Recovery of southern Appalachian streams from historical agriculture

Matthew E. McTammany

Dissertation submitted to the faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy
in
Biology

E. F. Benfield, Chair
H. M. Valett
J. R. Voshell
J. R. Webster
R. H. Wynne

March 18, 2004
Blacksburg, Virginia

Keywords: stream, agriculture, invertebrates, primary production, respiration, wood

Recovery of southern Appalachian streams from historical agriculture

Matthew E. McTammany

Abstract

Stream ecosystems are influenced by the surrounding landscape, and agriculture within their catchments has changed many characteristics of streams. Agriculture has been a prominent land use activity in the southern Appalachian Mountains of the eastern United States for over 500 years. However, recent socioeconomic changes in the region have caused many farmers to abandon agriculture leading to widespread reforestation of historical farmland. I investigated the influence of agriculture on the physical, chemical, and biological structure and ecosystem processes of streams in the southern Appalachians. In addition, I studied streams in watersheds previously agricultural but currently reforested to determine how historic agriculture generates long-term effects on streams. Stream draining agricultural catchments (i.e., agricultural streams) had higher temperatures, light inputs, nutrients, and suspended sediments than forested streams and contained smaller substrate, dominated by sand and silt. Temperature and light regimes recovered in streams of reforested catchments, but the other aspects of stream physicochemistry remained elevated or changed due to historical agriculture. I expected biological community structure and ecosystem processes to reflect these altered conditions in streams with current and historical agriculture. Higher chlorophyll, lower macroinvertebrate biodiversity, fewer shredder-detritivore invertebrates, and more pollution-tolerant organisms characterized agricultural streams compared to forested streams, but each of these biological features was similar in long-term forested streams and streams with reforested catchments but with agricultural histories. Agricultural streams had higher rates of gross primary production (GPP) and GPP to respiration (P/R) ratios than forested streams, indicating that agriculture enhances autotrophic metabolism in streams. Agriculture did not have a significant effect on wood breakdown or microbial biofilm development on wood substrates. Together, these data suggest that agriculture causes many different changes in stream physical and chemical properties and that many of these properties do not recover following reforestation of catchments over the past 50 years. However, biological community structure and ecosystem processes appear to respond to physical aspects of streams that do recover from historic agriculture including light, temperature, and organic matter supply and type.

Acknowledgments

I gratefully acknowledge the assistance my advisor, Fred Benfield, and the members of my doctoral committee. Fred and I have had some wonderful adventures in the field, and I greatly appreciated the wealth of information he possesses about the history of the region and its denizens. Fred's guidance has meant more to my life than he will ever know, and I thoroughly enjoyed working with him for both of my graduate degrees. Jack Webster and Reese Voshell served on my Master's committee and were foolish enough to agree to my doctoral committee as well. Jack has been a source of inspiration in my life and career and gave me many opportunities to work on and to publish projects in addition to my own research. I would like to thank Dr. Voshell for giving me the opportunity to teach aquatic entomology during his sabbatical. I would not have my current position at Bucknell University without that opportunity. Randy Wynne taught me everything I know about remote sensing and provided valuable assistance in understanding the capabilities and limitations of spatial data. Maury Valett has been a wonderful sounding board for ideas, whether we're in his office, on the golf course, or at a local watering hole. Doc Simmons filled in for Maury on my preliminary exam and provided many great experiences on Freshwater Ecology field trips. I consider each of these wonderful professors, mentors, and people my friend and hope to make each of them proud throughout my career.

The Virginia Tech Stream Team, an extremely interactive group of post-docs, lab technicians, graduate students, and undergraduates, was a huge source of information, support (professional and personal), assistance, and good times. Thank you to all the past and present VTST members and their families. You all have a very special place in my heart and are among my dearest friends and colleagues.

The Coweeta Long-term Ecological Research program is a fantastic group of people and provided much feedback at many different points throughout this project. Being a part of such a large field-oriented research team was very special to me, and I thoroughly enjoyed sharing my research with them.

The Aquatic Entomology Lab at Virginia Tech provided taxonomic assistance whenever asked and were an excellent resource. In particular, Steve Hiner and Amy Braccia were diligent in finding correct names for those nearly impossible to identify and seldom collected dipterans (even though I was left with a couple of unknowns that stumped all the experts).

The Biology Department (including all the faculty, staff, and graduate students) provided much needed support, encouragement, money, and opportunities to develop as a professional and colleague. In particular, Joe Cowles and Bob Jones gave me a great deal of guidance about my career and listened to my occasional whining about the unfair and inconsistent components of graduate life. Sue Rasmussen was one of the most supportive people in all of my graduate work by helping me get all aspects of my Master's and Ph.D. finished. Sue also provided a patient ear and very humorous retorts to my various rantings and ravings. I don't know if I could have finished without Sue, and I'm darn glad I didn't have to find out! The inviting people in the Bookkeeping office (Michelle, Melanie, Karen, and Robyn) were always sweet and caring and made visits to the second floor quite fun. The crazy ladies (Judy, Cathy, and Mary) in the GB labs were another wonderful source of conversation and advice for life. All the graduate students I have had the pleasure of working with during the past 8 years also deserve mention for their timely diversions, friendship, and hard work, but there are too many of you to list.

My new colleagues at Bucknell University have been very helpful in working through the last stages of my dissertation. In particular, I would like to thank Warren Abrahamson for

agreeing to teach the first half of Population and Community Biology this semester to give me the chance to finish my dissertation and defend without a teaching load. Bucknell University has given me the opportunity to teach at my alma mater, and I am looking forward to a great career in central Pennsylvania.

Finally, I would like to thank my friends and family for literally a lifetime of support. Most importantly, my wife, Wendy, who slaved at Blacksburg High School to support us, deserves my most sincere thanks and love. Our little daughter, Kassie, may only have been around for the end of this journey, but her arrival on February 8 helped down the stretch by providing the inspirational push to get this off my desk, finally.

Funding for my project was provided by a NSF grant (DEB9632854) to Coweeta Long-term Ecological Research site, Sigma Xi Grants-in-Aid of Research, Graduate Research Development Program at Virginia Tech, and the Biology Department at Virginia Tech.

Thanks to you all. I never would have made it without you.

Table of Contents

Chapter 1: General introduction

Chapter 2: The influence of historical and current agriculture on macroinvertebrate assemblages in southern Appalachian streams

Chapter 3: Recovery of stream ecosystem metabolism from historical agriculture

Chapter 4: Organic matter breakdown and microbial biofilm activity in agricultural streams

Chapter 5: Synthesis

Back Matter

List of Tables

List of Figures

CHAPTER 1

General introduction

Ecosystem stability involves two properties related to either the immediate impact or the eventual recovery of a system following disturbance (Holling 1973, Webster et al. 1975). Resistance is defined as the ability of a system to remain at or near pre-disturbance conditions during a disturbance. Resilience refers to the ability of a system to recover to pre-disturbance conditions following alteration caused by disturbance. When coupled, resistance and resilience determine the stability of an ecosystem and are usually inversely related (Webster et al. 1975, Fisher et al. 1998). Stream ecosystems are generally considered to have low resistance and high resilience to disturbances (Webster et al. 1983, Fisher 1990, Webster et al. 1992, Whiles and Wallace 1995, Fisher et al. 1998, Hutchens et al. 1998). Habitats that provide refugia for biota (Gurtz and Wallace 1984, Sedell et al. 1990), nutrients that sustain the resource base of an ecosystem (DeAngelis et al. 1989, Herbert et al. 1999), and retentive structures that minimize material export (Bilby and Likens 1980) can drive stream ecosystem resistance. Short life cycles of aquatic insects (Grimm and Fisher 1989, Wallace 1990), seasonality of leaf litter inputs to forested streams (Fisher and Likens 1973), and rapid recovery of algae (Grimm and Fisher 1989) enhance stream resilience to disturbance. However, given a persistent disturbance at broad spatial and temporal scales, such as agricultural activity within the catchment, these stabilizing properties may be insufficient to maintain stream structure and function.

Terrestrial conditions determine physical and chemical properties of streams (Minshall et al. 1983, Harding and Winterbourn 1995, Johnson et al. 1997), which influence the structure and function of stream ecosystems (Cummins 1974, Hynes 1975, Townsend et al. 1983, Richards and Host 1993, Wohl et al. 1995). In small, forested streams, the terrestrial-stream link is particularly strong because vegetation constitutes the primary organic resource base (as allochthonous detritus) and limits in-stream primary production (Fisher and Likens 1973). Clearing forested land for logging or conversion to agriculture causes many changes to streams including higher light and heat inputs, altered rates and types of organic matter supply, and higher nutrient and sediment inputs. These changes in stream physical and chemical conditions interact to affect biological community structure and ecosystem function. Agricultural land use results in increased nutrients and light, which causes algal production to increase in cleared streams (Webster et al. 1983, Lowe et al. 1986). Changing the dominant energy source in streams from allochthonous detritus to autochthonous production by algae can cause dramatic changes in benthic macroinvertebrate community structure (Gurtz and Wallace 1984, O'Hop et al. 1984, Wallace et al. 1988) and ecosystem metabolism (Young and Huryn 1999). In addition to changes in organic matter and nutrient supplies, agriculture can result in higher sediment inputs to streams (Waters 1995). Sediment in transport has direct, deleterious effects on many aquatic invertebrates (Wagener and LaPierre 1985, Culp et al. 1986, Doeg and Milledge 1991) and algae (Lloyd et al. 1987, Graham 1990). Sedimentation in streams results in low habitat heterogeneity, unstable substrate, and generally poor physical conditions for benthic animals (Lemly 1982, Mackay and Waters 1986, McClelland and Bruvsen 1986, Richards and Bacon 1994, Death and Winterbourn 1995), but some invertebrate populations, such as midge larvae

(Chironomidae) and segmented worms (Oligochaeta), flourish under the altered sediment conditions (Lenat et al. 1981, Lenat and Crawford 1994). Sediment can also bury organic matter, thereby altering leaf material processing (Herbst 1980, Webster and Waide 1982, Rounick and Winterbourn 1983) and potentially creating anoxic conditions in the streambed. While agricultural streams experience higher light and nutrient inputs with the potential to support primary production, sediment in suspension can limit light availability to reduce primary production rates (Wiley et al. 1990, Young and Huryn 1996). Ultimately, altered organic matter supply and type, increased nutrient and sediment loads, and altered stream temperature regimes result in major changes in biological structure and ecosystem function in agricultural streams (Benfield et al. 1977, Lemly 1982, Richards and Host 1993, Allan et al. 1997, Harding et al. 1998).

A good deal of our present knowledge regarding stream responses to agricultural practice comes from long-term studies of logging in headwater catchments (e.g., Marks and Bormann 1972, Webster et al. 1983, 1992). Initially, logging changes organic matter source in streams from allochthonous detritus to algal production (Lowe et al. 1986), but these effects are short-lived as reforestation rapidly eliminates light required for photosynthesis and returns detrital inputs to the stream (Marks and Bormann 1972, Bilby and Likens 1980, Webster et al. 1983, Likens 1984). Despite other long-lasting influences of logging in Appalachian streams (Webster et al. 1992, Swank and Vose 1997), benthic macroinvertebrate community structure recovers from logging within 20 years (Haefner and Wallace 1981, Stone and Wallace 1998). In contrast to logged catchments, agricultural land does not reforest immediately after forest clearing because the land is used for pastures or row crops. Therefore, agriculture presents more of a "press" disturbance (sensu Bender et al. 1984) to the landscape and streams draining agricultural catchments. Furthermore, reforestation occurring in agricultural areas is spatially patchy as a result of individual land ownership and variable in species composition (Foster 1992). The duration and extent of agriculture affects the rate of forest succession and species interactions during forest recovery (Pickett et al. 1987, Myster and Pickett 1994, Honnay et al. 1999). Forest recovery may require decades after logging or agriculture, but reforestation of entire catchments from agriculture likely requires more time due to spatial heterogeneity of reforestation within catchments and cumulative damage to soils during agricultural use (Stover and Marks 1998). Perhaps because of delays in forest recovery, macroinvertebrate assemblages in streams with reforested watersheds that were previously agricultural (~50 yrs. ago) were more similar to agricultural streams than to forested streams without agricultural history (Harding et al. 1998).

In the southern Appalachian Mountains of eastern United States, agriculture has been influencing streams for centuries. Prior to 1700, aboriginal settlements in river valleys throughout the region included bottomland farms (Bartram 1791, Yarnell 1998). Settlement of the southern Appalachians by Europeans did not occur until the late 18th century, when many families escaped indentured servitude in coastal cities by claiming land in the largely vacant Appalachian Mountains (Gray 1941). Agricultural practices of these early settlers were crude and focused on small fields because it was quite difficult to clear fields (Ayers and Ashe 1905). Farmers were forced to rotate their fields frequently due to poor soils (Cathey 1956). Subsistence farming was the rule for both native and early European settlers in the southern Appalachians until the late 19th century (Cathey 1956, Eller 1982, Otto 1983). At that time, the timber industry harvested vast expanses of hardwood forests in the southern Appalachians (Ayers and Ashe 1905, Otto 1983). By the mid-1930s, most of the primeval forests of the southern Appalachians was removed by harvest or killed by chestnut blight (Clark 1984). Land acquisition by logging and mining companies forced mountain farmers onto smaller plots of land, and the Great Depression forced many former miners and mill workers to begin farming their land (Eller 1982). This led to a dramatic increase in agricultural activity on marginal land around 1930 and eventual failure of many farms because of soil losses and nutrient depletion (Otto 1983). In addition, the U.S. government purchased a large amount of land, which had formerly been used for forest grazing of cows and pigs and row-crop agriculture, and converted the land to national forests and parks as part of the New Deal after the Great Depression (Yarnell 1998). By protecting land throughout the region, the U.S. government markedly decreased agricultural activities across the southern Appalachians (Eller 1982, Otto 1983).

Access to the southern Appalachians continued to develop as the U.S. added infrastructure to a previously inaccessible region (Otto 1983). World War II marked a turning point in agricultural development in the southern Appalachians because many young men entered the Armed Services. Following the War, thousands of veterans with newly acquired mechanical skills and worldliness emigrated from the southern Appalachians with their families to the booming industrial cities of the Midwest (Gade and Stillwell 1986). This exodus left many southern Appalachian farms, mostly small family operations, short-handed, and many families began to reduce their tillage (Otto 1983). Since 1950, a great deal of fallow agricultural land has been reforesting (Clark 1984). Agriculture is still a prominent feature of the landscape, but the extent of agriculture has decreased up to 30% in many counties since 1950 (Wear and Bolstad 1998) and is mainly confined to larger valleys (Otto 1983). Currently, the southern Appalachians are experiencing widespread reforestation from historical agriculture along with suburbanization and development of summer vacation homes (Wear and Bolstad 1998).

The history of human impact across the southern Appalachians presents ecologists with a unique opportunity to study ecosystems recovering from centuries of disturbance. Studies of broad-scale disturbances that affect streams often deal with the continuing effects of a single, often catastrophic, short-term event (e.g., logging, fire, flood). As discrete events, these disturbances may be large in a spatial context but temporally short-lived, but despite their brevity, they may have the potential to alter stream structure and function. In contrast, recovery from a disturbance that combines large spatial and temporal scales may be substantially different from recovery following disturbances with smaller spatial extent and considerably shorter time spans. My study explores the recovery of stream ecosystems from agriculture by measuring structural (i.e., physical, chemical, and biological) and functional (i.e., ecosystem processes) properties in streams draining catchments that have reforested over time following historical agriculture. The research addresses several questions:

1) How are in-stream physical and chemical conditions affected by agriculture?
2) What influence do changing in-stream conditions have on biological structure and ecosystem function in agricultural streams?
3) Which agricultural influences and alterations persist despite recovery of terrestrial forests?
4) Do these persistent alterations cause changes in present-day community structure and ecosystem processes of streams?

These questions were addressed by studying structural and functional aspects of streams with different current and historical agricultural use. I compared benthic macroinvertebrate community structure, ecosystem metabolism (primary production and respiration), organic matter breakdown, and microbial biofilm activity among streams with different amounts of agriculture and with extensive reforestation of agriculture in their watersheds. This dissertation is composed of 3 main chapters, an introduction, and a synthesis. General information about the study sites and benthic macroinvertebrate densities from each study sites are given in Appendix A and B, respectively.

Literature Cited

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37:149-161.

Ayers, H. B., and W. W. Ashe. 1905. The southern Appalachian forests. Series H, Forestry, Professional paper no. 37. U.S. Geological Survey. Government Printing Office, Washington, D.C.

Bartram, W. 1791. Travels. *In* The travels of William Bartram. F. Harper, editor, 1998. University of Georgia Press, Athens, GA.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1-13.

Benfield, E. F. 1995. Historical land-use and streams. Bulletin of the North American Benthological Society 12:241-248.

Bilby, R. E., and G. E. Likens. 1980. Importance of debris dams in the structure and function of stream ecosystems. Ecology 61:1107-1113.

Cathey, C. O. 1956. Agricultural developments in North Carolina 1783-1860. James Sprunt Studies in History and Political Science, Volume 38. University of North Carolina Press, Chapel Hill, NC.

Clark, T. D. 1984. The greening of the South. University of Kentucky Press, Lexington, KY.

Culp, J. M., F. J. Wrona, and R. W. Davies. 1986. Response of stream benthos and drift to fine sediment deposition versus transport. Canadian Journal of Zoology 64:1345-1351.

Cummins, K. W. 1974. Structure and function of stream ecosystems. Bioscience 24:631-641.

DeAngelis, D. L., P. J. Mulholland, A. D. Palumbo, M. A. Steinman, M. A. Huston, and J. W. Elwood. 1989. Nutrient dynamics and food web stability. Annual Review of Ecology and Systematics 20:71-95.

Death, R. G., and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. Ecology 76:1446-1460.

Doeg, T. J., and G. A. Milledge. 1991. Effect of experimentally increasing concentrations of suspended sediment on macroinvertebrate drift. Australian Journal of Marine and Freshwater Research 42:519-526.

Eller, R. D. 1982. Miners, millhands, and mountaineers: industrialization of the Appalachian South, 1880-1930. University of Tennessee Press, Knoxville, TN.

Fisher, S. G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. Environmental Management 14:725-736.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421-439.

Fisher, S. G., N. B. Grimm, E. Martí, R M. Holmes, and J. B. Jones. 1998. Material spiraling in stream corridors: a telescoping ecosystem model. Ecosystems 1:19-34.

Foster, D. R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80:753-772.

Gade, O., and H. D. Stillwell. 1986. North Carolina: people and environments. Geo-App Publishing Company, Boone, NC.

Graham, A. A. 1990. Siltation of stone surface periphyton in rivers by clay sized particles from low concentrations in suspension. Hydrobiologia 199:107-115.

Gray, L. C. 1941. History of agriculture in the southern United States to 1860. Carnegie Institution of Washington publication no. 430. Peter Smith, New York, NY.

Grimm, N. B., and S. G. Fisher. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society 8:293-307.

Gurtz, M. E., and J. B. Wallace. 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65:1556-1569.

Haefner, J. D., and J. B. Wallace. 1981. Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. Canadian Journal of Fisheries and Aquatic Sciences 38:353-359.

Harding, J. S., and M. J. Winterbourn. 1995. Effects of contrasting land-use on physico-chemical conditions and benthic assemblages of streams in a Canterbury (South Island, New Zealand) river system. New Zealand Journal of Marine and Freshwater Research 29:479-492.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Science 95:14843-14847.

Herbert, D. A., J. H. Fownes, and P. M. Vitousek. 1999. Hurricane damage to a Hawaiian forest: nutrient supply rate affects resistance and resilience. Ecology 80:908-920.

Herbst, G. N. 1980. Effects of burial on food value and consumption by aquatic invertebrates in a lowland forest stream. Oikos 35:411-424.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1-24.

Honnay, O., M. Hermy, and P. Coppin. 1999. Impact of habitat quality on forest plant species colonization. Forest Ecology and Management 115:157-170.

Hutchens, J. J., K. Chung, and J. B. Wallace. 1998. Temporal variability of stream macroinvertebrate abundance and biomass following pesticide disturbance. Journal of the North American Benthological Society 17:518-534.

Hynes, H. B. N. 1975. The stream and its valley. Verhandlung der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 19:1-15.

Johnson, L. B., C. Richards, G. E. Host, and J. W. Arthur. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. Freshwater Biology 37:193-208.

Lemly, D. 1982. Modification of benthic insect communities in polluted streams: combined effects of sedimentation and nutrient enrichment. Hydrobiologia 87:229-245.

Lenat D. R., and J. K. Crawford. 1994. Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. Hydrobiologia 294:185-199.

