

Wood Decomposition of *Cyrilla racemiflora* in a Tropical Montane Forest¹

Juan A. Torres

International Institute of Tropical Forestry, U.S.D.A. Forest Service, Call Box 25000, Río Piedras, Puerto Rico 00928-2500 U.S.A. and Biology Department, Bayamón Technological University College, Bayamón, Puerto Rico 00959-1919 U.S.A.

ABSTRACT

Changes in wood density, nutrient content, and invertebrate populations throughout the decay of *Cyrilla racemiflora* (Cyrillaceae) were compared with those observed in temperate woody tree species. Wood density tended to remain constant as decay advanced except in the late stages. Nutrients (N, P, Ca, Mg) were in highest concentrations in intact bark, surface wood, and wood in advanced decay. Concentrations of N and P were highly correlated, as were concentrations of Ca and Mg. The C/N ratio was determined mainly by changes in N because C tended to remain constant as decay proceeded. The C/N ratio of wood in advanced decay was 79, one of the lowest reported, and the concentration of N was one of the highest reported (0.69%) in studies of wood decomposition. Nitrogen and P were in greater concentrations in the feces of the cerambycid *Parandra cribrata* than in surrounding wood. A total of 138 invertebrate species was identified. The number of species increased as decay progressed. Termites (*Parvitermes discolor* and *Glyptotermes pubescens*) and ants (*Pheidole moerens*, *Paratrechina* spp. and *Solenopsis* spp.) were the most abundant invertebrates, with ants more abundant in snags than in logs. The scarcity of bark beetles and wood borers such as carpenter ants and bees in the wood of *C. racemiflora* contrasted with reports of their presence in dead wood from other tree species.

RESUMEN

Los cambios en la densidad de la madera, contenido de nutrientes y las poblaciones de invertebrados fueron examinados durante la descomposición de los árboles de *Cyrilla racemiflora*. La densidad de la madera mostró una tendencia a permanecer constante, excepto en la última etapa de descomposición. Los nutrientes (N, P, Ca, Mg) se encontraron en grandes concentraciones en la corteza firme, la superficie de la madera y la madera podrida. Las concentraciones de N y P estaban altamente correlacionadas, también las de Ca y Mg. La tasa de C/N fue determinada principalmente por los cambios en la concentración de N, ya que la concentración de C mostró una tendencia a permanecer constante según avanzó al proceso de descomposición. La tasa de C/N en la madera podrida fue de 79, una de las más bajas reportadas, y la concentración de N una de las más altas (0.69%). El N y P se encontró en mayor concentración en la excreta del cerambycido *Parandra cribrata* que en la madera que la rodeaba. En total 138 especies de invertebrados fueron identificados. El número de especies aumentó según avanzaba el proceso de descomposición. Las termitas (*Parvitermes discolor* y *Glyptotermes pubescens*) y las hormigas (*Pheidole moerens*, *Paratrechina* spp., y *Solenopsis* spp.) fueron los organismos más abundantes; las hormigas eran más abundantes en los árboles muertos de pie que en los que yacían en el suelo. La poca abundancia de escarabajos descortizadores de la madera y barrenadores como las hormigas y abejas carpinteras en *C. racemiflora* reflejó un contraste con los reportes de la presencia de estos organismos en la madera muerta de otras especies de plantas.

Key words: *Cyrilla racemiflora*; invertebrates; nutrients; Puerto Rico; tropics; wood decomposition.

DEAD WOOD, A LARGE RESERVOIR OF CARBON, may act as a sink for atmospheric carbon. It is also important in the process of soil organic matter accumulation (Lambert *et al.* 1980) and provides sites for nitrogen fixation (Ausmus 1977, Breznak 1982) and seedling establishment (McCullough 1948, Maser & Trappe 1984, Harmon *et al.* 1986). In addition, decomposing wood is an important habitat

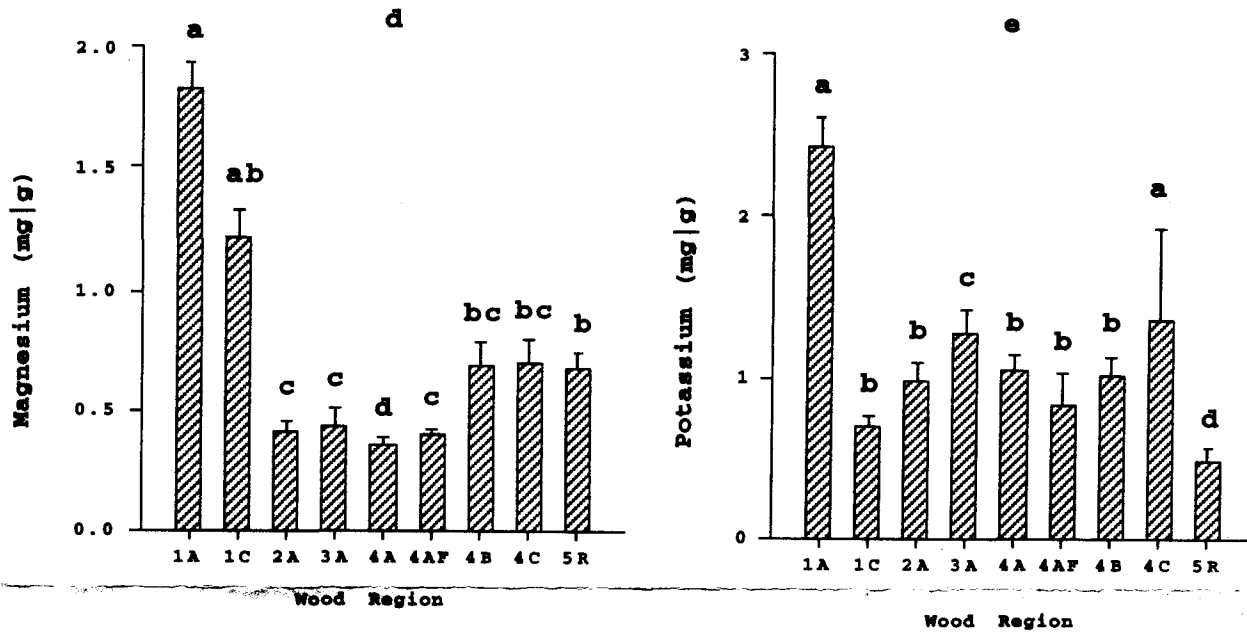
for wildlife (Elton 1966, Cline *et al.* 1980, Harmon *et al.* 1986). Studies on wood decomposition may be useful in the management of agro-forest systems. Litter input from crops generally lacks the lower quality woody components that stabilize nutrient cycling (Anderson & Swift 1983). The study of wood decomposition in the field has practical implications for wood salvage operations, wood selected for use in damp and shaded places, and the regeneration of damaged forest land.

