



Recovery of decomposition and soil microarthropod communities in an Appalachian watershed two decades after a clearcut

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Abstract

We examined decomposition rates of three substrates (*Quercus prinus* L., *Acer rubrum* L., and *Cornus florida* L.) in a watershed 21 years after it had been clearcut, and compared them to an adjacent control watershed. Previous investigations at these sites had shown that microarthropod populations, important components of the decomposer community, were considerably less dense in the clearcut watershed and that decomposition rates were reduced. Twenty-one years after clearcut decomposition rates in the clearcut watershed had reconverged with the control, and in the case of one substrate (*C. florida*) now exceeded the control. Microarthropods maintained denser populations in the clearcut watershed, and oribatid assemblages, the most abundant taxonomic group, were more diverse in that watershed. A contrast of the decomposition of the substrates 8 and 21 years after cable-logging revealed that decomposition was slower in the control watershed in the more recent observations, though this may reflect lower precipitation that year. These results seem to confirm that microarthropod recovery may be indicative of a restored decomposer community functioning, and that this may be reflective of reconverged abiotic conditions at the site.

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1. Introduction

The recovery of ecosystems after a disturbance remains a major theme for ecological research (DeAngelis, 1992; Pimm, 1984). Numerous studies have focused either on the reestablishment of biological communities (Niemela, 1997) or on the recovery of ecosystem processes after perturbations (Covington, 1981; Likens and Boorman, 1997). In circumstances where biota and process are closely linked, as they are in the case of decomposer organisms and the processes of organic matter decay and the mineralization of

nutrients, the recovery of the biota and ecosystem process can be usefully considered in tandem. The question of the degree to which biota must recover before the process is restored to pre-disturbance levels is clearly a crucial one, particularly in the context of ecosystem restoration where emphasis is often placed on restoring ecosystem structure (expressed often as mean species composition) or rehabilitation of function but rarely both simultaneously (Ehrenfeld and Toth, 1997). Indeed studies linking community structure and resilience of process have been generally rare in ecology (Vitousek, 1990).

Clearcutting of forests followed by the harvesting of marketable timber is clearly a disturbance with implications for the process of decomposition and amounts

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of carbon storage. Recovery of soil processes will have implications for the subsequent stand productivity, and all other parameters linked to productivity. The determining factors of leaf litter decomposition are both abiotic (climate, edaphic factors, substrate resource quality), and biotic (microbes and decomposer fauna). Both biotic and physical factors come into play in all terrestrial ecosystems; however their relative importance may vary along environmental gradients (Lavelle et al., 1993). A radical physical disruption on the scale of a watershed such as occurs during the clearcutting of a stand can have a dramatic impact on all of these factors. Such an impact moreover is likely to be long-lasting because the disruption will leave a legacy by way of modification of soil structure, changes in site hydrology, altered litter input as succession proceeds, and solar radiation flux changes, that will continue to influence the factors determining decomposition.

Clearcutting is likely to have both direct and indirect impacts on soil biota. The direct effects are as a consequence of the physical disruption of the environment. Indirect effects will stem from a modification of the abiotic habitat factors regulating the communities in the soil. In turn modified soil communities will affect rates of decomposition and mineralization of key nutrients. Soil fauna have been implicated as having an important regulatory role in a variety of ecosystem processes including decomposition and nutrient dynamics (Seastedt, 1984). Microarthropods—mainly free-living mites, Collembola, and Protura—which are relatively small contributors to ecological energetics appear to have a disproportionately prominent role in determining soil fertility through their regulatory effect on soil microbial communities. Although they are by no means the only fauna of importance in the process of decomposition, microarthropods have been implicated as playing a role in the decomposition of dead organic matter because of their ability to regulate below ground food-webs (Seastedt, 1984; Lussenhop, 1992). Reduction of microarthropod population can reduce rates of decomposition and can result in modified patterns in nutrient leaching in forest soil (Heneghan and Bolger, 1996).

