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THE INFLUENCE OF HYDROLOGIC CONDITIONS AND SUCCESSIONAL STATE ON DISSOLVED ORGANIC CARBON EXPORT FROM FORESTED WATERSHEDS[1]

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Abstract. Concentration and export of dissolved organic carbon (DOC) were compared in streams draining four southern Appalachian watersheds with different treatment histories in 1969–1970 and again in 1979–1980. In 1969–1970 the watersheds were: old field (1 yr old), hardwood coppice (7 yr old), white pine (13 yr old), and mature hardwood (undisturbed for at least 45 yr). DOC concentrations in 1969–1970 were three to four times greater than in 1979–1980 on all watersheds, and the differences among watersheds were consistent both years: old field > hardwood > pine > coppice. Concentrations were always greater during the growing season. Annual runoff was 50% greater in 1979–1980, and annual DOC export in 1979–1980 was half the 1969–1970 value in all watersheds. Annual export was greatest from the hardwood and old-field watersheds and least from the pine and coppice watersheds during both years. Although there appears to be a trend toward decreasing DOC concentration and export over the first two decades of secondary succession, differences caused by periodic variations in runoff are far more significant than any successional changes observed.

Key words: Coweeta Hydrologic Laboratory; disturbance; ecosystem recovery; hydrologic regime; long-term ecosystem changes; North Carolina; nutrient export; old field; pine plantation; succession.

INTRODUCTION

Dissolved organic carbon (DOC) is a major form of organic carbon transported in streams. For example, Wetzel and Manny (1977) found DOC to comprise 75% of all carbon transported in Augusta Creek, Michigan, and Fisher and Likens (1973) found that 47% of organic carbon transported by Bear Brook, New Hampshire, was in the dissolved form. DOC also plays a major role in the energetics of stream ecosystems (Fisher and Likens 1973, Lush and Hynes 1973, McDowell and Fisher 1976, Wetzel and Manny 1977). Studies which report DOC transport and dynamics are few. Moeller et al. (1979) summarize North American work on DOC, while others (Meybeck 1981, Schlesinger and Melack 1981) report total organic carbon transported by rivers throughout the world. Few studies specifically address the effect of perturbation (e.g., clear-cutting) on DOC dynamics in streams (Hobbie and Likens 1973, Dahm 1980, Meyer and Tate 1982), and no study addresses the question of how annual hydrologic conditions and secondary succession influence DOC dynamics in streams.

Although patterns of export of essential nutrients during forest succession have been explored (Vitousek and Reiners 1975, Bormann and Likens 1979), little is known of successional changes in DOC export. Export of essential nutrients is high immediately after disturbance, decreases to a minimum largely due to utilization by successional plant species, and then increases gradually to an asymptotic value with the mature forest (Vitousek and Reiners 1975, Bormann and Likens 1979). The temporal pattern of DOC export may be similar, although for different reasons. One source of streamwater DOC is leaching of forest floor organic matter, which decreases rapidly for several years after disturbance and then increases to an asymptote with regrowth of the mature forest (Covington 1981). Other watershed sources of DOC to the stream include leaching of leaf and wood litter from the riparian zone; one would expect an initially rapid increase with a gradual leveling off of these sources with revegetation. In addition, the nature of DOC inputs may change as forest species composition changes; for example, early successional, more rapidly decomposing species may contribute less refractory DOC to the stream. In-stream processes and hydrologic conditions will also influence DOC export. Hence the pattern of DOC export over time will not simply reflect changing amounts of DOC entering the stream from the successional watershed.

The purpose of this study was to examine changes in concentration and annual export of dissolved organic carbon from four watersheds with different treatment histories and at different stages of secondary succession at the beginning and end of a 10-yr period. The main objectives were: (1) to determine if disturbance and ecosystem recovery (succession) on a watershed have an influence on stream DOC concentrations and export, and (2) to compare the variation in DOC concentration and export due to annual hydrologic regime with the variation observed over a decade of successional change.

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TABLE 1. Summary of physical and chemical characteristics of the four watersheds and streams studied.

