

EARLY DETERIORATION OF COARSE WOODY DEBRIS¹

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Abstract—Coarse woody debris (CWD) is an important structural component of southern forest ecosystems. CWD loading may be affected by different decomposition rates on sites of varying quality. Bolts of red oak and loblolly pine were placed on plots at each of three (hydric, mesic, and xeric) sites at the Savannah River Site and sampled over a 16-week period. Major changes were in moisture content and nonstructural carbohydrate content (total carbohydrates, reducing sugars, and starch) of sapwood. Early changes in nonstructural carbohydrate levels following placement of the bolts were likely due to reallocation of these materials by sapwood parenchyma cells. These carbohydrates later formed pools increasingly metabolized by bacteria and invading fungi. Most prevalent fungi in sapwood were *Ceratocystis* spp. in pine and *Hypoxylon* spp. in oak. Although pine sapwood became blue stained and oak sapwood exhibited yellow soft decay with black zone lines, estimators of decay (specific gravity, sodium hydroxide solubility, and holocellulose content) were unchanged during the 16-week study period. A small effect of site was detected for starch content of sapwood of both species. Fungal biomass in sapwood of both species, as measured by ergosterol content, was detectable at week zero, increased somewhat by week three and increased significantly by week 16.

INTRODUCTION

Coarse woody debris (CWD) may influence a site for hundreds of years in the form of snags, logs, chunks of wood, large branches, or coarse roots. CWD has many characteristics that contribute to the health of forest ecosystems, such as creating habitats for wildlife, plants, and microorganisms. Through degradation these organisms recycle nutrients to the soil which enhances soil nutrient and energy content, thus creating richer soils for tree growth (Harmon and others 1986, Maser and others 1988, and Spies and Cline 1988). Mortality and breakage of living trees add CWD, as do harvest operations, while fire may remove or transform it (Van Lear 1996). Sporadic disasters such as hurricanes and insect and disease epidemics may also add CWD to the forested ecosystem.

Our understanding of the dynamics of CWD loading in southern forests is limited to one study (Waldrop 1996), which used a forest-succession model to predict loading. That study suggested that CWD dynamics could be strongly influenced if inputs (limbfall or tree mortality) and outputs (decomposition) of CWD vary between different types of forest sites. Little information is available on decomposition rates or the number and types of organisms that cause decay which occur on each site type.

This study examines the populations of bacteria and fungi that occur across three forest types. These sites were defined using the landscape ecosystem classification (LEC) approach developed by Barnes and others (1982) for forests in Michigan and applied to the South Carolina upper coastal plain by Jones (1991). To differentiate among sites there must be interrelationships between vegetation and landform, between vegetation and soils, and between landform and soils (Jones 1991). We previously reported the populations of bacteria that occurred in CWD by site class and species within the first 16 weeks following placement of bolts of red oak (*Quercus* spp.) and loblolly pine (*Pinus taeda* L.) on these sites (Porter and others 1998). In addition, chemical decomposition of the sapwood of both species was monitored during the 16-week period and it is the results of this aspect which are reported here.

METHODS

In April 1995 sample trees between 20-30 cm diameter at 1.4 m above ground were felled and cut into 0.5 m-long bolts. Red oaks were taken from the Clemson Experimental Forest, Pickens County, SC, and the loblolly pines were taken from the Savannah River Site, Aiken County, SC. The freshly cut bolts were placed on the study plots within 2-3 days after the trees were felled. The study sites were on LEC units established on the Savannah River Site and included three sites each of varying moisture availability: xeric, mesic, and hydric. The xeric sites were in pine plantations with little or no undergrowth. The mesic sites were also in pine plantations but there was more undergrowth and organic debris present. The hydric sites were located in mixed-species stands with dense understories. Since hydric sites were also located near streams, the soil was very moist during the study period and usually had some standing water. LEC classifications were used in other CWD studies by Bailey (1994) and Hare (1992).

On each LEC unit, a square plot was established and eleven sample bolts of each species were placed on the ground with the longitudinal axis of the bolt parallel with the ground. The surface of the bolt in contact with the ground was marked for orientation purposes during subsequent sample preparation.

The sample bolts were collected at 3, 6, 10, and 16 weeks after placement, in addition to controls processed immediately after the trees were felled. A randomized system for bolt selection was created by using a time schedule for the collection of two bolts of each species from each site during the different sampling periods. The bolts were taken to Clemson University and broken down for analysis the day following collections.