Although wood is the main constituent of tropical forests (Brown & Lugo 1982), few studies have

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ERRATA

1. The correct versions of Figs. 2d and 2e in Wood Decomposition of *Cyrilla racemiflora* in a Tropical Montane Forest (Biotropica 26(2): 124-140) are the following:



2. In Fig. 2c the superscript for the 1A bar is c.

3. In Fig. 3 the correct mean C/N in region 1A is 79.0 and in region 1C is 122.1

addressed the question of wood decomposition. Most decomposition studies of organic matter are based on litter breakdown. However, litter and wood differ in both chemical composition and hardness, and these differences affect the organisms and processes in decomposition (Anderson *et al.* 1978, Swift *et al.* 1979, Edwards 1982, Hong 1986).

The succession of organisms in decomposing logs has been studied for various plant species (Blackman & Stage 1924, Graham 1925, Park 1930, Savely 1939, Park & Auerbach 1954, Deyrup 1981). Invertebrates contribute to wood breakdown in several ways. They disintegrate plant tissues allowing the penetration of water, fungi, and bacteria (Graham 1925, Alle 1926, Batra & Batra 1967, Ausmus 1977). Fragmentation of wood by invertebrates facilitates decomposition by microorganisms (Van der Drift & Witkamp 1959, Edwards *et al.* 1970), increases the loss of material by leaching (Witkamp & Crossley 1966), and facilitates the aeration of wood permitting aerobic respiration (Fager 1968). Invertebrates create spatial heterogeneity, allow the penetration of roots in logs (Maser & Trappe 1984), and affect the distribution of nutrients by translocation and defecation (Savely 1939, Lofty 1974, Petal 1978).

Few studies exist on dead wood invertebrates, especially insects, in the tropics (see Morón *et al.* 1988, Constantino 1992). In Puerto Rico the studies on wood decomposition have been concentrated on the protection of wood against termites and fungi and the service life of fence posts under different preservative treatments (Wolcott 1924, 1946, 1947, 1950; Chudnoff & Goytia 1972).

Cyrilla racemiflora (Cyrillaceae) is a dominant plant species in the palo colorado forests of Puerto Rico. Large accumulations of dead wood of *C. racemiflora* are observed in these forests. The objective of the present study was to compare the changes that occur in wood density, nutrient concentrations, and invertebrates throughout the decomposition of *C. racemiflora* wood with those observed in temperate woods.

METHODS

STUDY SITE AND TREE DESCRIPTION.—The study was conducted during 1988–1989 within the Luquillo Experimental Forest (18°15'N, 65°45'W) in northeast Puerto Rico. The study site was in the Icacos Valley at an elevation of approximately 800 m in the subtropical lower montane wet forest life zone, where mean annual rainfall averages 400 cm and annual mean air temperature is about 22°C with

little month to month variation (Brown *et al.* 1983). The soil is at field capacity throughout most of the year (Ewel & Whitmore 1973).

Cyrilla racemiflora can reach 20 m in height and 2.6 m in diameter in Puerto Rico. In the United States *C. racemiflora* is a small tree or shrub found in swamps and on river banks in the southeast (Little & Wadsworth 1964, Weaver 1986). Mature trees of *C. racemiflora* possess smooth thin reddish-brown bark, the sapwood is light brown, and the heartwood dark reddish-brown. Fresh, green wood is hard (specific gravity about 0.53) and exhibits prominent growth rings (Little & Wadsworth 1964). The large, very old trunks are often crooked and usually hollow, serving as nesting cavities for bees and birds. In the Luquillo Mountains, *C. racemiflora* grows at elevations between 600 and 1000 m in the subtropical lower montane wet and rain forest life zones (Weaver 1986). Trees exhibit slow growth rates suggesting that some may be nearly 1000 years old.

FIELD MEASUREMENTS.—Four sequential states of decay were defined to classify the logs and snags (standing dead trees) (modified from Fogel *et al.* 1973 and Lambert & Cromack 1982). Class I logs (Log I) had bark intact and twigs less than 3 cm in diameter were present; wood texture was sound (visual inspection) and the log elevated from the ground on support points. Invading roots were absent or in the outer bark. Class II logs (Log II) had bark intact but twigs less than 3 cm in diameter were absent. Although the wood was mostly intact, the sapwood could be partly soft. The log was elevated from the ground on support points, and invading roots could be found in the outer and inner bark. Class III logs (Log III) did not have bark or it was partly removed. If present, the sapwood was soft, and the heartwood difficult to penetrate. The log was elevated from the ground on support points or sagging slightly. Invading roots were present in the border of the heartwood. Class IV logs (Log IV) did not have bark or twigs. Wood texture was soft and could be easily penetrated. All portions of the log were on the ground, and roots had invaded the border and interior of the heartwood. For snags, portions of the tree on the ground did not apply and members of Class IV (Snag IV) in most cases were held upright by the presence of the invading roots.

The red color of *C. racemiflora* wood was distinct from the color of other dead woods, thus facilitating its identification. Most of the *C. racemiflora* logs and snags found in the forest belonged to decay

class III. Log recruitment is irregular in space and time and is often episodic. This variability necessitates a large area for adequate sampling (Lambert *et al.* 1980). Therefore, I conducted a systematic sampling (Steel & Torrie 1960, p. 412) of *Cyrilla racemiflora* logs and snags in an effort to obtain equal numbers of samples for each decay class. I sampled 63 logs and 70 snags distributed as follows: Log I = 15, Log II = 19, Log III = 15, Log IV = 14, Class I snags (Snag I) = 16, Class II snags (Snag II) = 18, Class III snags (Snag III) = 18, Class IV snags (Snag IV) = 18.