	Watershed 6	Watershed 13	Watershed 17	Watershed 18
Vegetation type				
1969–1970	1-yr-old old field (weed, grass, shrubs)	7-yr-old hardwood coppice	13-yr-old white pine	Mature hardwood
1979–1980	Black locust, blackberry, herbaceous plants (11 yr old)	17-yr-old hardwood coppice	23-yr-old white pine	Mature hardwood
Watershed area (ha)	8.9	16.1	13.5	12.5
Runoff (cm)*				
44-yr average	...	...	...	103.0
1969–1970†	89.3	99.7	72.3	98.9
1979–1980†	131.3	153.0	111.4	156.7
Precipitation (cm)*				
1969–1970†	172	178	190	190
1979–1980†	234	228	256	256
Elevation (m)‡				
Minimum	699	725	742	721
Maximum	905	912	1021	1006
Slope (%)‡	54	49	57	52
Total channel length (m)	450§	604‡	210§	564§
Average channel width (m)	0.6§	...	1.2§	1.2§
Total channel area (m^2)	277§	...	380§	699§
Channel gradient (m/m)§	0.243	...	0.249	0.200
Water chemistry (mg/L)*,‖				
NO_3-N 1971–1972¶	0.657	0.055	0.177	0.003
1979–1980†	0.778	no data	0.128	0.004
NH_4-N 1971–1972¶	0.006	0.004	0.006	0.006
1979–1980†	0.003	no data	0.004	0.002
PO_4 1971–1972¶	0.004	0.002	0.003	0.003
1979–1980†	0.005	no data	0.005	0.003
Ca 1971–1972¶	1.084	0.487	0.560	0.676
1979–1980†	0.939	no data	0.490	0.577
K 1971–1972¶	0.574	0.423	0.442	0.481
1979–1980†	0.554	no data	0.405	0.427

* Data from Coweeta Hydrologic Laboratory.
† 1 July through 30 June.
‡ Data from Johnson and Swank (1973).
§ Data from Webster and Patten (1979).
‖ Values are means of monthly means.
¶ 1 November through 31 October. Complete nutrient data are not available for these watersheds prior to 1971.

STUDY SITE

The watersheds studied are a part of the 1625-ha Coweeta Basin located at the Coweeta Hydrologic Laboratory, Macon County, North Carolina. The four watersheds (WS) include an old field (WS 6), a hardwood coppice (WS 13), a white pine forest (WS 17), and a mature hardwood forest (WS 18). The old-field watershed has a long and varied treatment history. In 1958 the entire watershed was clear-cut, converted to fescue grass, and fertilized. Two more applications of fertilizer were added between 1959 and 1965. Beginning in May 1966 and for 2 yr thereafter, the grass was sprayed with herbicide. Since spring 1968 successional vegetation has been allowed to grow. In 1969 the watershed was dominated by grass, and in 1970 woody shrubs became abundant. In 1979 and 1980 the vegetation included herbaceous plants (e.g., blackberry), with black locust (*Robinia pseudo-acacia*) the dominant tree species (see Haefner and Wallace [1981] for pictures of this watershed in 1968 and 1978). A natural pertubation occurred during 1979–1980 when an outbreak of locust borers (*Megacyllene robiniae* Forst) killed or weakened many black locust trees.

The hardwood coppice watershed was first clear-cut in 1939 and 1940, and all wood was left in place. A forest regrew from stump and root sprouts until 1962 when the watershed was again clear-cut. Again no wood was removed, and the forest was allowed to regrow. The dominant vegetation was oaks, hickories, yellow poplar, and dogwoods.

Watershed 17 was clear-cut of hardwood vegetation in 1942. Logs, tree tops, and limbs were left on the watershed. Annual sprout growth was cut back from 1943 to 1955. In 1956 white pine (*Pinus strobus*) was planted, and competing hardwood sprouts were cut or sprayed with herbicides.