As the bolts were processed, freshly cut cross-sectional disks were removed and further subdivided into sapwood (upper and lower) and heartwood (upper and lower). After preliminary analyses indicated that there were no differences between upper and lower samples, they were

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combined. Fresh samples were weighed, dried at 105 °C to a stable weight, and then reweighed and moisture content determined based on oven dry weight. These samples were then used for extraction and quantification of various chemical components. Duplicate samples were also oven dried as described above and then briefly dipped in melted paraffin and specific gravity determined based on their water displacement and oven dry weight.

Non-Structural Carbohydrates

Non-structural carbohydrates are those components of woody cells that are located in the cytoplasm and are not a part of the cell wall matrix. Subsamples of 20-60 gm of oven-dried wood tissues were ground in a Wiley mill to pass a 40-mesh screen. Soluble sugars were extracted with 80 percent ethyl alcohol for 6 hours in Soxhlet extractors. Aliquants were assayed for total carbohydrate by the phenol-sulfuric acid method (Dubois and others 1965) and for reducing sugars (Nelson 1944). Starch was extracted enzymatically from the sugar-free residue by using Enzyme Method 3 of Rose and others 1991. All determinations were performed in triplicate.

Preparation of Extractive-Free Wood

For the subsequent chemical analysis, extractive-free wood was prepared using the procedure of ASTM D1105 (1980b).

One Percent Caustic Soda Solubility

This test measures the degree of decay that has taken place and mainly extracts hemicellulose and degraded cellulose.

The procedure outlined in ASTM D1109-56 (1980c) was utilized.

Holocellulose

This test measures holocellulose plus hemicellulose. Both components are easily degraded by many microorganisms. Each sample consisted of 2.0 g of extractive-free 60-80-mesh wood meal and was analyzed according to the procedure outlined in ASTM D1104 (1980a).

Fungal Biomass

Fungal biomass is difficult to quantify in woody tissues. Ergosterol is produced only by certain higher fungi and has been used as an estimator of fungal biomass. Ergosterol was extracted and saponified with irradiation (Young 1995). Ergosterol was separated from the alkaline methanol irradiation buffer using a lipophilic copolymer. Total ergosterol was measured by HPLC using a 4.6 X 150 mm Sentry Shield RP₈ 3.5 µm column (Waters Corporation, Milford, MA).

RESULTS AND DISCUSSION

Oak

The initial moisture content did not differ significantly between heartwood and sapwood (81.8/77.6 percent) (table 1), but a significant difference was detected by week 3 (72.1/65.5 percent), and both continued to decrease through week 16 (65.4/54.8 percent). Both heartwood and sapwood were drying out but the sapwood dried at a somewhat more

Table 1—Chemical composition of oak bolts

Attribute	Control	Weeks of exposure			
		3	6	10	16
Moisture content ^a					
Heartwood	81.82a ^b	72.08a	70.57a	67.93a	65.35a
Sapwood	77.62a	65.51b	61.89b	57.22b	54.78b
Specific gravity ^c					
Heartwood	.673a	.689a	.701a	.701a	.719a
Sapwood	.630b	.625b	.591b	.571b	.554b
Total carbohydrates ^d					
Heartwood	20.66a	13.80a	13.89a	12.17a	11.90a
Sapwood	18.72a	23.28b	10.76b	8.17b	6.36b
Reducing sugars ^d					
Heartwood	29.48a	13.96a	14.84a	9.82a	8.65a
Sapwood	11.15b	16.32a	5.16b	2.74b	3.36b
Starch ^d					
Heartwood	33.55a	35.16a	35.71a	30.34a	30.39a
Sapwood	50.15b	36.36a	34.12a	31.06a	30.74a
Caustic soda solubility ^e					
Heartwood	24.43a	22.66a	22.72a	22.00a	21.32a
Sapwood	23.42a	23.06a	21.79a	21.56a	20.71b
Holocellulose ^e					
Sapwood	71.24	73.07	71.65	71.56	71.86
Ergosterol ^f					
Sapwood	2.89	59.88	74.90	48.64	76.52

- ^a = (percent), of fresh wood, based on oven-dry weight.
^b = Means within a column followed by the same letter are not different at p = 0.05.
^c = Based on oven-dry weight and oven-dry volume.
^d = (mg/g), of oven-dry weight of unextracted wood.
^e = (percent), of oven-dry weight of unextracted wood.
^f = (µg/g), of oven-dry weight of unextracted wood.

