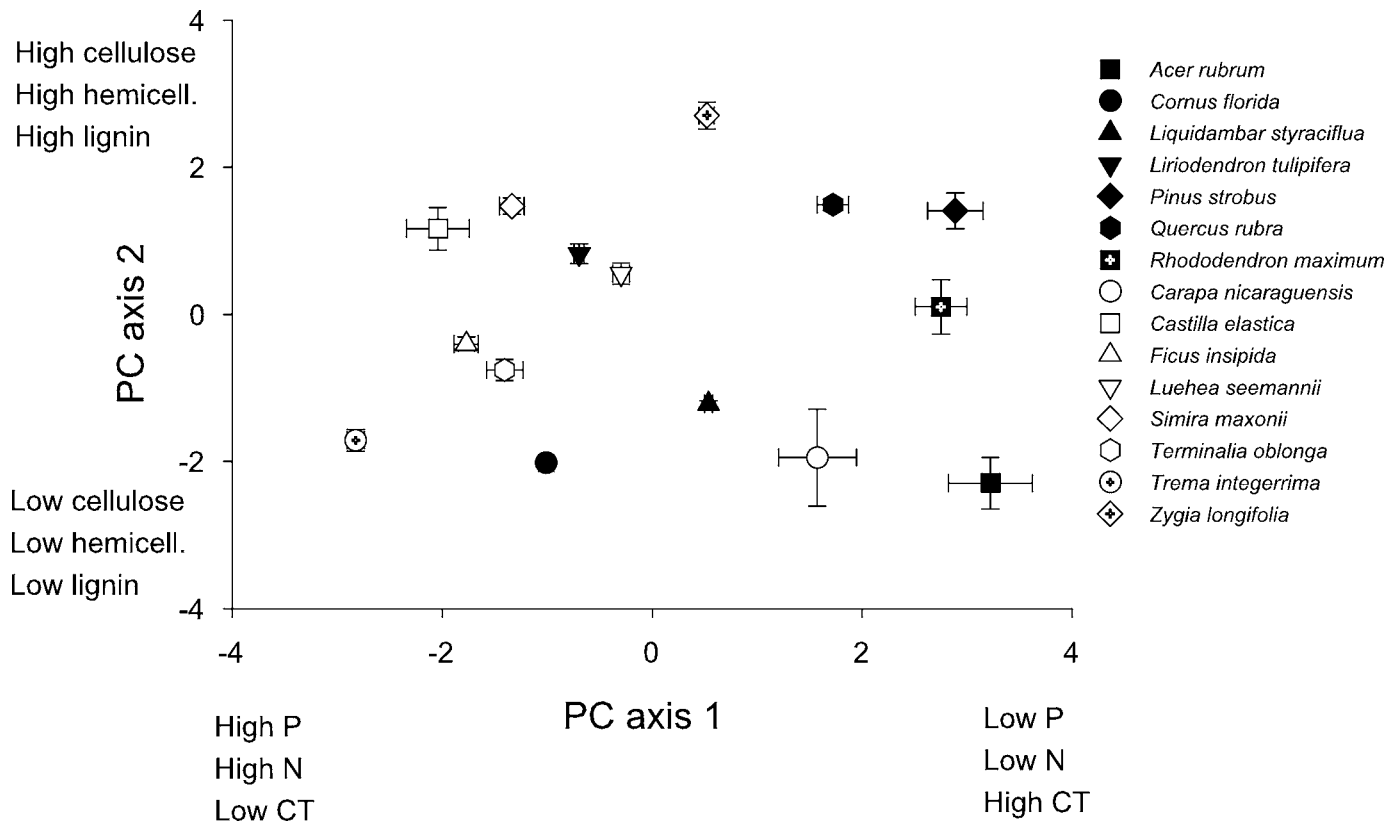
FIG. 2.   Principal component analysis (PCA) of leaf chemistry of 7 riparian species from Coweeta Hydrologic Laboratory, North Carolina, and 8 riparian species from La Selva Biological Station, Costa Rica. PC axis 1 explained 40% of the variation, and PC axis 2 explained 27% of the variation. Coweeta species are denoted by black symbols, La Selva species are denoted by white symbols. CT = condensed tannins, hemicell = hemicellulose. Error bars indicate 1 SD.

negatively correlated with P ($r = -0.40$) and N ($r = -0.39$) content. PC axis 2 explained 27% of the variation and was positively correlated with cellulose ($r = 0.52$), hemicellulose ($r = 0.50$), and lignin ($r = 0.37$) content.