The mature hardwood forest has remained undisturbed since at least 1924 except for the chestnut blight during the 1930s. It supports a hardwood forest of oaks, hickories, yellow poplar, and a dense riparian understory of rhododendron. Physical and chemical characteristics of all four streams are summarized in Table 1 (for a more complete description of the four watersheds, see Johnson and Swank [1973] and Webster and Patten [1979]).

Because of their varied treatment histories, these four watersheds cannot be positioned in a simple successional series. On the basis of plant species composition, the old-field watershed represents the earliest successional stage during the 2 yr, while the mature hardwood forest watershed represents the latest successional stage studied. The coppice watershed is of intermediate age, as is the pine plantation, although the latter does not represent a natural successional stage.

Methods

Two sampling designs were used during the 2 yr studied. The 1st yr, grab samples were collected weekly from July 1969 through December 1970. Samples were taken from midchannel just upstream of the ponding basin and filtered through glass fiber filters. Filtered water was acidified, and potassium persulfate was added. Samples were purged of inorganic carbon by bubbling with nitrogen, and were sealed in 5-mL ampoules. The ampoules were autoclaved, and CO_2 was measured by an infrared (IR) analyzer (Menzel and Vacarro 1964). These samples were collected under the direction of Dr. Philip L. Johnson (Oak Ridge Associated Universities) and analyzed by Dr. John E. Hobbie (Marine Biology Laboratory, Woods Hole). We are grateful to them for the use of these data. During 1979–1980, grab samples were collected at the same sites biweekly from July 1979 through June 1980. Samples were filtered through precombusted Gelman A/E glass fiber filters (nominal pore size 0.3 μm). The samples were analyzed with a Dohrmann Envirotech DC-54 carbon analyzer, which uses ultraviolet (UV) catalyzed oxidation in the presence of persulfate.

DOC export during the 2 yr was calculated by multiplying average concentration between sampling dates times the amount of water leaving the watershed during that period. Hence it was not possible to use statistical methods to analyze differences between years or among watersheds. In addition, this method of calculation underestimates total DOC export because increases in DOC concentration that occur during storms are not taken into account. Dahm (1980) found a 60% decrease in DOC export when storms were not included in export calculations for Oregon streams. In two second-order streams at Coweeta, Meyer and Tate (1982) found DOC export was underestimated by 35% in an undisturbed watershed and 50% in a clearcut watershed, by not accounting for changes in DOC concentrations during storms. However, our results are comparable to other studies of DOC export, since most investigators do not include results from intensive storm sampling in their estimates.

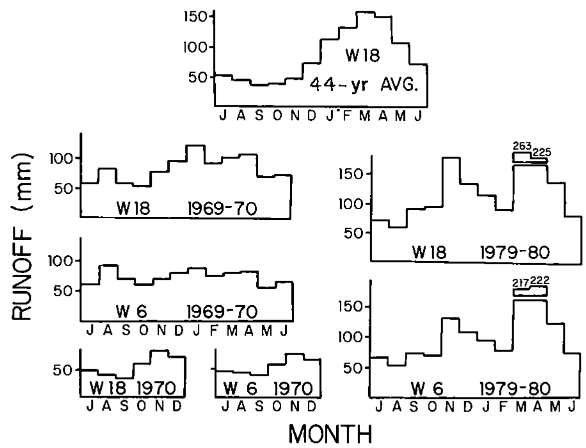

FIG. 1. Monthly runoff from watersheds 18 (mature hardwood) and 6 (old field) for 1969–1970, 1979–1980, and July–December 1970 as well as the 44-yr average runoff pattern for watershed 18. Data are from the Coweeta Hydrologic Laboratory.

To check methodological differences between years, we analyzed standards and samples from each watershed, using both analytical methods during 1980. DOC concentrations using the Menzel and Vaccarro (1964) method averaged 4% lower than the UV catalyzed oxidation method. Unfortunately, we do not know what type of filter was used during 1969–1970, although it was probably Whatman GF/C (nominal pore size 1.2 μm). Comparison of Whatman GF/C- with Gelman A/E-filtered water from Coweeta streams showed no detectable difference in DOC concentrations between the two.