Table 2—Chemical components of oak sapwood by LEC site

Attribute	Weeks of exposure			
	3	6	10	16
Moisture content ^a				
Hydric	64.49a ^b	65.76a	62.37a	60.52a
Mesic	66.34a	58.45a	56.85b	53.76b
Xeric	65.71a	61.45a	52.46b	50.08b
Specific gravity ^c				
Hydric	.622ab	.583a	.574a	.579a
Mesic	.599b	.590a	.563a	.538a
Xeric	.654a	.601a	.574a	.543a
Total carbohydrates ^d				
Hydric	24.63a	11.13a	8.37a	7.09a
Mesic	26.13a	10.77a	8.54a	6.36a
Xeric	19.06b	10.38a	7.60a	5.63a
Reducing sugars ^d				
Hydric	17.26ab	5.24a	2.99a	3.23a
Mesic	19.42a	5.28a	2.51a	3.90a
Xeric	12.28b	4.95a	2.72a	2.96a
Starch ^d				
Hydric	35.13a	32.97a	30.08b	34.50a
Mesic	38.09a	35.92a	34.07a	28.11b
Xeric	35.87a	33.49a	29.02b	29.62b
Caustic soda solubility ^e				
Hydric	23.62a	20.80a	21.34a	21.36a
Mesic	23.48a	22.44a	23.04a	21.15a
Xeric	22.09a	22.12a	20.71a	19.61a
Holocellulose ^e				
Hydric	73.32a	71.82a	71.81a	71.31a
Mesic	72.66a	71.66a	71.26a	71.85a
Xeric	73.24a	71.47a	71.60a	72.43a
Ergosterol ^f				
Hydric	25.76b	136.67a	26.92a	23.89a
Mesic	130.80a	39.19a	77.94a	124.93a
Xeric	8.91b	48.84a	51.92a	96.00a

^a = (percent), of fresh wood, based on oven-dry weight.

^b = Means within a column followed by the same letter are not different at $p = 0.05$.

^c = Based on oven-dry weight and oven-dry volume.

^d = (mg/g), of oven-dry weight of unextracted wood.

^e = (percent), of oven-dry weight of unextracted wood.

^f = ($\mu\text{g/g}$), of oven-dry weight of unextracted wood.

rapid rate. Site differences in moisture content began to show up by week 10 (table 2) with the sapwood of bolts on hydric sites having a higher moisture content (62.37 percent) than on mesic (56.8 percent) and xeric (52.5 percent) sites. By week 16 hydric sites had declined to 60.5 percent, mesic to 53.8 percent and xeric to 50.1 percent. The relative moistness of the three LEC units seems to be accurately reflected in the moisture content of sapwood of the oak bolts placed on those sites.

The initial specific gravity of heartwood and sapwood (0.6728/0.6301) was significantly different, a difference which increased through week 16. Specific gravity increased slightly in heartwood and decreased slightly in sapwood (0.7194/0.5537) over the 16-week period (table 1). There were essentially no differences in specific gravity due to site class (table 2) throughout the 16-week period. These data suggest that there was no major wood decay during this period. The slight, but not significant, declines during the

study are probably reflective of internal checking within the wood samples, yielding a somewhat erroneous specific gravity reading, rather than reflecting wood loss due to decay.

Because of their availability, non-structural carbohydrates are the first chemical components to be degraded by invading microorganisms. Nonstructural carbohydrate contents generally decreased throughout the 16-week period (table 1). Initially, there was no difference in total carbohydrates between heartwood and sapwood (20.7/18.7 mg/g), but by week 3 these declined somewhat in heartwood and then leveled off through week 16. In sapwood there was a slight increase in week 3 to 23.3 mg/g and then a sharp decline to 6.4 mg/g by week 16. In both of these tissues these declines suggest that the pool of total carbohydrates diminished over the 16-week period. There was no effect of site class on total carbohydrate content (table 2).

The reducing sugar contents generally paralleled those of total carbohydrates, from an initial high of 29.5 mg/g in heartwood and 11.2 mg/g in sapwood (table 1). Both tissues declined markedly in reducing sugar contents by week 16 (8.6/3.4 mg/g). There was no effect of site class on reducing sugar content (table 2). The decline in total carbohydrates and reducing sugars reflects the declining activity of parenchyma cells in the respective tissues as the increasing populations of bacteria and fungi began to metabolize these readily available carbon sources.

Starch content showed moderate decreases throughout the 16-week period, from a high of 33.6 mg/g in week 0, to 30.4 mg/g by week 16 (table 1). Sapwood had a higher content of starch (50.2 mg/g) than did heartwood and this decreased to 30.7 mg/g by week 16. Site class significantly affected starch decomposition. On the hydric sites there was no change in starch content over the 16-week period (table 2). On the mesic sites starch decreased from 34.1 mg/g at week 10 to 28.1 mg/g at week 16 (table 2). On the xeric sites starch decreased from 33.4 mg/g at week 6 to 29.0 mg/g at week 10 (table 2). It is postulated that on the hydric sites there was sufficient moisture imbibition from the soil to keep the sapwood parenchyma cells alive and this enabled them to resist invasion and colonization by microorganisms.