A cross sectional disk of approximately 5 cm in width was cut from each log or snag using a chain, coping, or bow saw. Since decay resistance increases slightly from the top to the base of a bole (Reis 1973) and density is lower in the extremes than in the center of a log (Healey & Swift 1971), I utilized a stratified random selection method to select the position of the cuts. Samples were taken 15 cm from each end of the bole and at the middle. Wood disks were placed in plastic bags and taken to the laboratory for detailed examination.

WOOD DISK REGIONS.—Using wood texture or structural integrity, I classified the regions of decay in each wood disk (Table 1). A drawing of each disk was made in order to calculate the area of the different regions using a Li-Cor area meter (model Li-3100). The volume of the disk was calculated by multiplying the mean area of the sides by the mean width.

WOOD DENSITY AND CHEMICAL ANALYSES.—A sample was taken from the midpoint of the different regions in each wood disk with a plug cutter or with a core soil sampler. Densities were calculated as the ratio of oven-dry weight (constant weight at 105°C) to fresh volume. Disk cross-sectional density was calculated by weighting cross-sectional density by area of each region.

Samples from the different wood regions in each disk were analyzed at the International Institute of Tropical Forestry laboratory for nitrogen, phosphorus, calcium, potassium, magnesium, and carbon. Before analyses, roots, lichens, plants, and invertebrates were removed from the wood samples. The samples were oven-dried to constant weight at 65°C and ground with a Willey mill through a 0.85 mm (20 mesh) stainless steel sieve. Nitrogen was determined using the semi-micro Kjeldahl procedure (Chapman & Pratt 1979). For P, Ca, K, and Mg, a Beckman plasma emission spectrometer (Spectra Span V) was used. The digestion method recom-

TABLE 1. Explanations of symbols used to classify wood regions.

Symbol	Wood region
1A	bark intact, no decay
1B	bark in advanced decay
1C	surface wood (outer edge)
2A	sapwood intact, no decay
2B	sapwood with fungi, but wood is hard
2C	sapwood with fungi, and wood is friable (could be crushed by hand)
3A	heartwood intact, no decay
4A ^a	xylem intact, no decay
4AF ^a	xylem with cerambycid frass
4B ^a	xylem with fungi, but wood is hard
4C ^a	xylem with fungi, and wood is friable (could be crushed by hand)
5R	humus, soil-like

^a These classifications were used when it was impossible to distinguish sapwood from heartwood by visual inspection.

mended by Luh Huang & Schulte (1985) was used for extraction. For ash content, 1 g of the ground material was burned in a muffle furnace at 490°C for eight hours. All nutrient concentrations are reported on an oven dry basis (105°C).

EXTRACTION AND IDENTIFICATION OF INVERTEBRATES.

—A strip of wood about 2.5 cm wide was cut along the center of each disk with a bench saw or hand ax. The strip was then cut with a hand ax and the pieces placed in a Berlese funnel for mite extraction. The rest of the disk was dissected with a knife or hand ax to extract other invertebrates. The location and abundance of the invertebrates were mapped. The invertebrates were sorted to the species level whenever possible. No attempt was made to classify mites (Acarina) into lower taxonomic units. In order to identify some insects, larvae were placed in petri dishes with the wood substrate in which they were found and raised to the adult stage. The petri dishes were put in a dark cabinet and a few drops of water were added weekly to keep the wood moist. All estimates of animal density and diversity were expressed per 1000 cm³ (average volume of samples was 1339 cm³, SE 130). Since it was not possible to control for the diameter of the wood disk, which affects the volume of the sample and in turn could affect the abundance and number of species, the measures of diversity and species number were weighted. The diversity (as measured by the Shannon-Wiener index) and the number of species for each sample were divided by the volume of the sample and multiplied by 1000 to express the values in terms of 1000 cm³. Each wood disk was defined

TABLE 2. Mean number \pm 1 standard error of invertebrates in 1000 cm³.

Taxon	Logs (N = 63)	Snags (N = 70)
Isoptera	14.99 \pm 9.43	18.51 \pm 10.23
Hymenoptera	7.00 \pm 3.94	36.32 \pm 23.08
Coleoptera	5.34 \pm 2.03	4.71 \pm 1.83
Arachnida	1.13 \pm 0.29	1.47 \pm 0.62
Collembola	1.86 \pm 0.90	0.67 \pm 0.29
Isopoda	0.73 \pm 0.45	0.55 \pm 0.21
Diptera	0.41 \pm 0.23	0.40 \pm 0.23
Diplopoda	0.74 \pm 0.32	0.33 \pm 0.13
Symphyla	0.53 \pm 0.35	0.61 \pm 0.28
Oligochaeta	0.47 \pm 0.32	0.14 \pm 0.08
Zoraptera	0.08 \pm 0.05	0.02 \pm 0.01
Diplura	0.27 \pm 0.11	0.15 \pm 0.12
Homoptera	0.09 \pm 0.06	0.25 \pm 0.21
Hemiptera	0.09 \pm 0.07	0.08 \pm 0.06

as an area of point diversity to obtain repeated estimates of diversity (Magurran 1988). To simplify the study of community patterns, the species were organized into groups of similar ecology (Table 2). The class Chilopoda was grouped together with the Arachnida because they are predators.

STATISTICAL ANALYSES.—Because variances in wood density and nutrient concentrations were not homogeneous and could not be made homogeneous by standard transformations, I conducted approximate tests of equality of means using the Games and Howell method (Sokal & Rohlf 1981, Day & Quinn 1989). All tests were conducted at the experimentwise error rate of 0.05. For carbon and nutrients, the results from logs and snags were combined to obtain larger sample sizes. Statistical analyses for regions 1B, 2B, and 2C were not performed because of small sample sizes for these categories. Only descriptive statistics are presented for the distribution of taxonomic groups between the logs and snags. For the Friedman multiple comparison procedure an experimentwise error rate of 0.10 was used to increase the test power (Daniel 1978). The Bonferroni method was used to adjust the significant level in the Spearman correlations (Day & Quinn 1989, Wilkinson 1989). The Terpstra-Jonckheere test (Jonckheere 1954, Daniel 1978) was used to test the hypotheses that number of species and diversity come from populations whose medians are in a specified order.