Leaf breakdown rate

Mean breakdown rates were 3× to 7× faster at La Selva (mean $k = 0.058/d$, 0.0023/dd) than at Coweeta (mean $k = 0.008/d$, 0.0008/dd; Table 2). The difference in breakdown rate between the slowest and the fastest species was much higher at La Selva (15× based on k [per d], 18× based on k [per dd]) than at Coweeta (5× based on k [per d] and 8× based on k [per dd]; Table 2). Breakdown rates (per dd) of the 4 slowest decomposing species in each site (i.e., *C. elastica, L. seemannii, Z. longifolia,* and *C. nicaraguensis* in La Selva; *A. rubrum, Q. rubra, P. strobus,* and *R. maximum* in Coweeta) were not significantly different ($F_{1,6} = 4.08$, $p = 0.08$; Fig. 3).

Overall, relationships between leaf chemical parameters and breakdown rates were stronger among Coweeta species than among La Selva species (Table 3). Breakdown rates (per dd) of Coweeta species were strongly correlated with lignin ($r = -0.94$, $p < 0.01$), cellulose ($r = -0.77$, $p < 0.05$), P ($r = 0.90$, $p < 0.01$), and condensed tannins ($r = -0.80$, $p < 0.05$; Table 3). Breakdown rates (per dd) of La Selva species were strongly correlated with structural compounds (cellulose, $r = -0.78$, $p < 0.05$) and %C ($r = -0.73$, $p < 0.01$; Table 3). Concentration of condensed tannins was not significantly correlated with breakdown rates (per dd) in La Selva species (Table 3). When all 15 species were analyzed together, breakdown rates (per dd) were strongly negatively correlated with %C ($r = -0.76$, $p < 0.01$) and lignin ($r = -0.66$, $p < 0.01$; Table 3) and marginally significantly negatively correlated with condensed tannins ($r = -0.53$, $p = 0.04$).

Discussion

Contrary to our initial predictions, secondary compounds were higher in species at the temperate (Coweeta) than the tropical (La Selva) site and concentrations of condensed tannins were correlated

TABLE 2. Breakdown rates calculated for 7 common riparian species from Coweeta Hydrologic Laboratory, North Carolina, and 8 species from La Selva Biological Station, Costa Rica. Breakdown rates (*k*) are classified as slow (S), medium (M), or fast (F) based on days (Webster and Benfield 1986) and on degree days (dd) (Cummins et al. 1989).

| | | *k* | |
Location	Species	(/d)	(/dd)
Coweeta	*Cornus florida*[a]	0.017 F	0.0017 F
	Liriodendron tulipifera	0.010 F	0.0011 M
	Liquidambar styraciflua	0.008 M	0.0009 S
	Acer rubrum	0.008 M	0.0008 S
	Quercus rubra	0.007 M	0.0007 S
	Rhododendron maximum	0.004 S	0.0004 S
	Pinus strobus	0.003 S	0.0002 S
La Selva	*Trema integerrima*	0.198 F	0.0076 F
	Ficus insipida	0.079 F	0.0031 F
	Simira maxonii	0.048 F	0.0018 F
	Terminalia oblonga	0.039 F	0.0015 M
	Castilla elastica	0.038 F	0.0014 M
	Luehea seemannii	0.033 F	0.0013 M
	Carapa nicaraguensis	0.023 F	0.0009 S
	Zygia longifolia	0.011 F	0.0005 S