Some studies, particularly in northern hardwoods, on the recovery of decomposition in clearcut watersheds have demonstrated or at least implied that

decomposition rates accelerate after the disturbance (Covington, 1981; Aber et al., 1978). In contrast, studies on decomposition of leaf litter and woody debris in a clearcut watershed at Coweeta Hydrological Laboratory, North Carolina, USA, have indicated that decomposition rates were lower than in an adjacent undisturbed control watershed (Abbott and Crossley, 1982; Seastedt, 1979; Blair and Crossley, 1988). Blair and Crossley (1988) established that decay rates remained depressed 8 years after the disturbance by as much as 46% for *Cornus florida*, the most rapidly decomposing substrate they examined. All three substrates they employed in the study decomposed more slowly in the disturbed watershed than in the control. Investigations of the response of decomposer organisms and microbial processes to tree harvesting have been similarly equivocal. Houston et al. (1998) showed that microbial responses to clearcutting in two Ontario hardwood forests were very slight. Striegl et al. (1998) report a reduction in soil respiration rates, measured as CO₂ evolved, as a consequence to clearcutting in Saskatchewan. Siira-Pietikäinen et al. (2001) conclude that forest harvesting had little impact on decomposers at a variety of trophic levels. These studies suggest that no generalizations can be made concerning the impact of clearcutting (Whitford et al., 1981; Will et al., 1983; Binkley, 1984).

Studies on decomposition in watershed 2 (WS2) and watershed 7 (WS7) at Coweeta have concentrated on tracking changes in this process subsequent to a clearcut in 1977. An assumption was made that microarthropod abundance was similar on WS7 and WS2 at Coweeta before WS7 was cable logged in 1977. After a year abundance was reduced by more than 50% in the clearcut watershed compared with an adjacent control (WS2) (Abbott et al., 1980; Seastedt and Crossley, 1981). Blair and Crossley (1988) suggest that microarthropod abundance which had remained 28% lower in the clearcut area than in the control may be responsible for the decreased decomposition rates.

The present study was motivated by observations (Heneghan, unpublished), that microarthropod population in the clearcut areas, exceeded the control watershed. That is, after two decades the fauna not only returned to predisturbance levels but in fact appeared to have exceeded it. These observations prompted a reinvestigation of the decomposition

dynamics of the substrates utilized in the study by Blair and Crossley (1988). We are not hypothesizing here that microarthropod populations are so tightly linked with the process of decomposition (a process constrained by myriad factors both abiotic and biotic) that an increase in their populations will be predictive of an acceleration in decomposition rates for a specified litter types by a predicted amount. However, we do hypothesize that elevated faunal populations will be indicative of overall acceleration of decomposition in the clearcut watershed.

2. Methods

2.1. Site description

Coweeta Hydrologic Laboratory, North Carolina, is a 2185 ha research facility dedicated to ecosystem research (Swank and Crossley, 1988). Located in the Nantahala Mountains—part of the Blue Ridge province in the southern Appalachians—the US Department of Agriculture (Forest Service) oversees it and research there focuses on long-term watershed-based research. The effects of disturbance and management history on hydrology, stream chemistry and soil nutrient dynamics have been a core of this research effort. Watershed treatments include prescribed burning, grazing and selective logging (Swank and Vose, 1997). WS7 is a 59 ha southfacing watershed. Human disturbances were restricted from 1924 until 1941 when it became the site of a grazing experiment until 1952. This watershed was cable logged in 1977. Harvesting of timber began in January 1977. Tractor skidding and a mobile cable system were used to remove the timber. Since this time the forest has been undisturbed and vegetation and soil recovery has been intensively monitored (Boring et al., 1981; Blair and Crossley, 1988; Swank and Vose, 1997; Knoepp and Swank, 1997; Elliott et al., 1997).

2.1.1. Vegetation and faunal recovery prior to the present study

Vegetational surveys have been conducted in 24 permanent plots since 1974. These plots were revisited in 1977, 1979, 1984, and 1993. The following short account of revegetation is drawn mainly from Elliott et al. (1997). In general, hardwood forests in the

Southern Appalachians revegetate quickly as a consequence of rapid reproduction and tree growth. *Carya* spp., which dominated in hardwood coves before the cut, has diminished to 1% of the trees in 1993. *Robinia pseudoacacia*, *Liriodendron tulipifera*, and *Acer rubrum*, all opportunistic species, have an increased representation during succession. In general species richness increased in the cove–hardwood and hardwood–pine plots within the watershed in the 17 years after clearcutting but remained relatively constant in mixed hardwood communities. Diversity, measured using the Shannon–Weaver index, decreased in the mixed hardwoods but remained constant in the cove–hardwoods and the hardwood–pine communities. The ground flora was in a transitional stage between early and late successional species 17 years after clearcutting. Early successional species such as *Aster*, *Salidago*, and *Eupatorium* have declined in abundance because of the rapid woody species growth and consequent canopy closure.

