Biol Fertil Soils (1989) 7:247–253

Biology and Fertility of Soils

Soil and detrital carbon dynamics following forest cutting in the Southern Appalachians

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Summary. Soil-system CO_2 efflux and detrital C pools were measured in three hardwood watersheds in the Southern Appalachians, USA. On two of the watersheds (hereafter referred to as clearcuts), forests were cut via clearcut logging methods and allowed to naturally regenerate; logging residue was removed on one clearcut and was left in place on the other. The third watershed was an uncut reference watershed. There was no statistically significant difference in CO_2 efflux between the two types of residue treatments on the clearcuts; however, CO_2 effluxes from the clearcuts were 33% less than effluxes from the uncut watershed. Lower CO_2 effluxes on the two clearcuts were associated with higher soil temperatures, smaller live-root masses, and larger forest-floor masses. No long-term (5–8 years) changes in soil C pools were apparent following forest cutting. Therefore, reductions in CO_2 efflux on the clearcuts appear to be due both to fewer live roots and to slower rates of forest-floor decomposition. Cutting of these forests followed by regeneration does not appear to result in large net C transfers to the atmosphere, as has been generally assumed.

Key words: CO_2 – Forest cutting – Detrital carbon – Soil – Forest floor

It has been postulated that removal of the forest canopy stimulates higher rates of organic-matter decay (Bormann et al. 1974). Modeling analyses have shown how forest cutting produces a net flux of CO_2 to the atmosphere (Aber et al. 1978; Houghton et al. 1983; Cropper and Ewel 1984). However, the assumption that cutting of forests causes losses of detrital C may be oversimplified. Distinctions are not usually made among the varying degrees of forest cutting and most data have come from surveys of cut areas without control over the methods of cutting.

Forest cutting may range in intensity from selection harvesting to deforestation. The latter, which often involves long-term conversion to non-forest uses and greater soil disturbance, has been associated with declines in soil C contents (reviewed by Allen 1985). However, causal explanations are confounded by further site disturbances such as burning, cropping, or site preparation. In contrast, studies of forest harvesting followed by rapid, natural regeneration and minor soil disturbance have shown only small changes in detrital C (Edwards and Ross-Todd 1983; Nakane et al. 1986). Other findings indicate that C losses may be a function of the degree of soil disturbance (Miller and Sirois 1986). Furthermore, the effect of forest harvesting on CO_2 effluxes is uncertain as both increases (Piene 1978; Sundman et al. 1978; Kawahara et al. 1979) and decreases (Edwards and Ross-Todd 1983; Hendrickson et al. 1985) in effluxes have been observed following harvests. It is impossible to interpret such changes when other pathways of the detrital C budget are not monitored.

To test the assumption that forest harvesting causes decreases in detrital C, we measured CO_2 effluxes from intact soils and forest floors on two commercially clearcut watersheds during the early years of forest regeneration following canopy closure. On one cut, the logging residue was left in place, and on the other, the logging residue was removed. Results from these clearcuts were compared to measurements from an uncut reference watershed. Watershed comparisons were also made with respect to forest-floor mass, soil C, mass of fine roots, soil temperature, and soil moisture. Pre- and postcut comparisons of soil C and forest-floor

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masses were also made. If large declines in detrital C were occurring on the clearcuts, we expected to detect associated increased rates of CO_2 effluxes. Furthermore, we expected that the clearcut with the residue removed would show the largest detrital C declines while the clearcut with the residue left would show the largest increases in CO_2 efflux.

Materials and methods

Site description. The study area comprised three south-facing, hardwood watersheds (WS 2, WS 7, and WS 48) at the Coweeta Hydrologic Laboratory located in the Southern Appalachian Mountains of North Carolina, USA (35° 04′ N, 83° 26′ W). Mean precipitation is 1820 mm year^{-1} and is evenly distributed annually with 95% falling as rain; mean temperature is 12.6 °C (Swift and Swank 1981; Swift et al. 1988). Major disturbances to the Coweeta area include logging up to 1923, and the chestnut blight beginning in 1925 (Day and Monk 1974). Current forests are maturing but not yet at peak biomass (Day and Monk 1974).

