Verh. Internat. Verein. Limnol.	24	1676–1680	Stuttgart, Juni 1991

Long-term studies of the influence of invertebrate manipulations and drought on particulate organic matter export from headwater streams

J. B. Wallace, T. F. Cuffney, B. S. Goldowitz, K. Chung and G. J. Lugthart

Introduction

Most of the energy inputs to small headwater streams in forested regions are in the form of coarse particulate organic matter (CPOM) from the surrounding forest, while outputs are primarily exported in the form of fine particulate organic matter (FPOM) and dissolved organic matter (DOM) (Webster et al. 1983). The biota, including microbes (Suberkropp & Klug 1980), can play an important role in the conversion of CPOM to both FPOM (Wallace et al. 1982) and DOM (Meyer & O'Hop 1983). In 1980, we treated one of two adjacent 1st-order streams with an insecticide which resulted in massive invertebrate drift and altered the community structure from one dominated by large shredders to one dominated by collector-gatherers and some predators. Rates of leaf litter processing and seston concentrations were significantly lower following treatments (Wallace et al. 1982). Within two years after treatment ceased, restoration of shredder biomass and FPOM concentrations occurred (Wallace et al. 1986). In 1984, a third stream was included as a new reference. Following a year of pretreatment data collection in the three streams, the reference stream from the previous study served as a "new" treatment stream. During this treatment period, the basin experienced its most severe drought in 54 years of record.

The objectives of this paper are to summarize the influence of insecticide treatment and drought on particulate organic matter export from the above three streams over a >4-year period.

Study sites and treatment

Three streams, draining Catchments (C) 53, 54, and 55 at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of western North Carolina, USA, were used in this study. The catchments are heavily shaded by deciduous forest, and rhododendron forms a dense understory which results in year-round shading of the stream bed.

Stream temperature extremes range from ca. 1.5 to 19.6 °C, and annual degree days range from 4541 (C 54) to 4696 (C 53). Starting in 1985 and continuing through early 1989, precipitation at Coweeta was below normal (long-term mean = ca. 180 cm $\cdot$ y^{-1}), and a record drought (precipitation = 63 % of normal) occurred during 1986. During the period of study, precipitation was highest in 1987 (85 % of the long-term average). Additional site descriptions can be found in Cuffney & Wallace (1988).

In December 1985, the stream draining C 54 was treated by spraying a 10 ppm solution of the insecticide methoxychlor (1,1,1-tri-chloro-2,2-bis[p-methoxyphenyl]ethane) along the entire 280 m being studied, from its spring seep source. Treatments were repeated seasonally (eleven times) from March 1986 to October 1988 (Wallace et al. 1989). The initial insecticide treatment of C 54 produced massive invertebrate drift and altered community structure (Wallace et al. 1989). Invertebrate shredder abundances in leaf bags were not significantly different among streams prior to treatment; following treatment, there were significantly fewer shredders in litterbags in C 54 than in C 53 and C 55 (Cuffney et al. 1990). Treatments also reduced leaf litter processing rates and FPOM export in C 54 relative to C 53 and C 55 without altering benthic leaf and wood respiration rates (Cuffney et al. 1990).

Methods

Each stream is equipped with a gaging flume connected to a stage recorder for continuous estimates of discharge. A Coshocton proportional sampler attached to each flume shunts ca. 0.6 % of stream discharge through a series of settling barrels designed to trap FPOM (<4 mm to >0.45 μm) (Cuffney & Wallace 1988). Barrels were sampled at weekly to biweekly intervals for FPOM using procedures described by Cuffney & Wallace (1988). At the same time, replicate instantaneous (grab) samples of seston were collected at each flume by filtering 2–6 l per sample through ashed and preweighed glass fiber filters (Gelman type A/E) (Cuffney & Wallace 1988).

We utilized linear regression to examine the relationship between maximum discharge (independent variable) and total FPOM export (barrel samplers) among individual sampling intervals (Cuffney & Wallace 1989).

CPOM export was collected continuously on each stream using a rectangular cage (ca. 6 m^3, galvanized 4 mm wire mesh) which was open on the upstream end.