[a] Previously reported in Wallace et al. (1982)

with breakdown rate only for species at Coweeta. When we combined both sites, condensed tannins were correlated with breakdown rate (per dd), but it was mostly driven by the Coweeta species. Use of standardized analytical techniques and incubation of leaves from native species in their natural habitat enabled us to compare leaf chemistry directly and to relate leaf chemistry to leaf breakdown across a tropical and temperate site. In contrast, previous studies of differences in leaf breakdown between temperate and tropical streams have relied on literature values for leaf chemistry (measured in a non-standardized manner; Stout 1989), have incubated leaf litter from tropical species in temperate streams (Campbell and Fuchshuber 1995, Wantzen et al. 2002), or have conducted cross-site transplants in which leaves from a tropical ecosystem were incubated in a temperate stream and vice versa (Stout 1989, Irons et al. 1994, Wantzen and Wagner 2006).

How do secondary compounds differ between a tropical and a temperate site?

Contrary to our predictions based on the literature (Levin 1976, Coley and Aide 1991), concentrations of condensed tannins were greater (2.6×, *p* < 0.001) in temperate Coweeta species than in tropical La Selva species (Fig. 1). In a study similar to ours, Campbell and Fuchshuber (1995) found no statistically significant differences in concentrations of condensed tan-

nins and phenolics in litter of 8 tropical and 10 temperate species in Australia. Their results, combined with ours, bring into question the generalization that concentrations of secondary compounds are greater in leaf litter from tropical than from temperate species. Of the species analyzed, temperate *P. strobus* had the highest concentration of condensed tannins. Conifers tend to have high concentrations of tannins and phenolics, which can inhibit breakdown (Ostrofsky 1997), and *P. strobus* is a poor resource for aquatic invertebrates (Whiles and Wallace 1997). Our decision to include *P. strobus* might have biased our results, but it is a species representative of poor quality litter that commonly enters Coweeta streams.

Concentrations of condensed tannins were more strongly related to breakdown rates of temperate Coweeta species than of tropical La Selva species, which also led to a significant correlation when we combined both sites (Fig. 1, Table 3). Evidence for an inhibitory role of condensed tannins and other phenolic compounds on leaf breakdown is stronger in temperate than in tropical streams. Ostrofsky (1997) found a significant negative relationship between condensed tannins and leaf breakdown rate for 48 temperate species. Gessner and Chauvet (1994) reported a negative relationship between condensed tannins and leaf breakdown rate of 5 species in a French stream. Hybridization in cottonwood plants increased condensed tannin concentrations and led to slower leaf breakdown in temperate streams (Driebe and Whitham 2000). Phenolic compounds in *Eucalyptus* leaves affect leaf breakdown by inhibiting fungal colonization (Bärlocher et al. 1995, Canhoto and Graça 1999) and invertebrate feeding (Canhoto and Graça 1999). In contrast, the few studies conducted with tropical species do not provide evidence for a strong role of secondary compounds in leaf breakdown (Campbell and Fuchshuber 1995, Ardón et al. 2006, Ardón and Pringle 2008) and do not support the hypothesis of Stout (1989) that condensed tannins inhibit leaf breakdown of tropical species.