One percent caustic soda solubility increased only slightly between heartwood and sapwood during the 16-week period (table 1), but there was a slight increase in sapwood only at 16 weeks. There were no effects of site class during the study (table 2).

Because the one percent caustic soda solubility test showed little decay loss, holocellulose content was assessed only for sapwood. Holocellulose content, likewise, did not vary over the study period (table 1), and was not affected by site class (table 2).

Inspection of the bolts during the course of the study indicated that there were visible stain/decay effects in sapwood but not in heartwood. The sapwood became a light yellowish color with black zone lines. For that reason, fungal biomass was estimated only in the sapwood. Initially, sapwood contained 2.89 µg ergosterol/g, which sharply increased to 59.88 µg/g in week 3, and eventually to 76.52 µg/g in week 16. Although there was quite a bit of variation, the data suggest that ergosterol content may have been greatest on the mesic sites (table 2). Most of this content is believed due to *Hypoxylon atropunctatum* (Schwein.:Fr.) Cooke, which is a common invader of oak sapwood of declined or dead trees and also an early invader of freshly milled lumber (Tainter and Baker 1996). It has a unique positional advantage because it colonizes the inner and outer bark of living oak trees as they grow and mature and is never more than a few cells away from the nutrient-rich sapwood of the living trees. The small, but detectable, amount of ergosterol in the control sapwood may reflect invasion of these bolts during the 2-3 days after their preparation before they could be processed.

Pine

The initial moisture content differed significantly between heartwood and sapwood (46.4/105.1 percent) (table 3).

Table 3—Chemical composition of pine bolts

Attribute	Weeks of exposure				
	Control	3	6	10	16
Moisture content ^a					
Heartwood	46.38a ^b	40.07a	41.93a	46.92a	48.45a
Sapwood	105.14b	91.05b	81.46b	75.03b	70.84b
Specific gravity ^c					
Heartwood	.449a	.512a	.482a	.493a	.452a
Sapwood	.554b	.592b	.576b	.582b	.572b
Total carbohydrates ^d					
Heartwood	8.06a	6.98a	8.03a	10.73a	6.46a
Sapwood	7.03a	4.68b	4.38b	4.59b	4.26b
Reducing sugars ^d					
Heartwood	6.98a	7.36a	8.56a	9.60a	7.14a
Sapwood	3.44a	1.81b	1.60b	1.60b	1.04b
Starch ^d					
Heartwood	11.36a	2.90a	2.06a	2.78a	.78a
Sapwood	12.64a	5.10b	2.69a	3.09a	1.40a
Caustic soda solubility ^e					
Heartwood	19.86a	23.10a	23.31a	27.89a	21.67a
Sapwood	13.51b	13.79b	12.85b	12.71b	12.80b
Holocellulose ^e					
Sapwood	66.51	67.05	66.98	67.76	67.41
Ergosterol ^f					
Sapwood	7.15	18.60	23.89	28.01	24.17

^a = (percent), of fresh wood, based on oven-dry weight.

^b = Means within a column followed by the same letter are not different at p = 0.05.

^c = Based on oven-dry weight and oven-dry volume.

^d = (mg/g), of oven-dry weight of unextracted wood.

^e = (percent), of oven-dry weight of unextracted wood.

^f = (µg/g), of oven-dry weight of unextracted wood.

The moisture content of heartwood did not decrease through week 16. However, sapwood moisture content decreased to 70.8 percent by week 16. The heartwood columns were relatively small in these bolts and were likely protected from drying by the much wetter and thicker sapwood. Site differences began to show up by week 3 with the hydric site at 107.7 percent, mesic at 91.0 percent and xeric at 74.5 percent (table 4), decreasing at week 16 for the hydric site to percent. As with the oak samples, the relative moistness of the three site classes seems to be reflected in the moisture content of sapwood of the pine bolts placed on these sites.

The initial specific gravity of heartwood and sapwood (0.4488/0.5537) was significantly different, a difference which was maintained through week 16, with no significant change in their relative amounts (table 3). There were no differences in specific gravity among the three site classes (table 4) throughout the 16-week period. As with the oak

data, there were no major chemical effects of wood decay during this time period.

Nonstructural carbohydrate contents generally decreased throughout the 16-week period (table 3). Initially there was no difference in total carbohydrates between heartwood and 89.9 percent, for mesic to 68.0 percent, and for xeric to 54.6 sapwood (8.06/7.03 mg/g), but by week 3 differences were evident (6.98/4.68 mg/g), holding steady through week 16 (6.46/4.26 mg/g) (table 3). There was no effect of site class on total carbohydrate content (table 4).