0368-0770/91/0024-1676 $ 1.25

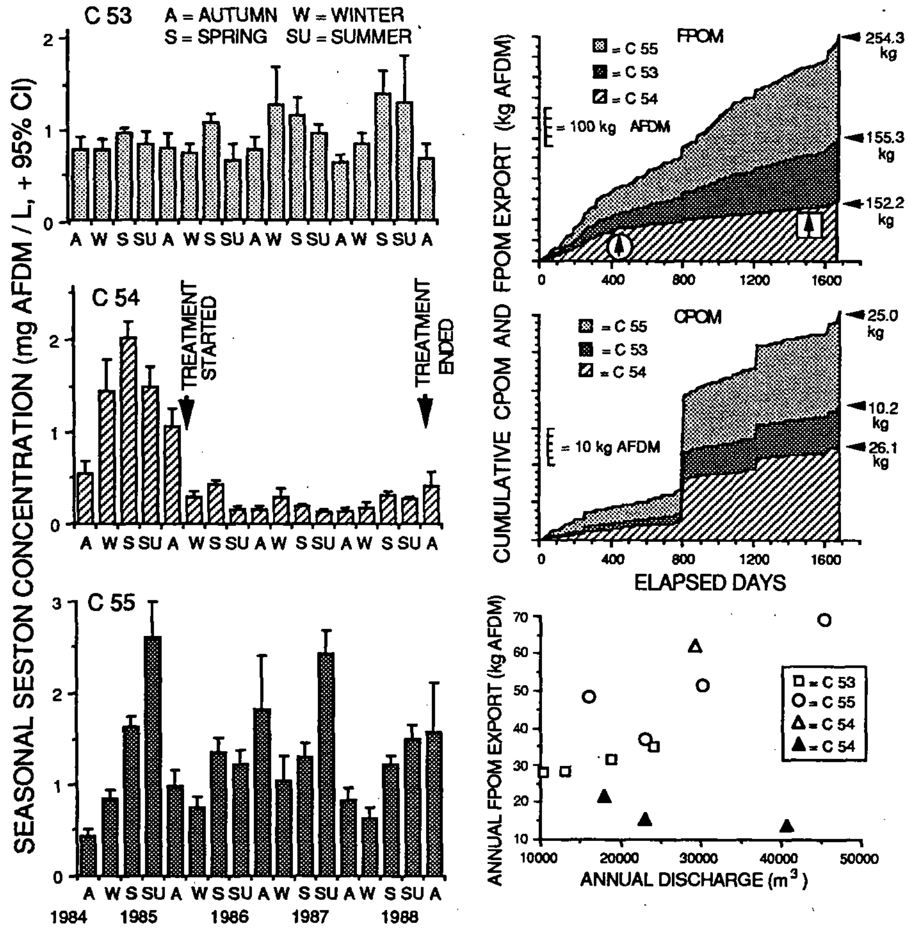

Fig. 1 – 3. Fig. 1, left column, organic seston concentrations in streams draining C 53, C 54, and C 55 based on instantaneous grab samples at 1 – 2 weeks intervals for the period of September 1984 through December 1988. Note treatment period (winter 1985 through autumn 1988) for C 54. Fig. 2, upper and middle right, cumulative FPOM and CPOM export for streams draining C 53, C 54, and C 55 for period of 26 September 1984 to 6 May 1989. The arrows on the FPOM figure denote start (circle) and termination (square) of seasonal treatments for C 54. Note the much lower slope of cumulative FPOM export during the treatment period of C 54 compared to those of C 53 and C 55. Fig. 3, lower right, total annual export of FPOM (barrel samples) versus annual discharge for 4-year period of December 1984 to December 1988 for C 53, C 54, and C 55. Open data points indicate untreated streams (squares and circles) or pretreatment values (open triangle) for C 54. Closed triangles represent the three treatment years for C 54.

Each cage sampled the entire stream flow 5 to 10 m above the flume of each catchment (see Cuffney et al. 1990). Contents of CPOM traps were collected at the same intervals as barrel samplers, separated by category (wood, leaves, moss, etc.) and AFDM determined. We estimated standing crop of leaf litter in each stream in August 1988 by wet weighing all leaf material across the wetted perimeter in 20 cm wide samples collected at 10 m intervals for the entire stream length. Subsamples were returned to the laboratory for wet weight-dry weight and AFDM determinations.