Our results underline the importance of structural compounds in inhibiting breakdown of both tropical and temperate leaves. Concentrations of cellulose and lignin in leaves were strongly correlated with breakdown rate at both sites (Table 3). Specialized enzymes are required to process recalcitrant forms of C, such as cellulose and lignin (Melillo et al. 1983). Our results agree with those of previous studies that have shown that high concentrations of recalcitrant forms of C, such as lignin, inhibit leaf breakdown (Melillo et al. 1983, Gessner and Chauvet 1994, Hutchens and Benfield 2000).
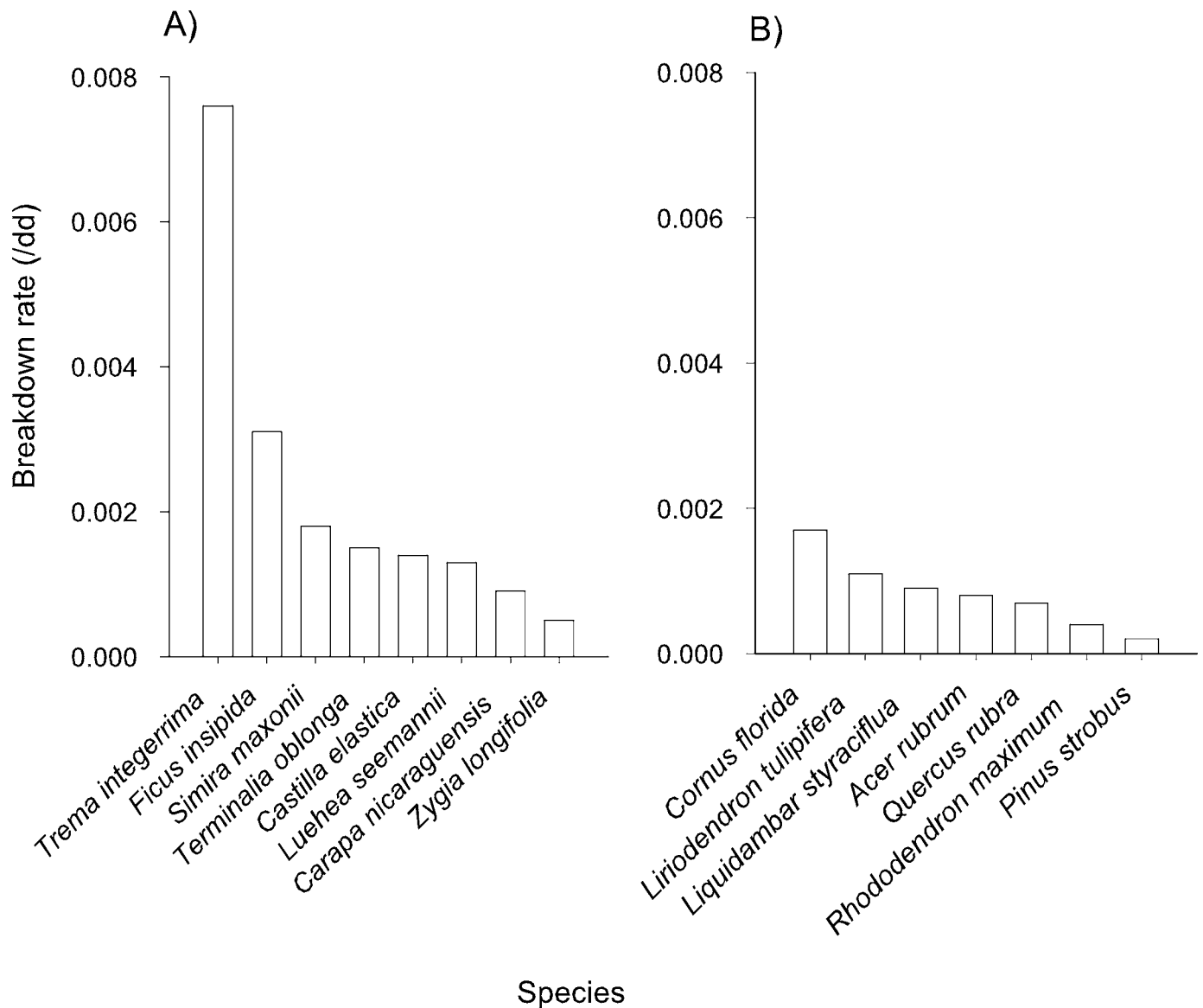
FIG. 3.   Breakdown rates (k/degree day [dd]) of leaves from common riparian species from (A) La Selva Biological Station, and (B) Coweeta Hydrologic Laboratory.

How do leaf breakdown rates differ between a temperate and a tropical stream?