Results

Runoff

The seasonal runoff pattern during 1969–1970 was similar to the 44-yr average, but the pattern during 1979–1980 was very different (Fig. 1). November, December, March, April, and May were unusually wet during this year. The seasonal runoff pattern was similar for all four watersheds during each year, with one exception (Fig. 1). One year after disturbance (1969), the old-field watershed showed very little seasonal variation in runoff. Eleven years after disturbance (1979) the runoff pattern more closely resembled that of the other watersheds during that year. This change in runoff pattern reflects the successional changes from herbaceous to woody vegetation.

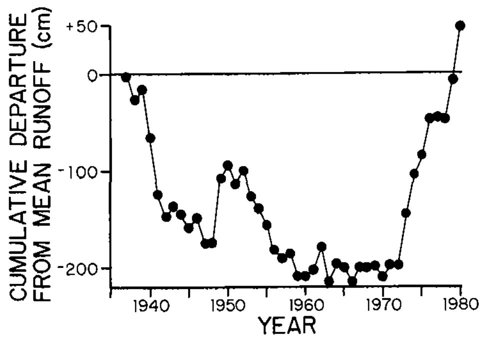

FIG. 2. Cumulative departure from mean runoff for the 44-yr period of record on watershed 18 (mature hardwood). Data are from the Coweeta Hydrologic Laboratory.

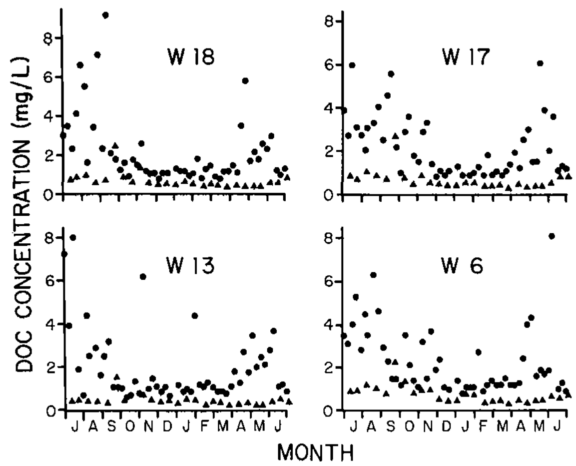

FIG. 3. DOC concentration in weekly or biweekly samples from watersheds 6, 13, 17, and 18 during 1969–1970 (●) and 1979–1980 (▲). The 1969–1970 data are courtesy of Dr. Philip Johnson, Oak Ridge Associated Universities.

Annual runoff for the 1969 year was 4% below average and the 1979 year was 52% above average for the undisturbed hardwood forest watershed. Runoff for July–December was 45, 9 and 117% above average for 1969, 1970, and 1979, respectively. Growing season (May–October) runoff was 13 and 56% above average for 1969–1970 and 1979–1980, respectively, while runoff during the dormant season (November–April) was 9% below and 61% above average.

The runoff data indicate that 1969–1970 was a year of average runoff, while 1979–1980 was a wet year. DOC export from a watershed will be strongly influenced by the amount of runoff during that year, but it may also reflect moisture conditions during previous years, i.e., whether there has been a prolonged dry or wet period (Cummins et al., *in press*). This can be examined by plotting cumulative departure from mean runoff (Fig. 2). In this plot, a negative slope (e.g., 1937–1947) represents a period of below-average runoff, a positive slope (e.g., 1970–1976) a period of above-average runoff, and zero slope (e.g., 1967–1969) a period of average runoff. It is clear from the data in Fig. 2 that 1969–1970 was preceded by a decade of below-average runoff and then a decade of average runoff. On the other hand, the decade of this study, preceding 1979–1980, had several years of above-average runoff.

DOC concentration

Discharge-weighted DOC concentrations from all watersheds were approximately three to four times greater in 1969–1970 than in 1979–1980 (Table 2). These concentration differences are not due to methodological or sampling problems. When we use the two methods on the same water sample, the method used during 1969–1970 slightly underestimates rather than overestimates DOC concentration. Furthermore, stream discharge on sampling days was generally lower in 1969–1970 than in 1979–1980; i.e., the concentration

TABLE 2. Summary of DOC concentration and export from four watersheds.