Lenat, D. R., D. L. Penrose, and K. W. Eagleson. 1981. Variable effects of sediment addition on stream benthos. Hydrobiologia 79:187-194.

Likens, G. E. 1984. Beyond the shoreline: a watershed-ecosystem approach. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1-22.

Lloyd, D. S., J. P. Koenings, and J. D. LaPerriere. 1987. Effects of turbidity in fresh waters of Alaska. North American Journal of Fisheries Management 7:18-33.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221-229.

Mackay, R. J., and T. F. Waters. 1986. Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67:1680-1686.

Marks, P. L., and F. H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady state nutrient cycling. Science 176:914-915.

McClelland, W. T., and M. A. Bruvsen. 1980. Effects of sedimentation on the behavior and distribution of riffle insects in a laboratory stream. Aquatic Insects 2: 161-169.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs 53:1-25.

Myster, R. W., and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr. in 10 contrasting old fields. Ecology 75:387-392.

O'Hop, J., J. B. Wallace, and J. D. Haefner. 1984. Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. Freshwater Biology 14:13-21.

Otto, J. S. 1983. The decline of forest farming in southern Appalachia. Journal of Forestry 27:18-27.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms, and pathways of succession. Botanical Review 53:335-371.

Richards, C., and G. E. Host. 1993. Identification of predominant environmental factors structuring stream macroinvertebrate communities within a large agricultural catchment. Freshwater Biology 29:285-294.

Richards, C., and K. L. Bacon. 1994. Influence of fine sediment on macroinvertebrate colonization of surface and hyporheic stream substrates. Great Basin Naturalist 54:106-113.

Rounick, J. S., and M. J. Winterbourn. 1983. Leaf processing in two contrasting beech forest streams: Effects of physical and biotic factors on litter breakdown. Archiv fur Hydrobiologie 96:448-474.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford, and C. P. Hawkins. 1990. Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14:711-724.

Stone, M. K., and J. B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39:151-169.

Stover, M. E., and P. L. Marks. 1998. Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. Journal of the Torrey Botanical Society 125:150-164.

Swank, W. T., and J. M. Vose. 1997. Long-term nitrogen dynamics of Coweeta forested watersheds in the southeastern United States of America. Global Biogeochemical Cycles 11:657-671.

Townsend, C. R., A. G. Hildrew, and J. Francis. 1983. Community structure in some southern English streams: the influence of physicochemical factors. Freshwater Biology 13:521-544.

Wagener, S. M., and J. D. LaPerriere. 1985. Effects of placer mine drainage on the invertebrate communities of interior Alaska streams. Freshwater Invertebrate Biology 4:208-214.

Wallace, J. B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. Environmental Management 14:605-620.

Wallace, J. B., M. E. Gurtz, and T. F. Cuffney. 1988. Long-term comparisons of insect abundances in disturbed and undisturbed Appalachian headwater streams. Verhandlungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie 23:1224-1231.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Waters, T. F. 1995. Sediment in streams; sources, biological effects and control. American Fisheries Society Monograph 7. Bethesda, Maryland, USA.

Wear, D. N. and P. V. Bolstad. 1998. Land-use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Webster, J. R., and J. B. Waide. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. Freshwater Biology 12:331-344

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient cycling and stability of ecosystems. Pages 1-27 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral Cycling in Southeastern Ecosystems. ERDA Symposium Series, Washington, DC.

Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. 1983. Stability of stream ecosystems. Pages 355-395 *in* J. R. Barnes and G. W. Minshall, editors. Stream Ecology. Plenum Publishing Corp., New York.

Webster, J. R., S. W. Golladay, E. F. Benfield, J. L. Meyer, W. T. Swank, and J. B. Wallace. 1992. Catchment disturbance and stream response: an overview of stream research at

Coweeta Hydrologic Laboratory. Pages 231-253 *in* P. J. Boon, P. Calow and G.E. Petts, editors. River Conservation and Management. John Wiley and Sons Ltd., New York.

Whiles, M. R., and J. B. Wallace. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. Canadian Journal of Fisheries and Aquatic Sciences 52:2402-2422.

Wiley, M. J., L. L. Osborne, and R. W. Larimore. 1990. Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 47:373-384.

Wohl, D. L., J. B. Wallace, and J. L. Meyer. 1995. Benthic macroinvertebrate community structure, function, and production with respect to habitat type, reach and drainage basin in the southern Appalachians. Freshwater Biology 34:447-464.

Yarnell, S. L. 1998. The southern Appalachians: a history of the landscape. General report SRS-18. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Young, R. G., and A. D. Huryn. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian Journal of Fisheries and Aquatic Sciences 53:2199-2211.

Young, R. G., and A. D. Huryn. 1999. Effects of land use on stream metabolism and organic matter turnover. Ecological Applications 9:1359-1376.

CHAPTER 2

The influence of historical and current agriculture on macroinvertebrate assemblages in southern Appalachian streams

Abstract

Agriculture has affected stream ecosystems in the southern Appalachians for centuries. Recent socioeconomic changes in the region have resulted in numerous abandoned farms, resulting in reforestation of large tracts of historically agricultural land. I created a watershed database of forest cover in 1950 and 1993 for 4 counties in western North Carolina and southwestern Virginia. I used this database to place streams into categories representing a gradient of agriculture (no change over time) and into categories showing reforestation from historical agriculture. I compared physico-chemistry and benthic macroinvertebrate community structure among streams with different agricultural intensity and history. Agricultural and reforested streams had higher dissolved inorganic nitrogen, higher suspended solids, and smaller substrate particle size than forested streams. Agricultural streams also had more degree-days and chlorophyll *a* standing crop than forested streams, but these variables were not different between reforested and forested streams. Macroinvertebrate density and diversity were not significantly different among stream types, but functional feeding group composition and pollution tolerance metrics showed influences of current agriculture on macroinvertebrate assemblages. Gatherers made up a significantly larger proportion of invertebrates in currently agricultural streams than in both forested and reforested streams, while shredders showed the opposite pattern. The ratio of scrapers to shredders was significantly lower in forested streams regardless of land-use history suggesting that detritus returns to importance rapidly during reforestation from agriculture. Agricultural streams had macroinvertebrate communities comprised mostly of pollution tolerant taxa with fewer sensitive representatives in the community. However, reforested streams had macroinvertebrate communities similar to forested streams with no agricultural history. I related macroinvertebrate metrics to forest cover at different spatial scales and physico-chemistry to explore potential mechanisms controlling long-term influences of agriculture on stream recovery. Most macroinvertebrate metrics were most strongly correlated with current riparian forest cover, chlorophyll concentration, and degree-days. Therefore, despite long-term influences of agriculture on water chemistry, seston, and in-stream habitat, macroinvertebrate communities in the present study appeared to reflect current forest cover and are related to organic matter supply and type.

Keywords: land-use, disturbance, recovery, GIS, diversity, functional feeding groups, pollution-tolerance, spatial scale

Introduction

Resistance and resilience describe mechanisms of stability that enable ecosystems to maintain their structure and function in the context of a given disturbance regime (Webster et al. 1983). However, some disturbances affect conditions at very broad scales thereby altering multiple ecosystems. Connections between different ecosystems are often critical determinants of structure and function of ecosystems. For example, stream ecosystems are intimately linked to the surrounding landscape through hydrology, organic matter inputs, and geology (Hynes 1975). Disturbances that affect terrestrial ecosystems likewise affect stream ecosystems, and streams will remain affected until terrestrial ecosystems recover and in-stream conditions stabilize (Niemi et al. 1990, Golladay et al. 1992, Webster et al. 1992, Valett et al. 2002).

For a given ecosystem, disturbance regimes vary in terms of the frequency, intensity, extent, and duration of disturbance (Pickett and White 1985). Given similar disturbance extent, ecosystems are likely to be more resilient to short-duration (PULSE) than to long-duration disturbances (PRESS; *sensu* Bender et al. 1984). Recovery of stream ecosystems from pulse disturbances, such as floods or toxic chemical spills, is related to colonization of streams and is subsequently fairly rapid (e.g., Whiles and Wallace 1995). However, recovery of streams from press disturbances, such as logging or mining that substantially alter in-stream habitat, may require long periods for the system to return to original conditions (Niemi et al. 1990).

Clearing forested land is a dramatic disturbance to watersheds and has major influences on stream ecosystems. Streams in logged watersheds require several decades to centuries to recover from a relatively short-duration disturbance (Webster et al. 1992). Properties of streams related to forest cover, such as organic matter supply, shading, temperature, and gross primary production, recover rapidly following logging (Webster et al. 1983, Swift 1988). Other properties, such as nutrient concentrations (Swank and Vose 1997), sediment composition (Brown and Krygier 1971, Davies and Nelson 1993), and organic matter quality (Stout et al. 1993) remain influenced by logging for longer periods of time. For the most part, however, responses are rapid. In contrast, converting land to support agriculture may cause prolonged alterations to the stream, even after the land is allowed to reforest. Nutrient supply to watersheds is dramatically enhanced during agricultural periods (e.g., Karr and Schlosser 1978) and likely requires major sequestration by aggrading forests to reduce supply to streams. Stream channel morphology is dramatically altered by agriculture (Wark and Keller 1963) and may require geologic time frames to recover. Sediments that enter agriculture headwater streams might require several major floods to reach a large river due to suspension and deposition at different points in the stream network (Trimble 1999).

Conversion of forested land to agriculture can also have significant influences on stream macroinvertebrate communities. Removal of streamside vegetation increases light to streams and removes allochthonous organic matter supply resulting in dramatically different carbon sources to the stream (Webster et al. 1992, Sweeney 1993). Organisms that feed on in-stream primary production may benefit from land clearing (Woodall and Wallace 1972), while many detritivores cannot survive without the annual pulse of organic matter provided by autumnal leaf fall in deciduous catchments (Wallace et al. 1997). In addition, agriculture increases sediment loads (Waters 1995), nutrient loads (Karr and Schlosser 1978), and summer temperatures (Rutherford et al. 1997) in streams resulting in degradation of habitat and water quality for many aquatic organisms. Many benthic macroinvertebrates require clean substrate and low temperatures (i.e., high oxygen) to complete their life cycles (Merritt and Cummins 1996).

Properties of macroinvertebrate and fish assemblages of streams have been linked to historical agriculture in the southern Appalachians (Harding et al. 1998), but the physical and chemical factors linking agricultural history to current stream diversity are unknown.

In the southern Appalachian Mountains, agriculture has been a major land use influencing streams for centuries. Native American settlements throughout the region included bottomland farms (Bartram 1791, Yarnell 1998). European settlement of the region occurred in the late 18th century, and the influx of people resulted in use of mountainous land for farming (Ayers and Ashe 1905, Gray 1941, Cathey 1956). Native and early European settlers survived in the southern Appalachins by subsistence farming until the late 19th century (Cathey 1956, Eller 1982) at which time the timber industry began harvesting trees from the region (Ayers and Ashe 1905, Otto 1983). By the mid-1930s, most of the primeval forests of the southern Appalachians were either harvested or killed by chestnut blight (Clark 1984). Many mining and timbering operations were closed during the Great Depression, which forced many former miners and mill workers to begin farming their land (Eller 1982). This led to a dramatic increase in agricultural activity on marginal land, which eventually led to failure of many farms because of soil losses and nutrient depletion (Otto 1983). In addition, the U.S. government purchased large amounts of agricultural land and converted the land to national forests and parks as part of the New Deal after the Great Depression (Yarnell 1998). Following World War II, thousands of veterans with newly acquired mechanical skills emigrated from the southern Appalachians with their families to industrial cities of the Midwest (Gade and Stillwell 1986), which left many farms in the southern Appalachians without labor (Otto 1983). Since 1950, large tracts of fallow agricultural land have been reforesting (Clark 1984). Agriculture is still a prominent feature of the landscape, but the extent of agriculture has decreased up to 30% in some areas since 1950 (Wear and Bolstad 1998) and is mainly confined to larger valleys (Otto 1983).

The pattern of forest cover through time in the southern Appalachians has created a natural experiment to test the stability of streams in this region to agricultural disturbance. Specifically, streams located within catchments of protected forest, varying agricultural intensity, and extensive reforestation of historically agricultural land were studied to determine the influence of current agriculture on streams and the nature of recovery from historical agriculture. The study objective was to determine how land use (i.e., agricultural land conversion and use) and catchment recovery (i.e., reforestation) influence benthic community structure in streams. Multiple streams were selected using specific criteria to establish a gradient in agricultural land cover among study sites. Further, temporal comparison of land cover was used to identify streams draining catchments that have variably reforested since 1950. Several metrics representing macroinvertebrate abundance, diversity, composition, trophic structure, and pollution tolerance were compared among streams. Similar values for metrics in reforested and currently agricultural streams were interpreted to illustrate a legacy of agricultural influence and no recovery for this metric. On the other hand, similarities between reforested streams and long-term forested streams were interpreted as providing evidence of benthic macroinvertebrate recovery. In addition, I measured physical and chemical conditions in each stream to assess recovery of factors potentially affecting macroinvertebrate community structure.

Methods

Study sites

Study streams (2^{nd} and 3^{rd} order) were located in the southern Appalachian Mountains of western North Carolina and southwestern Virginia, USA (Figure 1). Headwater streams in the Blue Ridge physiographic province of the southern Appalachians are typically slightly acidic and have low conductivity and dissolved ion concentration reflecting granitic and micaceous parent lithology (Simmons and Heath 1979). Forests in the region are maturing second-growth (logged ~ 75-100 years ago) and are dominated by oak (*Quercus* spp.), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*) with an understory of *Rhododendron*, mountain laurel (*Kalmia latifolia*), and dogwood (*Cornus florida*). Agricultural activity across the region is mainly cattle pasture with isolated row crop (primarily tobacco and corn). Agriculture occurs primarily in bottomland along streams, but many farmers have upland pastures. Riparian zones along agricultural streams frequently lack woody vegetation entirely or are vegetated with a narrow strip of trees, particularly black walnut (*Juglans nigra*), river sycamore (*Platanus occidentalis*), black locust (*Robinia pseudoacacia*), red maple, and oak (Neatrour et al. 2004).

Site selection and categorization

A total of 30 streams from select regions of the southern Appalachians of North Carolina and Virginia were used following a specific site selection procedure. I created a database of past land cover (% forest in 1950) and more recent land cover (1993) for watersheds in the southern Appalachians using a geographic information system (GIS). Land cover data and watershed boundaries were obtained from Coweeta Hydrologic Laboratory for 4 counties: Grayson County, Virginia; Buncombe, Macon, and Madison Counties, North Carolina. Land cover plots of 100 m width delineated riparian corridors for streams in each watershed with stream vectors centered in the plot (i.e., 50 m to each side of the stream) for the entire stream length. Forest cover was determined for each watershed and associated riparian corridor by overlaying these spatial zones on a land cover map from each year and quantifying % forest cover.

Site eligibility was restricted to watersheds with areas between 500 and 3000 ha and stream outlet elevations between 600 and 1000 m to help standardize for confounding factors (Resh et al. 1988). I categorized these 500 watersheds into 6 groups based on the historical and current amount of forest in their watersheds. Four categories were chosen to represent a gradient of extant agriculture with no change over time (FOR >98 % forest; AG-L 90-95 % forest; AG-M 70-80 % forest; AG-H < 60 % forest). Two categories were used to represent different stages of watershed recovery from agriculture by reforestation (REC-1 < 60 % forest in 1950 to > 80 % forest in 1993; REC-2 < 75 % forest in 1950 to > 90 % forest in 1993). Streams of the REC-1 category have undergone considerable reforestation (> 20 %) over the past 50 years, but they have less current forest cover than REC-2 streams. Forest cover in riparian corridors was used to verify category assignment, and streams with riparian forest cover that was dramatically different than watershed category designations were not considered for our study. Each category initially included 5 study streams based on site access, landowner cooperation, and on-site validation of category assignment.

Final catchment characterization was calculated for portions of the watershed up gradient of the specified study site for each stream. These spatial zones were whole watershed, 100-m riparian corridor, and 100-m riparian corridors 1 and 2 km upstream of each sampling site. I used forest cover data in 1950 and 1993 at all spatial scales from these 30 sites to confirm assignments of streams to forest cover categories using principle component analysis. Principle component analysis was able to separate sites into groups, which conformed to our land cover categories (Figure 2). The first principle component explained 92.1 % of the variance and was most significantly correlated with % forest in whole watersheds and riparian corridors (Table 1). The second principle component contained less information (4.8 % variance) and was correlated most strongly with % forest at sub-corridor spatial scales (Table 1). Therefore, % forest at broad spatial scales primarily separated sites in land cover space. Based on the distribution of sites in land cover space, it appeared that spatial restriction of land cover analysis to areas upstream of my study sites resulted in 2 sites having incorrect categories. I changed the categories of one REC-1 site to AG-M and one AG-M site to AG-H. This re-categorization resulted in an unbalanced design (REC-1, *n* = 4 and AG-H, *n* = 6). Figure 1 shows the appropriate categories for each site based on principle component analysis.

Physical and chemical measurements

Stream monitoring included measuring physical and chemical characteristics at the study sites on a bi-monthly basis from November 2000 to August 2001 during baseflow conditions. I estimated discharge from velocity measured with an electronic flow meter (Marsh-McBirney Flo-Mate, Marsh-McBirney, Incorporated, Frederick, Maryland) and cross-sectional area of the stream channel. Temperature was monitored continuously at 6-hour intervals throughout the study period using data loggers (HOBO Temp, Onset Corporation, Bourne, Massachusetts). For each site and data, I collected samples to characterize suspended sediment, dissolved nutrients, and epilithic chlorophyll. Triplicate 1-L water samples for determination of suspended solids were filtered through pre-ashed and weighed glass fiber filters (Gelman Type AE, 1-µm nominal pore size). Filters were dried to constant weight, weighed, and ashed (550ºC for 1 hour) to quantify organic (combustible) and inorganic (ash) suspended material. Three other samples were collected, filtered in the field using pre-soaked membrane filters (Whatman nylon, 0.45-µm pore size), and frozen before analysis. Samples were analyzed for nitrate-nitrogen (NO_3-N) and ortho-phosphate (PO_4-P) using a Dionex DX500 Ion Chromatograph (Dionex Corporation, Sunnydale, California) and ammonium-nitrogen (NH_4-N) using the OPA fluorometric method (Holmes et al. 1999). Total dissolved inorganic nitrogen (DIN) was determined as the sum of NO_3-N and NH_4-N. Specific conductance was measured bi-monthly using a field probe (YSI Model 30/50 conductivity meter). Alkalinity was measured once at the beginning of the study using acid titration (APHA 1998). Chlorophyll *a* (chl-*a*) at each site was determined for 5 randomly selected rocks during April, June, and August. Algae were scrubbed from rocks and collected onto filters. Chlorophyll was analyzed following extraction in basic acetone (Steinman and Lamberti 1996) with a Shimadzu UV-VIS model 1601 spectrophotometer (Shimadzu Corporation, Kyoto, Japan). During July 2001, size-frequency analysis of streambed substrate was carried out at each site. Streambed particles (n = 100) from a 100-m study reach were randomly selected and passed through a USGS gravelometer with 0.5 Φ-size holes (Wolman 1954). From these data, mean particle size was determined for each stream reach by calculating average Φ-size and converting to mm (Gordon et al. 1992). Substrate composition in each reach was then represented by the percent of selected particles ≤ 1 mm (% fines) and the ratio of cobbles:fines (particles ≥ 64 mm / particles ≤ 1 mm). A visual habitat assessment of each study reach employed the Rapid Habitat Assessment Protocol (RHAP, Barbour et al. 1999). RHAP scores were determined using combined values of several physical properties of the stream channel, stream banks, and riparian vegetation. Physical variables measured once (watershed area, degree-days, sediment composition) were compared among forest cover categories using one-way ANOVA and sequential Bonferroni pair-wise comparisons. Variables measured repeatedly were compared among forest cover categories using one-way repeated measures ANOVA and sequential Bonferroni pair-wise comparisons. Variables not meeting assumptions of normality or homogeneity of variance were compared using ANOVA on Ranks with Dunn's pair-wise comparisons. All statistical analyses were performed in SAS version 8.0 (SAS Institute, Cary, NC).

Macroinvertebrates

In April 2001, I collected 5 benthic macroinvertebrate samples from each site using a quantitative kick-net procedure. For each sample, I disturbed the substrate inside a metal frame placed on the stream bottom (0.34 x 1.0 m) to a depth of 10 cm for 90 sec by vigorous kicking followed by 30 sec of hand-rubbing all large substrate to dislodge clinging invertebrates. All material dislodged from the sampling area was collected in a wide-frame net (0.4 m wide, 353-μm mesh) at the downstream end of the sampling unit, transferred to Whirl-pak bags, and preserved with formalin (5% final concentration). After several days in formalin, samples were rinsed using a 250-μm sieve, and then contents were stored in 80% ethanol.