RESULTS

DENSITY.—Mean density of class IV logs did not differ from class IV snags. Logs and snags from

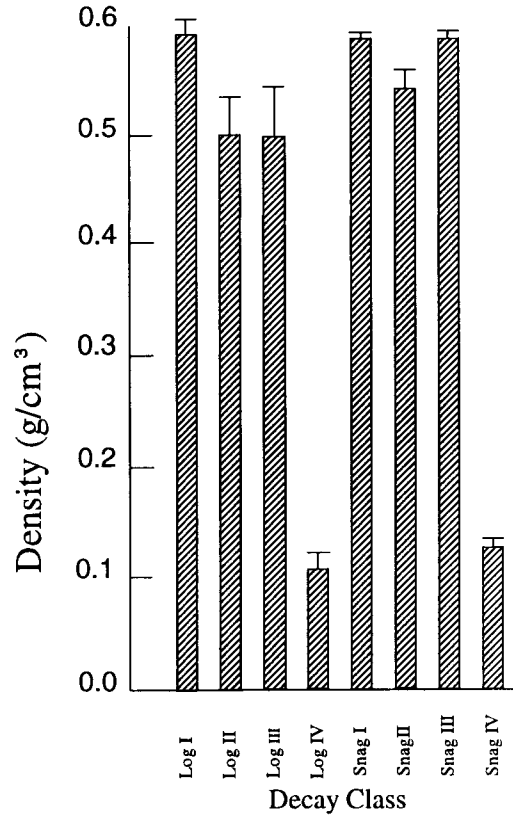


FIGURE 1. Wood density in *Cyrilla racemiflora* decay classes. Bars represent mean values, vertical lines SE.

class IV differed from all other means. No other means differed (Fig. 1). There is a tendency for density in snags to be higher than in logs (while not significant, note that the Games and Howell test is only an approximation and *a posteriori* test with low power). This could be explained by the requirement of greater strength to keep a bole standing than laying down. Also, the variances in wood density tend to be lower in the standing dead than in the laying down boles, which can be related to the need of an adequate strength to remain standing.

CARBON AND NUTRIENTS.—Patterns of distribution of nitrogen and phosphorus in different wood regions were similar (Fig. 2a and 2b). The humus/soil-like (5R), the surface wood (1C), and intact bark (1A) showed the highest concentrations. The presence of cerambycid frass increased concentrations in the heartwood significantly.

Concentrations of calcium (Fig. 2c) and magnesium (Fig. 2d) in the intact bark were the highest. Intact sapwood and heartwood did not differ in

concentration. There was a tendency for both elements to increase as decay proceeded.

The distribution of potassium (Fig. 2e) was quite different from the distribution of other nutrients. The surface wood (1C) and humus/soil-like (5R) regions had the lowest concentrations of potassium. This is related to the fact that potassium is highly mobile and subject to leaching. Intact bark had the highest K concentration. The C/N ratios were highest in the intact wood (2A, 3A, 4A) and lowest in bark, surface wood, and humus/soil-like (Fig. 3). These changes in the C/N were principally influenced by the variability in the concentration of nitrogen. The highest ratios were found in the heartwood and intact xylem (4A). The presence of cerambycid frass and fungi in the xylem lowered this ratio.

Spearman correlations using Bonferroni-adjusted probabilities showed that the distributions of nitrogen and phosphorus were highly correlated ($r = 0.89$, $P < 0.001$, $N = 291$). Concentrations of the multivalent cations (Mg^{2+} and Ca^{2+}) were also highly correlated ($r = 0.77$, $P < 0.001$, $N = 291$). Carbon was negatively correlated with all the elements studied. The highest negative correlations corresponded to carbon-phosphorus ($r = -0.72$, $P < 0.001$) and carbon-nitrogen ($r = -0.70$, $P < 0.001$). Although significant, the correlations of potassium with phosphorus, calcium, and magnesium were low. There was no significant correlation between potassium and nitrogen ($r = 0.14$, $P = 0.28$).

INVERTEBRATES.—A total of 138 different species was identified in the decomposing wood. Densities in different decay classes are indicated in Appendix 1. The medians of species' numbers increased with decay class for the logs (Jonckheere-Terpstra test, $Z = 5.82$, $P < 0.001$) and the snags ($Z = 5.42$, $P < 0.001$) (Fig. 4a). The medians of diversity (Fig. 4b) in each wood disk increased with decay class in the logs (Jonckheere-Terpstra test, $Z = 5.63$, $P < 0.001$) and the snags ($Z = 5.68$, $P < 0.001$).