	Dissolved organic carbon							
	Old field (WS6)		Coppice (WS13)		Pine (WS17)		Hardwood (WS18)	
	Export (kg/ha)	Concentration (mg/L)	Export (kg/ha)	Concentration (mg/L)	Export (kg/ha)	Concentration (mg/L)	Export (kg/ha)	Concentration (mg/L)
1969–1970*	20.83	2.33	18.76	1.88	14.28	1.98	20.62	2.08
1979–1980*	8.92	0.680	6.88	0.450	6.64	0.596	10.11	0.633
1969–1970 Growing†	12.77	3.09	10.01	2.35	7.95	2.97	11.72	2.94
1979–1980 Growing†	4.34	0.939	2.93	0.531	3.08	0.894	4.74	0.861
1969–1970 Dormant‡	8.06	1.68	8.75	1.53	6.32	1.39	8.90	1.51
1979–1980 Dormant‡	4.59	0.536	3.95	0.404	3.56	0.463	5.37	0.513
1969 July–December	12.36	2.79	9.64	2.10	7.57	2.47	11.06	2.57
1970 July–December	4.89	1.52	5.48	1.70	4.35	1.90	5.25	1.63
1979 July–December	4.88	0.967	3.40	0.585	3.54	0.823	5.55	0.863

* From 1 July to 30 June.
† From 1 May to 31 October.
‡ From 1 November to 30 April.

differences are not a consequence of greater sampling during storms in 1969–1970.

Although the discharge-weighted DOC concentrations for 1969–1970 were greater than during 1979–1980, mean annual concentration decreased in the order: old field > hardwood > pine > coppice during the 2 yr (Table 2). Concentrations were always higher during the growing season than during the dormant period. During the growing seasons, mean concentrations decreased in the order: old field > pine > hardwood > coppice.

Weekly DOC concentrations during 1969–1970 were higher and more variable than during 1979–1980 (Fig. 3). The differences between years were greatest during the growing season. In both years concentrations were higher and more variable during the growing season than during dormancy for all watersheds (Fig. 3). These seasonal changes are far greater than any diel changes in DOC concentration in Coweeta streams (Meyer and Tate 1982). During 1979–1980, DOC concentrations in subsurface water seeps were similar for all four watersheds (0.15–0.24 mg/L), and concentrations increased from the source to the weir.

DOC export

DOC export during 1969–1970 was approximately two times greater than in 1979–1980 for all watersheds (Table 2), despite less runoff during 1969–1970 (Table 1). The differences between years were greatest during the growing season. During both years, export was greatest from the hardwood and old-field watersheds and least from the pine watershed. Export from the old-field and hardwood watersheds was essentially the same in 1969–1970, but by 1979–1980 export from the old field was somewhat less than that from the undisturbed watershed.

Temporal changes in discharge, DOC concentration, and export

To compare the disturbed watersheds better over time, we calculated the ratio of discharge, DOC concentration, and export for each disturbed watershed to the corresponding value for the undisturbed hardwood watershed for each year studied (Table 3). Hence we are comparing each disturbed watershed to the undisturbed "reference." This facilitates a comparison of temporal trends among watersheds that is less influenced by the difference in discharge for the 2 yr.

There was little change in the relationship between the pine and hardwood watersheds over the decade. Ratios of discharge, DOC concentration, and export remained constant (Table 3). In contrast, ratios for both the coppice and old-field watersheds declined significantly for export and concentration, while the discharge ratio remained constant over the decade. These results indicate some change in DOC concentration and export over a decade of succession in the old-field and coppice watersheds, but little change in the pine plantation.

TABLE 3. A comparison of discharge, DOC concentration, and DOC export from four watersheds. The values are the ratio of each parameter for a disturbed watershed divided by that parameter for the undisturbed watershed.