Prior to clearcut it is assumed that there was no significant differences between microarthropod densities in the two watersheds (Abbott et al., 1980; Seastedt and Crossley, 1981). In the study by Blair and Crossley (1988) the populations were shown to have recovered somewhat from the strong reductions noted after year 1 (remaining 28% lower in the clearcut watershed in the Blair and Crossley study). There was a differential response among the microarthropod groups. Mesostigmata and oribatid mites in the clearcut site were still 50% less abundant compared to the control. Abbott et al. (1980) found that within a year of the cut the proportional abundance of the most dominant species, *Tectocephus velatus*, was only 14.5%. The proportional abundance of the most dominant species in the control watershed, *Oppiella nova*, was 27.1%.

2.1.2. Litterbag experiment

Litterbags with an internal dimension of 10 cm × 10 cm, constructed with fiberglass window screen were used in this study. Recently fallen leaves of chestnut oak (*Quercus prinus* L.), red maple (*A. rubrum* L.) and dogwood (*C. florida* L.) were collected from a number of low elevation watersheds and pooled by species, mixed thoroughly (to ensure that all the leaves in a single bag were not derived from a single tree). Approximately 2.5 g of air-dried material was

placed in litterbags. Five bags were oven-dried at 95 °C to establish relationship between air-dried and oven-dried mass loss. Litterbags of each species were placed in three plots in each of the two watersheds in January 1998. All plots matched for altitude, aspect and slope. Five bags were taken up immediately to establish mass loss from handling. Litterbags were collected every 2 weeks for 18 months. Bags were oven-dried at 50 °C, the litter reweighed, ground and subsamples were placed in a muffle furnace at 500 °C for 4 h to obtain an estimate of biomass ash content. This value was subtracted from oven-dried mass to obtain ash-free mass. Nitrogen and carbon percent of the litter at the beginning of the study were determined by combustion using a Carlo Erba C/N analyser (instrument NA1500).

2.1.3. Statistical analysis of litterbag experiment

Decomposition rates were fitted using the single negative exponential decay model (Olson, 1963). Significant differences in mass remaining were determined using paired one-tailed *t*-tests on the decomposition rate constants (*k*) determined from the model. These tests assessed the null hypothesis that decomposition rate remained lower in the clearcut area than in the paired control watershed. First-year decomposition rate of each substrate was analyzed between years using paired *t*-tests. All statistics were performed on SAS.

2.1.4. Soil fauna: methodology

Six samples of litter measuring 27 cm × 27 cm were collected from randomly chosen points in each of the two watersheds in July 1998. The litter samples primarily comprised litter material, though no attempt was made to separate out coarse woody debris. Prior

studies (Heneghan, unpublished) had demonstrated that there were no differences in the volume of litter when the two watersheds were compared. These observations were based upon three replicates from quadrats measuring a meter squared. Microarthropods were extracted from the samples using standard Tullgren funnels and the fauna were stored in 70% ethanol before being separated into Prostigmata, Mesostigmata, Oribatei, Collembola, and Protura. Oribatei were sorted to morphospecies. Total abundance of each taxonomic group was recorded and species richness, Shannon diversity, and Shannon evenness was measured for Oribatei. Assemblages of oribatids in each of the samples from both watersheds were analyzed using principal components analysis using multivariate statistical package (MVSP). Similarities among these samples were analyzed using Jaccard's index (Magurran, 1988).

2.1.5. Soil fauna: statistical analysis

Differences between proportions of microarthropods were tested using *t*-tests (arcsine transformed). Potential differences between measures of richness and diversity were examined using *t*-tests, after a test for homogeneity of variances.

3. Results

Twenty-one years after clearcut decomposition rates of all substrates had either reconverged, or in the case of one species, *C. florida*, had very slightly surpassed that of the control watershed (Fig. 1). First-year decomposition rates for each substrate are provided in Table 1 for precut measurements until 21 years after clearcut.