Precut vegetation on the three watersheds included *Quercus* spp., *Carya* spp., *Acer rubrum, Liriodendron tulipifera, Tsuga canadensis, Rhododendron maximum, Kalmia latifolia, Oxydendrum arboreum,* and *Robinia pseudoacacia* (Swank 1979; Boring et al. 1981; Berish and Ragsdale 1986). The watersheds are characterized by deep, permeable soils formed on steep slopes from folded gneiss. The dominant soil series along the streams and at the lower elevations is the Tusquitee, a member of the coarse-loamy, mixed, mesic family of Umbric Dystrochrepts; ridge and slopes are dominated by the Chandler series, a member of the coarse-loamy, micaceous, mesic family of Typic Dystrochrepts, and by the Fanin series, a member of the fine-loamy, micaceous, mesic family of Typic Hapludults.

WS 2 is a 12-ha, uncut, reference catchment, with an elevation of 720 – 1000 m and an average slope of 47%. No manipulations have occurred on WS 2 since 1934.

WS 7 is a 59-ha catchment adjacent to the west edge of WS 2. The elevation of WS 7 ranges from 700 to 1000 m and slopes vary between 20% and 80%. The only manipulations to WS 7 between 1934 and the time of forest-cutting occurred during 1941 – 1951 when six cattle were grazed for 4 months each year (Swank and Douglass 1975). In 1977, the forest on WS 7 was cut as part of a study to assess the effects of disturbance on nutrient cycling. Merchantable trees were cut and their boles removed using a mobile cable system operating from a series of three permanent roads. Next, all remaining standing trees were felled and left on the site. Mineral soil exposure was limited to 5.1% of the non-road area (J. Buchanan, Coweeta Office Report).

WS 48 is a 0.67-ha catchment located 2.0 km west of WS 2 and WS 7. The elevation of WS 48 ranges from 950 to 1010 m; the average slope is 56%. No manipulations occurred on WS 48 from 1934 until 1980, when the forest was cut. Merchantable timber and firewood were removed by a mobile cable system and the remaining woody residue was removed by hand.

All measurements and sample collections were made inside a series of plots, the locations of which were stratified by the precut vegetation. The soil samples were dried at 105 °C for 24 h; the organic-matter content of the forest floor and roots was determined by drying at 65 °C and ashing at 500 °C. During the study period, 1982 – 1984, WS 48 was in its 3rd through 5th years and WS 7 was in its 6th through 8th years of regeneration. Regeneration on the clearcuts was rapid; the leaf area index on WS 7 during year 3 was 4.2% or 68% of a mature forest (Boring et al. 1988). Canopy height on the clearcuts varied between 2 and 6 m.

Measurement of CO_2 efflux. Soil-system CO_2 efflux, the diffusion of CO_2 from the forest floor and soil, was measured using the static technique (Anderson 1982). Twenty aluminum cylinders (10 cm in diameter and 12 cm long) were inserted 2 cm into the soil at randomly located positions on WS 7, 11 were inserted on WS 48, and 16 on WS 2. The cylinders were not moved between measurements. The clearcuts were sampled during the entire study period and WS 2 was included during April – October 1984. CO_2 efflux was measured during the same 24-h periods on all watersheds. Soil temperature data (10 cm) and moisture samples (gravimetrically, 0 – 10 cm) were collected at the beginning of each measurement.

Forest floor. Forest-floor samples were collected three times during 1983 on the clearcuts inside 25-×25-cm quadrats. These mull forest floors did not always have a clear boundary between the H layer and the soil. Questionable material was included in the H layer collections instead of the soil collections since the forest-floor material was to be ashed and inclusion of questionable material with the H layer would cause less bias than inclusion of such material with the soil. This method gave mean organic-matter contents for the non-woody portions in the H layer of 41% (s.d. 14.2, $n = 43$), consistent with Federer's (1982) recommendation.

The total organic-matter mass of the clearcut forest floors was compared to that of WS 2 (Berish and Ragsdale 1986), and the L+F layer of the clearcuts was compared to earlier estimates of forest floor O1+O2 layers (Seasedt and Crossley 1981; W. T. Swank, unpublished data 1981). In the earlier estimates, the H layer as defined in this study was not collected as O2 but as soil (L. Reynolds, pers. comm. 1982 and K. G. Mattson, pers. obs. 1982). The L and F layers were sampled in this study to correspond to the earlier O1 and O2 layers, respectively.