		DOC	
	Discharge	Concentration	Export
1969–1970			
Old field/hardwood	0.90	1.12	1.01
Coppice/hardwood	1.01	0.90	0.91
Pine/hardwood	0.73	0.95	0.69
1979–1980			
Old field/hardwood	0.82	1.07	0.88
Coppice/hardwood	0.96	0.71	0.68
Pine/hardwood	0.70	0.94	0.65

DISCUSSION

DOC concentration in streamwater

The low DOC concentrations on all watersheds during 1979–1980 were probably due to the consistently higher runoff throughout the year and during the previous several years (Fig. 2), causing a washout of stored DOC and stored sources of DOC (e.g., leachable particulate organic carbon [POC]) within the watershed and stream. During 1979–1980 all watersheds had a similar and low DOC concentration in the subsurface water; therefore, the consistent increase in DOC concentration observed downstream appears to be contributed from riparian sources or from sources within the streams such as leaching of leaves or wood. After several wet years, these DOC sources would probably be depleted. Hence DOC concentrations in streamwater during a wet year (such as 1979–1980) more closely reflect concentrations of the subsurface waters.

The higher DOC concentration on all watersheds in 1969–1970 was probably a consequence of lower and more evenly distributed runoff during that year and the preceding decade (Fig. 2). Not only was there less dilution of the DOC being produced in the watershed and stream, but there probably was also more DOC and leachable POC stored in the streambed. We have noted higher DOC concentrations during dry years in other Coweeta streams (J. L. Meyer and C. M. Tate, *personal observation*), and Dahm (1980) also found that DOC concentration was higher during periods of consistently low flow in Oregon streams. In addition to the lower annual runoff during 1969–1970, maximum discharge was also less than in 1979–1980. The recurrence interval of the maximum discharge in 1969–1970 was 2 yr, while in 1979–1980 it was 6 yr (recurrence intervals calculated from empirical regressions in Douglass [1974]). Furthermore, there was a 10-yr flood in 1978 and a 100-yr flood in 1976, while the greatest discharge

TABLE 4. Summary of DOC concentration and export from disturbed and undisturbed North American watersheds. All streams are first or second order.

Watershed	Area (km^2)	Discharge-weighted concentration (mg/L)	Annual runoff (cm)	Annual DOC export ($g \cdot m^{-2} \cdot yr^{-1}$)	Symbol*	Reference
New Hampshire (Hubbard Brook)						
W2* (1967–1969, mean)	0.156	0.94	122.1	1.03	A	Hobbie and Likens (1973)
W6‡ (1967–1969, mean)	0.132	0.94	96.2	1.02	B	Hobbie and Likens (1973)
Bear Brook‡	1.30	1.10	72.0	1.31	C	Fisher and Likens (1973)
Tennessee						
Walker Branch‡	0.384	0.56	156	1.04	D	Comiskey (1978)
Oregon (H. J. Andrews)						
W10† (1977)	0.102	2.74	78.2	2.06	E	Dahm (1980)
W2‡ (1977)	0.603	1.92	36.5	0.71	F	Dahm (1980)
W10† (1978)	0.102	1.87	186	3.44	G	Dahm (1980)
W2‡ (1978)	0.603	1.77	143	2.52	H	Dahm (1980)
Devil's Club Creek‡	0.20	1.60	26.8	0.43	I	Moeller et al. (1979)
Pennsylvania						
White Clay Creek‡	0.30	2.6	58.8	1.53	J	Moeller et al. (1979)
White Clay Creek‡	1.8	2.6	50.8	1.32	K	Moeller et al. (1979)
Michigan						
Smith Creek‡	0.78	3.9	56.6	2.21	L	Moeller et al. (1979)
Idaho						
Camp Creek‡	0.80	1.1	150	1.65	M	Moeller et al. (1979)
North Carolina (Coweeta)						
W18‡ (1969)	0.125	2.08	98.9	2.06	N	This study
W18‡ (1979)	0.125	0.63	156.7	1.01	O	This study
W17† (1969)	0.134	1.98	72.3	1.43	P	This study
W17† (1979)	0.134	0.60	111.4	0.66	Q	This study
W13† (1969)	0.161	1.88	99.7	1.88	R	This study
W13† (1979)	0.161	0.45	153.0	0.69	S	This study
W6† (1969)	0.089	2.33	89.3	2.08	T	This study
W6† (1979)	0.089	0.68	131.3	0.89	U	This study