Prior to sorting, samples were rinsed and large debris was removed and discarded. In some cases, subsampling was used if it was estimated based on the amount of debris remaining in the sample that sorting would require more than 3 hours. If subsampling was deemed necessary, I poured the entire sample into a gridded tray (9 x 12 in.) with 12 squares and randomly selected squares (minimum of 3). I removed material from selected squares with a spatula and checked to ensure that all macroinvertebrates were removed from each square. Subsamples ranged from 3/12 to 8/12 of my original samples. Macroinvertebrates were sorted under 40x magnification and placed in 80% ethanol for storage prior to identification. I identified and counted macroinvertebrates to the lowest practical taxonomic level (genus for insects, order for mollusks and crustaceans, class for segmented worms, and phylum for other invertebrates). Chironomids from each sample were subsampled, cleared in 10% KOH, mounted in CMC media (Master's Company, Inc., Des Plaines, Illinois), and identified to genus using regional keys (Epler 2001). Macroinvertebrate densities were corrected for sampling area and subsampling (when appropriate) after identification and enumeration.

For each site, I pooled subsample-corrected abundance data from all 5 benthic samples to obtain one set of macroinvertebrate data per stream. I then calculated total density, total taxa richness, Simpson's diversity (1/D), Shannon diversity (H'), and Shannon evenness (H'/Hmax). I also calculated percent of invertebrates in functional feeding groups (FFG, *sensu* Merritt and Cummins 1996) and calculated the ratio of scrapers to shredders as an index of the relative importance of autochthonous and allochthonous organic matter. Several calculated metrics related to sensitivity of macroinvertebrates to disturbance and pollution included EPT taxa richness (number of Ephemeroptera, Plecoptera, and Trichoptera genera), % EPT, % Chironomidae + Oligochaeta, % 5 dominant taxa, and the North Carolina Biotic Index (NCBI, Lenat 1993), which uses taxon-specific tolerance values (ranging from 1-10) and relative density to assess the overall sensitivity of macroinvertebrate assemblages.

In addition to calculated metrics, differences in macroinvertebrate community composition among sites were determined using several multivariate procedures in PCORD version 3.18 (MjM Software, Gleneden Beach, Oregon). Non-metric multidimensional scaling (NMS) was used to distribute sites in taxonomic space from density of each macroinvertebrate taxon. The NMS procedure used the Sorensen distance measure with 2 axes at 100 iterations from a random starting point. NMS axis scores were then correlated with macroinvertebrate densities to determine which taxa were driving separation of streams in taxonomic space. Two-way indicator species analysis (TWINSPAN) was also performed to separate or group sites using distinct or shared macroinvertebrate taxa. TWINSPAN settings were conservative (6 group maximum and 5 sites per group to divide) to avoid unrealistic separation of streams into different taxonomic groups. Ecological properties of taxa (FFG, pollution-tolerance) separating sites in NMS and TWINSPAN were investigated.

Macroinvertebrate metrics were compared among forest cover categories using ANOVA and sequential Bonferroni pair-wise comparisons in SAS version 8.0. Stepwise multiple linear regressions were used to explore relationships between forest cover (1950 and 1993 at different spatial scales) and biological variables. In-stream physical and chemical variables were also used to explain variability in macroinvertebrate metrics using stepwise multiple linear regressions. Multiple regression analyses were performed using SAS PROC REG, STEPWISE procedure with *F* to enter model = 4.0. Macroinvertebrate densities and proportions were transformed prior to analysis using ln (x+1) and arcsine square root, respectively.

Results

Forest cover

Percent forest cover was higher in 1993 than in 1950 in all categories, and % forest was lower in riparian corridors 1 and 2 km upstream of sampling sites than at a whole-watershed scale (Table 2). Forest cover in the riparian corridor 1 km of the heavily forested (FOR) sites was > 95% in both 1950 and 1993, but riparian forest cover was < 30% both in 1950 and 1993 for AG-H sites. Forest cover increased from 1950 to 1993 in watersheds and riparian zones of both classes of recovering catchments (REC-1 and REC-2). By 1993, % forest in the 100-m wide riparian corridor of the recovering catchments was 85.4% in REC-1 sites and 94.6% in REC-2 sites, indicating that reforestation was not as extensive in riparian corridors of the first class of recovering sties (REC-1) compared to the second (REC-2). REC-1 sites also had lower % forest cover (66.4%) than REC-2 sites (84.4%) within the riparian area 1 km upstream of the study sites in 1993. In 1950, riparian forest cover 1 km upstream of REC-1 sites was only 29%, while REC-2 sites had 62.4% forest cover in the same zone, which suggests that REC-1 catchments had more agricultural land cover than REC-2 sites historically.

Physico-chemistry in forest cover categories

Elevation among sites varied from 576 to 861 m and was not significantly different among categories (Table 3). Watershed area varied from 320.5 to 2130.5 ha. AG-L and AG-M watersheds were significantly ($P < 0.05$) larger than FOR and REC-2 watersheds. Discharge was not significantly different among categories. Mean discharge for each forest cover category was typically around 65 L / s but varied from 29 to 102 L / s among study sites. Specific conductance varied from 11.9 to 98.4 µS / cm and was highest in AG-L streams. Alkalinity varied from 4 to 21 mg $CaCO_3$ / L among sites and was significantly lower in FOR streams compared with AG-M and AG-H streams.

DIN varied from 21 to 1118 µg / L among sites and was significantly higher in AG-H streams than in FOR, AG-L, and REC-2 streams (Table 3). DIN values for AG-M and REC-1 streams fell between values for AG-H and REC-2 streams. PO_4-P varied from 3 µg / L to 25 µg / L among sites and did not differ significantly among categories. Cumulative degree-days above 0ºC from November 2000 to August 2001 varied from 2172 to 3218 among sites. Degree-days were significantly higher in high agriculture (AG-H) and medium agriculture (AG-M) streams compared to long-term forested (FOR), low agriculture (AG-L), and mostly reforested (REC-2) streams. Degree-days were significantly higher in slightly reforested (REC-1) streams than FOR streams, but the differences among REC-1 streams and other categories was not significant. Mean chl-*a* concentration varied from 2.60 mg/m^2 in REC-2 streams to 9.14 mg/m^2 in AG-H streams. Chl-*a* was significantly lower in REC-2 streams than in AG-M, AG-H, and REC-1 streams. FOR and AG-L streams also had low mean chl-*a*, but these values were not significantly lower than other categories.

Forested sites had lower total suspended solids (TSS) than all other sites, even those with extensive reforestation in their catchments (Figure 3A). TSS varied from 4 mg/L in FOR streams to >10 mg/L in REC streams. In addition, inorganic sediment comprised >50% of suspended particle composition in AG and REC streams (up to 72% in AG-M), while suspended particles in FOR streams was mostly organic material (Figure 3B). Mean substrate particle size ranged from ~ 60 mm (very coarse gravel) to ~ 25 mm (coarse gravel) and was significantly smaller in AG-M, AG-H, REC-1, and REC-2 streams than in FOR and AG-L streams (Figure 4A). % Fine substrate was significantly lower in FOR and AG-L streams than in AG-M, AG-H, REC-1, and REC-2 streams (Figure 4B). FOR and AG-L streams also had higher amounts of cobble relative to fine substrates when compared with other categories (Figure 4C). RHAP scores were highest at FOR sites and lowest at AG-M and AG-H sites with AG-L, REC-1, and REC-2 sites at intermediate values (Figure 4D).

Macroinvertebrates

Total density varied from 3000 to 5000 individuals/m^2 but there was no significant difference among forest cover categories (Figure 5A). Total species richness varied from 39 to 81 among the 30 streams, but mean richness was similar among forest cover categories (~61 taxa, Figure 5B). Mean values of the Simpson index varied among categories from 9.55 in AG-H to 16.43 in FOR (Figure 5C), but this difference was not statistically significant. Shannon diversity (Figure 5D) and evenness (Figure 5E) were also lowest in AG-H streams and highest in FOR streams but were not significantly different among forest cover categories.

Filterers comprised an average of 5.3 to 8.6% of invertebrates in REC-1 and AG-M categories, respectively (Figure 6A), and this percentage was not significantly different. Gatherers made up 45-65% of invertebrates collected from each stream, and the mean percentage of gatherers was significantly higher in AG-M and AG-H streams compared to FOR and AG-L streams (Figure 6B). Predators comprised approximately 8-10% of the invertebrate assemblage at each site (Figure 6C), and this percentage did not vary with forest cover category. Percent scrapers varied from 16.6% in AG-M sites to 28.7% in AG-L sites (Figure 6D), but this difference was not statistically significant. The percentage of invertebrates categorized as shredders was highest in streams with forested catchments (10.0 ± 1.8%, Figure 6E) and declined steadily among agricultural categories to a minimum of 1.2 ± 0.4% in streams with high agriculture catchments. Percent shredders were significantly lower ($P < 0.05$) in medium and high agriculture streams compared to forested and low agriculture streams (Figure 6E). At the same time, % shredders in recovering streams were of similar value to forested and low agriculture streams (Figure 6E). The ratio of scrapers to shredders, an index of autochthonous and allochthonous carbon supply, varied from 3.2 ± 0.8 in FOR sites to 23.4 ± 7.2 in AG-H sites (Figure 6F) and was significantly higher in medium and high agriculture streams, lower in forested streams, and intermediate in recovering and low agriculture streams (Figure 6F).

EPT taxa richness ranged from 7 to 37 among sites, but was not significantly different among forest cover categories (Figure 7A). Percent composition of invertebrates in EPT orders (mayflies, stoneflies, and caddisflies) varied from 56.7 ± 2.1% in low agriculture streams to 19.2 ± 5.4% in high agriculture streams (Figure 7B) and was significantly higher in forested, low agriculture, and recovering streams than in medium and high agriculture streams. In contrast, percentage of chironomids and oligocheates were significantly higher in medium and high agriculture (49.8 ± 9.1% and 56.6 ± 8.5%, respectively) compared to forested, low agriculture, and recovering (25.7 ± 4.2%, 23.2 ± 2.8%, 23.2 ± 2.2%, respectively) streams (Figure 6C). Organisms from the 5 most dominant taxa made up 37-83% of the benthic macroinvertebrates among all streams, but this percentage did not differ significantly among forest cover categories

(Figure 6D). NCBI scores were highest in streams with high agriculture and medium agriculture (5.29 ± 0.44 and 4.89 ± 0.60) catchments and were lower in forested and reforested sites, which all had scores between 2.8 and 4 (Figure 6E).

Several benthic macroinvertebrate metrics (Simpson's index, Shannon index, Shannon evenness, % gatherers, % scrapers, scrapers/shredders, EPT taxa, % EPT, % C+O, % 5 dominant, and NCBI) were related to % forest in a 100-m riparian corridor in 1993 (Table 4). Macroinvertebrate density was negatively related to % forest at the watershed scale in 1993, and % shredders was most strongly related to % forest in the riparian corridor 2 km upstream of sampling sites in 1950. Total richness was not significantly related to % forest cover in either year or at any spatial scale. Most relationships showed higher diversity, higher % shredders, and more pollution-sensitive taxa with increasing forest cover and less agricultural influence.

In addition to forest cover, stepwise multiple regression of benthic macroinvertebrate metrics and various physical, chemical, or biological variables, suggested some possible links between forest cover and macroinvertebrate metrics. Chl-*a* was the single best predictor of several metrics, including total density, Shannon index, Shannon evenness, % gatherers, scrapers/shredders, and % 5 dominant (Table 5). Other physical or chemical variables added predictive power to some regression models, including degree-days, % inorganic seston, % fine substrate, RHAP, TSS, and PO_4-P.

Non-metric multidimensional scaling (NMS) ordination separated sites according to macroinvertebrate density by taxon, and these taxonomic differences appeared to distinguish sites along a forest cover gradient corresponding roughly to forest cover categories. Medium and high agriculture sites occupied taxonomic space with high axis 1 and axis 2 values, and long-term forested sites generally had low scores for both axes (Figure 8). Reforested sites (REC-1 and REC-2) and low agriculture sites occupied intermediate positions on both axes. High values on axis 1 were correlated with high density of *Orthocladius*, Oligochaeta, Nematoda, and *Cryptochironomus*, all taxa generally tolerant of poor water quality (Table 6). Sites with high density of the stonefly genera *Amphinemura*, *Sweltsa*, and *Tallaperla*, and the mayfly genera *Cinygmula* and *Epeorus* had low axis 1 scores (Table 6). Distribution of sites along axis 2 was correlated with density of many more taxa than axis 1. In addition to the 4 taxa correlated with axis 1, axis 2 scores were positively correlated with density of *Nigronia*, *Cheumatopsyche*, *Polypedilum*, *Chironomus*, *Psephenus*, and *Oecetis* (Table 6). Axis 2 scores were negatively correlated with density of *Epeorus* and *Cinygmula* (like axis 1) and the following taxa: *Acentrella*, *Oulimnius*, *Diplectrona*, *Prosimulium*, *Dicranota*, *Drunella*, *Pteronarcys*, *Baetis*, *Cambarus*, and *Leuctra*.

Density of particular macroinvertebrates was used to separate and group sites based on pair-wise comparisons of assemblages in a two-way indicator species analysis (TWINSPAN). The first separation of sites was based on presence or absence of *Tallaperla*, *Ophiogomphus*, and Ancylidae (Figure 9). These 3 taxa appeared to separate all forested, low agriculture, and reforested sites from medium and high agriculture sites (with one AG-L and one REC-1 site). A variety of other genera further distinguished site groups taxonomically, but these divisions did not appear to follow forest cover categories.

Discussion

Effects of agriculture on physical and chemical stream conditions

Streams showed elevated nutrients and temperature in response to historical and current agriculture. Streams in different categories were not significantly different in elevation or discharge making land use the single factor likely to have caused these physical and chemical differences in streams. Other studies have demonstrated elevated nutrients and temperature in agricultural streams (e.g., Karr and Schlosser 1978, Peterjohn and Correll 1984, Lowrance et al. 1985). Historical agriculture had a persistent effect on water chemistry but not on water temperature regime. DIN concentrations in REC-2 streams were between values for streams with similar past (AG-M) or present (AG-L) amounts of agriculture, which suggests that nutrient concentrations might be declining in reforesting streams. However, elevated nutrients in streams have been observed decades following logging in the southern Appalachians as a result of mineralization of nutrients from organic material in the catchment (Swank and Vose 1997). Forest development in historically agricultural watersheds was likely dense enough to shade streams resulting in lower stream temperatures than agricultural streams. Swift (1983) showed that stream temperature recovers quickly (within 5 years) during reforestation from clear-cutting. However, reforestation on abandoned agriculture generally takes longer than reforestation from logging because soils are compacted by livestock or farm machinery (Myster and Pickett 1994). Fifty years appears to be enough time for streams to establish a pre-agriculture temperature regime as a result of reforestation.

Increased sediment load has been one of the most documented influences of agricultural land use on streams (Wark and Keller 1963, Waters 1995). In the present study, baseflow suspended particle concentrations were 3X higher in agricultural streams and streams with agricultural histories than in forested streams. These high TSS concentrations were coupled with higher % inorganic sediment content, which results in ~ 4X higher inorganic suspended load in agricultural streams than in forested streams.

Natural resource managers seek to reduce suspended sediment load, but most studies indicate that TSS remain elevated following reforestation from logging or agricultural management. For example, logging results in higher TSS transport and shifts composition from organic to inorganic (Webster et al. 1988), and these changes require decades to recover following reforestation (Swift 1988, Webster et al. 1992, Davies and Nelson 1993). Ursic and Dendy (1965) found that reforested old fields had slightly lower sediment yield than cultivated cropland or pasture but that sediment yield from old fields was still higher than long-term woodlands. Furthermore, implementation of best management practices on cropland in the Midwest U.S. has reduced alluvial deposition in streams but not suspended sediment load (Trimble 1999). Suspended sediments could be arising either from exposed stream banks not stabilized by vegetation or from streambed sediments during high flows. Despite the transition from agriculture to forest in many watersheds studied here, reforested streams continue to carry higher amounts of sediment than forested streams without historical agricultural use, most likely due to suspension of material from banks or the streambed.

In addition to suspended particle concentration and composition, in-stream substrate was dramatically altered in agricultural streams. Agricultural streams had smaller mean particle size, larger amounts of fine substrate, and lower ratios of cobble to fine substrate than forested streams. Infiltration of fine sediment to substrate is one of the most common effects of logging (e.g., Davies and Nelson 1993), agriculture (e.g., Richards et al. 1996), and urbanization (e.g., Sponseller et al. 2001). These geomorphic changes seem to persist in streams after cessation of agriculture and subsequent reforestation, which is indicated by the similarity of substrate in reforested and agricultural streams in the present study. Alteration in-stream habitat from historical land use activities (i.e., siltation) has been suggested as one of the longest lasting influences on stream ecosystems (Benfield 1995, Harding et al. 1998). For example, streams with previously logged catchments retain sediment introduced during logging for decades, despite periods of suspension and deposition of this sediment (Brown and Krygier 1971) primarily associated with storms (Golladay et al. 1987). Although maintenance of forested buffer strips along streams has been linked to reductions of soil loss (Peterjohn and Correll 1984, Robinson et al. 1996), sediment in streams from historical land use might continue to affect in-stream habitat.

Chl-*a* concentration was dramatically higher in agricultural than forested streams, presumably resulting from higher nutrients and light. High light intensity and nutrients are associated with algal productivity in agricultural streams (Reed et al. 1994, Corkum 1996), and nutrients have been strongly correlated with algal growth in the absence of light limitation (Lowe et al. 1986, Lohman et al. 1992, Mosisch et al. 2001). In the current study, agricultural streams had ~3X the amount of chl-*a* as forested streams, but these higher chl-*a* values in agricultural streams (~ 9 mg/m^2) were lower than chl-*a* in some forested streams of the southern Appalachians during the same times of year (e.g., 13.5 to 93.4 mg/m^2 in Hill and Dinick 2002). Chl-*a* was lower in REC-1 and REC-2 streams than AG streams suggesting that reforestation may limit algal growth in historically agricultural streams despite elevated nutrient concentrations. Stream shading recovers rapidly (within 5 years) following logging in the southern Appalachians and limits algal growth and primary production (Webster et al. 1983). Given the return of temperature and chl-*a* to amounts typical of forested streams, terrestrial vegetation appears to have recovered enough to provide shading to REC streams.

Effects of agriculture on macroinvertebrates

Diversity (richness and calculated indices) of benthic macroinvertebrates was not significantly different among forest cover categories. Many other studies found macroinvertebrate diversity to be similar among agricultural and forested streams (e.g., Reed et al. 1994, Quinn et al. 1997, Townsend et al. 1997, Harding et al. 1999). At the same time, macroinvertebrate communities in these studies, and the present research, displayed compositional changes in response to land use. I found that diversity indices were positively related to forest cover in riparian zones (Table 4), even though differences in mean values for these indices were not significant among forest cover categories. In the present study, categories were determined using watershed-scale forest cover, but forest cover in riparian corridors was a stronger predictor of macroinvertebrate diversity and might have been a better spatial scale to use in categorizing streams based on forest cover. Metrics that measured distribution of individuals among taxa (i.e., evenness) responded to forest cover more predictably than species richness. Stone and Wallace (1998) suggested that using multiple indices to assess long-term influences of logging on streams provides more information than is gained by considering only species richness. I contend that the same is true when considering other agricultural influences.

Some functional feeding groups differed among forest cover categories and displayed strong linear relationships with forest cover in the riparian corridor. Percentage of shredders was much higher in forested streams compared to streams with current agricultural activity and varied from >10% of benthic macroinvertebrate abundance in forested streams to <1% in high agriculture streams. The lower shredder abundance was likely caused by two factors: availability of coarse organic matter and water quality. Shredder production and abundance have been linked to the availability of organic matter, as shown by studies of logged streams (Haefner and Wallace 1981, O'Hop et al. 1984, Stout et al. 1993, Stone and Wallace 1998) and of forested streams with reduced allochthonous organic matter supply (Wallace et al. 1997, Eggert and Wallace 2003, Johnson et al. 2003). Agriculture, like logging, results in reductions in coarse organic matter supply to streams (Karr and Schlosser 1978), which likely leads to lower abundance of shredders in agricultural streams. In addition, most shredder taxa in the southern Appalachians are sensitive to different forms of pollution including high temperatures, high sediment load, and chemicals (Morse et al. 1993). Agricultural streams in this study had lower water quality than forested streams, which likely contributed to lower shredder abundance in agricultural streams than in forested streams.