Soil C and roots. Soil was sampled during 1984 in nine plots on WS 7, six plots on WS 48, and four plots on WS 2. The forest floor was removed using the same criteria for H-layer determination as described above. Soil was sampled at three depths: (1) 0 – 10 cm, (2) 10 – 30 cm, and (3) 30 – 60 cm, using a soil-tube sampler with an inside diameter of 2.1 cm. For depths 1 and 2, the soil sample from each plot was composed of nine subsamples all taken within 10 m of each other. Each bulk sample was analysed for bulk density of the <2 mm fraction, soil C content of the <2 mm fraction, and fine roots (≤ 5 mm). Live and dead roots were separated from the soil before it was dried (Mattson 1986). The sampler diameter is not thought to affect fine-root estimates (McClaugherty et al. 1982). Such a narrow tube sampler may compress the soils while sampling; as long as this was avoided, no bias was detected in total bulk density when values were compared to those from a tube of 4 cm diameter.

The bulk density of the <2 mm fraction was calculated by dividing the dry mass of sieved soil by the net soil volume (sampler volume less volume of rocks between 2 and 20 mm). Sieved soil was analysed for soil C content using a Leco C analyser; no inorganic C (Nelson and Sommers 1982) was detected. The mass of soil C for each plot was calculated as the product of bulk density and soil C content. This slightly overestimates watershed C because a small volume of the soil is occupied by rocks. The volume of rocks between 2 and 20 mm in diameter was similar across the watersheds and averaged 1.9%, 2.8%, and 6.9% for depths 1, 2, and 3, respectively. No estimates were made for larger rocks, but they, too, occupied a relatively small volume. The mass of soil C per watershed was estimated as the mean across the plots sampled.

Statistical analyses. Square root transformations were applied to the CO_2 and soil-moisture data to equalize the variance (Zar 1974). The effects of watershed and date on CO_2 efflux, soil temperature, and soil moisture were analysed factorially by a two-way analysis of variance using the GLM procedure, type III sum of squares (SAS

Institute 1982). The F statistic, mean square error (MSE), degrees of freedom (df), and the probability of type I error (P) are reported. Multiple comparisons of means were made using Bonferroni's t-test. Comparison of forest-floor masses of the clearcuts were made using two-tailed t-tests. Watershed differences in soil C and roots were analysed by an one-way analysis of variance. Due to smaller sample sizes, the watershed differences in soil C and roots were considered significant at $\alpha = 0.10$; $\alpha = 0.05$ was used for all other effects.

Results

CO_2 efflux

CO_2 effluxes from the two clearcuts (WS 7 and WS 48) were similar and paralleled each other over a seasonal, periodic pattern (Fig. 1a). Date effects were highly significant; watershed effects between the clearcuts were not significant.

CO_2 effluxes from the clearcuts were consistently less than effluxes from the uncut watershed (WS 2) during the spring, summer, and early fall of 1984. Watershed date, and watershed-by-date interactions were all significant during April–October 1984 (for watershed effects: $F = 39.21$; $MSE = 0.099$; df = 2,270; $P = 0.0001$; WS 2 > WS 48 = WS 7). When analysed by separate dates, the CO_2 efflux from WS 2 was significantly greater than that from WS 7 for five of the six measurement dates, and significantly greater than the efflux from WS 48 for three of the six measurement dates (Fig. 2).

CO_2 effluxes were calculated by summing the areas beneath the curves in Figs. 1a and 2 (Table 1). The mean CO_2 efflux over both years was 5710 and 5780 kg C ha^{-1} year^{-1} for WS 48 and WS 7, respectively. A yearly variation in CO_2 efflux on the clearcuts was apparent, as shown by an average increase of 28% in CO_2 during 1983–1984. During April to October 1984, the clearcuts produced, on average, 33% less CO_2 than the uncut watershed (WS 48 was 27% less than WS 2 and WS 7 was 38% less than WS 2).