Table 1

Annual decomposition rates (*k*) (derived from a negative exponential decay model) (percentage of original mass remaining after 12 months in parentheses)^a

	Precut		Year 1 (1978)		Year 8 (1985)		Year 21 (1998)	
	Clearcut (1974–1975)	Control (1975–1976)	Clearcut	Control	Clearcut	Control	Clearcut	Control
<i>Q. prinus</i>	-0.37 (69.3)	-0.29 (72.2)	-0.29 (76.7)	-0.43 (65.2)	-0.19 (78.1)	-0.27 (73.1)	-0.28 (72.73)	-0.24 (75.54)
<i>C. florida</i>	-1.31 (27.8)	-0.71 (47.8)	-0.63 (55.6)	-1.17 (34.3)	-0.71 (51.3)	-0.85 (45.8)	-0.38 (61.32)	-0.32 (64.98)
<i>A. rubrum</i>	-0.53 (49.0)	-0.48 (57.9)	-0.37 (70.5)	-0.62 (53.7)	-0.55 (62.4)	-0.64 (52.9)	-0.343 (65.22)	-0.3508 (64.16)

^a Climatic data associated with these years is shown in Fig. 5.

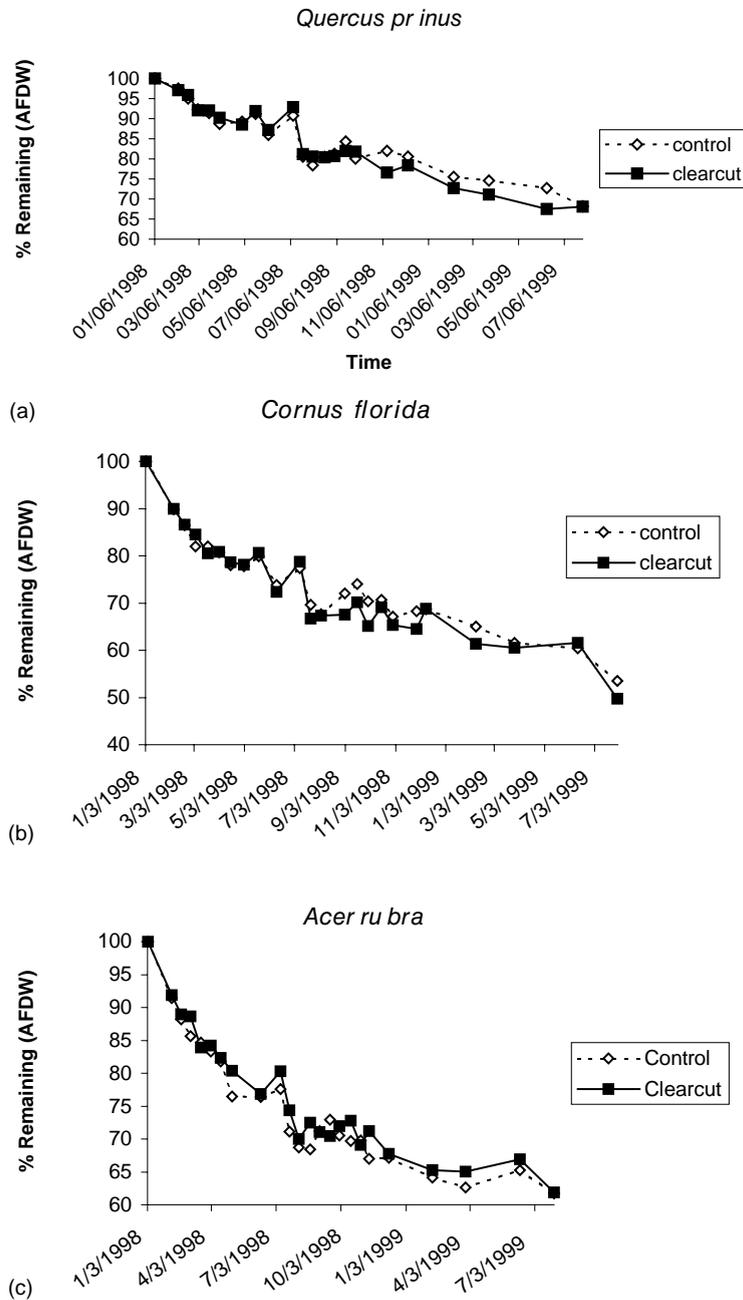


Fig. 1. Mass loss of: (a) *Q. prinus*; (b) *C. florida*; (c) *A. rubrum* in clearcut and control watershed at Coweeta Hydrologic Station, North Carolina.