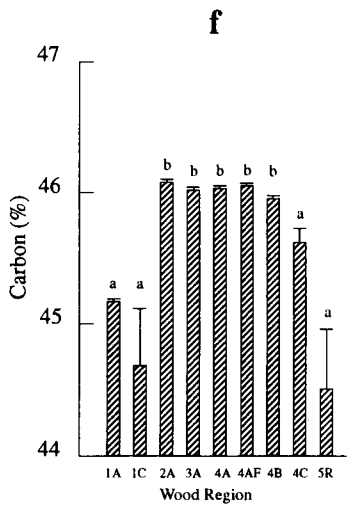
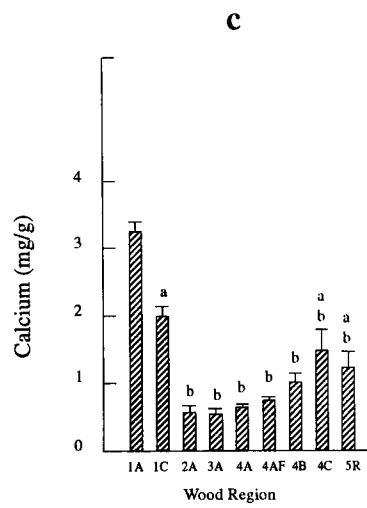
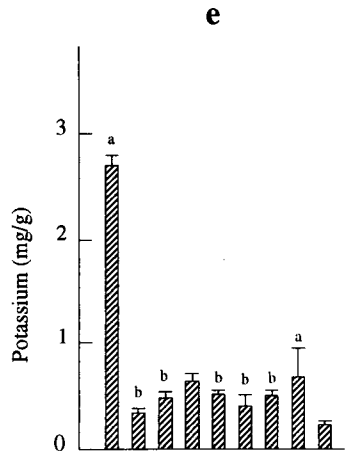
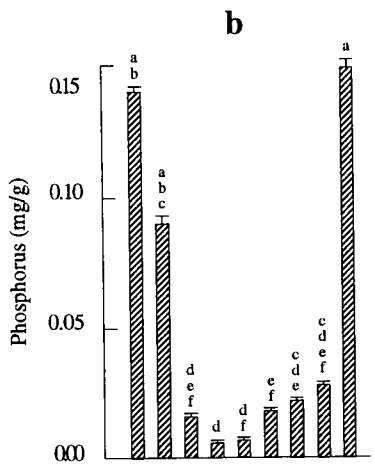
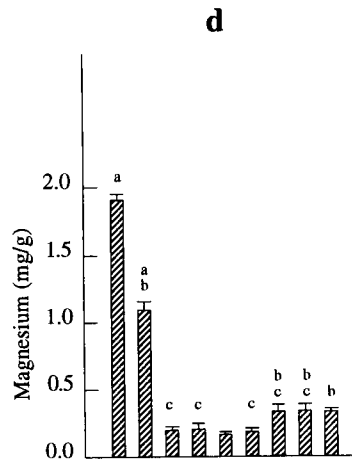
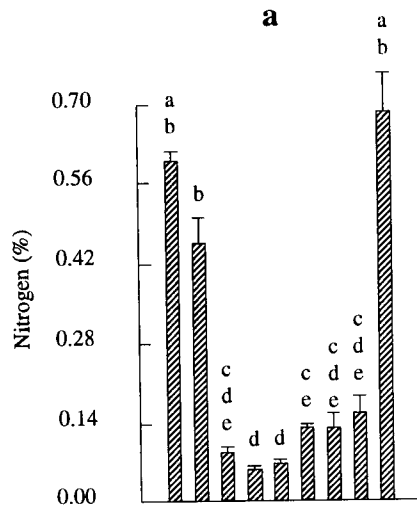
The densities of the taxonomic groups (Table 2) depended on the decay class (Friedman test statistic = 52.48, $P < 0.001$ assuming χ^2 with 7 df).

A multiple-comparison procedure (Daniel 1978, $\alpha = 0.10$) showed the community in Log IV differed from the others except Snag III and Snag IV. The community found in Snag IV differed from Log I, Log II, Snag I, and Snag II. In summary, there was a tendency for the organisms found in the first two decay classes to co-occur. Similar species were also observed in the last two stages of decay in logs and snags.

Termites (Isoptera) were the most abundant invertebrates, followed by ants (Hymenoptera: Formicidae) and then Coleoptera (Table 2). The termite *Glyptotermes pubescens* was not found in highly decayed wood, but *Parvitermes discolor* thrived. Members of the following groups were more common in logs than in snags: Collembola, Diplopoda, Oligochaeta, Zoraptera, and Diplura (Table 2). These groups tend to be associated with the soil fauna and increased in abundance in the last stages of decay because they cannot tunnel into sound wood. Predators (Arachnida, Chilopoda, and Hemiptera) were more common in the late stages and presumably use the wood as refugia, breeding, or hunting grounds. The predators could not become part of the decomposer community until borers (beetles and termites) made channels in the wood. Diptera larvae were uncommon in the first stages of decomposition most likely because of the lack of mouthparts to tunnel into the wood, and the absence of fungi for larval consumption (Deyrup 1976).

Ants were more common in snags. Higher abundance of ant nest in snags could be related to a lower moisture environment. The ant species with the highest number of nests was a predator Ponerinae, *Pachycondyla stigma*, which is rarely seen foraging outside the wood in which it nests. *Pheidole moerens* (Myrmicinae) was next in nest abundance and is considered a generalized scavenger. The carpenter ant, *Camponotus* sp., and *Myrmelachista ramulorum* are abundant in dead dry wood (Smith 1936) but were found only once in *C. racemiflora*. The carpenter bee *Xylocopa mordax* which uses many species of trees for nesting was also absent from *C. racemiflora*. Wood density might have been the reason for the scarcity of these species in *C. racemiflora*.

FIGURE 2. Nutrient concentrations in different wood regions. See Table 1 for explanations of symbols. Bars represent mean values and vertical lines SE. Sample size 1A = 65, 1C = 22, 2A = 17, 3A = 19, 4A = 64, 4AF = 32, 4B = 28, 4C = 9, and 5R = 35. Bars with different superscripts are significantly different according to the Games and Howell Test.



The cerambycid *Parandra cribata* was found in all stages of decay. It bored the sound heartwood of *Cyrilla racemiflora* creating channels that allowed penetration of roots and other organisms into the boles. *Parandra cribata* created circular channels across the wood of *C. racemiflora* that were invaded by a white polypore fungus. In this manner, the cerambycid and the fungus were responsible for the creation of cavities in the trees. Common entrance points for the cerambycids were broken tree limbs.

The order Coleoptera exhibited the highest number of species, however members of the Scolytidae (bark beetles) were rare. Only four specimens belonging to three species of scolytids were found. The scolytids were restricted to decay class Snag I. A large proportion of the coleopterans were immature. Larvae of the tenebrionid *Arrhabeus* sp. were one of the few organisms that could penetrate the dead sound wood of this tree. Though the adult of this species is about 2 mm in length, it takes several months for the larvae to reach the adult stage. After reaching the adult stage, this species remained in torpor.

Patterns of distribution of organisms showed that wood regions with high nitrogen and phosphorus concentration, such as intact bark and sapwood, had very few organisms. However, elemental analysis is difficult to interpret in terms of the accessibility of the nutrients to the organisms (Swift *et al.* 1979). The highest concentrations of organisms were found in the surface wood (1C) and the humus/soil-like (5R). These regions were high in nutrient concentrations and were soft, which could explain the presence of higher numbers of organisms because of low mechanical constraints to penetration.