Soil temperature and moisture

Soil temperatures for the two clearcuts were not significantly different from each other and closely paralleled the CO_2 effluxes. However, the average soil temperature for the two clearcuts for any measurement date during April–October 1984 was between 0.2 and 2.5 °C higher than the soil temperatures of the uncut watershed (Fig. 1b). Effects due to watershed, date, and watershed-by-date interactions were all significant (for watershed effects: $F = 3.73$; $MSE = 2.67$; df = 2,91; $P = 0.028$; WS 48 > WS 2). When analysed by separate dates, the soil temperature for WS 48 was significantly greater than that for WS 2 only during April ($F = 5.48$; $MSE = 5.53$; df = 2,24; $P = 0.011$). Failure

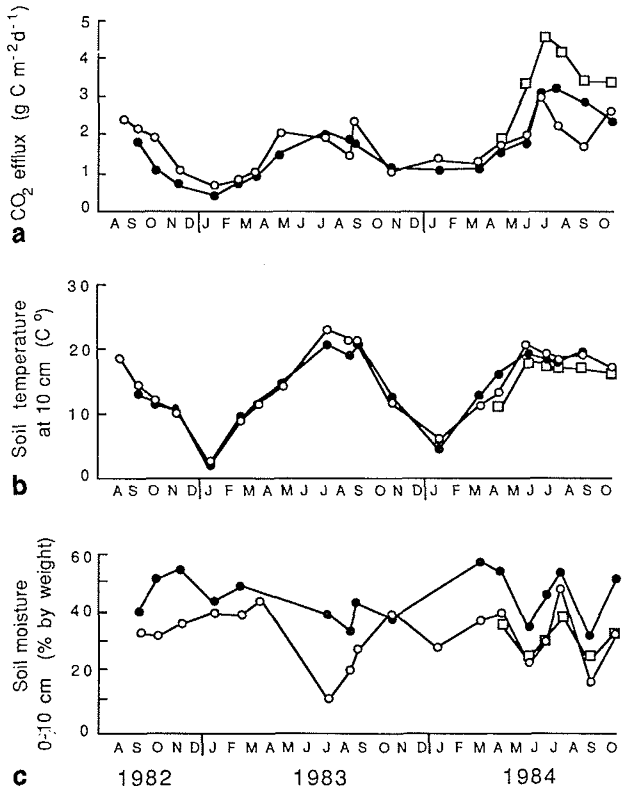

Fig. 1 a–c. Watershed (WS) CO_2 efflux with simultaneous environmental measures. WS 7: ○——○, clearcut with residue left. WS 2: □——□, uncut reference watershed. WS 48: ●——●, clearcut with residue removed. **a** CO_2 efflux. Coefficient of variation: WS 7 = 47%, WS 48 = 44%, WS 2 = 31%. **b** Soil temperature. Standard deviation: WS 7 = 1.30 °C, WS 48 = 1.03 °C, WS 2 = 1.00 °C. **c** Soil moisture. Coefficient of variation: WS 7 = 23%, WS 48 = 22%, WS 2 = 13%

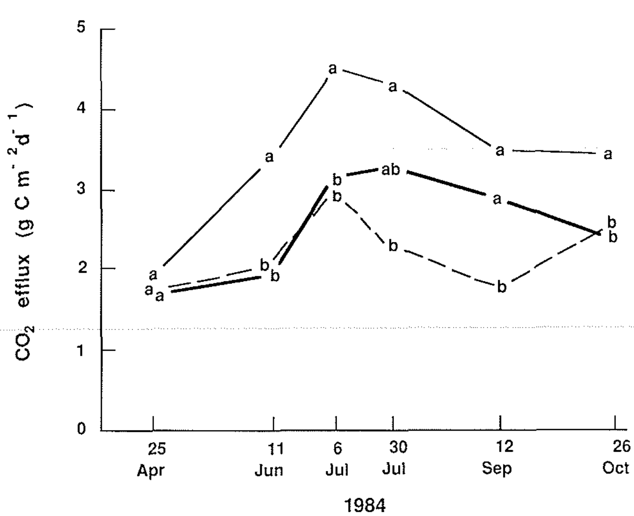

Fig. 2. Watershed effects on CO_2 efflux: results of an analysis of variance by separate dates. Mean efflux for different watersheds within a date are not significantly different if represented by the same letter ($\alpha = 0.05$). WS 2, uncut reference: ———, WS 48, clearcut with residue removed: ▬▬▬, WS 7, clearcut with residue left: – – –

to detect differences in soil temperatures between watersheds at other dates was probably due to small sample sizes and small differences in temperature. Higher CO_2 effluxes on the clearcuts in 1984 versus 1983 (Table 1) are associated with higher winter soil temperatures but lower summer soil temperatures during 1984 (Fig. 1b).