A comparison of the decomposition rates of each substrate 8 and 21 years after the clearcut revealed some difference in decomposition rates in the clearcut watershed but also for the same substrates in the

control watershed. Differences in decomposition rates of chestnut oak in the cleared watershed were marginally significant ($t = 2.26, P = 0.087$). No differences were detected in the control watershed. Differences

Table 2

Mean and standard error of abundance of each microarthropod group from six samples (27 × 27 cm) from both clearcut (WS7) and control (WS2) watersheds

	Mean (S.E.)		T (d.f.)	Significance
	WS7 abundance	WS2 abundance		
Collmbola	52 (12.04)	28 (6.64)	1.71 (10)	ns
Astigmata	119 (38.24)	66 (27)	1.10 (10)	ns
Mesostigmata	27 (8.23)	16 (7.96)	1.02 (10)	ns
Oribatid	302 (44.73)	134 (47)	2.58 (10)	*
Proturan	28 (26.49)	6 (4.66)	1.92 (10)	ns
Prostig				ns
Others	59 (22.09)	19 (14.21)	1.5 (10)	ns
Total	530 (70.68)	260 (85.91)	2.43 (10)	*

* Significant difference at $P < 0.05$ level.

for dogwood were significant across years in the clearcut watershed ($t = 11.09$, d.f. = 4, $P = 0.0004$) and between control watersheds ($t = 11.34$, d.f. = 4, $P = 0.003$). Differences were detected between maple decomposition rates between years in the clearcut watershed ($t = 3.31$, d.f. = 4, $P = 0.03$) and the control watershed ($t = 5.95$, d.f. = 4, $P = 0.004$).

3.1. Microarthropod inventory

Twenty-one years after the clearcut watershed, microarthropod populations were more abundant in WS7 than in the control watershed (Table 2). Among the constituent groups of microarthropods significant differences in density were detected only for oribatid mites (Table 2). Oribatid mites were the most prevalent microarthropods, occupying close to 50% of the fauna in WS2 and approximately 57% in WS7. There were no

Table 3

Proportion of abundance in each microarthropod group from six samples from both clearcut (WS7) and control (WS2) watersheds

	WS7 (%)	WS2 (%)
Astigmata	0.03	0.13
Collmbola	9.74	9.96
Mesostigmata	5.25	5.44
Oribatid	56.90	55.87
Proturan	5.37	4.76
Others	11.06	10.34
Prostig	22.40	23.03
Total	100.00	100.00

Table 4

Species richness and Shannon diversity and evenness, with associated test statistic for clearcut and control watersheds

	Mean (S.E.)		t-Test, probability
	Clearcut (WS7)	Control (WS2)	
Species richness	34 (2.64)	21.66 (4.43)	0.04
Shannon diversity	1.31 (0.04)	1.05 (0.10)	0.06
Shannon evenness	0.86 (0.01)	0.84 (0.04)	ns

significant differences detected in the proportion of animals in any of the microarthropod groups (Table 3). Twenty-five percent of the variance in the PCA was explained along the first axis. The cumulative percent variance explained by the first four axes extracted was 62%. Most of the samples drawn from the clearcut watershed clustered together in the PCA plot (Fig. 2). Jaccard's similarity index that shows a consistent similarity in oribatid assemblage between samples drawn from the same watershed (Fig. 3).

Differences in the diversity in the two watersheds were detected (see Fig. 4, species rank curve). There was elevated species richness of oribatid mites in WS7 ($t = 2.38$, d.f. = 10, $P = 0.04$). Differences in Shannon diversity were marginally significant ($t = 2.33$, d.f. = 6.3, $P = 0.056$) (Table 4). No differences were found in Shannon evenness.

4. Discussion

After 21 years, decomposition rates in a clearcut watershed had reconverged or surpassed (in the case of one substrate, *C. florida*) the decomposition rates of an adjacent control watershed at Coweeta Hydrologic Laboratory, North Carolina. Before this study, previous observations (up to year 8 after clearcut) on decomposition at this site revealed slower decomposition rates in the disturbed watershed.