Differences in breakdown rates between the slowest and the fastest decomposing species at La Selva were much greater (15–18×) than the differences between slow and fast decomposing species at Coweeta (5–8×). The large difference among tropical species was driven mostly by the extremely fast breakdown rate of *T. integerrima*. The difference in breakdown rate between the 2nd fastest (*F. insipida*) and the slowest (*Z. longifolia*) decomposing species at La Selva was similar (6–7×) to the difference between slow and fast decomposing species at Coweeta (5–8×). This result suggests that the

range of the processing continuum (i.e., range of breakdown rates of leaves entering a stream; Petersen and Cummins 1974) might not be very different between a tropical and a temperate site when exceptionally fast decomposing species are excluded. However, it remains to be determined how many species in tropical streams are processed as fast as *T. integerrima*. *Trema integerrima* is common along streams in La Selva and in much of Costa Rica (Hartshorn 1983) and is a high quality, but transient, resource for invertebrates.

On average, breakdown rates tended to be faster in La Selva. However, breakdown rates did overlap between the 2 sites. Breakdown rates (per dd) of the

TABLE 3. Pearson correlation coefficients between breakdown rates (per degree day) and concentrations of chemical constituents of leaf litter from 7 riparian species from Coweeta Hydrologic Laboratory, North Carolina, and 8 riparian species from La Selva Biological Station, Costa Rica. Bold font indicates statistically significant correlations. $* = p < 0.05$, $** = p < 0.01$.

Chemical constituent	Coweeta	La Selva	Both sites
C	**−0.79***	**−0.73***	**−0.76***
N	0.58	0.03	0.37
P	**0.90****	−0.01	0.29
Lignin	**−0.94****	−0.65	**−0.66***
Cellulose	**−0.77***	**−0.78***	−0.49
Hemicellulose	−0.34	−0.37	−0.16
Condensed tannins	**−0.80***	−0.60	**−0.53***
Total phenolics	−0.10	−0.50	−0.37
Hydrolyzable tannins	−0.06	−0.46	−0.44
C:N	**−0.75***	−0.38	−0.47
N:P	−0.38	−0.10	−0.07

4 slower decomposing species in each site (i.e., *C. elastica*, *L. seemannii*, *Z. longifolia*, and *C. nicaraguensis* in La Selva; *A. rubrum*, *Q. rubra*, *P. strobus*, and *R. maximum* in Coweeta) did not differ significantly ($F_{1,6} = 4.08$, $p > 0.05$). Our results suggest that slow decomposing species in tropical streams can break down at rates similar to those of slow decomposing species in temperate streams. Leaves from *Z. longifolia* lost 95% of their mass in 686 d in headwater streams at La Selva (Ardón et al. 2006), a period that is similar to the 656 d to 95% mass loss reported for *R. maximum* in Coweeta headwater streams (Greenwood et al. 2007).

Differences in leaf breakdown rates between Coweeta and La Selva could have been confounded by the fact that rates were measured in a 3rd-order stream at La Selva and a 1st-order stream at Coweeta. Physical abrasion caused by greater discharge fluctuations in the Sabalo might have led to faster breakdown rates than would have been observed had rates been measured in a smaller stream. Breakdown rates of 4 species measured in the Sabalo stream were 2× to 3× faster than rates of the same species measured in a 1st-order stream at La Selva (Table 4), but the relative differences among species were similar in both streams. For example, the difference in breakdown

rate between *T. integerrima* and *Z. longifolia* was 15× in the Sabalo study stream (Table 4) and 11× in a 1st-order stream (Ardón et al. 2006). Our results agree with previous reports of relatively constant differences in breakdown rates among species under different stream conditions (Webster and Benfield 1986). If all breakdown rates measured in La Selva were scaled to be similar in magnitude to rates at Coweeta (i.e., decreased by a factor of 3), k [per d] would be 2× faster at La Selva than at Coweeta, but k [per dd] would be very similar between sites (mean $k/dd = 0.0008$ in La Selva, 0.0008 in Coweeta). This result supports the hypothesis that the *ranges* in breakdown rates are similar between tropical and temperate streams when breakdown rates are expressed in degree days (Irons et al. 1994).