The reducing sugar contents generally paralleled those of total carbohydrates in heartwood, from 6.98 mg/g to 7.14 mg/g in heartwood of control bolts over the 16-week period (table 3). In sapwood, however, the initial reducing sugar content of 3.44 mg/g steadily decreased to 1.04 mg/g at week 16, but effect of site class on these contents was not clear (table 4).

Table 4—Chemical components of pine sapwood by LEC site

Attribute	Weeks of exposure			
	3	6	10	16
Moisture content ^a				
Hydric	107.68a ^b	92.37a	90.32a	89.92a
Mesic	91.01ab	84.32a	71.56b	68.01b
Xeric	74.48b	67.68b	63.21b	54.58c
Specific gravity ^c				
Hydric	.601a	.575a	.555a	.578a
Mesic	.569a	.554a	.592a	.559a
Xeric	.605a	.600a	.600a	.578a
Total carbohydrates ^d				
Hydric	3.88b	3.76a	4.34a	3.97a
Mesic	5.32a	4.80a	4.78a	4.62a
Xeric	4.83ab	4.58a	4.63a	4.18a
Reducing sugars ^d				
Hydric	2.21a	2.14a	2.21a	1.37a
Mesic	1.75a	1.57ab	1.63a	.64a
Xeric	1.46a	1.08b	.96b	1.12ab
Starch ^d				
Hydric	4.12a	2.81a	1.30b	.78b
Mesic	5.82a	2.70a	3.81a	1.96a
Xeric	5.38a	2.55a	4.18a	1.46ab
Caustic soda solubility ^e				
Hydric	13.97a	12.94a	13.69a	13.69a
Mesic	13.72a	12.70a	12.70ab	12.06a
Xeric	13.69a	12.90a	11.74b	12.66a
Holocellulose ^e				
Hydric	67.11a	67.11a	67.34a	67.52a
Mesic	66.96a	66.91a	68.02a	66.59a
Xeric	67.19a	66.91a	67.91a	68.11a
Ergosterol ^f				
Hydric	3.94b	9.97a	9.11b	13.07b
Mesic	11.20b	24.56a	7.28b	6.65b
Xeric	40.66a	34.81a	67.64a	52.80a

^a = (percent), of fresh wood, based on oven-dry weight.

^b = Means within a column followed by the same letter are not different at $p = 0.05$.

^c = Based on oven-dry weight and oven-dry volume.

^d = (mg/g), of oven-dry weight of unextracted wood.

^e = (percent), of oven-dry weight of unextracted wood.

^f = (μ g/g), of oven-dry weight of unextracted wood.

Starch content showed dramatic decreases throughout the 16-week period, from initial highs in heartwood and sapwood (11.36/12.64 mg/g) (table 3), decreasing to 2.90/5.10 mg/g by week 3 and decreasing even more (0.78/1.40 mg/g) by week 16. Starch decreased more slowly on hydric sites (table 4).

At the beginning of the study, one percent caustic soda solubility was significantly different between heartwood and sapwood (19.86/13.51) and these relative amounts did not change throughout 16 weeks (table 3). Site class had no effect on this measure of decay (table 4).

Holocellulose content of sapwood did not vary over the study period (table 3) or by site class (table 4).

Initially, ergosterol content of sapwood was 7.15 µg/g and this measure of fungal biomass rose to 18.60 µg/g by week 3, and to 24.17 µg/g by week 16 (table 3). Blue stain, caused by *Ceratocystis* spp. or *Ophiostoma* spp., was very evident in these bolts as the study progressed. A detectable amount of ergosterol in sapwood of initial samples likely reflects the rapid invasion and colonization of these bolts during the 2-3 days before they could be taken to the laboratory and processed. Although there was considerable variation in the data, it was clear that ergosterol was most abundant in sapwood of pine bolts placed on the xeric sites (table 4). Since the bolts were randomized before placement, it is unlikely that this is a reflection of pre-existing colonization.

CONCLUSIONS

This study suggests that there are detectable increases in fungal populations during the first 16 weeks when freshly cut bolts of pine and oak are placed on the forest floor and allowed to deteriorate. The bolts begin to dry and the rate of drying is reflective of site class influences. Declines in total nonstructural carbohydrate contents, which also were affected by site class to a limited extent, suggest an increasing utilization of these carbon sources by invading microorganisms. The 16-week period, though, was not sufficiently long enough to allow detectable deterioration of woody cells.

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