Percent shredder abundance was the only macroinvertebrate metric more strongly related to forest cover in 1950 than to forest cover in 1993 and to forest cover in the riparian zone 2 km upstream of the study sites instead of the entire riparian corridor or watershed. Most of the coarse organic matter to support shredder populations in streams is derived from vegetation within 1 km upstream (Johnson and Covich 1997), so it is not surprising that shredders were most strongly related to forest cover at this spatial scale. While riparian forest cover within 2 km upstream of the study site in 1950 was the strongest correlate with % shredders, forest cover in 1993 at the same spatial scale was the second best predictor of % shredders (data not shown). Furthermore, shredder abundance was significantly higher in reforested streams than in agricultural streams suggesting that shredder abundance had recovered from historical agriculture. In logged streams, shredder abundance and production return to pre-logging levels within 10 years (Haefner and Wallace 1981, O'Hop et al. 1984, Stout et al. 1993, Stone and Wallace 1998). Although shredder abundance appears to have recovered from historical agriculture through reforestation, shredder assemblage composition was slightly different in reforested streams compared to forested streams. Shredder assemblages in forested streams had higher numbers of *Pteronarcys* and *Tallaperla* than reforested sites, whose shredder assemblages were dominated by *Leuctra*, *Brillia*, and Stratiomyidae (Appendix B). Considering biomass of these shredder taxa might provide further insight into the differences in the shredder assemblages among streams with catchments reforested from historical agriculture and those with long-term forested catchments.

Other functional feeding groups did not respond to the gradient of forest cover represented by my study sites. Filterers and predators were not significantly different among forest cover categories and were not related to forest cover at any spatial scale or year. Filterers might be expected to increase in agricultural streams because of high organic loads from cattle, but it appears that in-stream habitat alteration negatively affected filterers in agricultural streams in the present study. Scrapers, on the other hand, have been shown to increase as a result of forest clearing (Woodall and Wallace 1972) and to return to pre-logging abundances rapidly in southern Appalachian streams (Haefner and Wallace 1981, Stone and Wallace 1998). It is reasonable to expect scrapers to be more abundant in agricultural streams due to higher primary production, as others have shown (Behmer and Hawkins 1986, Dudgeon and Chan 1992, Reed et al. 1994). In the current study, scraper abundance did not differ significantly among forest cover categories and was positively correlated with forest cover (i.e., high forest cover = high % scrapers). However, pollution-tolerant gatherers (e.g., Chironomidae and Oligochaeta) dominated benthic macroinvertebrate communities in AG streams (>60%) resulting in lower proportional abundance of scrapers in AG streams. Proportional abundance of gatherers was also negatively related to forest cover suggesting that AG streams supported large populations of gatherers relative to macroinvertebrates from other functional feeding groups. In New Zealand, gatherer (browser) density and proportional abundance were higher in pastoral streams than in forested streams (Townsend et al. 1997), but other studies did not find consistent patterns of gatherer abundance with agricultural influence on streams (e.g., Reed et al. 1994).

Although scraper abundance was not higher in agricultural streams, the ratio of scrapers to shredders, an index of the relative importance of primary production or allochthonous organic matter as food for macroinvertebrates (Stone and Wallace 1998), was significantly higher in agricultural streams than in forested and reforested streams. In addition, scraper:shredder was negatively related to riparian forest cover in 1993 suggesting that benthic macroinvertebrates in streams with high forest cover rely on allochthonous detritus more than in-stream production for carbon. Given the strong response of shredders to agriculture and reforestation, it seems that organic matter source has a dramatic influence on benthic macroinvertebrate communities in streams influenced by agriculture. Cummins et al. (1981) found that ratios of shredders to collectors decreased and scrapers to collectors increased along a river continuum in response to changing organic matter supply from allochthonous leaf fall to primary production. Furthermore, Stone and Wallace (1998) used the ratio of shredders to scrapers to assess recovery of benthic macroinvertebrate communities from clear-cut logging and found that this index recovered to pre-logging levels within 5 years. Results from the current study support the contention that macroinvertebrate metrics linked to organic matter source recovered quickly from changes caused by land clearing.

Pollution-tolerant organisms dominated benthic macroinvertebrate communities in agricultural streams, and these streams had lower densities of sensitive taxa compared to forested and reforested streams. EPT richness has been shown to respond predictably to land use (Lenat and Crawford 1994, Wallace et al. 1996), but this metric did not differ among forest cover categories identified for this study and was only weakly related to forest cover. Quinn et al. (1997) also found no difference in EPT richness but significantly higher EPT density in pasture than in forest streams in New Zealand. While the present study did not detect differences in EPT richness or density, EPT insects made up a much greater proportion of the macroinvertebrate communities in forested streams (> 50%) than in agricultural streams (~ 20%). Changing food resources from detritus to algae might have caused similarity in EPT richness in forested and agricultural streams because shredder-detritivore taxa (many Plecoptera and Trichoptera) might be replaced by scraper taxa (many Ephemeroptera and some Trichoptera) without affecting overall EPT richness. EPT composition varied quite dramatically among forest cover categories, which may help explain the lack of differences in EPT richness and percent composition. Forested sites had much higher abundances of *Pteronarcys*, *Tallaperla*, *Swetlsa,* and *Rhyacophila* and lower abundances of *Ephemerella* and *Drunella* compared to other categories. Reforesting streams shared several EPT taxonomic patterns with forested streams including presence of *Cinygmula*, *Amphinemura*, and *Diplectrona*. Agricultural streams had high abundances of *Stenacron*, *Isoperla*, *Alloperla*, Capniidae, *Hydropsyche*, *Cheumatopsyche*, and

Leucotrichia. Agricultural and reforested streams shared the presence of *Baetisca*, which was not found in any of the forested streams.

Low percentages of EPT were coupled with high proportions of chironomids and oligochaetes, two groups generally considered tolerant to pollution. Organic enrichment from cattle or sewage effluent has been linked to high density of chironomids and oligochaetes (Townsend et al. 1983, Lenat 1984), and these taxa increased along the agricultural gradient represented by forest cover categories. NCBI scores showed trends similar to % EPT and % chironomid + oligochaete in response to agriculture. The NCBI was developed for streams in North Carolina, USA and has been used effectively to determine benthic macroinvertebrate community responses to insecticides (Wallace et al. 1996), logging (Stone and Wallace 1998), agriculture (Harding et al. 1998), and urbanization (Sponseller et al. 2001) in southern Appalachian streams. The NCBI is based on tolerance values for each macroinvertebrate taxon (higher numbers indicate pollution tolerance) and relative abundance of each taxon, so macroinvertebrate communities with a large proportion of pollution-tolerant taxa receive higher NCBI scores than communities with pollution-sensitive taxa. NCBI scores were higher in agricultural streams than in forested and reforested streams and were negatively correlated with riparian forest cover in 1993. Based on % EPT, % Chironomidae + Oligochaeta, and NCBI scores, agricultural streams had higher relative abundances of pollution-tolerant organisms than forested and reforested streams. Stone and Wallace (1998) found that NCBI values did not recover as rapidly as other invertebrate metrics in streams reforesting from logging and suggested that, as a result, the NCBI is a valuable tool for assessing subtle patterns of recovery from logging. However, none of the tolerance-based invertebrate metrics, including the NCBI, calculated in the present study differed significantly among forested streams with agricultural histories and long-term forested streams.

In their study, Harding et al. (1998) found that forested and agricultural streams were separated in an ordination based on macroinvertebrates. However, they found that some reforested sites grouped with current agriculture sites instead of forested sites (Harding et al. 1998). In the present study, grouping sites based on macroinvertebrate composition using multivariate techniques supported the taxonomic similarities between long-term forested streams and reforested streams and the separation of sites by taxa sensitive to water quality. In NMS and TWINSPAN, reforested sites grouped very close to forested or low agriculture sites, and high densities of pollution-sensitive taxa (e.g., *Tallaperla*, *Epeorus*, *Cinygmula*, *Diplectrona*, *Pteronarcys*, etc.) drove these groupings. Furthermore, sites with extensive agriculture activity in their catchments (AG-M, AG-H) typically contained dense populations of pollution-tolerant organisms (e.g., chironomids, oligochaetes, nematodes) and facultative EPT taxa (e.g., *Cheumatopsyche*). Interestingly, several taxa found in high density in forested and reforested streams belong to the shredder trophic group, while several taxa common to medium and high agriculture sites were collector-gatherers. This observation supports functional-feeding group composition results previously discussed.

Forest cover in the riparian zone had strong relationships with most macroinvertebrate metrics, which is similar to several studies that found strong relationships between riparian forest cover and macroinvertebrate or fish metrics (Roth et al. 1996, Allan et al. 1997). However, some studies have found strong relationships between macroinvertebrate metrics and forest cover at either broader (i.e., whole watershed; Lenat and Crawford 1994, Harding et al. 1998) or finer (i.e., sub-corridor; Richards et al. 1997, Sponseller et al. 2001) spatial scales. Despite the differences among these studies, processes at different spatial scales within watersheds likely control mechanisms affecting stream biota as a result of land use. Richards et al. (1996) showed that the physical and chemical factors that best predicted macroinvertebrate assemblages were influenced by land use at the broadest spatial scales (whole watershed and 100m riparian for the entire stream length). Scott et al. (2002) found that land use at the watershed scale was the best predictor of physical and chemical variables in streams of the southern Appalachians. In-stream habitat features have been accurately predicted using landscape features at a broad scale (Davies et al. 2000). Nitrogen concentration and deposited sediment in streams have been linked to agriculture at the watershed scale, while phosphorus and suspended solids were positively related to land use at more local scales (Johnson et al. 1997).

Because reforested streams had higher nutrient concentrations and altered sediment composition and transport than forested streams, I expected historical agriculture to have long-term influences on macroinvertebrate community structure. It appears though that regulation of organic matter source via riparian vegetation was more important than in-stream habitat or water chemistry in determining benthic macroinvertebrate community structure. Most macroinvertebrate metrics were strongly related to chlorophyll concentrations and/or cumulative degree-days, both strongly linked to riparian forest cover (Sweeney 1993). In the present study, sediment composition was assessed at a reach scale and therefore may be inappropriate for linking directly to macroinvertebrate data collected in riffles within reaches because the two measurements do not necessarily assess the same space. However, microhabitat restoration by altering variability and heterogeneity of substrate particle sizes resulted in no net effect on macroinvertebrate community structure (Brooks et al. 2002). Furthermore, recovery of streams from logging has been strongly linked to organic matter or “trophic status” as opposed to in-stream sedimentation (Murphy et al. 1981). These other studies support the conclusion that recovery of benthic macroinvertebrate community structure from agriculture relies on shading and organic matter supply more than in-stream physicochemistry.

Current forest cover (i.e., 1993) was a more robust predictor of macroinvertebrate community structure than were historical patterns, and reforested streams supported macroinvertebrate communities very similar to long-term forested streams. These results contrast with those of Harding et al. (1998) who found that historical forest cover was a stronger predictor of benthic macroinvertebrate community structure than current forest cover and suggested that present-day invertebrate diversity in streams results from historical land use. Both spatial and temporal scales of agricultural influences on streams may tax the resilience of biological communities. Degradation of ecosystems at regional scales might make recovery more difficult because multiple stresses cause synergistic influences on biodiversity and ecosystem function (Niemi et al. 1990, Rapport and Whitford 1999). In addition, the pool of species available to colonize disturbed habitats following stress removal may be severely reduced or even absent in the event of broad-scale regional disturbances (Rapport et al. 1985, Palmer et al. 1997). However, in the southern Appalachians, agricultural streams exist in a matrix of protected national forest land (Gade and Stillwell 1986), and degradation of aquatic habitats has not resulted in regional reductions of diversity (Wallace et al. 1992). In particular, agricultural streams frequently have forested headwaters or share a watershed boundary with an adjacent forested stream (Otto 1983). These nearby forested streams support macroinvertebrate and fish communities that can rapidly colonize streams by downstream and upstream movement or by over-land flight and oviposition (Williams and Hynes 1976, Gore and Milner 1990) but only when conditions are suitable for survival (Poff and Ward 1990). Therefore, macroinvertebrate communities might be resilient to long-term agriculture once reforestation occurs to reestablish organic matter and thermal conditions in streams. This finding holds promise for watershed managers and restoration planners because it suggests that biodiversity of streams influenced by decades of agriculture may be restored to pre-agricultural levels if agriculture is replaced with forest across the landscape. However, the present study considered relatively small streams (2nd-3rd order), which are not indicative of all southern Appalachian streams. In particular, Harding et al. (1998) included several large streams (5th-6th order) in their study, and these large systems might require longer periods to recover from historical disturbance due to inertia and larger watersheds with complex land use patterns.

Because of the dramatic changes to geomorphology and substrate in streams with disturbed catchments, models generally predict long recovery times for stream macroinvertebrate communities (Niemi et al. 1990), a suggestion initially supported by Harding et al. (1998). Given the PRESS (*sensu* Bender et al. 1984) nature of agriculture as a disturbance to streams, I expected recovery of biological components in these streams to take extremely long periods for several reasons: 1) stream recovery from watershed disturbance depends on recovery of terrestrial (allogenic) drivers like organic matter supply (Golladay et al. 1992); 2) in-stream substrate requires long periods to return to pre-disturbance conditions (Brown and Krygier 1971, Trimble 1999); and 3) stream nutrient concentrations remain high following disturbance even in reforested streams (Swank and Vose 1997). While my results support the long-term presence of sediment and elevated nutrients in streams after reforestation of agricultural catchments, macroinvertebrate data were more strongly correlated with variables other than substrate and chemistry (i.e., chlorophyll and degree-days). Chlorophyll concentration and temperature were similar among reforested and long-term forested streams indicating that over the course of 40 years these variables had recovered from historical land use while substrate composition and water chemistry had not. In this sense, some features of stream ecosystems may remain altered by historical agriculture practices, but these long-lasting changes are not evident in benthic macroinvertebrate community structure.

Acknowledgments

Funding for this project was provided by Sigma Xi, the Graduate Student Assembly and Biology Department of Virginia Tech, and the National Science Foundation grant DEB9632854 to the Coweeta Hydrologic Laboratory Long-Term Ecological Research site. Special thanks to all the landowners who gave me access to their properties and provided many anecdotes about the history of the region and their land. I would also like to thank the Virginia Tech Stream Team for valuable help in data collection and Paul Bolstad and Ned Gardiner for providing GIS data.

Literature Cited

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land use on stream integrity across multiple spatial scales. Freshwater Biology 37:149-161.

APHA (American Public Health Association, American Water Works Association, and Water Environment Federation). 1998. Standard methods for the examination of water and wastewater, 20th edition. American Public Health Association, Washington, DC.

Ayers, H. B., and W. W. Ashe. 1905. The southern Appalachian forests. Series H, Forestry, Professional paper no. 37. U.S. Geological Survey. Government Printing Office, Washington, DC.

Barbour, M. T., J. Gerritsen, B. D. Snyder, and J. B. Stribling. 1999. Rapid bioassessment protocols for use in streams and wadeable rivers: periphyton, benthic macroinvertebrates and fish, second edition. EPA 841-B-99-002. U.S. Environmental Protection Agency, Office of Water, Washington, DC.

Bartram, W. 1791. Travels. *In* The travels of William Bartram. F. Harper, editor, 1998. University of Georgia Press, Athens, GA.

Behmer, D. J., and C. P. Hawkins. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. Freshwater Biology 16:278-300.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1-13.

Benfield, E. F. 1995. Historical land-use and streams. Bulletin of the North American Benthological Society 12:241-248.

Brooks, S. S., M. A. Palmer, B. J. Cardinale, C. M. Swan, and S. Ribblett. 2002. Assessing stream ecosystem rehabilitation: limitations of community structure data. Restoration Ecology 10:156-168.

Brown, G. W., and J. T. Krygier. 1971. Clear-cut logging and sediment production in the Oregon Coast Range. Water Resources Research 7:1189-1199.

Cathey, C. O. 1956. Agricultural developments in North Carolina 1783-1860. James Sprunt Studies in History and Political Science, Volume 38. University of North Carolina Press, Chapel Hill, NC.

Clark, T. D. 1984. The greening of the south. University of Kentucky Press, Lexington, KY.

Corkum, L. D. 1996. Responses of chlorophyll-a, organic matter, and macroinvertebrates to nutrient additions in rivers flowing through agricultural and forested land. Archiv fur Hydrobiologie 136:391-411.

Cummins, K. W., M. J. Klug, G. M. Ward, G. L. Spingler, R. W. Speaker, R. W. Ovink, D. C. Mahan, and R. C. Petersen. 1981. Trends in particulate organic matter fluxes, community processes and macroinvertebrate functional groups along a Great Lakes drainage basin river continuum. Verhandlung der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 21:841-849.

Davies, N. M., R. H. Norris, and M. C. Thoms. 2000. Prediction and assessment of local stream habitat features using large-scale catchment characteristics. Freshwater Biology 45:343-369.

Davies, P. E., and M. Nelson. 1993. The effect of steep slope logging on fine sediment infiltration into the beds of ephemeral and perennial streams of the Dazzler Range, Tasmania, Australia. Journal of Hydrology 150:481-504.

Dudgeon, D., and I. K. K. Chan. 1992. An experimental study of the influence of periphytic algae on invertebrate abundance in a Hong Kong stream. Freshwater Biology 27:53-63.

Eggert, S. L., and J. B. Wallace. 2003. Reduced detrital resources limit *Pycnopsyche gentilis* (Trichoptera:Limnephilidae) production and growth. Journal of the North American Benthological Society 22:388-400.

Eller, R. D. 1982. Miners, millhands, and mountaineers: industrialization of the Appalachian South, 1880-1930. University of Tennessee Press, Knoxville, TN.

Epler, J. H. 2001. Identification manual for the larval Chironomidae (Diptera) of North and South Carolina. Special Publication SJ2001-SP13. North Carolina Department of Environment and Natural Resources, Raleigh, NC and St. Johns River Water Management District, Palatka, FL.

Gade, O., and H. D. Stillwell. 1986. North Carolina: people and environments. Geo-App Publishing Company, Boone, NC.

Golladay, S. W., J. R. Webster, and E. F. Benfield. 1987. Changes in stream morphology and storm transport of organic matter following watershed disturbance. Journal of the North American Benthological Society 6:1-11.

Golladay, S. W., J. R. Webster, E. F. Benfield, and W. T. Swank. 1992. Changes in stream stability following forest clearing as indicated by storm nutrient budgets. Archiv fur Hydrobiologie 1:1-33.

Gordon, N. D., T. A. McMahon, and B. L. Finlayson. 1992. Stream hydrology: an introduction for ecologists. John Wiley and Sons, Chichester, England.

Gore, J. A., and A. M. Milner. 1990. Island biogeographical theory: can it be used to predict lotic recovery rates? Environmental Management 14:737-753.

Gray, L. C. 1941. History of agriculture in the southern United States to 1860. Carnegie Institution of Washington publication no. 430. Peter Smith, New York.

Haefner, J. D., and J. B. Wallace. 1981. Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. Canadian Journal of Fisheries and Aquatic Sciences 38:353-359.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones III. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Science 95:14843-14847.

Harding, J. S., R. G. Young, J. W. Hayes, K. A. Shearer, and J. D. Stark. 1999. Changes in agricultural intensity and river health along a river continuum. Freshwater Biology 42:345-357.

Hill, W. R., and S. M. Dimick. 2002. Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. Freshwater Biology 47:1245-1256.

Holmes, R. M., A. Aminot, R. Kerouel, B. A. Hooker, and B. J. Peterson. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 56:1801-1809.

Hynes, H. B. N. 1975. The stream and its valley. Verhandlung der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 19:1-15.

Johnson, B. R., W. F. Cross, and J. B. Wallace. 2003. Long-term resource limitation reduces insect detritivore growth in a headwater stream. Journal of the North American Benthological Society 22:565-574.

Johnson, L. B., C. Richards, G. E. Host, and J. W. Arthur. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. Freshwater Biology 37:193-208.

Johnson, S. L., and A. P. Covich. 1997. Scales of observation or riparian forests and distributions of suspended detritus in a prairie river. Freshwater Biology 37:163-175.

Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. Science 201:229-234.

Lenat D. R., and J. K. Crawford. 1994. Effects of land use on water quality and aquatic biota of three North Carolina Piedmont streams. Hydrobiologia 294:185-199.

Lenat, D. R. 1984. Agriculture and stream water quality: a biological evaluation of erosion control practices. Environmental Management 8:333-344.