Differences in breakdown rates between the 2 sites also could have been confounded by the difference in sizes of the litter bags used at the 2 sites (Coweeta, 15 g; La Selva, 5 g). Breakdown rates in litter bags with high initial litter mass are slower than are rates in litter bags with lower initial mass (Reice 1974, Benfield et al. 1979, Campbell et al. 1994, Ruetz et al. 2006). However, the results from these studies are difficult to generalize. Reice (1974) found decreasing breakdown rates of litter packs with increasing pack size only in summer and not in other seasons. Benfield et al. (1979) reported decreasing breakdown rates with increasing leaf mass, but their results were confounded by changes in both leaf pack size and exposure method (packs vs bags of different meshes). Campbell et al. (1994) found that breakdown rates were faster in bags with 0.5 g initial mass than in bags with 3 g initial mass, but breakdown rates were slowest in bags with 1 g initial mass. Ruetz et al. (2006) reported that breakdown rates tended to be slower when leaf mass was higher, but the trend was not statistically significant. These studies illustrate that leaf mass in packs or bags affects breakdown rate, but the direction and magnitude of the effect are difficult to predict. Ruetz et al. (2006) suggested that the size of leaf packs and bags should be carefully selected and that the best approach might be to imitate the natural size of leaf accumulations occurring at each site (as was done in our study).

TABLE 4. Breakdown rates (/d) of 4 common riparian species in the Sabalo (3rd-order stream) and Saltito −100 (1st-order stream) in La Selva Biological Station. F values are from analysis of covariance (ANCOVA). $* = p < 0.05$, $** = p < 0.01$, $*** = p < 0.001$.

Species	Sabalo	Saltito-100	F	Source
Trema integerrima	0.198	0.067	37.74***	Ardón et al. (2006)
Ficus insipida	0.079	0.053	22.53***	Stallcup et al. (2006)
Castilla elastica	0.038	0.010	117.40***	Ardón et al. (2006)
Zygia longifolia	0.013	0.006	8.79**	Ardón et al. (2006)

Are shredders or microbes differentially affecting leaf breakdown in these 2 sites?

Irons et al. (1994) suggested that microbes might be more important than shredders in tropical streams, whereas shredders might be more important than microbes in higher latitude streams. In agreement with this hypothesis, recent studies have reported a paucity of shredders in tropical streams relative to temperate streams (Dobson et al. 2002, Wantzen et al. 2002, Wantzen and Wagner 2006). However, macroinvertebrate shredders do occur in high abundance in some tropical streams (Benstead 1996, Cheshire et al. 2005, Yule et al. 2009). One proposed hypothesis to explain the difference in shredder abundance between temperate and tropical streams is high concentrations of secondary compounds in tropical plant species (Stout 1989, Dobson et al. 2002, Wantzen et al. 2002). Our results do not support this hypothesis. Concentrations of secondary compounds were higher in leaves of species at Coweeta than of species at La Selva, but shredders were more prevalent at Coweeta than at La Selva. Higher abundance (range = 75–164 individuals/litter bag) and biomass (range = 6.4–84 mg/litter bag) of macroinvertebrate shredders occur in Coweeta streams (Wallace et al. 1982, Whiles and Wallace 1997, Eggert and Wallace 2003, Greenwood et al. 2007) than in La Selva streams (abundance 0–2 individuals/litter bag, biomass 0–0.65 mg/litterbag; Rosemond et al. 1998, Ardón et al. 2006, Ardón and Pringle 2008) (based on the same methods used in our study).

Higher water temperatures in tropical than in temperate streams might lead to greater microbial activity in tropical than in temperate streams and might accelerate breakdown rates in tropical streams. Fungal biomass on submerged leaves is higher at La Selva (range = 10–200 mg/g leaf AFDM; Ardón and Pringle 2008) than at Coweeta (range = 5–35 mg/g leaf AFDM; Gulis and Suberkropp 2003). Bacterial biomass on submerged leaves in La Selva also is high (range = 0.01–1 mg C/g AFDM; Ardón and Pringle 2008) and is similar to that observed on *A. rubrum* leaves in an artificially nutrient-enriched stream in Coweeta (range = 0.1–0.9 mg C/g AFDM; Gulis and Suberkropp 2003). These differences in microbial and invertebrate biomasses support the hypothesis that microbial processing might be more important in tropical than in temperate streams, whereas invertebrate shredders might be more important in temperate than in tropical streams (Irons et al. 1994).