Although the rates converged, contrasts between decomposition rates of the substrates 8 and 21 years after clearcut indicated that for the more rapidly decomposing of the three substrates, the rates in fact were lower after 21 years than after 8 years. That is, both *C. florida* and *A. rubrum* decomposed more slowly in both the previously clearcut and control watersheds. *Q. prinus* decomposition rates remained the same in the control watershed, but slowed margin-

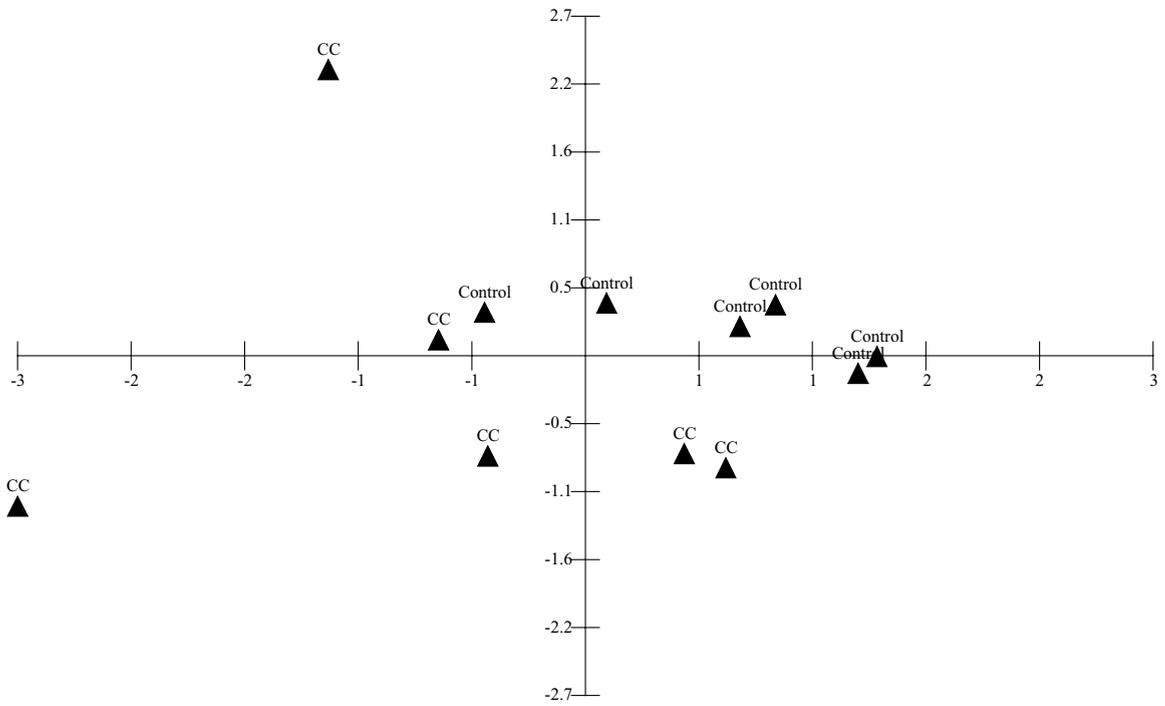


Fig. 2. PCA plot of oribatid morphospecies, showing six samples from clearcut (CC) and control (Control) watersheds.