Lenat, D. R. 1993. A biotic index for the southeastern United States: derivation and list of tolerance values, with criteria for assigning water-quality ratings. Journal of the North American Benthological Society 12:279-290.

Lohman, K., J. R. Jones, and B. D. Perkins. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. Canadian Journal of Fisheries and Aquatic Sciences 49:1198-1205.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221-229.

Lowrance, R. R., L. S. Altier, J. D. Newbold, R. R. Schnabel, P. M. Groffman, J. M. Denver, D. L. Correll, J. W. Gilliam, J. L. Robinson, R. B. Brinsfield, K. W. Staver, W. Lucas, and A. H. Todd. 1997. Water quality functions of riparian forest buffers in Chesapeake Bay watersheds. Enviromental Management 21:687-712.

Lowrance, R. R., R. A. Leonard, L. E. Asmussen, and R. A. Todd. 1985. Nutrient budgets for agricultural watersheds in the southeastern coastal plain. Ecology 66:287-296.

Merritt, R. W., and K. W. Cummins, editors. 1996. An introduction to the aquatic insects of North America, 3rd edition. Kendall-Hunt Publishing Company, Dubuque, IO.

Morse, J. C., B. P. Stark, and W. P. McCafferty. 1993. Southern Appalachian streams at risk: implications for mayflies, stoneflies, caddisflies, and other aquatic biota. Aquatic Conservation: Marine and Freshwater Ecosystems 3:293-303.

Mosisch, T. D., S. E. Bunn, and P. M. Davies. 2001. The relative importance of shading and nutrients on algal production in subtropical streams. Freshwater Biology 46:1269-1278.

Murphy, M. L., C. P. Hawkins, and N. H. Anderson. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society 110:469-478.

Myster, R. W., and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr. in 10 contrasting old fields. Ecology 75:387-392.

Neatrour, M. A., J. R. Webster, and E. F. Benfield. 2004. The role of floods in particulate organic matter dynamics of a southern Appalachian river-floodplain ecosystem. Journal of the North American Benthological Society 23:198-213.

Niemi, G. J., P. DeVore, N. Detenbeck, D. Taylor, A. Lima, J. Pastor, J. D. Yount, and R. J. Naiman. 1990. Overview of case studies on recovery of aquatic systems from disturbance. Environmental Management 14:571-587.

O'Hop, J., J. B. Wallace, and J. D. Haefner. 1984. Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. Freshwater Biology 14:13-21.

Osborne, L. L., and D. A. Kovacic. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. Freshwater Biology 9:243-258.

Otto, J. S. 1983. The decline of forest farming in southern Appalachia. Journal of Forestry 27:18-27.

Palmer, M. A., R. F. Ambrose, and N. E. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology 5:291-300.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65:1466-1475.

Pickett, S. T. A., and P. S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, London, UK.

Poff, N. L., and J. V. Ward. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environmental Management 14:629-645.

Quinn, J. M., A. B. Cooper, R. J. Davies-Colley, J. C. Rutherford, and R. B. Williamson. 1997. Land use effects on habitat, water quality, periphyton, and benthic invertebrates in Waikato, New Zealand, hill-country streams. New Zealand Journal of Marine and Freshwater Research 31:579-597.

Rapport, D. J., and W. G. Whitford. 1999. How ecosystems respond to stress. Bioscience 49:193-203.

Rapport, D. J., H. A. Regier, and T. C. Hutchinson. 1985. Ecosystem behavior under stress. American Naturalist 125:617-640.

Reed, J. L., I. C. Campbell, and P. C. E. Bailey. 1994. The relationship between invertebrate assemblages and available food at forest and pasture sites in three southeastern Australian streams. Freshwater Biology 32:641-650.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. J. Sheldon, J. B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433-455.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Sciences 53:295-311.

Richards, C., R. J. Haro, L. B. Johnson, and G. E. Host. 1997. Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biology 37:219-230.

Robinson, C. A., M. Ghaffarzadeh, and R. M. Cruse. 1996. Vegetative filter strip effects on sediment concentration in cropland runoff. Journal of Soil and Water Conservation 50:227-230.

Roth N. E., J. D. Allan, and D. L. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.

Rutherford, J. C., S. Blackett, C. Blackett, L. Saito, and R. J. Davies-Colley. 1997. Predicting the effects of shade on water temperature in small streams. New Zealand Journal of Marine and Freshwater Research 31:707-721.

Schlosser, I. J., and J. R. Karr. 1981. Water quality in agricultural watersheds: impact of riparian vegetation during base flow. Water Resources Bulletin 17:233-240.

Scott, M. C., G. S. Helfman, M. E. McTammany, E. F. Benfield, and P. V. Bolstad. 2002. Multiscale influences on physical and chemical stream conditions across Blue Ridge landscapes. Journal of the American Water Resources Association 38:1379-1392.

Simmons, C. E., and R. C. Heath. 1979. Water-quality characteristics of streams in forest and rural areas of North Carolina. Pages B1-B33 in Water quality of North Carolina streams. Geological Survey Water-Supply Paper 2185 A-D. North Carolina Department of Natural and Economic Resources, Raleigh, NC.

Sponseller, R. A., E. F. Benfield, and H. M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biology 46:1409-1424.

Steinman, A. D., and G. A. Lamberti. 1996. Biomass and pigments of benthic algae. Pages 295-313 in Methods in Stream Ecology. F. R. Hauer and G. A. Lamberti, editors. Academic Press, Inc., San Diego, California, USA.

Stone, M. K., and J. B. Wallace. 1998. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. Freshwater Biology 39:151-169.

Stout, B. M., III, E. F. Benfield, and J. R. Webster. 1993. Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. Freshwater Biology 29:59-69.

Swank, W. T., and J. M. Vose. 1997. Long-term nitrogen dynamics of Coweeta forested watersheds in the southeastern United States of America. Global Biogeochemical Cycles 11:657-671.

Sweeney, B. W. 1993. Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in Eastern North America. Proceedings of The Academy of Natural Sciences of Philadelphia 144:291-340.

Swift, L. W., Jr. 1983. Duration of stream temperature increases following forest cutting in the southern Appalachian Mountains. Pages 273-275 *in* A. I. Johnson and R. A. Clark, editors. International Symposium on Hydrometeorology. American Water Resources Association, Bethesda, MD.

Swift, L. W., Jr. 1988. Forest access roads: design, maintenance, and soil loss. Pages 313-324 *in* W. T. Swank and D. A. Crossley, Jr., editors. Forest Hydrology and Ecology at Coweeta. Springer-Verlag, New York.

Townsend, C. R., A. G. Hildrew, and J. Francis. 1983. Community structure in some southern English streams: the influence of physicochemical factors. Freshwater Biology 13:521-544.

Townsend, C. R., C. J. Arbuckle, T. A. Crowl, and M. R. Scarsbrook. 1997. The relationship between land use and physicochemistry, food resources and macroinvertebrate communities in tributaries of the Taieri River, New Zealand: a hierarchically scaled approach. Freshwater Biology 37:177-191.

Trimble, S. W. 1999. Decreased rates of alluvial sediment storage in the Coon Creek basin, Wisconsin. Science 285:1244-1246.

Ursic, S. J., and F. E. Dendy. 1965. Sediment yields from small watersheds under various land uses and forest covers. Pages 47-52 *in* Proceedings, Federal Interagency Sedimentation Conference, 1963. U.S. Department of Agriculture Miscellaneous Publication 970. Washington, DC.

Valett, H. M., C. L. Crenshaw, and P. F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. Ecology 83:2888–2901.

Wallace, J. B, J. R. Webster, and R. L. Lowe. 1992. High gradient streams of the southern Appalachians. Pages133-191 *in* T. Hackney, S. M. Adams, and W. A. Martin, editors. Biodiversity of the southeastern United States/aquatic communities. John Wiley and Sons, Inc., New York.

Wallace, J. B., J. W. Grubaugh, and M. R. Whiles. 1996. Biotic indices and stream ecosystem processes: results from an experimental study. Ecological Applications 6:140-151.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Wark, J. W., and F. J. Keller. 1963. Preliminary study of sediment sources and transport in the Potomac River basin. Interstate Commission on the Potomac River Basin Technical Bulletin 1963-11. Washington, DC.

Waters, T. F. 1995. Sediment in streams; sources, biological effects and control. American Fisheries Society Monograph 7. Bethesda, MD.

Wear, D. N. and P. V. Bolstad. 1998. Land-use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Webster, J. R., E. F. Benfield, S. W. Golladay, R. F. Kazmierczak, W. B. Perry, and G. T. Peters. 1988. Effects of watershed disturbance on stream seston characteristics. Pages 279-294 *in* W. T. Swank and D. A. Crossley, Jr., editors. Forest Ecology and Hydrology at Coweeta. Springer-Verlag, New York.

Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. 1983. Stability of stream ecosystems. Pages 355-395 *in* J. R. Barnes and G. W. Minshall, editors. Stream Ecology. Plenum Publishing Corp., New York.

Webster, J. R., S. W. Golladay, E. F. Benfield, J. L. Meyer, W. T. Swank, and J. B. Wallace. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. Pages 231-253 *in* P. J. Boon, P. Calow and G.E. Petts, editors. River Conservation and Management. John Wiley and Sons Ltd., New York.

Whiles, M. R., and J. B. Wallace. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. Canadian Journal of Fisheries and Aquatic Sciences 52:2402-2422.

Williams, D. D., and H. B. N. Hynes. 1976. The recolonization mechanisms of stream benthos. Oikos 27:265-272.

Wolman, M. G. 1954. A new method of sampling coarse riverbed. Transactions of the American Geophysical Union 35:951-956.

Woodall, W. R., Jr., and J. B. Wallace. 1972. The benthic fauna of four small southern Appalachian streams. American Midland Naturalist 88:393-407.

Yarnell, S. L. 1998. The southern Appalachians: a history of the landscape. General report SRS-18. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Table 1. Results from Pearson product moment correlations between land cover at different scales and site scores for the first two principle component axes. Lateral spatial scale is indicated by WS (whole watershed) or RIP (100-m riparian corridor). Extent refers to longitudinal spatial scale. Values shown are correlation coefficients (*r*, *n* = 30 streams) with strongest correlations in bold ($P < 0.0001$). The first and second principle component axes explained 92.1% and 4.8% of the variance among sites, respectively.

Spatial scale				
Lateral	Extent	Year	PCA-1	PCA-2
WS	Whole catchment	1950	**-0.952**	0.282
WS	Whole catchment	1993	**-0.932**	-0.232
RIP	Whole stream	1950	**-0.936**	0.248
RIP	Whole stream	1993	**-0.937**	-0.257
RIP	2 km corridor	1950	**-0.907**	**-0.853**
RIP	2 km corridor	1993	**-0.865**	**-0.794**
RIP	1 km corridor	1950	**-0.776**	**-0.829**
RIP	1 km corridor	1993	**-0.869**	**-0.780**

Table 2. Historical and current forest cover (%) at different spatial scales for streams in each forest cover category. Percent forest cover of sites in "extant" categories has remained constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Lateral spatial scale is indicated by WS (whole watershed) or RIP (100-m riparian corridor). Extent refers to longitudinal spatial scale. Values are means ± 1 SE.

Spatial scale			Extant				Recovering	
Lateral	Extent	Year	FOR	AG-L	AG-M	AG-H	REC-1	REC-2
WS	Whole catchment	1950	99.9 ± 0.1	87.5 ± 3.0	60.0 ± 6.3	52.7 ± 6.5	79.6 ± 5.2	77.6 ± 7.8
WS	Whole catchment	1993	99.3 ± 0.3	94.9 ± 1.9	83.6 ± 2.8	74.1 ± 4.8	94.9 ± 1.0	94.8 ± 1.1
RIP	Whole stream	1950	99.8 ± 0.2	84.2 ± 3.1	42.0 ± 8.0	29.3 ± 3.8	57.5 ± 8.4	75.5 ± 6.9
RIP	Whole stream	1993	99.9 ± 0.1	96.3 ± 0.9	72.2 ± 5.2	58.4 ± 2.3	85.4 ± 3.0	94.6 ± 2.0
RIP	2 km corridor	1950	99.7 ± 0.3	74.6 ± 3.8	13.7 ± 4.7	11.3 ± 5.1	40.4 ± 11.6	71.7 ± 6.1
RIP	2 km corridor	1993	96.8 ± 1.2	89.2 ± 3.0	47.7 ± 5.2	32.2 ± 6.6	76.7 ± 4.9	91.2 ± 1.4
RIP	1 km corridor	1950	99.1 ± 0.9	58.6 ± 12.2	12.6 ± 3.8	9.6 ± 3.5	29.0 ± 11.7	62.4 ± 6.3
RIP	1 km corridor	1993	96.6 ± 1.3	78.1 ± 12.1	43.8 ± 4.2	25.5 ± 7.5	66.4 ± 4.9	84.4 ± 3.7

Table 3. Physical and chemical characteristics of study sites by forest cover category. Values are means with standard errors in parentheses. Within a row, means with different superscripts are significantly different ($P < 0.05$). Discharge, specific conductance, dissolved inorganic nitrogen (DIN), and phosphate-phosphorus (PO_4-P) were measured semi-monthly at each site from November 2000 to August 2001.

	Extant				Recovering	
	FOR ($n = 5$)	AG-L ($n = 5$)	AG-M ($n = 5$)	AG-H ($n = 6$)	REC-1 ($n = 4$)	REC-2 ($n = 5$)
Elevation	767	710	641	676	754	776
(m)	(25)	(44)	(32)	(24)	(45)	(37)
Watershed area [1]	617.6^{a}	1403.2^{bc}	1842.5^{c}	1311.8^{abc}	667.0^{ab}	599.8^{a}
(ha)	(149.1)	(175.0)	(92.0)	(247.4)	(154.2)	(166.5)
Discharge	70	92	64	62	67	63
(L / s)	(4)	(4)	(8)	(10)	(9)	(6)
Specific conductance [2]	20.1^{a}	72.1^{c}	31.6^{ab}	38.0^{ab}	58.7^{bc}	52.9^{bc}
(µS / cm)	(2.8)	(9.0)	(4.8)	(4.0)	(10.9)	(10.0)
Alkalinity [3]	5.4^{a}	7.4^{ab}	13.0^{b}	13.7^{b}	11.5^{ab}	10.6^{ab}
(mg $CaCO_3$ / L)	(0.5)	(1.3)	(1.5)	(2.4)	(1.6)	(1.1)
DIN [2]	93^{a}	109^{a}	420^{ab}	643^{b}	287^{ab}	244^{a}
(µg / L)	(34)	(37)	(127)	(111)	(90)	(55)
PO_4-P	4	8	11	8	11	9
(µg / L)	(1)	(4)	(4)	(2)	(3)	(2)
Degree-days [1]	2543^{a}	2600^{ab}	3013^{c}	3158^{c}	2844^{bc}	2546^{ab}
	(62)	(109)	(88)	(117)	(88)	(49)
Chlorophyll *a* [2]	3.41^{ab}	3.85^{ab}	8.11^{b}	9.14^{b}	6.48^{b}	2.60^{a}
(mg / m^2)	(0.69)	(0.67)	(2.07)	(1.53)	(1.76)	(0.30)

[1] One-way ANOVA and sequential Bonferroni pair-wise comparisons, $P < 0.05$

[2] Repeated-measures ANOVA and sequential Bonferroni pair-wise comparisons, $P < 0.05$

[3] Differences based on ANOVA on Ranks and Dunn's pair-wise comparisons, $P < 0.05$

Table 4. Regression coefficients (r^2) from the most significant regression ($n = 30$ streams, $P < 0.05$) between macroinvertebrate metrics and historic (1950) or contemporary (1993) forest cover at each spatial scale (WS is whole watershed upstream and laterally; RIP is 50 m on both sides of the stream; 2km is 2 km upstream of sampling site; 1km is 1 km upstream of sampling site). Slope indicates direction of relationship. NS = not significant.

Metric	Forest cover variable	r^2	P	Slope
Total density	WS-1993	0.207	0.012	-
Richness	NS	--	--	
Simpson index (1/D)	RIP-1993	0.451	< 0.001	+
Shannon index (H')	RIP-1993	0.467	< 0.001	+
Evenness (H'/Hmax)	RIP-1993	0.544	< 0.001	+
% Filterers	NS	--	--	
% Gatherers	RIP-1993	0.583	< 0.001	-
% Predators	NS	--	--	
% Scrapers	RIP-1993	0.260	0.004	+
% Shredders	RIP-2km-1950	0.537	< 0.001	+
Scrapers/Shredders	RIP-1993	0.351	< 0.001	-
EPT Taxa	RIP-1993	0.195	0.014	+
% EPT	RIP-1993	0.720	< 0.001	+
% C + O	RIP-1993	0.645	< 0.001	-
% 5 dominant	RIP-1993	0.511	< 0.001	-
NCBI	RIP-1993	0.740	< 0.001	-

Table 5. Results of stepwise multiple regressions between macroinvertebrate metrics and physical and chemical parameters measured at each site (*n* = 30 streams). NS = not significant.

Metric	Independent variables	Model r^2	Model *P*
Total density	Chlorophyll *a*	0.175	0.021
Richness	NS	--	--
Simpson index (1/D)	Chlorophyll *a*, % inorganic seston	0.370	0.002
Shannon index (H')	Chlorophyll *a*	0.323	0.001
Evenness (H'/Hmax)	Chlorophyll *a*	0.417	< 0.001
% Filterers	% fine substrate, % inorganic seston	0.270	0.014
% Gatherers	Chlorophyll *a*	0.421	< 0.001
% Predators	% inorganic seston	0.138	0.044
% Scrapers	Degree days	0.169	0.024
% Shredders	Degree days, RHAP, % fines	0.628	< 0.001
Scrapers/Shredders	Chlorophyll *a*	0.338	< 0.001
EPT Taxa	NS	---	---
% EPT	Chlorophyll *a*, Degree days, PO_4-P	0.729	< 0.001
% C + O	Chlorophyll *a*, Degree days, TSS	0.681	< 0.001
% 5 dominant	Chlorophyll *a*	0.336	<0.001
NCBI	Chlorophyll *a*, Degree days, TSS	0.720	< 0.001

Table 6. Macroinvertebrate taxa strongly ($r \geq 0.4$ or ≤ -0.4, $n = 30$ streams) correlated with axis scores from non-metric multidimensional scaling ordination. Taxa are listed in descending order of correlation strength with positively correlated taxa at the top of the table. Taxa listed in bold are strongly correlated with both NMS axes.

Correlates with axis 1		Correlates with axis 2	
Taxon	*r*	Taxon	*r*
Orthocladius	0.703	***Orthocladius***	0.645
Oligochaeta	0.563	**Oligochaeta**	0.555
Nematoda	0.454	*Nigronia*	0.522
Cryptochironomus	0.414	*Cheumatopsyche*	0.511
		Cryptochironomus	0.492
		Polypedilum	0.491
		Nematoda	0.478
		Chironomus	0.465
		Psephenus	0.409
		Oecetis	0.406
Amphinemura	-0.609	***Epeorus***	-0.665
Cinygmula	-0.575	*Acentrella*	-0.585
Epeorus	-0.465	*Oulimnius*	-0.575
Sweltsa	-0.424	*Diplectrona*	-0.560
Tallaperla	-0.405	*Prosimulium*	-0.507
		Dicranota	-0.456
		Drunella	-0.447
		Pteronarcys	-0.444
		Baetis	-0.430
		Cambarus	-0.416
		Cinygmula	-0.403
		Leuctra	-0.400

Figure Captions

Figure 1. Map showing study sites in relation to the area of the southern Appalachian portion of the Blue Ridge physiographic province (inset, gray ellipse). Study sites are categorized according to historical and current forest cover at different spatial scales (● FOR, ■ AG-L, ○ AG-M, Δ AG-H, □ REC-1, ▲ REC-2).

Figure 2. Principle component ordination of sites using historical (1950) and current (1993) land cover (% forest) within several spatial scales (whole watershed, 100-m riparian zone, 100-m riparian zone 1 and 2 km upstream of sampling site). These first two principle components explained 96.9% of the total variance in forest cover among sites (92.1% by axis 1, 4.8% by axis 2). Symbols that are circled indicate sites that were originally in different categories (open circle was originally categorized as REC-1 but was changed to AG-M; open triangle was originally categorized as AG-M but was changed to AG-H).

Figure 3. Total suspended solids (A) and % inorganic seston (B) based on bimonthly grab samples taken at seasonal base flow. Bars are grand means for each forest cover category + 1SE. Forest cover of sites in "extant" categories has remained relatively constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Bars with shared letters are not significantly different ($P < 0.05$).