Recent studies have focused on the effects of larger macroinvertebrates (shrimp and crabs) on breakdown rates in tropical streams (March et al. 2001, Dobson et al. 2002, Wright and Covich 2005, Crowl et al. 2006). The mesh size of our litter bags probably prevented large macroinvertebrates from entering bags and, thus, reduced their effects on leaf breakdown in La Selva. However, exclusion of large macroinvertebrates with electricity and meshes of different sizes did not significantly alter leaf breakdown rate of *F. insipida* in the Sabalo (Rosemond et al. 1998). Thus, large macroinvertebrates probably do not play a major role in leaf breakdown at La Selva.

Use of standardized analytical techniques to measure leaf chemistry

Use of standardized analytical methods to measure leaf chemistry would facilitate future cross-site comparisons. We selected methods that are widely used by terrestrial ecologists and that are commonly regarded to be the most accurate. The forage fiber technique was used to measure structural compounds because this technique is simpler and more accurate than other commonly used techniques (Ryan et al. 1990). Standard colorimetric assays with standards made from purified tannins from our own samples (i.e., *self-standards*; Appel et al. 2001) were used to measure secondary compounds. Most studies conducted in streams have used commercial tannic acid as a standard, despite recognition in the terrestrial literature that commercial tannic acid can overestimate or underestimate concentrations by up to a factor of 2 (Hagerman and Butler 1989, Appel et al. 2001). Colorimetric methods (after acid-digestion of leaf material) can provide accurate and comparable results for both N and P (Flindt and Lillebo 2005).

In conclusion, our results suggest that leaf chemistry is not as different as expected among these 8 riparian species from La Selva and 7 riparian species from Coweeta (Stout 1989, Wantzen et al. 2002). Contrary to expectations, concentrations of secondary compounds were correlated with breakdown rates of Coweeta species but not of La Selva species. The wider range of breakdown rates of La Selva than of Coweeta species was mainly a consequence of the very fast decomposition rate of *T. integerrima,* and comparisons based on the other species suggest that the variation in breakdown rates is not very different between these 2 sites. However, this conclusion should be interpreted with caution because we sampled only a small fraction of the possible species entering La Selva and Coweeta streams. La Selva has >2000 species in an area ½ the size of Coweeta. Thus, the detritus base of La Selva streams appears to be more species rich than that of Coweeta streams. Future studies should examine the chemical diversity of the detritus base of tropical and

temperate streams with standardized analytical techniques to facilitate comparisons of leaf litter chemistry.

Acknowledgements

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APPENDIX. Common species found along rivers, streams, and wetlands in La Selva Biological Station, compiled from the literature (Lieberman et al. 1985, Hartshorn and Hammel 1994), and expert opinion of O. Vargas (Organization for Tropical Studies), N. Zamora (INBio), M. Grayum (Missouri Botanical Garden), and B. Hammel (Missouri Botanical Garden). Species denoted with an asterisk were used for stream leaf breakdown experiments.