* Symbol for watershed used in Fig. 4.
† Disturbed watershed.
‡ Undisturbed watershed.

in the decade prior to 1969 was a 10-yr flood in 1964. Thus it appears that 1979–1980 was a year when terrestrial and aquatic DOC sources and storage sites had been depleted by storm flows, and when their contribution to streamwater DOC was diluted by a larger volume of water.

The relationship among DOC concentrations in the streams from the four watersheds remained constant for the 2 yr studied: old field > hardwood > pine > coppice. Thus during both years, concentration was highest in the most recently disturbed watershed and lowest in the watersheds of intermediate age since disturbance. Johnson and Swank (1973) also observed this pattern on these watersheds for export of the cations Na^+, K^+, Ca^{++}, and Mg^{++} during 1969–1971. This pattern follows the successional trend for forest floor organic matter (Covington 1981) discussed earlier.

In 1979–1980, 11 yr had passed since the major disturbance of the old field. One might predict that at this time DOC concentrations would be lower than in the undisturbed watershed, because that was observed in 1969–1970 with the 7- and 13-yr-old coppice and pine watersheds; instead average DOC concentration was slightly higher than on WS 18. The 1979 natural perturbation by the locust borer appears to have disrupted the trend of decrease in streamwater DOC concentration during early succession. This perturbation had a similar effect on streamwater nitrate concentrations, which was most dramatic in 1980 (W. Swank, *personal communication*; Table 1).

DOC concentrations were always higher during the growing season than the dormant period. During the growing season the major sources of DOC are in-stream biological activity, leaching and decomposition within the stream, and leachate from the riparian zone. These within-stream and riparian sources overwhelm the subsurface DOC concentrations during the growing season, whereas the soil and subsurface DOC sources predominate during the winter dormant season.

DOC export from upland watersheds

DOC export from Coweeta watersheds is similar to that observed from other small upland watersheds in North America (Table 4). Export from the undisturbed watershed is virtually identical with that from an undisturbed Tennessee watershed for a year of similar runoff (Table 4; Comiskey 1978).

Other workers have reported a significant relationship between annual runoff and annual total organic carbon export from small upland watersheds (Brinson 1976, Mulholland and Kuenzler 1979). Since DOC is a major form of organic carbon in transport, we expected to see a similar relationship between annual runoff and DOC export. As is apparent in Fig. 4, there is no relationship between annual runoff and DOC export for several small upland forested watersheds (r^2 = .074). The relationship is not significantly improved by considering only undisturbed watersheds (r^2 = .089). This suggests that the relationship between runoff and total organic carbon export noted by others may be largely due to the relationship between runoff and particulate organic carbon (POC) export rather than runoff and DOC export. This may simply be a consequence of the fact that POC concentration is more sensitive to increasing discharge during spates than is DOC concentration; POC can increase by two to three orders of magnitude, while DOC increases at most by one order of magnitude. It is also apparent in Fig. 4 that DOC export from some of these watersheds falls very close to the regression line for total organic carbon export calculated from small upland watersheds (Mulholland and Kuenzler 1979). That suggests that this regression may underestimate total organic carbon loss in many watersheds.

The absence of a positive relationship between DOC export and annual runoff is somewhat surprising, since higher DOC export with greater runoff has been reported in some streams (Hobbie and Likens 1973, Dahm 1980), although our Coweeta data do not show this, largely because of antecedent hydrologic conditions. Using a wider range of watershed and stream sizes, Moeller et al. (1979) report that discharge and stream link magnitude (the total number of channels [source to confluence] in a drainage network) are good predictors of DOC export. However, for small, forested, upland watersheds in several physiographic regions with differing amounts of runoff, DOC export appears to be remarkably similar at $\approx 1.5 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (mean of values in Table 2). In many cases, the variation between years on one watershed is as great as the variation among watersheds.