Figure 4. Results from measurement of physical habitat properties of each site (A-median particle size, B-% fine substrate, C-cobble:fine substrate ratio, D-EPA Rapid Habitat Assessment Protocol score). Forest cover of sites in "extant" categories has remained relatively constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Bars are means for each forest cover category + 1SE, and bars with shared letters are not significantly different ($P < 0.05$).

Figure 5. Density (A) and diversity (B-richness, C-Simpson's index, D-Shannon index, E-Shannon evenness) metrics of benthic macroinvertebrates based on forest cover category (means + 1SE). Forest cover of sites in "extant" categories has remained relatively constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Means were not significantly different among forest cover categories for any variable.

Figure 6. Proportion of benthic macroinvertebrates in each functional feeding group (A-E) and the ratio of scrapers to shredders (F) in streams based on forest cover category (means + 1SE). Forest cover of sites in "extant" categories has remained relatively constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Bars with shared letters are not significantly different ($P < 0.05$).

Figure 7. Pollution tolerance metrics (A-EPT richness, B-% EPT, C-% Chironomidae + Oligochaeta, D-% 5 dominant, E-NCBI) based on benthic macroinvertebrate taxonomic composition in streams of different forest cover categories (means + 1SE). Forest cover of sites in "extant" categories has remained relatively constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Bars with shared letters are not significantly different ($P < 0.05$).

Figure 8. Non-metric multidimensional scaling (NMS) ordination of sites based on densities of macroinvertebrate taxa. This ordination plots sites on the first two axis scores from a 3-axis NMS with stress = 10.151. Sites are labeled with forest cover categories. Table 6 shows taxa densities most strongly correlated with each axis.

Figure 9. Diagram of sites separated and grouped using densities of macroinvertebrate taxa by two-way indicator species analysis (TWINSPAN). Each split shows taxa driving the separation or grouping of sites along with the eigenvalue (λ). Dots represent intermediate groups comprised of all the sites below them on the tree. Sites in boxes were not separated further using TWINSPAN parameters established for the test.

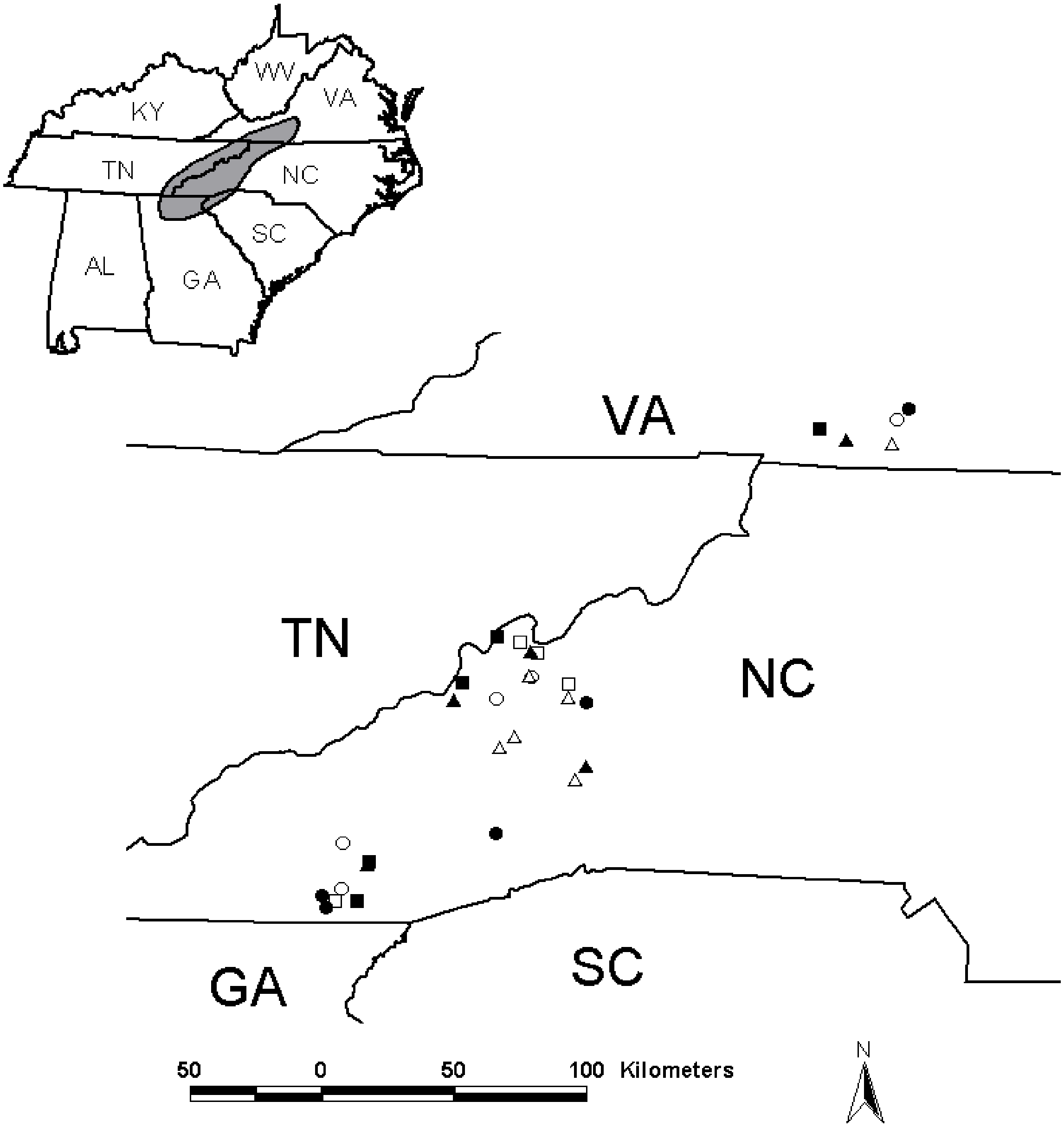
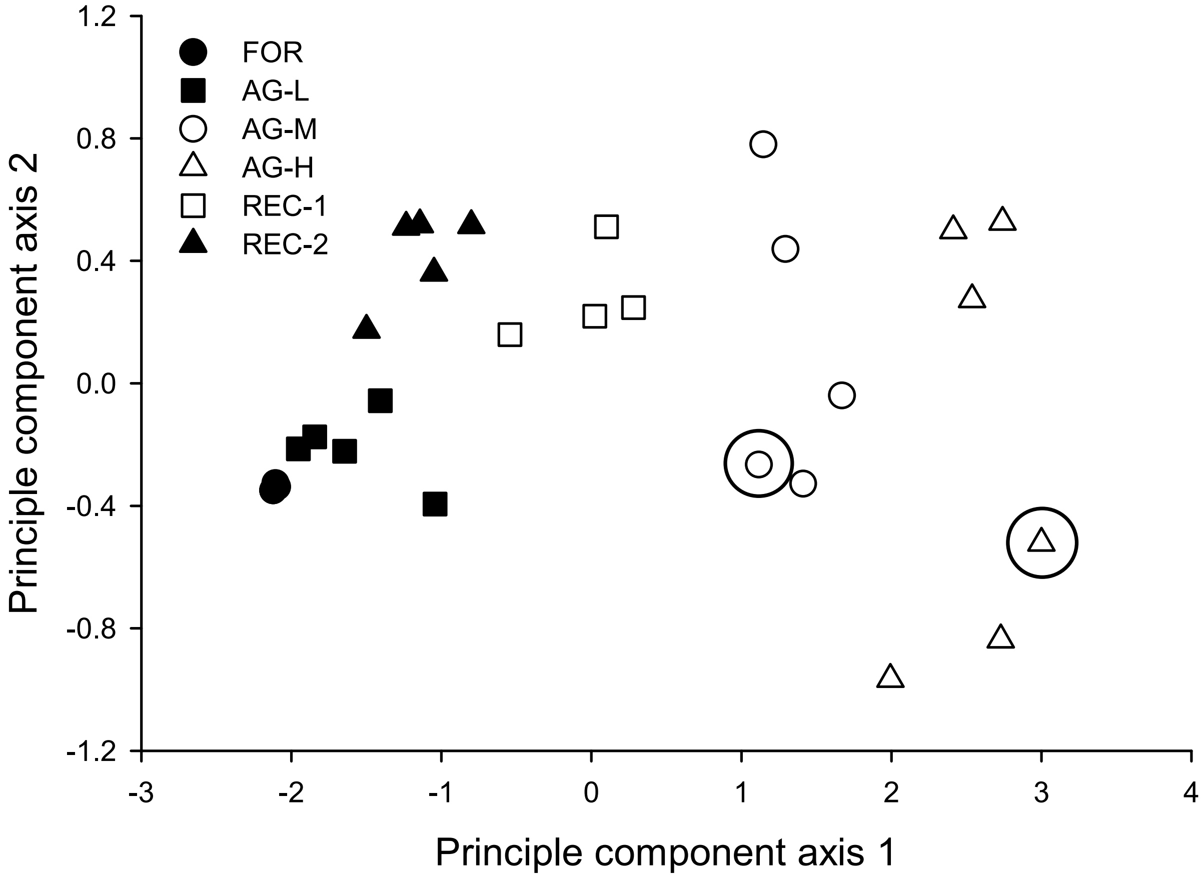


FIGURE 1



1.2
0.8
0.4
0.0
-0.4
-0.8
-1.2
-3
-2
-1
0
1
2
3
4
Principle component axis 2
Principle component axis 1
● FOR
■ AG-L
○ AG-M
△ AG-H
□ REC-1
▲ REC-2

FIGURE 2

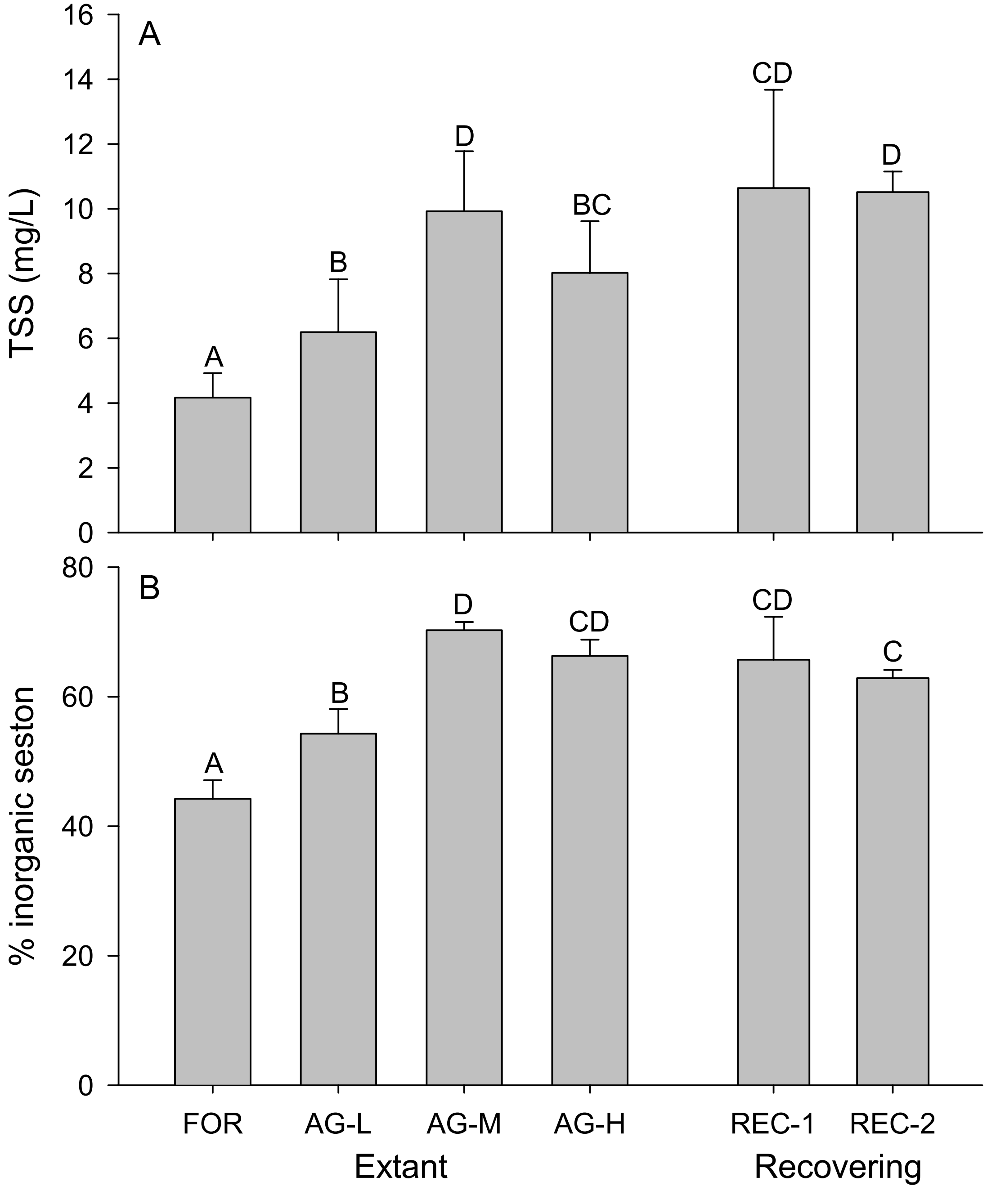

A
TSS (mg/L)
0
2
4
6
8
10
12
14
16
A
B
D
BC
CD
D
B
% inorganic seston
0
20
40
60
80
A
B
D
CD
CD
C
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 3

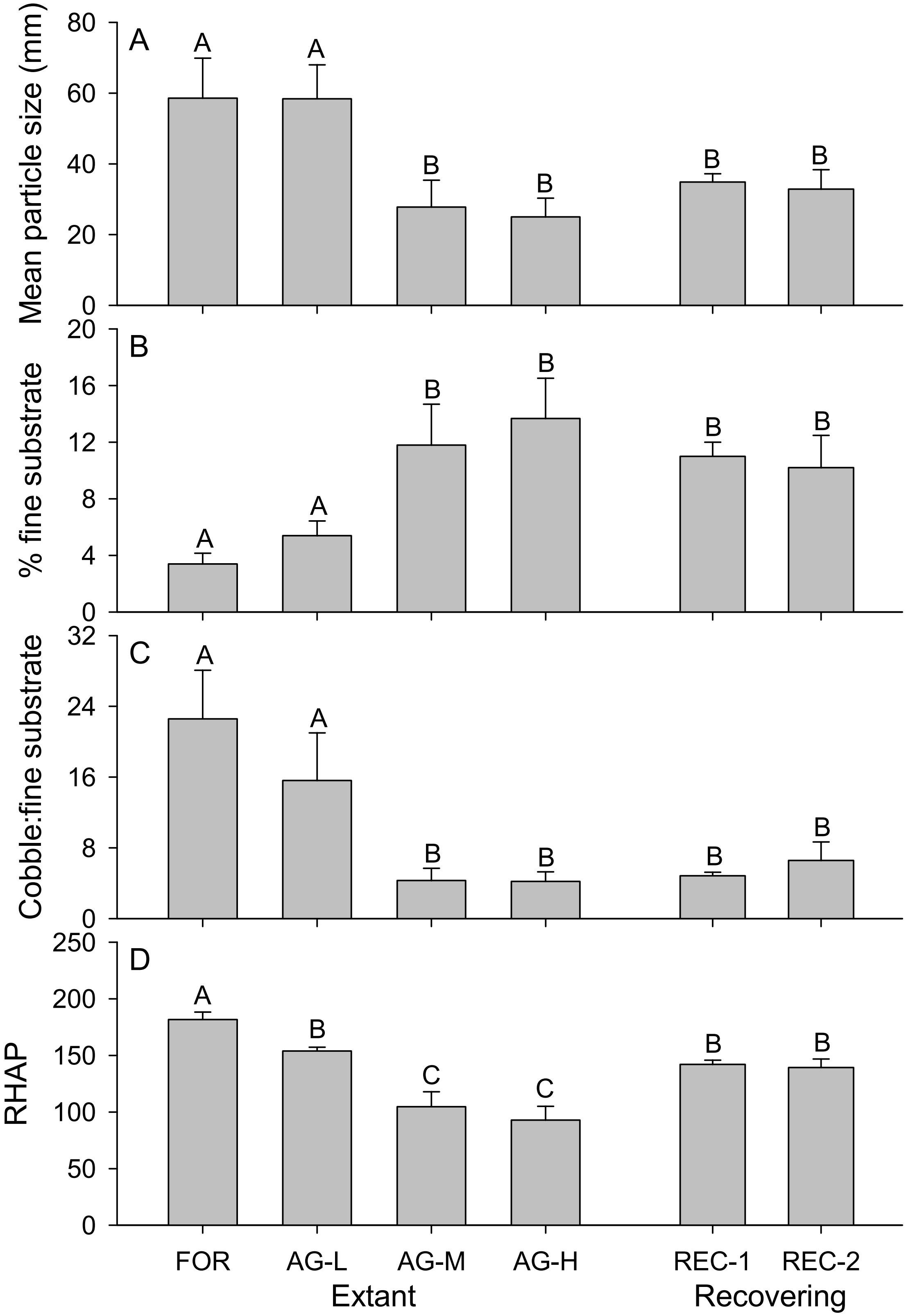

A
Mean particle size (mm)
0
20
40
60
80
A
A
B
B
B
B
B
% fine substrate
0
4
8
12
16
20
A
A
B
B
B
B
C
Cobble:fine substrate
0
8
16
24
32
A
A
B
B
B
B
D
RHAP
0
50
100
150
200
250
A
B
C
C
B
B
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 4

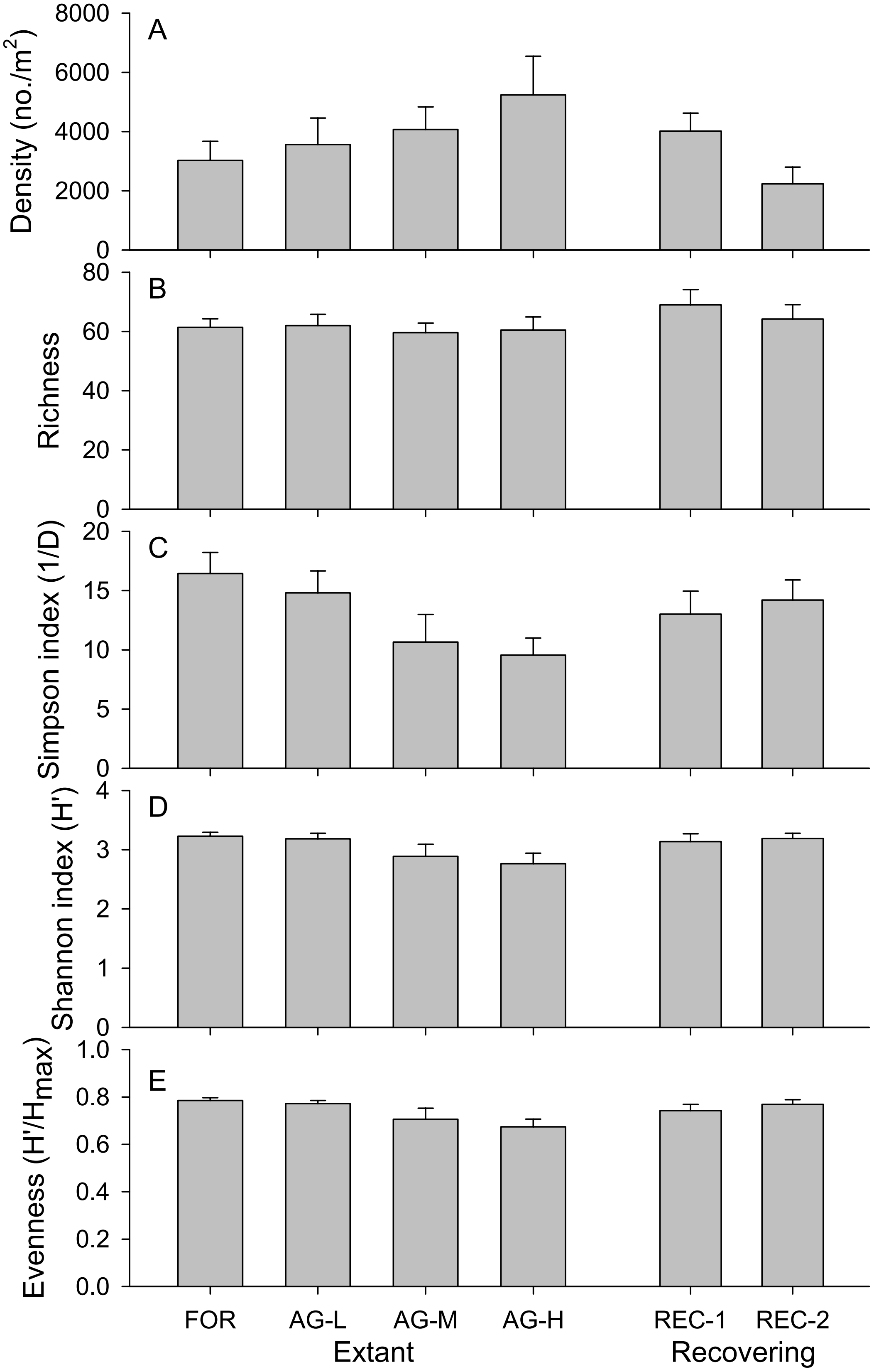

A
B
C
D
E
Density (no./m^2)
8000
6000
4000
2000
0
Richness
80
60
40
20
0
Simpson index (1/D)
20
15
10
5
0
Shannon index (H')
4
3
2
1
0
Evenness (H'/H$_{max}$)
1.0
0.8
0.6
0.4
0.2
0.0
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 5