The decomposition on *C. racemiflora* differed from the pattern observed in other species (Maser & Trappe 1984). Usually the inner bark is the first substrate attacked by insects followed by the sapwood. In *C. racemiflora*, the heartwood is frequently the first substrate attacked by *P. cribata* and the tenebrionid *Arrhabeus* sp. This could be one of the reasons explaining the propensity for cavity development in the heartwood of this species. However, due to its greater volume, the heartwood takes longer to decompose than the other wood regions. Standing dead *C. racemiflora* trees in the first decay class were extremely rare. *Cyrilla racemiflora* starts new sprouts when it contains just a small amount of live bark and sapwood. Aboveground adventitious roots, which extract nutrients from dead areas of the same tree or nearby trees, allow recovery of *C. racemiflora*.

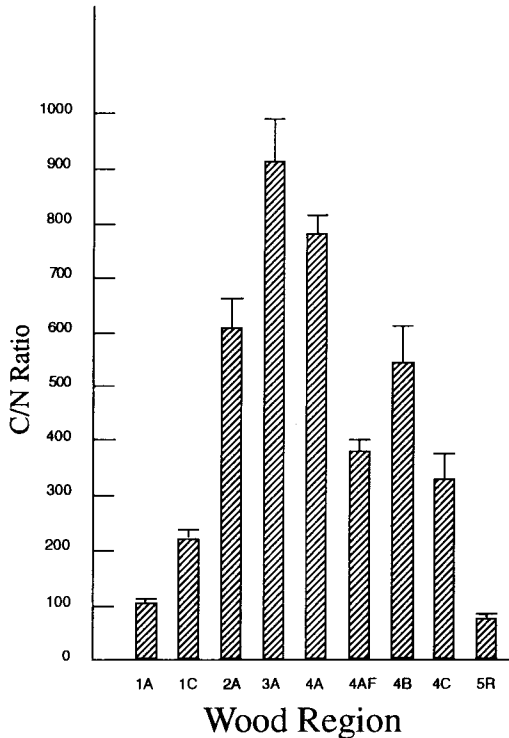
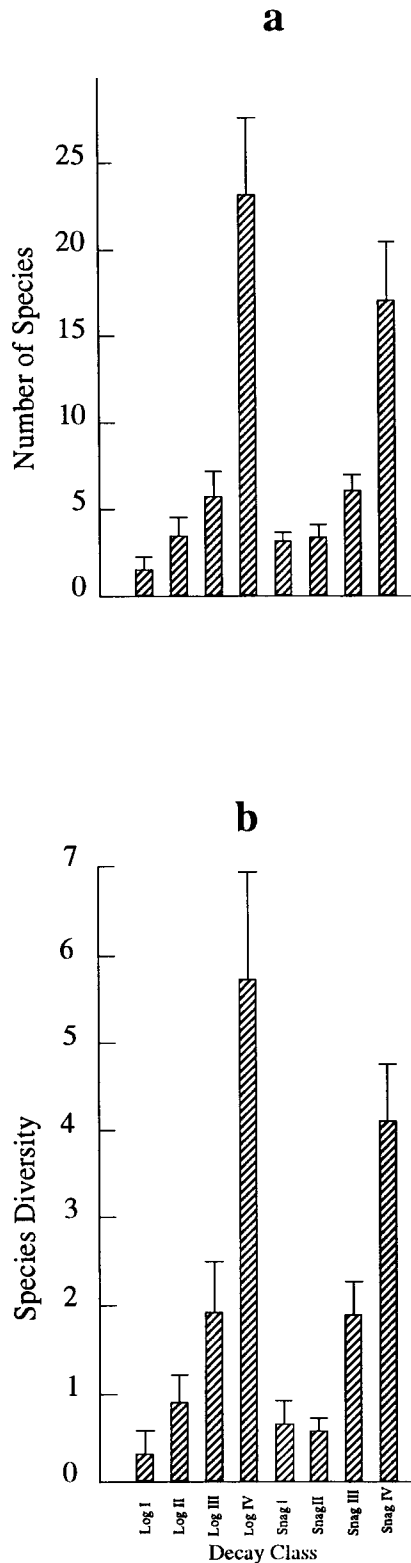


FIGURE 3. Carbon nitrogen ratio in different wood regions.

DISCUSSION

WOOD DENSITY.—Wood density tended to remain constant (except decay class IV) as decay proceeded in *C. racemiflora*. This is related to the fact that heartwood density was higher than sapwood density, and sapwood decomposes faster than heartwood. As decay proceeded, the sapwood tended to slough off and the density of the log corresponds mainly to the heartwood. Sometimes disk cross-sectional density increased as decay proceeded. This tendency is expected in trees with heartwood higher in density than sapwood and heartwood highly resistant to decomposition. Consequently the use of density as an indicator of decay stage is unreliable. Also, Harmon *et al.* (1987) found that density stays fairly constant despite decay in *Pinus jeffreyi* logs. Decay rates may be underestimated when only changes in density are taken in account (Graham & Cromack 1982).

CARBON AND NUTRIENTS.—Carbon concentration tended to remain close to 46 percent as decay proceeded in *C. racemiflora*. The value is smaller than is reported from temperate zone logs. The C con-



centration in temperate zone logs exhibits a tendency toward constancy between 50 and 60 percent as decay proceeds (Ausmus 1977, Lambert *et al.* 1980, Harmon *et al.* 1987). The present study confirms that carbon/element ratios in wood regions mainly reflect changes in concentration of the element in the denominator because of constancy in C concentration (Lambert *et al.* 1980).

The C/N ratio in advanced decay of *C. racemiflora* is one of the lowest reported. This is related to the high N content (0.69%). Harmon *et al.* (1987) reported an average N concentration of 0.26 percent in well decayed wood from four temperate plant species. Nitrogen in intact bark of *C. racemiflora* was higher than in temperate zone trees (Merrill & Cowling 1966, Allen *et al.* 1974, Anderson *et al.* 1978, Harmon 1992). The concentration of N in *C. racemiflora* sapwood (intact) and heartwood (intact) was similar to that in temperate zone trees, but sapwood N concentration was lower than in most tropical tree species (Merrill & Cowling 1966). Also, the percent of N in bark and wood in advanced decay was lower in balsam fir (*Abies balsamea*) than in *C. racemiflora* (Lambert *et al.* 1980).