Soil moisture showed a high variation between measurement dates and no seasonal patterns (Fig. 1c). WS 48 held significantly greater soil moisture than WS 7 ($F = 69.39$; MSE = 0.66; df = 1,184; $P = 0.0001$) and greater soil moisture than both WS 7 and WS 2 during April–October 1984 ($F = 13.68$; MSE = 0.64; df = 2,64; $P = 0.0001$). One reason why WS 48 had higher soil moisture was that this watershed received 21% more precipitation than WS 7 during 1983–1984 (Mattson 1986). Soil moisture did not differ significantly between WS 2 and WS 7, but WS 2 showed less variability by date than both the clearcuts. Soil moisture may have been important in reducing CO_2 effluxes during periods when values fell below 20% on WS 7, or in enhancing CO_2 during periods of greater moisture variability such as June–October 1984 (Figs. 1a and 1c).

Forest floor

The organic-matter masses of the forest floors on both clearcuts were larger than that of the uncut watershed (Table 2). The forest-floor mass of WS 7 was significantly larger than that of WS 48 ($P = 0.008$) and the difference was significant for the non-woody fractions of all layers ($P \leq 0.04$). However, there was no significant difference in the amount of wood fragments in the forest floor between the clearcuts. It is surprising that no larger masses of wood fragments were measured in the forest floor of WS 7 where 121 Mg/ha of logging residue was left on the site. Mattson et al. (1987) estimated that 5.7 Mg/ha^2 of bark and 11.2 Mg/ha^2 of small woody material had been transferred from the logging residue to the forest floor during the first 6 years following cutting on WS 7. It is possible that much of this wood was decayed beyond the point of easy separation from other forest-floor material and may have contributed to the large H-layer mass on WS 7.

Comparison of the L+F components measured during 1983 with the earlier forest-floor estimates indicated that an increase in the mass of the forest floor occurred on both clearcuts during the first year following the harvest operations (Table 3). The forest floor on WS 48 (without residue) appeared to return to near precut levels by 1983, while the forest floor on WS 7 appeared to maintain larger masses due to the inputs from the decomposing logging residue.

Soil C and roots

The percentage of soil C was consistently higher at all three depths for WS 48 compared to WS 2 and 7, particularly so at greater depths. Bulk densities were consistently higher at all three depths on WS 2. The resul-

Table 1. CO_2 effluxes (kg C ha^{-1}) from clearcut watersheds (WS 48 and WS 7) and from an uncut reference watershed (WS 2)

Period of measurement	Watershed		
	48	7	2
23 Oct. 82 – 5 Nov. 83	4660	5410	–
5 Nov. 83 – 26 Oct. 84	6760	6150	–
26 Apr. 84 – 26 Oct. 84	4710	3970	6490

Table 2. Forest-floor organic-matter mass (g m^{-2}, mean and SE) by layers on clearcut watersheds (WS 48 and WS 7) and on an uncut reference watershed (WS 2). Data for WS 2 are from Berish and Ragsdale (1986)

		Non-woody	Woody	Total
WS 48 ($n = 30$)	L	207 (22)	117 (30)	324 (27)
	F	302 (28)	216 (47)	519 (67)
	H	420 (80)	74 (16)	495 (91)
	Total	930	407	1338
WS 7 ($n = 36$)	L	353 (22)	152 (41)	505 (47)
	F	416 (46)	238 (61)	653 (98)
	H	943 (170)	77 (28)	1020 (186)
	Total	1712	466	2179
WS 2 ($n = 16$)	Litter			805 (71)
	Humus			340 (47)
	Total			1145