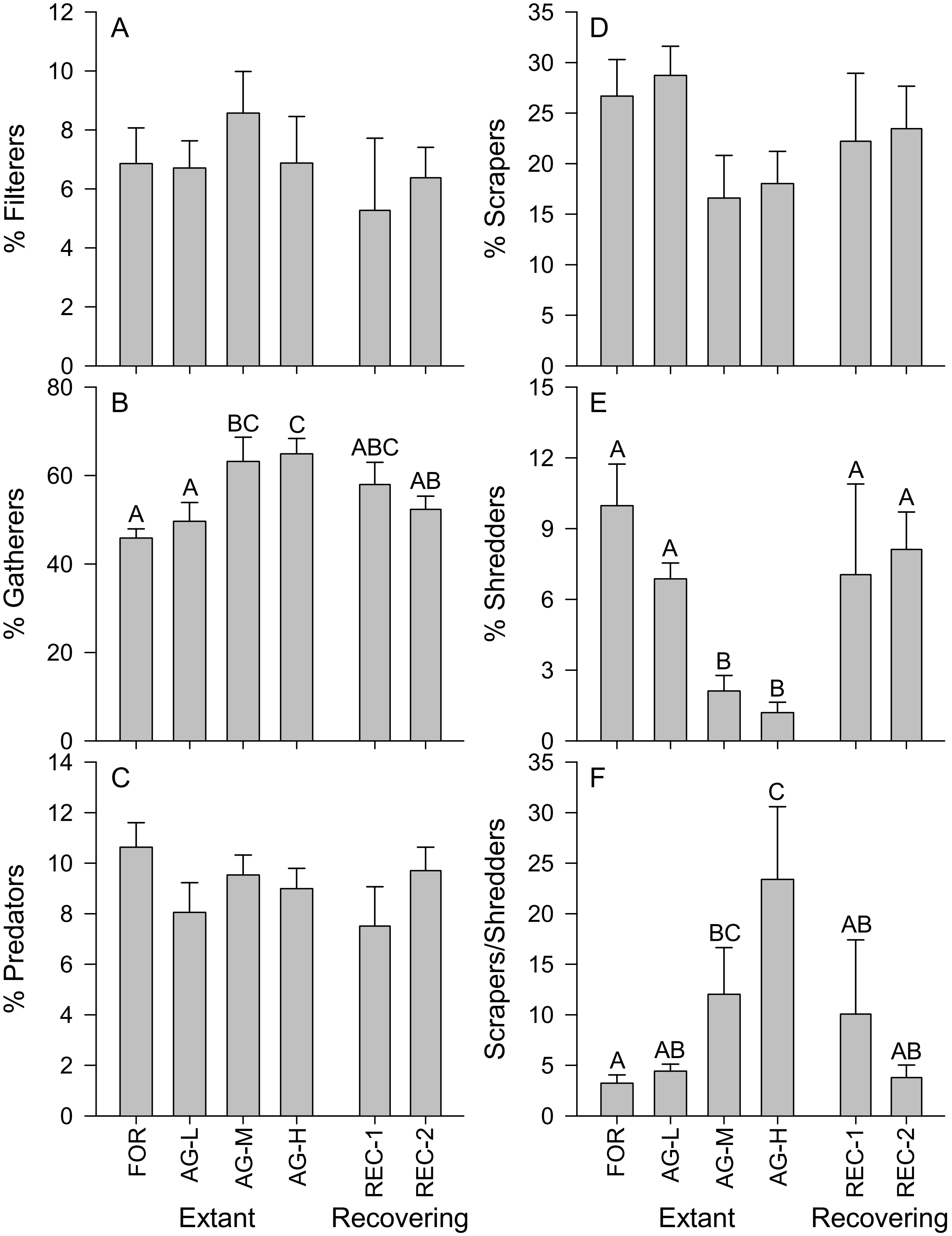
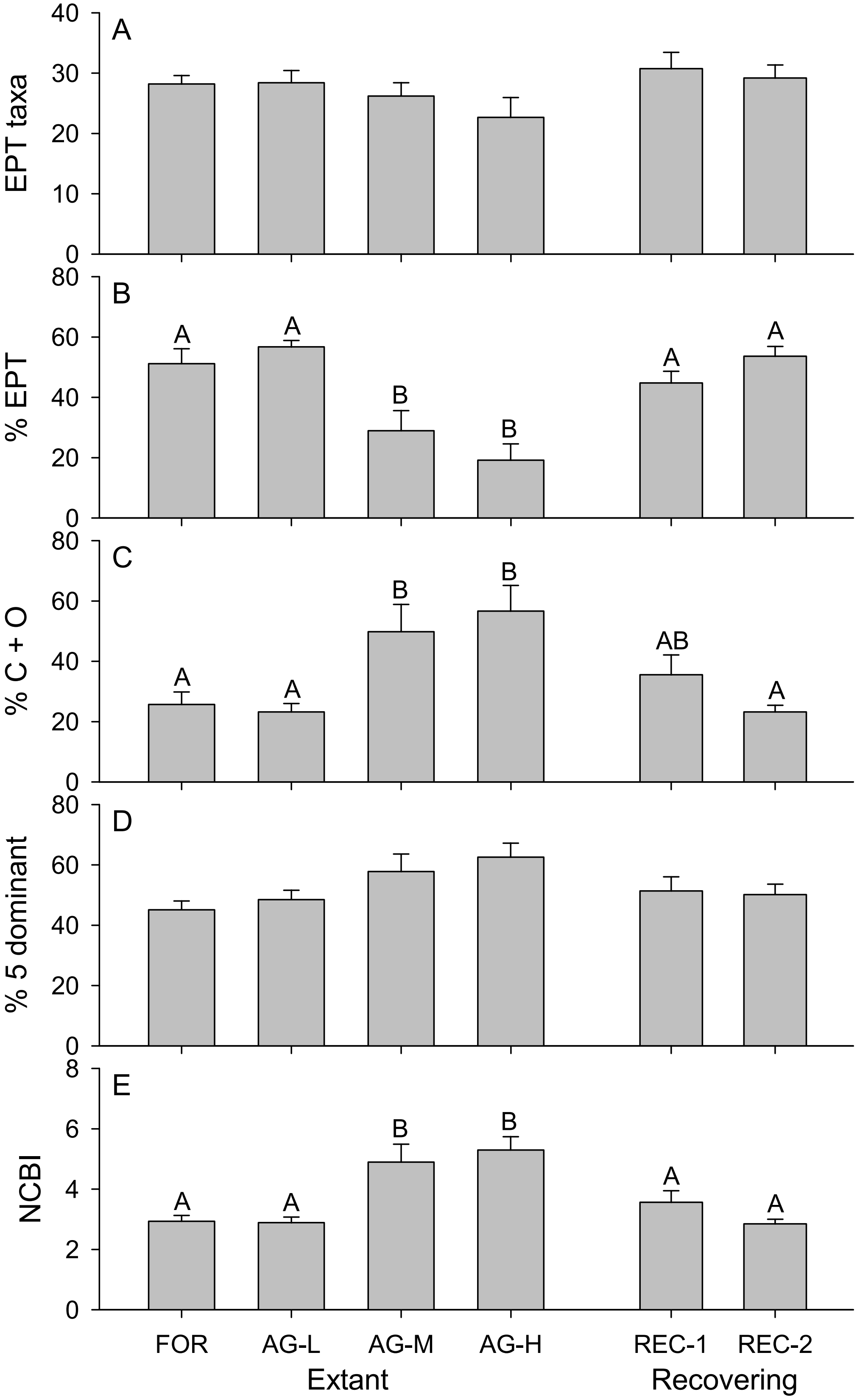
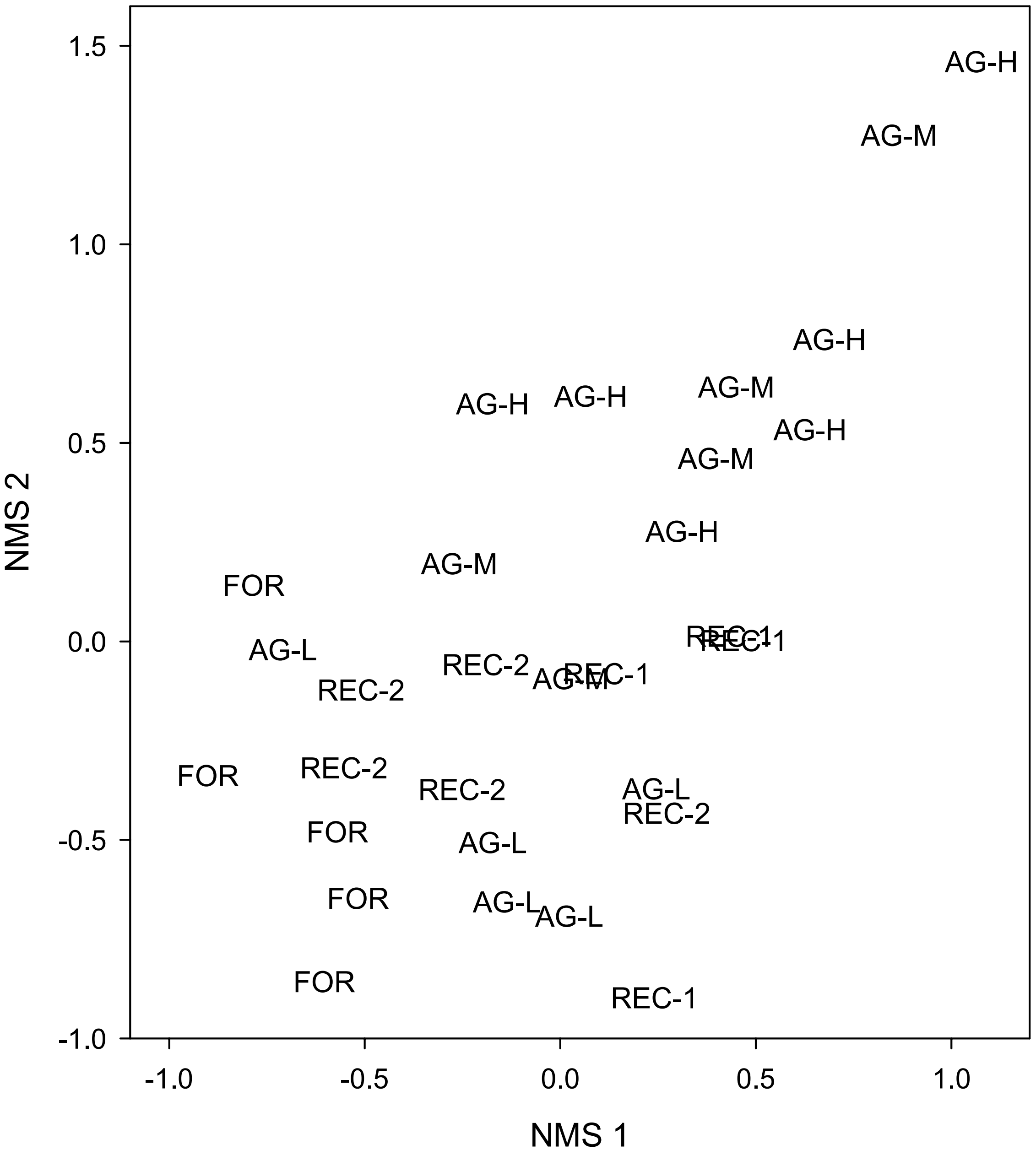

A
% Filterers
0
2
4
6
8
10
12
B
% Gatherers
0
20
40
60
80
A
A
BC
C
ABC
AB
C
% Predators
0
2
4
6
8
10
12
14
D
% Scrapers
0
5
10
15
20
25
30
35
E
% Shredders
0
3
6
9
12
15
A
A
B
B
A
A
F
Scrapers/Shredders
0
5
10
15
20
25
30
35
A
AB
BC
C
AB
AB
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 6



A
EPT taxa
0
10
20
30
40
B
% EPT
0
20
40
60
80
A
A
B
B
A
A
C
% C + O
0
20
40
60
80
A
A
B
B
AB
A
D
% 5 dominant
0
20
40
60
80
E
NCBI
0
2
4
6
8
A
A
B
B
A
A
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 7



AG-H
AG-M
AG-H
AG-H
AG-H
AG-M
AG-H
AG-M
AG-H
FOR
AG-M
REC-1
REC-1
AG-L
REC-2
AG-M
REC-1
REC-2
FOR
REC-2
REC-2
AG-L
REC-2
FOR
AG-L
FOR
AG-L
AG-L
FOR
REC-1
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0
NMS 2
NMS 1

FIGURE 8

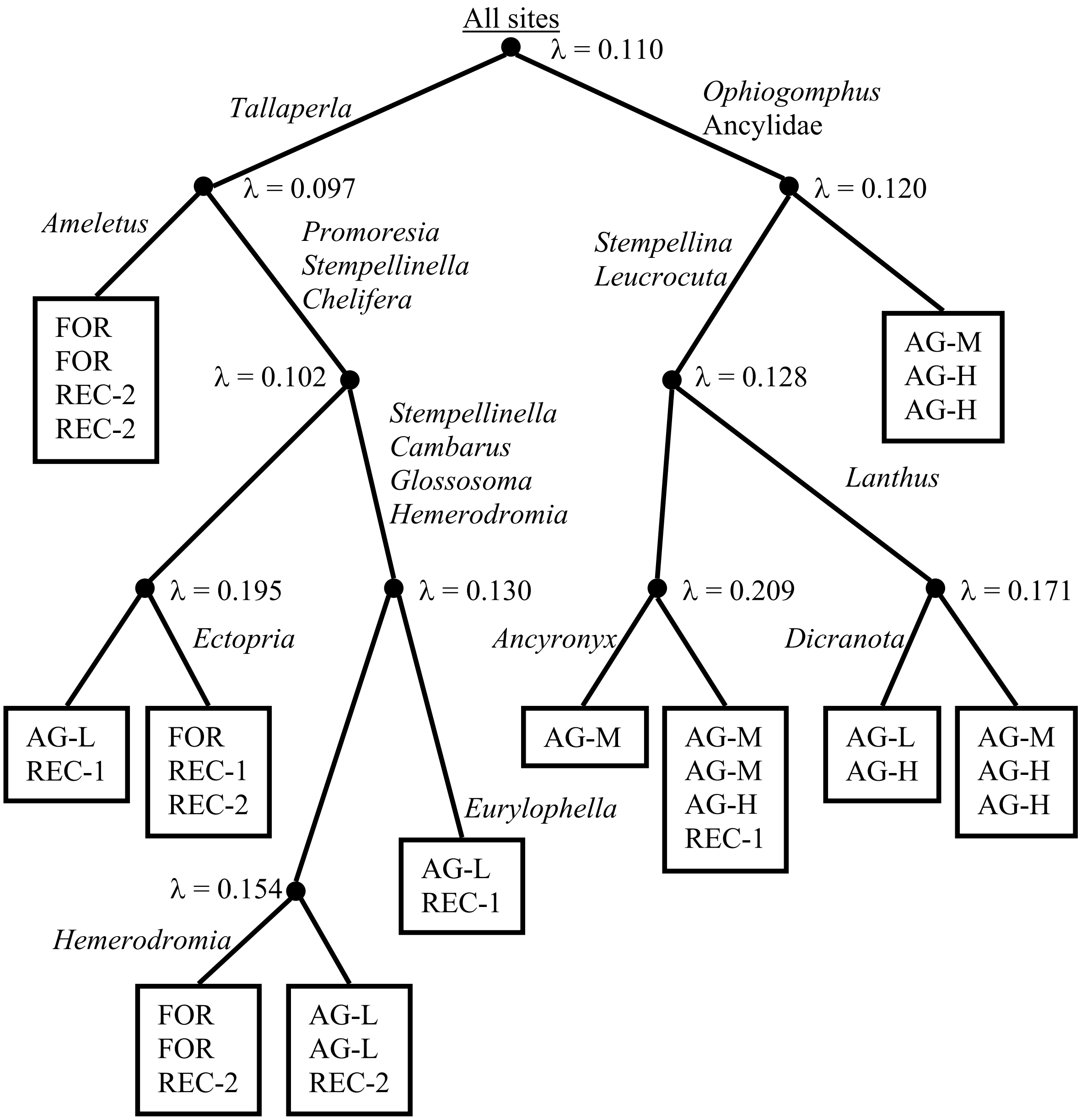

All sites
λ = 0.110
Tallaperla
Ophiogomphus
Ancylidae
λ = 0.097
λ = 0.120
Ameletus
Promoresia
Stempellinella
Chelifera
Stempellina
Leucrocuta
FOR
FOR
REC-2
REC-2
AG-M
AG-H
AG-H
λ = 0.102
λ = 0.128
Stempellinella
Cambarus
Glossosoma
Hemerodromia
Lanthus
λ = 0.195
λ = 0.130
λ = 0.209
λ = 0.171
Ectopria
Ancyronyx
Dicranota
AG-L
REC-1
FOR
REC-1
REC-2
AG-M
AG-M
AG-M
AG-H
REC-1
AG-L
AG-H
AG-M
AG-H
AG-H
Eurylophella
λ = 0.154
AG-L
REC-1
Hemerodromia
FOR
FOR
REC-2
AG-L
AG-L
REC-2

FIGURE 9

CHAPTER 3

Recovery of stream ecosystem metabolism from historical agriculture

Abstract

Primary production is limited in most forested streams by extremely low light and nutrients due to terrestrial vegetation shading streams and retaining nutrients. However, agricultural land-use practices have caused increased light, nutrients, and sediment to reach many streams. These agricultural influences have led to increased algal growth, higher primary production, and changes in stream ecosystem energetics. In the southern Appalachians, agricultural activity has influenced streams for centuries, but recent socioeconomic trends in the region have led to extensive reforestation of agricultural land. As watersheds reforest, stream ecosystem metabolism may recover from historical agricultural influences, particularly as streams become shaded by terrestrial vegetation. I determined historical (1950) and current (1993) forested land cover in 2nd and 3rd order watersheds in 4 counties of the southern Appalachians using a geographic information system and used this information to categorize streams based on percent forested land cover in their watersheds and riparian zones. Categories included 4 levels of agriculture with no change in % forest over the past 50 years and 2 levels of reforestation from agriculture due to land abandonment. I then selected 3 streams from each category to determine the effect of current and historical agriculture on stream metabolism and to explore the influence of agriculture on factors potentially controlling stream metabolism. I measured primary production (GPP) and respiration (R_{24}) in 18 streams where the watersheds have experienced different amounts of historical and current agricultural activity. I also calculated net metabolism (NEP and P/R) to compare ecosystem energetics among land-use types. I estimated metabolism using a two-station diurnal oxygen change technique and gas releases to determine the reaeration rate. In addition, I measured nutrient concentrations (DIN and PO_4-P), light (PAR), temperature (degree-days), seston concentrations (TSS), and algae (chl-*a* and AFDM) to determine if these factors were affected by current or historical agriculture and were correlated with metabolism. Agricultural streams had significantly higher DIN, PO_4-P, PAR, degree-days, TSS, and algae than did forested streams. Nutrient concentrations and TSS were also higher in reforested streams than in forested streams despite reforestation from agriculture, but PAR and degree-days were similar to values for forested streams. Chl-*a* and algal AFDM were also similar in reforested and forested streams, most likely because light became limiting during reforestation from agriculture. GPP varied from < 0.1 g O_2 m^{-2} d^{-1} in forested streams to 1.0 g O_2 m^{-2} d^{-1} in agricultural streams. Reforested streams had GPP similar to forested streams suggesting that shading due to reforestation may reduce GPP to pre-agricultural levels. R_{24} was much higher (4-20 times) than GPP in all stream types, resulting in highly negative NEP. Although NEP was always negative, streams with current agriculture had less negative NEP than forested and reforested streams. Agriculture could cause small shifts toward autotrophy in these streams, but these shifts were not enough to compensate for total ecosystem respiration. The extremely low NEP and P/R consistently < 1 could be due to allochthonous organic matter from remnant forested land (up to 75% forest) in agricultural watersheds. GPP and P/R were strongly correlated with PAR, degree-days, and algae suggesting that light limited primary production in the streams studied. Nutrients and TSS were positively correlated with R_{24}, which suggests that nutrients and TSS may stimulate respiration. Agricultural influences on stream metabolism seem to recover following watershed reforestation. This may lend hope to restoration efforts focused on reducing agricultural influence by maintaining streamside forests.