Results

Pretreatment grab seston concentrations (autumn 1984 through autumn 1985) were variable among streams (Fig. 1). Those of C 54 were higher than either C 53 or C 55 during winter and spring 1985, and summer 1985 concentrations were highest in C 55. There were no differences among streams in autumn 1985. Following initial treatment of C 54 (December 1985), seasonal seston concentrations

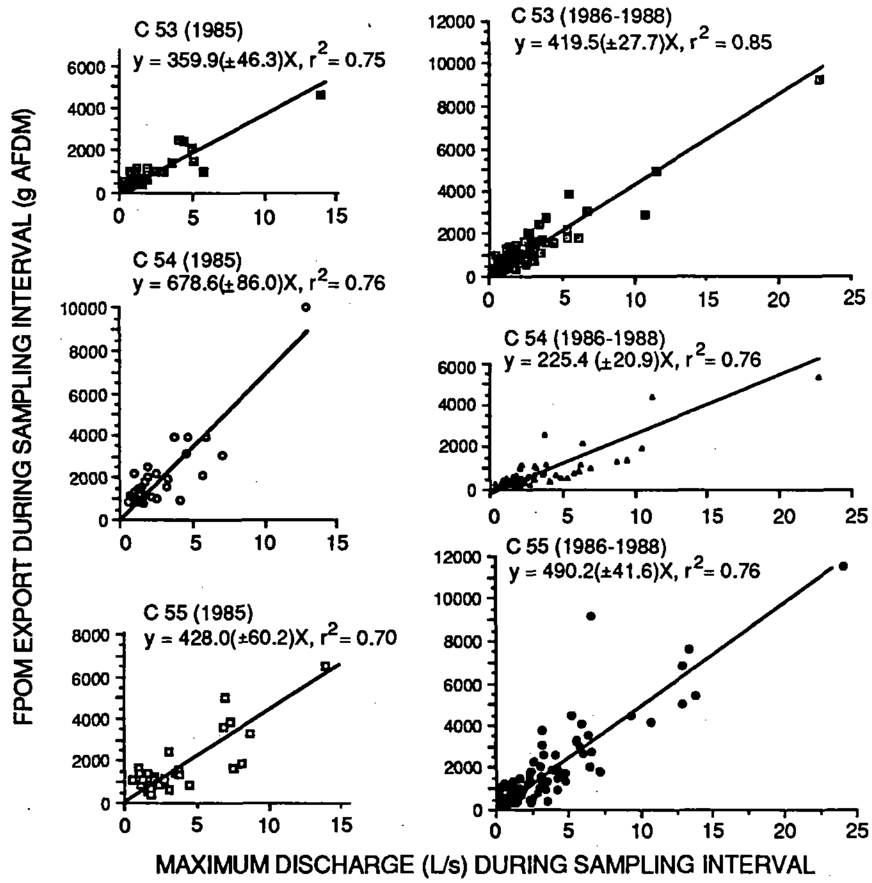

Fig. 4. Linear regressions through the origin relating g AFDM of FPOM export (y, from barrel samplers) to maximum discharge (X) during collection intervals for C 53, C 54, and C 55. Regression equations give slope (b) value (± 95 % CI of slope) and r^2. Values for 1985 (pretreatment) follow CUFFNEY & WALLACE (1989). The time periods correspond to pretreatment (1985) and 3-year treatment periods (1986–1988) for C 54. Note the large decrease in slope per unit maximum discharge for C 54 during the 3-year treatment period compared with C 53 and C 55.

remained consistently lower than either C 53 or C 55 throughout the 3-year treatment period.

Total FPOM export during the period of September 1984 to early May 1989 is shown in Fig. 2. During the pretreatment year (December 1984 to December 1985), more FPOM was exported from C 54 (67.6 kg AFDM) than either C 53 (35.4 kg) or C 55 (55.9 kg). During the 3-year treatment period (December 1985 to December 1988), annual export of FPOM from C 54 averaged only 25.6 % (range = 21.3 to 32.3 %) of the pretreatment year (Fig. 3). In contrast, annual FPOM export from the two untreated streams averaged 87.1 % (C 53, range = 78.6 to 102.2 %) and 92.3 % (C 55, range = 65.9 to 126.7 %) of the pretreatment year. These differences in annual export among untreated streams are attributable to high variability in precipitation, discharge (Fig. 3) and storms among years. Total annual export of FPOM showed trends related to discharge in untreated streams, as well as in C 54 during the pretreatment year. During the treatment years, FPOM export from C 54 was consistently lower than either untreated stream and did not show any positive relationship with discharge.