Temporal variation in DOC export

During the 2 yr studied, the youngest and oldest watersheds had the greatest export, while intermediate-aged watersheds had the lowest export (Table 2). The greatest decrease in export over the decade was observed on the two youngest watersheds (Table 3). Although this is the successional relationship predicted earlier in this paper, caution is necessary in interpreting this pattern as being purely a consequence of successional change. In addition to the differences in quantity and quality of decomposing material on the

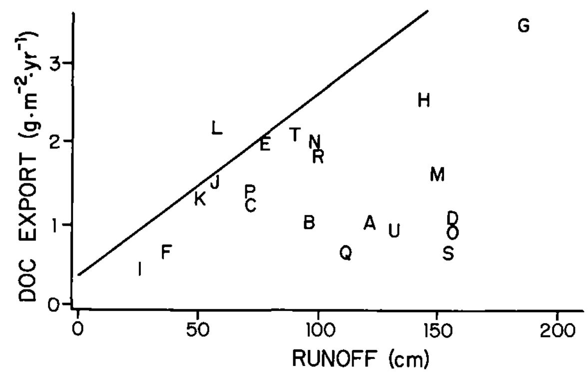

FIG. 4. Annual DOC export per square metre of watershed area from 15 North American watersheds vs. annual runoff. The letters represent individual watersheds described in Table 4. The solid line is the regression of total organic carbon export vs. runoff presented by Mulholland and Kuenzler (1979).

forest floor due to variable treatment histories of the watersheds, there are differences in the riparian zone and in streambed morphology on the four watersheds. If in-stream sources of DOC are important, some of the differences in DOC export may be a consequence of stream size. In fact, when DOC export is expressed as carbon per metre of stream channel, it is remarkably similar on all but the pine watershed: 0.41–0.50 kg/m in 1969–1970 and 0.18–0.22 kg/m in 1979–1980. The values for the pine watershed are 0.92 and 0.42 kg/m, respectively. The consistent increase in DOC concentration from the headwater seep to the weir observed in these and other Coweeta streams, plus the fact that subsurface water has consistently lower DOC concentration than stream water (Meyer and Tate 1982) point to the importance of in-stream generation of DOC. In an undisturbed Coweeta stream, DOC inputs in subsurface water and throughfall were only 70% of DOC exports (Meyer and Tate 1982); the remainder plus any additional DOC taken up by the stream community (Lush and Hynes 1978, Dahm 1981) would have to be supplied by in-stream generation, for example leaching and microbial processing of leaf and wood litter. If subsurface water inputs comprise a similar percentage on these watersheds, then from 8 to 20% of leaf litter inputs (based on 1979–1980 litter inputs to an undisturbed Coweeta watershed [Meyer and Tate 1982]) would have to be processed to DOC in the stream to account for the remainder of DOC exported from the stream during the 2 yr. Since 5–27% of leaf C can be leached within the 1st wk of stream residence (Anderson and Sedell 1979), this figure appears quite reasonable.

Successional changes in the terrestrial ecosystem would be expected to have the strongest effect on sources of DOC to the stream. These sources include subsurface water inputs and riparian contributions of throughfall and leaf and wood litter, which are then processed to DOC in the stream. These sources would be high immediately after a disturbance like clear-cutting, drop to a fairly low value, and then increase as forest biomass accumulated. The data presented here suggest that DOC export from streams is affected in part by these successional changes in magnitude of DOC sources, but that export is more strongly influenced by variations in hydrology. The change in DOC export from a watershed due to differences in annual runoff appears to be at least a two-fold change (Table 2), while the change due to succession and different treatment histories is more on the order of 10–20% (Table 3). We conclude that in the small, upland watersheds studied, succession has a minor effect, and periodic variations in hydrology exert a more profound influence on DOC concentration and export in streamwater.

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