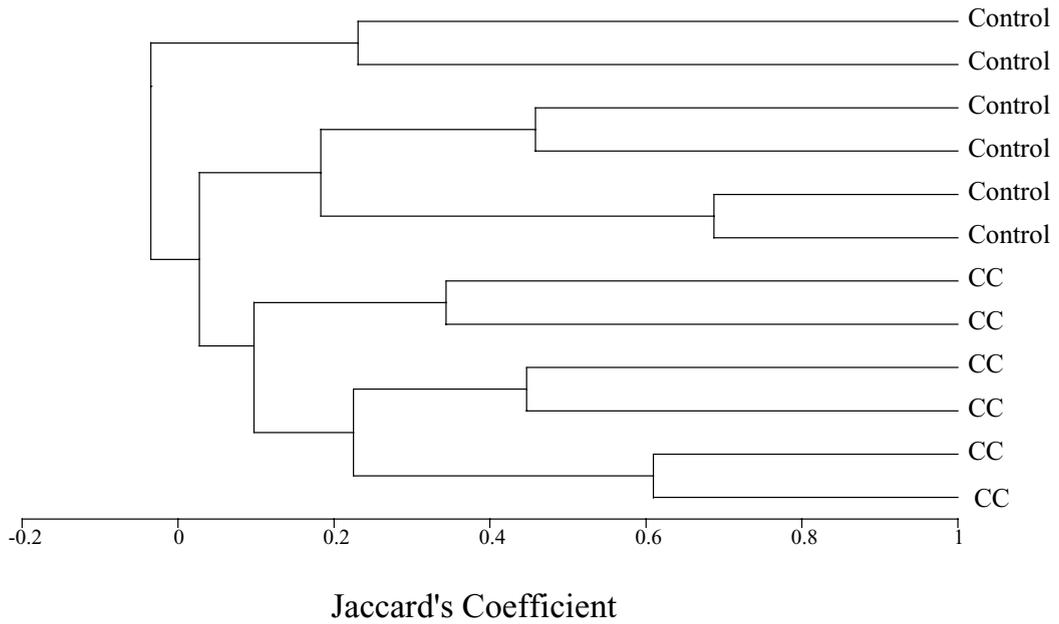


Fig. 3. Dendrogram showing Jaccard's coefficient for oribatid morphospecies from control (WS2) and clearcut (WS7) watersheds.

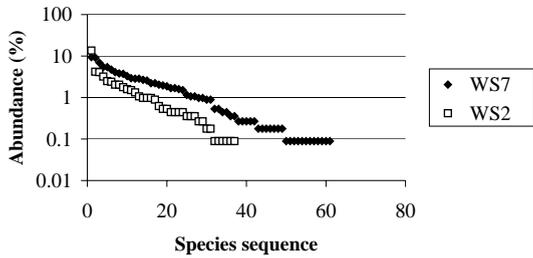


Fig. 4. Rank abundance curves for oribatid mite assemblages from control (WS2) and clearcut (WS7) watersheds.

Table 5

Percent nitrogen and carbon:nitrogen ratios for three substrates used in 1984 and 1996 experiment

	N (%)	C:N
Oak (1984)	0.87	55.7
Oak (1996)	0.88	54.96
Dogwood (1984)	0.56	85.7
Dogwood (1996)	0.96	50.67
Maple (1984)	0.75	62.9
Maple (1996)	0.98	47.52

ally in the disturbed one. The percent N in the litter of both of these litter types was greater in year 21 (Table 5). Percent nitrogen in leaves can vary greatly from tree to tree and from year to year for different species (Nordell and Karlsson, 1995). Although there

is often an increase in decomposition rates associated with elevated leaf nitrogen content, analysis of percent N does not reliably indicated substrate quality, as this nitrogen can be incorporated into a variety of recalcitrant molecules (Taylor et al., 1989). Arguably,