The highest concentrations of Mg, Ca, and K were found in the intact bark. The concentration of N and P in bark was the second highest, comparable to the concentration in advanced decay logs. This pattern is consistent with studies in temperate trees where intact bark has a higher nutrient concentration than intact wood (Merrill & Cowling 1966, Allen *et al.* 1974, Basham & Cowling 1976, Lambert *et al.* 1980, Abbott & Crossley 1982, Harmon 1992) and stresses its importance as a nutrient pool for several elements. Although *C. racemiflora* whole bark (intact) was rich in nutrients, few invertebrates were located in it. Phosphorus in bark appears to be higher in *C. racemiflora* than in temperate zone trees, and its concentration in sapwood and heartwood was low, similar to trees in that zone (Harmon 1992).

The sequence from 3A (intact heartwood) to 5R (humus/soil-like) (Figs. 2a-f) represents a progression in wood decomposition. In the sequence, Ca increased in concentration except in the humus/soil-like. This was contrary to findings in balsam fir where Ca diminishes as decay proceeds and then increases in concentration in buried wood (Lambert

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FIGURE 4. Number of species per 1000 cm³ (a) and the Shannon-Wiener diversity index (b) by decay class. Bars represent means and vertical lines SE.

et al. 1980). Both N and P increased as decay proceeded. Potassium did not exhibit a consistent pattern; the lowest concentrations of K were associated with wood regions that exhibit greater exposed areas (surface wood, heartwood with frass, humus/soil-like). The boring activities of invertebrates in these areas increased the penetration of water and the likelihood of K leaching. Magnesium tended to remain close to 0.40 mg/g in less decayed wood and then increased in concentration to 0.68 mg/g which remained almost constant in more decayed wood. The dynamics of Mg differed from that observed in balsam fir where an orderly decline in the concentration of Mg was observed (Lambert *et al.* 1980).

The presence of apogeotropic and adventitious roots in *C. racemiflora* could be an alternate route for the removal of nutrients from dead wood. This tree can send roots to the dead parts of the tree and the bark of live trees to obtain nutrients. This mechanism of nutrient conservation may be more common in montane rain forest tree species as compared to lowland tropical rain forest species (Herwitz 1991). Also, decayed hollow cores as found in many *C. racemiflora* trees have been proposed as a mechanism of mineral trapping (Janzen 1976).

INVERTEBRATES.—The 138 invertebrate species identified in *Cyrtilla racemiflora* were low compared with wood invertebrates in temperate zone dead trees (Savely 1939; Howden & Vogt 1951; Wallace 1954; Fager 1968; Deyrup 1975, 1976). The low species number in *C. racemiflora* is believed to be a reflection of insularity, elevation, high humidity, and probably chemical composition (Martorell 1945; Peck 1970, 1972; Nevling 1971; Allan *et al.* 1973; Benedict 1976; Snyder *et al.* 1987; Liebherr 1988). Dead trees from lower elevations in the Luquillo Experimental Forest (*e.g.*, *Sloanea berteriana*, *Inga vera*) show a higher diversity of invertebrates, that may surpass the diversity reported from temperate zone logs.

In the order Hymenoptera, parasitic species were absent in *C. racemiflora* and only the family Formicidae was present. A greater number of Hymenoptera families inhabit temperate logs, among them several parasitic hymenopterans that attack bark beetles (Savely 1939, Howden & Vogt 1951, Deyrup 1975). The low abundance of bark beetles in *C. racemiflora* could explain the absence of parasitic Hymenoptera. However, the number of ant species (16 species) was higher in *C. racemiflora* compared to Douglas-fir (4 species) and *Pinus virginiana* (9 species). Savely (1939) reported only five ant species

on pines and seven on oaks, but ants were present either under bark or running over the logs in every oak log on the ground for 3 years. Members of the ant genus *Camponotus* did not play an important role in the decomposition of *C. racemiflora* as they do in Douglas fir (Maser & Trappe 1984).

Beetles (Coleoptera) exceed other insect groups in number of species in temperate zone trees in the United States (Wallace 1954, Deyrup 1976). There are 223 species of beetles known to breed in bark and wood of Douglas fir (Deyrup 1976). Among them are 52 species of cerambycids, and 22 species of buprestids (Deyrup 1981). In contrast, only 3 species of cerambycids but no buprestid were found in *C. racemiflora*. Members of the Siricidae (Hymenoptera), present in temperate dead wood, were also absent in *C. racemiflora*. Fifty species of scolytids inhabit Douglas fir (Deyrup 1976), but only three species were found in *C. racemiflora*. Although beetles were the dominant order in terms of species numbers, the proportion of beetles in *C. racemiflora* was lower (38%) than in the pine and oak logs (63%) examined in the temperate United States (Savely 1939). This is related to the low number of scolytids, cerambycids, and buprestid and a high number of ant species in *C. racemiflora*. Savely (1939) listed several species of mollusks in his study, but mollusks were not encountered in the present study.

The number of invertebrate species increased as decay proceeded in *C. racemiflora*. In pine stumps located in clearings, Wallace (1954) encountered an increasing number of insect species as decay proceeded but in the contiguous forest there was a decrease in species numbers after the cambium feeders vanished. In *Pinus virginiana* the number of species diminished through time (Howden & Vogt 1951). The decrease in *P. virginiana* was related to a reduction in nutrients for the wood-boring forms which were replaced by saprovores in the late stages of decay. An apparent reduction in species number was also observed in pines as phloem feeders were replaced by saprophytic or mycetophagous insects, but an increase in species numbers was observed in oaks (Savely 1939).