Table 3. Forest-floor organic-matter mass (g/m^2) on clearcut and uncut watersheds. Layers measured during precut years, first-year postcut, and 1978 (O1 + O2) are compared against equivalent layers (L + F) measured during 1983. Rationale for comparison is explained in text

Clearcut watersheds			
WS	Precut[a]	1st year postcut	1983
7	816[b]	970[b]	1158
48	774[b]	1122[c]	843
Uncut reference watershed			
WS		1978	1983
2		880[b]	805[d]

[a] WS 7 was cut in 1977; WS 48 was cut in 1980
[b] Seastedt and Crossley (1981)
[c] W.T. Swank (unpublished data 1981)
[d] Berish and Ragsdale (1986)

Table 4. Soil carbon data and roots ≤5 mm diameter (mean, SE, *n*) on clearcut watersheds (WS 48, WS 7) and on an uncut, reference watershed (WS 2)

Watershed	Soil depth (cm)	% C	Bulk density ($g\ cm^{-3}$)	Soil carbon ($g\ C\ m^{-2}$)	Live roots ($g\ m^{-2}$)	Dead roots ($g\ m^{-2}$)
48	1 (0–10)	3.16 (0.27) 6[b]	0.63 (0.03) 6	1982 (81) 6	196 (35) 6	450 (57) 6
	2 (10–20)	1.73 (0.37) 6	0.81 (0.06) 6	2763 (527) 6	221 (46) 6	346 (50) 6
	3 (30–60)	1.17 (0.58) 4	0.94 (0.06) 4	3157 (1433) 4	88 (10) 4	229 (80) 4
	Total[a]	*1.60*	*0.85*	7882	505	1025
7	1	2.94 (0.21) 9	0.63 (0.03) 9	1806 (113) 9	251 (14) 8	446 (59) 8
	2	1.35 (0.17) 9	0.69 (0.04) 9	1869 (231) 9	190 (32) 8	303 (55) 8
	3	0.56 (0.09) 5	0.92 (0.11) 4	1507 (302) 4	57 (18) 5	49 (41) 5
	Total	1.10	0.80	5182	498	798
2	1	2.94 (0.22) 3	0.73 (0.08) 3	2106 (89) 3	310 (71) 3	316 (132) 3
	2	1.30 (0.14) 4	0.85 (0.05) 4	2200 (212) 4	353 (131) 4	171 (16) 4
	3	0.36 (–) 1	1.25 (–) 1	1367 (–) 1	106 (–) 1	212 (–) 1
	Total	0.92	1.03	5673	769	699

[a] Total = 0–60 cm soil depth; % C is the soil-mass-weighted mean (i.e., bulk density × depth); total bulk density is the depth-weighted mean; all others are algebraic sums

[b] Mean % C on WS 48 = 2.89, 1.37, 0.59 for depths 1, 2, 3, respectively, if one plot with high carbon values is deleted

tant calculated masses of soil C were fairly similar between watersheds for depth 1; masses were higher on WS 48 at greater depths, producing greater total soil C (Table 4). The differences shown in Table 4 were generally not statistically significant. Precut soil C contents for depth 1 were 3.4% and 2.8% for WS 48 and WS 7, respectively (W. T. Swank unpublished data 1976, 1981). Thus, there is no evidence of large declines in soil C for years 5 and 8 following cutting on these two watersheds.

While there were no large differences among watersheds in the total mass of fine roots (live plus dead), the clearcuts had smaller live-root masses (Table 4). No significant differences were found between watersheds for the mass of live or dead roots at any depth. However, when data for depths 0–10 and 10–30 cm were combined, WS 2 had a significantly greater live-root mass and all three watersheds had significantly different dead-root masses.

Discussion

Forest cutting on the two watersheds was associated with a 33% reduction in CO_2 efflux; there was no effect on CO_2 efflux due to treatment of the logging residue. The reduction in CO_2 on the two clearcuts was also associated with a trend of higher soil temperature, larger forest-floor masses, no change in soil C, and decreases in live, fine roots.