Regressions of maximum discharge versus FPOM export were relatively similar between the pretreatment year (1985) and treatment years (1986–1988) for untreated streams (C 53 and C 55) (Fig. 4). The 95 % CI of slopes did differ among reference streams between pretreatment and treatment periods (e.g. C 53 in 1985 versus C 55 in 1986–1988 and C 53 versus C 55 during treatment years (Fig. 4)). Much of this discrepancy is attributable to early September 1987, when C 55 experienced 3 brief thunderstorms spaced several days apart during a single sampling interval. More FPOM was exported (ca. 9 kg AFDM) during these 3 sequential storms than was predicted based on maximum discharge ($6.5 \, l \cdot s^{-1}$) during the barrel sampling interval. Exclusion of this single sampling interval increased the r^2 for C 55 from 0.76 to 0.85, and the slope decreased from 490 to 470.

During the pretreatment year, the slope of maximum discharge versus FPOM export for C 54 was higher than that of either C 53 or C 55 (Fig. 4). In contrast, during treatment of C 54 (1986–1988), significantly less FPOM was exported per unit maximum discharge in C 54 than in either C 53 and C 55 (Fig. 4).

Leaves and woody debris accounted for ≥ 90% of all CPOM export (Table 1). The cumulative export of CPOM displayed a much more punctuated pattern than that of FPOM (Fig. 2) and was distinctly related to major storms. During the 2-year treatment period, the ratio of CPOM/FPOM export for C 54 was >3 × that of the untreated streams (Table 2). Over the period of 26 September 1984 to 6 May 1989 (1683-d), total CPOM export was only ca. 0.9% (C 53), 2.1% (C 54), and 2.4% (C 55) of total CPOM inputs (based on measurements of direct litterfall and lateral movement). Over 50% to 60% of total CPOM export from all streams occurred during three storms; a single storm in late November 1986 accounted for 35 to 47% of the total for the entire 56 mo period. Although this storm had a recurrence interval of only 1.8 year, it occurred shortly after litterfall during a record (>54-year) drought.

Table 1. Total export (kg AFDM) and % composition of CPOM for the three catchments during the period of 26 September 1984 to 6 May 1989.

	C 53	C 54	C 55
Total Export (kg)	10.24	26.08	24.96
Leaves (%)	55.44	66.07	50.83
Wood (%)	34.26	31.57	39.39
Fruit & Seed (%)	7.51	0.71	3.49
Moss (%)	0.10	0.13	0.05
Miscellaneous (%)	0.05	0.37	0.10
Sediment (>4 mm) (%)	2.64	0.55	6.14

Table 2. Ratio of CPOM/FPOM export (kg AFDM) for each stream for pretreatment (September 1984 to December 1985), treatment (C 54, December 1985 to December 1988), and post-treatment (December 1988 to May 1989) periods for each of the study streams.

	C 53	C 54	C 55
Pretreatment	0.039	0.042	0.068
Treatment (C 54)	0.086	0.359	0.111
Post-treatment	0.030	0.150	0.093

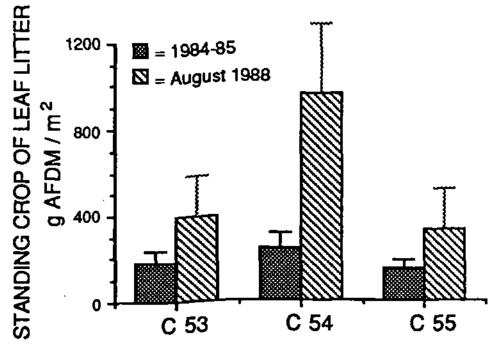

Fig. 5. Benthic standing crop of leaf material (± 95% CL) in each stream in 1984–1985 (pretreatment year) and in August 1988 following 3-year treatment of C 54.

Standing crops of leaf litter in stream channels during August 1988 were significantly higher in C 54 than in C 53 or C 55, whereas data from pretreatment (1984–85) benthic core samples indicated no significant difference among streams (Fig. 5).

Discussion

Seston concentrations changed significantly following initial treatment of C 54 and remained depressed throughout the 3-year treatment period (Fig. 1). In addition, the response of FPOM export to storms (as indicated by lower slope, Fig. 4) decreased significantly in C 54 during the treatment period.

The decline in FPOM export from C 54 is undoubtedly related to both direct and indirect effects of the insecticide on stream macroinvertebrate populations. Comparisons with pretreatment conditions and the two untreated streams indicate that methoxychlor did not affect bacterial densities or leaf, wood, and benthic respiration rates in the treated stream (Cuffney et al. 1990).