Parandra cribata, the most common cerambycid in *C. racemiflora*, persisted through almost the entire process of decomposition. Cavities created by the feeding activities of this cerambycid permitted the penetration of fungi and water into boles thus facilitating wood decomposition. Cerambycids can digest cellulose with the help of bacteria in their hindgut, which makes them one of the most important wood decomposers (Edwards 1974). In ad-

dition, the presence of higher N and P concentrations in the frass of this cerambycid could hasten decomposition (Van der Drift & Witkamp 1959, Bletchly 1969, Reis 1973, Käärik 1974, Swift 1977, Swift *et al.* 1979, Lambert *et al.* 1980, Aumen *et al.* 1983, Maser *et al.* 1988). Probably the activity of microorganisms was the factor responsible for the higher N concentration in the cerambycid frass (Ausmus 1977). Also, P is the element most in demand by wood-decomposer fungi (Frankland 1982) and the rate of decay of wood by fungi is directly related to its N content (Merrill & Cowling 1966). Since wood usually contains less than 1 percent of N as protein or protein precursors, this material might limit the organisms that a log can support (Fager 1968). The supply may be increased by nitrogenous excretory products, especially from those animals such as ants, spiders, and centipedes that feed largely outside the logs. Nevertheless, leaf litter rich in N retards lignin decomposition (Berg 1986), and soft-rot fungi attack on *Pinus radiata* sapwood decreases as the concentration of N or P increases (Butcher 1976).

Termites and ants were the dominant insect groups in *C. racemiflora*, but only two species of termites were found in *C. racemiflora*. The low number of termite species in *C. racemiflora* is related to insularity and elevation (Martorell 1945, Collins 1989, Constantino 1992). Members of the beetle families Passalidae and Melolonthidae, important in the decomposition of wood in the tropics (Morón *et al.* 1988), were absent from *C. racemiflora*.

Heteromurus sp. (Collembola) was found in almost all decay classes. The other six collembolan species were located mostly in fallen logs. The number of collembolan species is comparable with those found in pine and oaks by Savely (1939), but in Savely's work the collembolans seem to discriminate less between decay stages.

RATES OF DECOMPOSITION.—The Lang and Knight (1979) proposition that wood in the tropics decomposes much faster than in the temperate zone, largely

because it is attacked more by termites and ants, is not completely correct. Ants do not use wood as food. Ants use wood only as nesting sites, and few species have the capacity to chew sound wood. Many ants depend on wood borers (mostly coleopterans) to penetrate the wood. In highly decayed wood, ants can excavate their own galleries. However, ants can be important in wood decomposition by bringing limiting nutrients from the outside to the interior of the logs. Termite abundance and many insect species tend to decrease with elevation (Martorell 1945, Flint 1964, Darlington 1970, Janzen 1973, Janzen *et al.* 1976, Torres & Canals 1983, Snyder *et al.* 1987, Collins 1989), suggesting that decomposition rates are different in different tropical life zones. Lang and Knight (1979) also proposed that the warm and humid forest floor in the tropics favors invertebrate activity through the year. *Cyrtilla racemiflora* is mainly located in the subtropical lower montane wet and rain forests in Puerto Rico, where dead wood is waterlogged most of the time thus retarding decomposition. Wood whose void volume is filled with water will decay slowly because of the exclusion of oxygen required by decomposers (Boyce 1929, Hunt & Garratt 1967, Käärik 1974, Swift *et al.* 1979, Harmon *et al.* 1986). Furthermore, the cool temperature of the subtropical lower montane and rain forests in Puerto Rico (caused by cloud cover, rainfall, and sometimes winds) also contributes to the low decay rate of *C. racemiflora*.

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APPENDIX. Continued.

Class	Order	Family	Species	Decay class									
				LogI	LogII	LogIII	LogIV	SnagI	SnagII	SnagIII	SnagIV		
			<i>Linepithema mellea</i>	0.22	—	—	—	—	—	0.07	—	—	—
			<i>Myrmelachista ramulorum</i>	—	—	—	—	—	—	—	—	0.04	—
			<i>Pachycondyla stigma</i>	—	0.06	1.29	0.95	—	—	0.14	0.18	1.38	—
			<i>Paratrechina cispa</i>	—	—	—	14.20	—	—	—	—	0.65	—
			<i>Paratrechina myops</i>	—	—	—	0.36	—	—	—	—	—	—
			<i>Paratrechina steinheili</i>	—	—	—	—	—	—	0.07	—	31.4	—
			<i>Pheidole moerens</i>	—	0.03	5.10	5.46	1.98	—	0.11	0.11	13.10	—
			<i>Solenopsis azteca?</i>	—	—	—	—	—	—	—	—	1.16	—
			<i>Solenopsis corticalis</i>	—	—	—	—	—	—	—	—	4.21	—
			<i>Solenopsis pygmaea</i>	—	—	—	—	—	—	0.04	—	0.07	—
			<i>Strumigenys rogeri</i>	—	—	4.34	—	—	—	—	—	—	—
			<i>Wasmannia auropancinctata</i>	—	—	—	—	—	—	—	—	0.07	—
Isoptera		Kalotermitidae	<i>Glyptotermes pubescens</i>	—	4.77	1.83	—	34.00	—	8.39	11.9	—	—
		Termitidae	<i>Parvitermes discolor</i>	—	2.67	28.10	17.6	7.84	—	1.08	—	6.97	—
Microcoryphia		Machilidae	sp1	—	—	—	0.36	—	—	—	—	—	—
Neuroptera		— ^b	sp1 (larvae)	—	—	—	0.12	—	—	—	—	—	—
Orthoptera		Blattellidae	<i>Aglaopteryx</i> sp.	—	—	—	—	0.08	—	—	—	0.29	—
		Gryllidae	<i>Orocharis</i> sp.	—	—	0.03	0.59	—	—	—	0.04	1.09	—
Psocoptera		Liposcelidae	<i>Liposcelis</i> sp.	—	—	—	—	—	—	—	—	0.07	—
		Psocidae	sp1	—	—	—	0.12	—	—	—	—	—	—
		— ^b	sp1	—	—	—	—	0.08	—	—	—	—	—
Thysanoptera		Phlaeotripidae	sp1	0.04	—	—	—	—	—	—	—	—	—
Zoraptera		Zorotypidae	<i>Zorotypus barberi</i>	—	0.27	0.13	0.24	—	—	0.04	0.14	—	—
Oligochaeta	— ^c	—	—	0.09	0.06	0.03	0.95	—	—	0.04	0.25	0.22	—
Symphyla	none	Scolopendrellidae	sp1	—	0.12	0.09	0.95	—	—	0.36	0.07	1.45	—

^a Dashes represent a density of 0.00.

^b Undetermined.

^c The orders Tubificida and Lumbricina were present.