Since the treatments did not have true controls, we cannot infer that the observed differences were due to cutting alone. We can show that there were no large watershed differences before cutting, so that a stronger case can be made for cutting effects. Precut forest-floor masses on WS 7 and WS 48 were similar to those on the uncut WS 2 (Table 3), and the soil C levels of WS 7 were similar to those of WS 2; WS 48 soil C levels were higher. Precut soil CO_2 effluxes for WS 7 (J. B. Waide and R. L. Todd, unpublished data 1976) indicate that annual effluxes varied between 7500 and 9000 kg C ha^{-1}. The annual efflux from WS 2 was estimated at 8600 kg C ha^{-1} by extrapolating the observed 50% higher efflux of WS 2 to the measured average annual efflux of 5745 from the clearcuts (Table 1). There are insufficient data to allow precut CO_2-efflux estimates for WS 48. The highest mean precut soil temperature on WS 7 was 18.5 °C (W. T. Swank and J. B. Waide, unpublished data 1976), which is similar to the maximum mean soil temperature measured on WS 2 during this study (Fig. 1 b). These comparisons show that watershed differences were slight before cutting and suggest that much of the observed differences were associated with cutting.

The reasons for reduced CO_2 effluxes on the clearcuts are somewhat speculative. We suggest that the reduced CO_2 effluxes were due to decreased C flows through the root systems and to decreased rates of forest-floor decomposition. Reduced carbon flows through root systems logically follow the observation of smaller live, fine root standing stocks on the clearcuts. However, we can also show that it is unlikely that the entire reduction in CO_2 is due to reduced live-root pools. If we assume that (1) only live, fine roots contribute to root respiration and that (2) root respiration is a direct function of live mass, then the amount of decrease in total CO_2 efflux due to the decrease in live roots can be estimated by the product of the proportional decrease in live roots and the proportion of total efflux that is root-derived. Estimates of root respiration suggest that between 30% and 50% of total respiration is root-derived (Edwards and Sollins 1973; Nakane et al. 1983). Since the reduction in live, fine roots appears to be 30% on the clearcuts (Table 4), we estimate that the reduction in total respiration due to reduced root respiration was at most 15% (0.5×0.3), or approximately half the observed decrease. The rates of respiration per gram of root may have decreased following cutting, but we have no evidence to either support or refute this possibility.

The reduced soil CO_2 effluxes on the clearcuts may also have been due to decreased rates of forest-floor decomposition following cutting. This speculation is supported by the increases in forest-floor mass, which admittedly could also have been caused by high inputs during the harvest. It is also supported by the decreases observed in litterbag decay rates on WS 7 compared to WS 2 during the first 2 years following cutting (J. B. Waide, unpublished data 1978), and by lower microarthropod densities on WS 7 following cutting (Seasedt and Crossley 1981). Decreased decomposition may be due to altered microclimatic conditions exceeding those optimal for decay (Whitford et al. 1981). If decomposition is still occurring at a slower rate on the regenerating watersheds, it is not known why the decreased decomposition persists or how long it may last.

The reduction in CO_2 efflux and the lack of decline in detrital C pools following forest harvest in this study are not unique; other studies have failed to find large declines in detrital C following harvests (Gholz and Fisher 1982; Edwards and Ross-Todd 1983; Nakane et al. 1986). Allen (1985) suggested that the degree of C loss may be a function of soils and of the type of ecosystem. Our findings show that C loss may also be a function of the type of disturbance. Forest clearing in the tropics often involves burning and one to several years of agricultural use as part of the rotation before forest regrowth is allowed to occur. This practice may cause greater system disturbance, triggering C losses from the soil. The harvests at Coweeta caused little disturbance to the forest floor or to the regeneration mechanisms (i.e. seedlings, root systems, and seed pools). These comparisons suggest that greater site specificity involving local processes may be needed in models of C loss following landscape manipulations.

Acknowledgments. This research was supported in part by LTER Grant BSR 8012093, and in part by the Coweeta Hydrologic Laboratory, Otto, North Carolina and the Institute of Ecology at the University of Georgia. Influential ideas came from Jack Waide, Lindsay Boring, and Lee Reynolds. Technical help came from Mark Lawson, Ron Evon, Rick Schueder, Tony Parnell, Robin Klem, and Thelma Richardson.

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Received May 6, 1987