Reduced macroinvertebrate abundances and biomass, especially those of leaf shredders, lowered rates of leaf litter processing and FPOM generation. In addition, overall ingestion and defecation of FPOM by collector macroinvertebrates were reduced (SCHURR 1989). Such activities may contribute significantly to entrainment and subsequent transport of particles in streams. These direct effects may explain the rapid decline in seston concentrations of C 54 following treatment (CUFFNEY et al. 1990).

Loss of most leaf-shredding macroinvertebrates also indirectly altered physical retention within C 54. As a result of lower leaf litter processing rates standing crop of leaf litter following the 3-year treatment was over 2 × greater than C 53 or C 55 (Fig. 5). Accumulated leaves can enhance physical retention of FPOM (SHORT & WARD 1981). Storms in these streams tend to produce abrupt, short-term increases in discharge (CUFFNEY & WALLACE 1989), and the rate of increase in discharge during rising hydrographs influences seston concentration (WEBSTER et al. 1987). Due to lower invertebrate feeding activities, greater accumulations of leaf litter during treatment years in C 54 obviously reduced the transportability of particles compared to reference streams (Figs. 3 and 4).

The higher ratio of CPOM/FPOM exported from C 54 (Table 2) is primarily attributable to reduced FPOM export rather than large increases in CPOM export. In contrast to FPOM, total CPOM export from C 54 was only slightly greater than that of C 55 (Table 1) despite a much higher leaf litter standing crop in C 54 (Fig. 5). This is attributable to both high retention of CPOM and the low frequency of major storms during the study period.

Conclusions

Our 3-year manipulation of C 54 reinforces the findings of the previous (1980) experiment, which showed that reducing macroinvertebrate populations has profound effects on particulate organic matter dynamics in Appalachian headwater streams. These effects include: reduced processing and increased storage of CPOM (leaves), lower concentrations of FPOM in stream water and reduced export of FPOM, and reduced FPOM export per unit increase in storm discharge.

Acknowledgements

This research was supported by NSF grants BSR-8316082 and BSR-87-18005. A. LINGLE, P. EGENS, D. IMM, F. SMITH-CUFFNEY, G. SCHURR, P. VILA, and M. WHILES assisted with laboratory and field work.

References

CUFFNEY, T. F. & WALLACE, J. B., 1988: Particulate organic matter export from three headwater streams: discrete versus continuous measurements. – *Can. J. Fish. Aquat. Sci.* **45:** 2010–2016.

– – 1989: Discharge-export relationships in headwater streams: influence of invertebrate manipulations and drought. – *J. N. Amer. Benthol. Soc.* **8:** 331–341.

CUFFNEY, T. F., WALLACE, J. B. & LUGTHART, G. J., 1989: Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. – *Freshwat. Biol.* **23:** 281–299.

MEYER, J. L. & S'HOP, J., 1983: Leaf-shredding insects as a source of dissolved organic carbon in headwater streams. – *Amer. Midl. Nat.* **109:** 175–183.

SCHURR, G. A., 1989: Seasonal variation in the turnover of organic matter by Chironomidae (Diptera) in southern Appalachian streams. – Unpubl. M. Sc. thesis, Univ. of Georgia, Athens, GA. U.S.A., 54 pp.

SHORT, R. A. & WARD, J. V., 1981: Benthic detritus dynamics in a mountain stream. – *Holarctic Ecol.* **4:** 31–35.

SUBERKROPP, K. & KLUG, M. J., 1980: The maceration of deciduous leaf litter by aquatic hyphomycetes. – *Canadian J. Botany* **58:** 1025–1031.

WALLACE, J. B., LUGTHART, G. J., CUFFNEY, T. F. & SCHURR, G. A., 1989: The impact of repeated insecticidal treatments on drift and benthos of a headwater stream. – *Hydrobiologia* **179:** 135–147.

WALLACE, J. B., VOGEL, D. S. & CUFFNEY, T. F., 1986: Recovery of a headwater stream from an insecticide-induced community disturbance. – *J. N. Am. Benthol. Soc.* **5:** 115–126.

WALLACE, J. B., WEBSTER, J. R. & CUFFNEY, T. F., 1982: Stream detritus dynamics: regulation by invertebrate consumers. – *Oecologia* (Berl.) **53:** 197–200.