Species

Emergent and canopy tree species restricted to large rivers
  Ficus insipida Willd. (Moraceae)
  Zygia longifolia (Humb. and Bonpl. Ex Willd.)
    Britton and Rose (Fabaceae)
  Ceiba pentandra L. Gaertn. (Malvaceae)
  Cordia lucidula I.M. Johnston (Boraginaceae)
  Inga marginata Willd. (Fabaceae)
  Nectandra reticulata Ruíz and Pavón (Lauraceae)
  Posoqueria latifolia (Rudge) Roem. and Schult (Rubiaceae)
Species of emergent trees common along rivers, streams, and swamps
  Apeiba membranacea Spruce ex Benth (Tiliaceae)
  Carapa nicaraguensis C. DC. (Meliaceae)
  Castilla elastica Sessé ex Cerv. (Moraceae)
  Cecropia obtusifolia Bertol. (Cecropiaceae)
  Clusia minor L. (Clusiaceae)
  Goethalsia meiantha (Donn. Sm.) Burret (Tiliaceae)
  Hernandia didymantha Donn. Sm. (Hernandiaceae)
  Iriartea deltoidea Ruíz and Pavón (Arecaceae)
  Inga ruiziana G. Don. (Fabaceae)
  Luehea seemannii Triana and Planchon (Tiliaceae)
  Myrcia splendens (Sw.) DC. (Myrtaceae)
  Otoba novogranatensis Moldenke (Myristicaceae)
  Pachira aquatica Aublet (Bombacaceae)
  Pentaclethra macroloba (Willd.) Kuntze (Fabaceae)
  Protium panamense (Rose) I.M. Johnst. (Burseraceae)
  Pterocarpus officinalis Jacq. (Fabaceae)
  Socratea exorrhiza (C. Martius) Wendland
  Trema integerrima (Beurl) Standl (Ulmaceae)
  Terminalia oblonga (Ruiz and Pav.) Steud. (Combretaceae)
  Terminalia bucidoides Standl. and L.O. Williams
    (Combretaceae)
  Virola koschnyi Warb. (Myristicaceae)
  Welfia georgii Wenland ex Burret (Arecaceae)
Subcanopy trees and shrubs common along rivers, streams, and swamps
  Acalypha diversifolia Jacq. (Euphorbiaceae)
  Adelia triloba (Muell. Arg.) Hemsl. (Euphorbiaceae)
  Astrocaryum alatum H.F. Loomis (Arecaceae)
  Bactris longiseta Wendland ex Hemsley (Arecaceae)
  Carludovica rotundifolia Wendland ex Hooker F.
    (Cyclanthaceae)
  Calyptrogyne ghiesbreghtiana (Linden and
    H. Wendl.) H. Wendl. (Arecaceae)
  Colubrina spinosa Donn. Sm. (Rhamnaceae)
  Coussarea impetiolaris Donn. Sm. (Rubiaceae)
  Cuphea epilobiifolia Koehne (Lythraceae)
  Cuphea hyssopifolia Kunth (Lythraceae)
  Cuphea utriculosa Koehne (Lythraceae)
  Chione costaricensis Standley (Rubiaceae)
  Cyathea bicrenata Liebm. (Cyatheaceae)
  Grias cauliflora L. (Lecythidaceae)
  Hoffmannia valerioi Standl. (Fabaceae)

APPENDIX. Continued.

Species

  Lonchocarpus oliganthus F.J. Herm (Fabaceae)
  Malvaviscus arboreus Cav. (Malvaceae)
  Miconia impetiolaris (Sw.) D. Don ex
    DC (Melastomataceae)
  Miconia affinis DC (Melastomataceae)
  Myriocarpa longipes Liebm. (Urticaceae)
  Neea laetevirens Standl. (Nyctaginaceae)
  Ocotea cernua (Nees) Mez (Lauraceae)
  Parathesis microcalyx Donn. Sm. (Myrsinaceae)
  Piper auritum Kunth (Piperaceae)
  Piper biolleyi C. DC. (Piperaceae)
  Piper decurrens C. DC. (Piperaceae)
  Piper friedrichsthalii C. DC. (Piperaceae)
  Piper reticulatum L. (Piperaceae)
  Pleuranthodendron lindenii (Turcz.) Sleumer (Salicaceae)
  Psychotria chagrensis Standley (Rubiaceae)
  Psychotria graciliflora Benth. (Rubiaceae)
  Psychotria psychotriifolia (Seem.) Standl. (Rubiaceae)
  Simira maxonii (Standl.) Steyerm. (Rubiaceae)
  Urera laciniata (Goudot) Wedd. (Urticaceae)