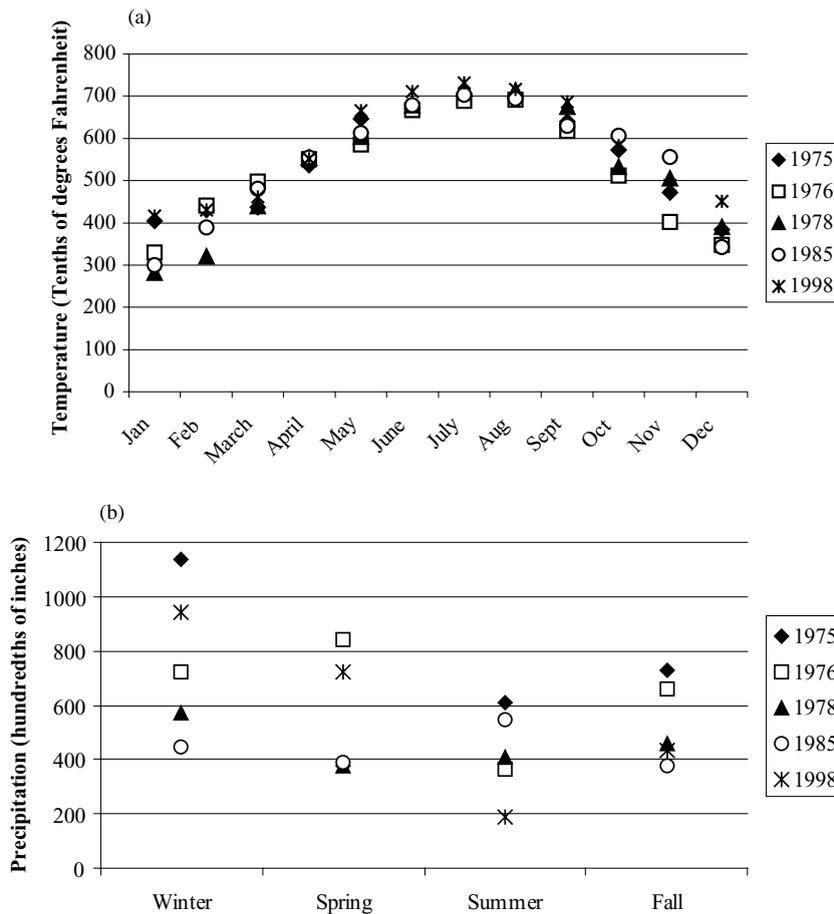


Fig. 5. Climatic data for Coweeta LTER: (a) monthly temperature (tenths of degree Fahrenheit) for all years for which annual decomposition rates are available; (b) seasonal precipitation for all years for which annual decomposition rates are available.

differences in climate between the 2 years that we compared could be partially responsible for the differences in decomposition rates. To test this we utilized monthly climatic data collected from the National Climatic Data Center and made available through the Coweeta LTER web page (<http://coweeta.ecology.uga.edu/>). The average temperature was warmer by about 2 °F for year 21 than for year 8 (Fig. 5a). However, total precipitation in both summer and fall was lower in year 21 than in year 8 (Fig. 5b). This droughtiness has important implications for decomposition rates and may have been responsible for the observations of lower decomposition rates for *C. florida* and *A. rubrum*.

These results suggest that there has been a recovery in the clearcut watershed of a variety of factors, both abiotic and biotic, that ultimately controls the breakdown of leaf material. Blair and Crossley (1988) attributed the substantially lower decomposition rates after 8 years in the clearcut watershed than in the control to differences in microarthropod abundance. In their study they noted that microclimatic extremes were greater in the clearcut watershed than in the control. This, they argued, created a situation unfavorable for microarthropods. Though we have not presented data on microclimate here, the large abundances of microarthropods in the disturbed watershed suggest that severe abiotic constraints on the growth rates of faunal populations have recovered.

A comparison of microarthropod abundance in the two watersheds reveals a greater density of microarthropods in WS7. The density of oribatid mites, elevated in the disturbed watershed, was largely responsible for this overall increase. The proportions of organisms in each broad taxonomic group were similar. The proportion of oribatids was the highest of all groups examined, and this contrasts with results from 8 years after the clearcut when prostigmatid mites were proportionately the most prevalent. Blair and Crossley (1988) reported on animals extracted directly from the litterbags whereas we looked at extractions from the forest floor adjacent to the litterbags. There is no reason to suspect that fauna in litterbags should be colonized preferentially by different taxonomic groups (Heneghan et al., 2002). Differences in diversity are detected and the Jaccard's similarity measure suggested that samples drawn from each watershed are self-similar, however PCA showed

some overlap between the assemblages of oribatids on the two sites. There is not a complete separation of samples along the first two axes of the PCA.

This study attempted to answer one question, had decomposition rates in a watershed that had been clearcut more than two decades prior to the initiation of the study recovered in comparison to an adjacent control watershed? We predicted, based upon the recovery of some decomposer populations, that the answer would be yes. In fact, further analysis of microarthropod populations revealed that the abundance and diversity was now greater in the previously clearcut watershed, and that decomposition rates of one substrate now exceeded the decomposition rates in the control.

Subsequent investigations on decomposition at these two watersheds will be important. Twenty-one years after a clearcut three substrates chosen to reflect a range of substrate qualities had comparable or faster decomposition rates than in an adjacent control watershed. Important biotic contributors to decomposition, namely microarthropod populations have recovered, and in fact are now higher. Well-controlled longitudinal studies may reveal if the behavior of the systems remains comparable, or if the legacy of the clearcut persists with the younger system establishing a swifter decomposition rates for some time.

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