WEBSTER, J. R., BENFIELD, E. F., GOLLADAY, S. W., HILL, B. H., HORNICK, L. E., KAZMIERCZAK, R. F. & PERRY, W. B., 1987: Experimental studies of physical factors affecting seston transport in streams. – *Limnol. Oceanogr.* **32:** 848–863.

WEBSTER, J. R., GURTZ, M. E., HAINS, J. J., MEYER, J. L., SWANK, W. T., WAIDE, J. B. & WALLACE, J. B., 1983: Stability of stream ecosystems. – In: BARNES, J. R. & MINSHALL, G. W. (Eds.): *Stream Ecology*: 355–395. – Plenum Press.

Authors' addresses:

J. B. WALLACE, B. S. GOLDOWITZ, K. CHUNG, and G. J. LUGTHART, Department of Entomology, University of Georgia, Athens, Georgia 30602, USA.

T. F. CUFFNEY, Environmental Safety Department, Procter & Gamble Company, Cincinnati, Ohio 45217, USA.

:E, J. B., 1988: Particulate
·rt from three headwater
rsus continuous measure-
Aquat. Sci. 45: 2010–2016.
<port relationships in head-
ce of invertebrate manipula-
J. N. Amer. Benthol. Soc. 8:

B. & LUGTHART, G. J., 1989:
:e quantifying the role of
in organic matter dynamics
ıs. – *Freshwat. Biol.* 23:

33: Leaf-shredding insects as
ırganic carbon in headwater
l. Nat. 109: 175–183.
al variation in the turnover
Chironomidae (Diptera) in
. streams. – Unpubl. M. Sc.
rgia, Athens, GA. U.S.A.,

V., 1981: Benthic detritus
in stream. – *Holarctic Ecol.*

J., 1980: The maceration of
y aquatic hyphomycetes. –
: 1025–1031.
, G. J., CUFFNEY, T. F. &
'he impact of repeated insec-
drift and benthos of a head-
obiologia 179: 135–147.
& CUFFNEY, T. F., 1986: Re-
· stream from an insecticide-
isturbance. – *J. N. Am. Ben-*

R. & CUFFNEY, T. F., 1982:
nics: regulation by inverte-
ecologia (Berl.) 53: 197–200.
F., GOLLADAY, S. W., HILL,
E., KAZMIERCZAK, R. F. &
: Experimental studies of
cting seston transport in
ceanogr. 32: 848–863.
E., HAINS, J. J., MEYER, J. L.,
E, J. B. & WALLACE, J. B.,
tream ecosystems. – In:
HALL, G. W. (Eds.): *Stream*
Plenum Press.

GOLDOWITZ, K. CHUNG, and
partment of Entomology,
ia, Athens, Georgia 30602,

ironmental Safety Depart-
able Company, Cincinnati,

This is a reprint of

Verhandlungen – Proceedings – Travaux

of the International Association for Theoretical and Applied Limnology, Congress in Munich 1989

If you are a member of this association you receive these "Proceedings" against your yearly membership fee of Swiss Francs 50.–

Please notice also the

Archiv für Hydrobiologie

an official organ of the International Association for Theoretical and Applied Limnology (SIL), and its Supplements.

Edited by: Prof. Dr. H. KAUSCH, Hamburg, Germany West and
Prof. Dr. W. LAMPERT, Plön/Holstein, Germany West.

As a member of SIL you are entitled to receive this important journal at a special membership price.

True to its tradition this periodical serves freshwater research in the widest sense, including treatment of problems of brackish and seawater as far as they bear a relationship to limnology. It is the editors' aim to devote increased attention to ecology in association with experimental, above all physiological works corresponding to the more recent developments in limnology. Finally, it is intended that the "Archiv" should continue to form a bridge between theoretical and applied water research.

For details please write to the Publishers E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Johannesstraße 3 A, D-7000 Stuttgart 1.

If you are interested in

Archiv für Hydrobiology, Supplements

and in the special issues

Ergebnisse der Limnologie/Advances in Limnology

these are available also against a special membership price; for details please ask the Publishers (for address see above).

If you are interested in being a member of the International Association for Theoretical and Applied Limnology, please write to the General Secretary-Treasurer:

Prof. Dr. R. G. WETZEL, Department of Biology,
The University of Alabama, Tuscaloosa, Alabama 35487-0344/USA