Keywords: primary production, respiration, light, nutrients, algae, agriculture, southern Appalachians

Introduction

Streams are intimately linked to their watersheds through fluxes of chemistry, hydrology, and terrestrial vegetation (Hynes 1975). Streamside vegetation reduces light inputs and supplies organic matter to streams (Sweeney 1993). In-stream metabolism is affected by the availability of light and nutrients because of their influence on primary production and respiration associated with detritus decomposition. As a result, metabolism in forested streams is generally heterotrophic (i.e., dominated by respiration and limited primary production; Odum 1956, Fisher and Likens 1973, Webster et al. 1995, Mulholland et al. 2001). Humans have dramatically altered watersheds in forested biomes by removing terrestrial vegetation for agriculture and other land uses resulting in higher light inputs, increased temperatures, and reduced allochthonous carbon supply to stream ecosystems (e.g., Webster et al. 1983). In addition, agriculture causes increased nutrient and sediment inputs (Karr and Schlosser 1978, Lowrance et al. 1985, Waters 1995). The combination of higher light and nutrient availability may lead to high primary production in agricultural streams with a subsequent autotrophic shift in net metabolism (Brown and King 1987, Wiley et al. 1990, Young and Huryn 1999, Bunn et al. 1999). However, suspended sediment in agricultural streams may limit primary production by reducing the amount of light reaching the stream bottom (Young and Huryn 1996) or scouring algae from the surfaces of rocks (Horner et al. 1990). In addition, deposited sediment may provide inhospitable substrate for attached algae (Waters 1995).

Streams are generally thought of as resilient ecosystems (i.e., they recover quickly following disturbance; Webster and Patten 1979). However, watershed disturbances, such as logging or agriculture, require that terrestrial vegetation recover prior to recovery of stream conditions (Webster and Patten 1979, Gurtz et al. 1980, Valett et al. 2002). Changes in streams as a result of watershed disturbance can be extremely long lasting, even after terrestrial areas re-vegetate. Examples from logged watersheds show little recovery of water chemistry, wood input, and physical structure over decades, while other ecosystem properties (e.g., light inputs, quantity of allochthonous input) recover within a few years (Webster et al. 1992). Agriculture may have a longer influence on streams because the disturbance occurs over decades or centuries rather than over a much shorter, discrete time frame. Thus, conversion of forest to agricultural land use acts as a “press” disturbance (*sensu* Bender et al. 1984) to the streams that drain the disturbed watersheds. Furthermore, reforestation of agricultural land is slowed compared to post-logging recover due to soil disturbance (e.g., compaction, erosion) and limited colonization by trees (Myster and Pickett 1994, Stover and Marks 1998, Honnay et al. 1999). In comparison, logging can be thought of as a pulse disturbance (Bender et al. 1984), at least with respect to the forest. Research has already shown that old-field succession takes much longer than reforestation from logging (Foster 1992), so it is reasonable to predict that the influences of agriculture will persist in streams longer than logging’s effects.

In the southern Appalachians, large amounts of historically agricultural land are reforesting as a result of socioeconomic changes in the region (Otto 1983, Clark 1984, Wear and Bolstad 1998). These changes have provided the opportunity to study stream ecosystems as their watersheds reforest in order to determine the nature of stream recovery from agriculture during natural reforestation of their watersheds. Following logging, reforestation reestablishes shading and allochthonous inputs (Webster et al. 1983). However, nutrients likely remain elevated (Vitousek and Reiners 1975), and quality of allochthonous input is altered due to terrestrial tree species composition (Webster et al. 1983). The legacy of agriculture affects biological community structure in streams (Harding et al. 1998), and these lasting agricultural influences may influence ecosystem metabolism as well.

In this study, the effects of current and historical agriculture on stream ecosystem metabolism were assessed using a comparative approach. Objectives were to compare rates of GPP and respiration among streams with different land-use patterns, determine how physical and chemical factors (e.g., nutrients, light, sediment) are most related to land use, and assess how they may influence metabolism. To address recovery from agricultural influences, metabolism in streams reforested from historical agriculture were compared with rates in forested streams to determine the influence of watershed reforestation.

Methods

Study sites

Study streams (2nd and 3rd order) were located in the southern Appalachian Mountains of western North Carolina and southwestern Virginia, USA (Figure 1). Headwater streams in the Blue Ridge physiographic province of the southern Appalachians are typically slightly acidic and have low conductivity and dissolved ion concentration reflecting granitic and micaceous parent lithology (Simmons and Heath 1979). Forests in the region are maturing second-growth (logged ~ 75-100 years ago) and are dominated by oak (*Quercus* spp.), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*) with an understory of *Rhododendron*, mountain laurel (*Kalmia latifolia*), and dogwood (*Cornus florida*). Agricultural activity across the region is mainly cattle pasture with isolated row crop (primarily tobacco and corn). Agriculture occurs primarily in bottomland along streams, but many farmers have upland pastures. Riparian zones along agricultural streams frequently lack woody vegetation entirely or are vegetated with a narrow strip of trees, particularly black walnut (*Juglans nigra*), river sycamore (*Platanus occidentalis*), black locust (*Robinia pseudoacacia*), red maple, and oak (Neatrour et al. 2004).

Site selection and categorization

Streams were selected to represent six land-use categories (3 streams per category) based on the current and historical extent of agriculture within their basins. I created a database of past land cover (% forest in 1950) and more recent land cover (1993) for watersheds in the southern Appalachians using a geographic information system (GIS). Land cover data and watershed boundaries were obtained from Coweeta Hydrologic Laboratory for 4 counties: Grayson County, Virginia; Buncombe, Macon, and Madison Counties, North Carolina. Land cover plots of 100 m width delineated riparian corridors for streams in each watershed with stream vectors centered in the plot (i.e., 50 m to each side of the stream) for the entire stream length. Forest cover was determined for each watershed and associated riparian corridor by overlaying these spatial zones on a land cover map from each year and quantifying % forest cover.

Site eligibility was restricted to watersheds with areas between 500 and 3000 ha and stream outlet elevations between 600 and 1000 m to help standardize for confounding factors (Resh et al. 1988). I categorized these 500 watersheds into 6 groups based on the historical and current amount of forest in their watersheds. Four categories were chosen to represent a gradient of extant agriculture with no change over time (FOR >98 % forest; AG-L 90-95 % forest; AG-M 70-80 % forest; AG-H < 60 % forest). Two categories were used to represent different stages of watershed recovery from agriculture by reforestation (REC-1 < 60 % forest in 1950 to > 80 % forest in 1993; REC-2 < 75 % forest in 1950 to > 90 % forest in 1993). Streams of the REC-1 category have undergone considerable reforestation (> 20 %) over the past 50 years, but they have less current forest cover than REC-2 streams. Forest cover in riparian corridors was used to verify category assignment, and streams with riparian forest cover that was dramatically different than watershed category designations were not considered for our study.

The study streams were selected from the pool of candidates by considering access to sampling locations, land owner cooperation, distribution across the region, and ground-truthing of land use category assignments. For each chosen stream, final catchment characterization was calculated for portions of the watershed up gradient of the specified study site. These spatial zones were whole watershed, 100-m riparian corridor, and 100-m riparian corridors 1 and 2 km upstream of each sampling site.

Physical and chemical measurements

Stream monitoring included measuring physical and chemical characteristics of the study sites on a bi-monthly basis from November 2000 to August 2001 during baseflow conditions. I estimated discharge from velocity measured with an electronic flow meter (Marsh-McBirney Flo-Mate, Marsh-McBirney, Incorporated, Frederick, Maryland) and cross-sectional area of the stream channel. Temperature was monitored continuously at 6-hour intervals throughout the study period using data loggers (HOBO Temp, Onset Corporation, Bourne, Massachusetts). For each site and data, I collected samples to characterize suspended sediment, dissolved nutrients, and epilithic chlorophyll. Triplicate 1-L water samples for determination of suspended solids were filtered through pre-ashed and weighed glass fiber filters (Gelman Type AE, 1-µm nominal pore size). Filters were dried to constant weight, weighed, and ashed (550°C for 1 hour) to quantify organic (combustible) and inorganic (ash) suspended material. Three other samples were collected, filtered in the field using pre-soaked membrane filters (Whatman nylon, 0.45-µm pore size), and frozen before analysis. Samples were analyzed for nitrate-nitrogen (NO_3-N) and ortho-phosphate (PO_4-P) using a Dionex DX500 Ion Chromatograph (Dionex Corporation, Sunnydale, California) and ammonium-nitrogen (NH_4-N) using the OPA fluorometric method (Holmes et al. 1999). Total dissolved inorganic nitrogen (DIN) was determined as the sum of NO_3-N and NH_4-N. Specific conductance was measured bi-monthly using a field probe (YSI Model 30/50 conductivity meter). Alkalinity was measured once at the beginning of the study by acid titration (APHA 1998).

Algae

Epilithic algal biomass was determined on rocks collected in April, June, and August 2001. On each date, 5 rocks from each stream were placed in a dark cooler on ice for transport to the lab where the upper surface of each rock was scrubbed with a wire brush in water to remove epilithon. Scrubbed material was filtered onto pre-ashed and weighed glass-fiber filters (Gelman type A/E, 1 µm pore size). Each filter was cut in half for separate analysis of photosynthetic pigments (chlorophyll *a*) and ash free dry mass (AFDM). Chlorophyll *a* (chl *a*) was measured using a procedure similar to that outlined by Steinman and Lamberti (1996). Chl *a* from each rock was extracted in 90% basic acetone for 20 hours. After extraction, absorbances at 750, 664, and 665 nm were measured before and after acidification with 1N HCl on a Shimadzu UV-1601 Spectrophotometer (Shimadzu Corporation, Kyoto, Japan). The other portion of the filter was used for determination of epilithic organic standing stock. Filters were dried to constant weight, ashed, re-wetted, re-dried to constant weight, and re-weighed to determine epilithon AFDM. Area scrubbed on each rock was determined by wrapping the upper surface of each rock in aluminum foil, weighing the foil, and using a weight-area conversion.

Chl *a* and AFDM were multiplied by 2 to account for filter splitting and divided by scrubbed rock surface area to represent chl *a* and epilithic biomass per unit area.

Metabolism

During summer 2001, whole streams metabolism was measured using the open system, two-station diurnal oxygen change method (Odum 1956, Marzolf et al. 1994). Dissolved oxygen concentration and temperature were recorded at 5-min intervals over a 24-hour period at two stations in each stream using Hydrolab sondes (Hydrolab Minisonde 4a, Hydrolab-Hach Company, Loveland, Colorado). Oxygen probes were calibrated in water-saturated air (100% dissolved oxygen) at deployment elevation. To correct for differences in calibration and probe drift, probes were placed together for 30-60 min at the beginning and end of each 24-hour measurement period. Recording stations were 200 m apart in each stream. Sondes were secured to the stream bottom in well-mixed stream segments with the probes pointing into the current at approximately half-depth.

Reach travel time (20-50 min.) was determined by releasing a slug of NaCl upstream of the study reach, recording conductivity readings as it passed upstream and downstream stations, and calculating the time for the NaCl slug to pass through the reach. Water velocity through the reach was estimated by dividing reach distance by the travel time (t). Transects were established every 50 m in the study reach to estimate width and depth (at least 10 depth readings per transect). Discharge at upstream and downstream sites was then calculated as the product of water velocity and cross-sectional area.

The reaeration coefficient (K_2) was estimated using volatile gas-conservative tracer solute injections at each site. Background water samples were collected at 50-m intervals along the 200-m study reach. Velocity, width, and slope were used to determine the minimum stream length required for complete mixing of solutes (Kilpatrick et al. 1989). Volatile gas (sulfur hexafluoride, SF_6) and conservative tracer (Cl^- or Br^-) were simultaneously released at a location at least 1 mixing length upstream of the study reach. SF_6 was released at a constant rate in deep runs from 3 bubbling air-stones to maximize contact between gas and water. Cl^- or Br^- was released at constant rate using a fluid-metering pump (FMI, Inc., Syossett, New York) into a constrained riffle portion of stream to optimize mixing. Gas and tracer were both released for at least 3 times the reach travel time (t) to reach steady-state (plateau) solute concentrations (Genereux and Hemond 1992, Marzolf et al. 1994). Triplicate water samples (gas and tracer) were collected every 50 m along the study reach after the stream reached plateau. Gas samples were obtained by collecting 45 mL of stream water in a 60-mL syringe, adding 15 mL of atmospheric air (away from the sampling reach to avoid SF_6 contamination), and shaking for 10 min to equilibrate SF_6 in the headspace. The headspace was then injected into 15-mL vacuumed, air-sealed glass vials. SF_6 was quantified with an SRI-8610 Gas Chromatograph (SRI Instruments, Torrance, California) equipped with an electron-capture detector. Water samples for tracer analysis were placed on ice for transport to the lab where they were anyzed for Cl^- or Br^- using a Dionex DX-500 Ion Chromatograph equipped with an A514A column. I calculated K_2 for each stream using the method and equations of Wanninkhof et al. (1990) and Wanninkhof (1992). K_2 values were converted from ambient stream temperature to standard temperature (20ºC) for comparison among sites following Elmore and West (1961).

Change in dissolved oxygen (DO) over each 200-m study reach (ΔDO) was determined by subtracting the oxygen concentration of the downstream site at time t_0+t from the upstream site at time t_0. I used the average oxygen saturation deficit, K_2, and reach travel time to correct for the flux of oxygen due to reaeration (Marzolf et al. 1994, Young and Huryn 1998). The saturation deficit is the difference between measured oxygen values and equilibrium concentrations at stream temperature and ambient barometric pressure. Stream temperature was measured on the Hydrolab minisondes concurrently with DO while barometric pressure was measured continuously using a Vaisala pressure transmitter equipped with a Campbell data logger (Campbell Scientific, Incorporated, Logan, Utah). I also measured photosynthetically active radiation (PAR) continuously at the stream surface of each study site using a LI-COR quantum sensor (LI-COR Biosciences, Incorporated, Lincoln, Nebraska) on the Campbell data logger. Discharge measures at upstream and downstream ends of each study reach were nearly identical suggesting that the influence of inflowing water was negligible.

From the resulting reaeration-corrected ΔDO, I calculated gross primary production (GPP) and respiration (R) following Marzolf et al. (1994). GPP was calculated by integrating the reaeration-corrected ΔDO curve from dawn to dusk (times determined from PAR). Daytime R was estimated by assuming a linear change from R at dawn and dusk. From this curve, I estimated R_{24} by integrating the reaeration-corrected ΔDO from midnight to midnight. GPP and R were converted to area estimates by dividing by mean depth along the reach. I used GPP and R to calculate net ecosystem metabolism (NEP = GPP - R) and the ratio of GPP:R (P/R).

Statistical analysis

I used one-way ANOVA to compare differences in metabolic variables among categories with streams as replicates within categories. Physicochemistry, chl *a*, and epilithic AFDM were compared using repeated-measures (RM) ANOVA with land-use category as factors and streams as replicates. To explore factors controlling metabolism, I correlated metabolic parameters with physicochemistry, chl *a*, and epilithic AFDM using Pearson product moment correlation. All variables were tested for normality prior to analysis and were transformed if found to have non-normal distributions.

Results

In general, % forest was higher at broader spatial scales (watershed and riparian corridor) than at sub-corridor scales within land-use categories (Table 1). In addition, most land-use categories showed higher amounts of forested land cover at all spatial scales in 1993 than in 1950. However, reforestation was more extensive in stream basins of the two recovery stages (REC-1 and REC-2) than in the agricultural reference (AG) streams. AG streams adequately represented a gradient of agriculture from low (AG-L) to high (AG-H) at all spatial scales. Streams in both stages of recovery had similar amounts of forest in their watersheds, but streams in the later stage of recovery (REC-2) had more forest cover in their riparian zones than did REC-1 streams.

Elevation varied from 576 to 861 m and was generally lower in AG streams, although differences were not significant among land-use categories (Table 2). Watershed area was significantly higher for AG-M streams, and REC-2 streams had the smallest watershed areas (ANOVA: $P < 0.001$). However, discharge at the time of sampling did not vary significantly among categories. Specific conductance varied from 11.9 to 98.4 μS/cm among all streams and was highest in AG-L streams (ANOVA: $P = 0.011$). Alkalinity was slightly higher in AG-M, AG-H, and REC-1 sites (ANOVA: $P = 0.031$), but mean values ranged only 6.4 mg $CaCO_3$/L from 5.3 to 11.7 mg $CaCO_3$/L (Table 2).

Nutrient concentrations, light, and cumulative degree-days were significantly higher in streams draining watersheds with more agricultural land use (Figure 2). Average DIN among categories varied from 75 μg / L in AG-L to 582 μg / L in AG-H. DIN values were lowest in FOR streams and highest in AG-H streams; REC streams fell between these values and were significantly higher than FOR streams. PO_4-P was below or near the analytical detection limit in FOR and AG-L streams (mean < 5 μg / L, detection limit 4 μg / L). All other categories had higher PO_4-P concentrations than FOR and AG-L. PAR varied from a mean of 0.74 mol m^{-2} d^{-1} at FOR sites to 26.16 mol m^{-2} d^{-1} at AG-H sites (Figure 2). AG-M and AG-H had significantly higher PAR than all other categories, and AG-L and REC-2 had higher PAR than FOR sties. Cumulative degree-days were higher in AG-M and AG-H streams than in FOR, AG-L, and REC-2 streams (Figure 2).

Suspended solids also differed among land cover categories (Figure 3). TSS was lowest in FOR and AG-L streams and was highest in AG-M and REC-2 streams. REC-1 and REC-2 streams had significantly higher total suspended solids than FOR and AG-L streams. Approximately 50 % of the seston in FOR and AG-L streams was inorganic material, but ~ 75 % of seston was inorganic in AG-M and AG-H. Seston in REC streams was comprised of more inorganic material than FOR and AG-L streams.

Reaeration coefficients ($K_{2(20°C)}$) varied from 14.7 to 204.1 d^{-1} among all sites and were highly variable within land-use categories (Table 2). FOR sites had the highest average $K_{2(20°C)}$ (113.5 d^{-1}), but mean values did not vary significantly among land-use categories due to the high variability observed within categories. In general, however, agricultural sites had lower values for $K_{2(20°C)}$ than forested or recovering streams.

Chl *a* varied from ~ 2 mg / m^2 in REC-2, FOR, and AG-L sites in August to ~12 mg / m^2 in AG-M and AG-H sites in June (Figure 4). All categories, except REC-1, had their highest chl *a* in June. Across seasons, chl *a* was lowest in REC-2 and FOR streams compared to AG-H and REC-1 streams. AFDM was generally highest in April and declined throughout the summer

(Figure 4); however, only AG-H had significantly higher epilithic AFDM than any other category.

Metabolism varied greatly among streams within land-use categories, but several significant differences were observed based on land-use. GPP was significantly higher in AG-M and AG-H sites (1.19 ± 0.19 and 0.66 ± 0.18 g O_2 m^{-2} d^{-1}, respectively) compared with all other categories where rates varied from 0.10 to 0.23 g O_2 m^{-2} d^{-1} (Figure 5). GPP in the recovering streams (REC-1 and REC-2) was similar to GPP in forested and low agriculture streams. R varied from ca. 4-7.5 g O_2 m^{-2} d^{-1}, was 4 to 40 times higher than GPP, and was not significantly different among categories (Figure 5). High R relative to GPP resulted in negative NEP for all sites and values similar to R (Figure 5). NEP did not vary significantly among land-use treatments. Mean P/R varied from 0.013 ± 0.008 in long-term forested sites to 0.183 ± 0.049 in medium agriculture sites (Figure 5) and was significantly higher in medium and high agriculture sites than in forested, low agriculture, and reforested sites.

Physical properties, water chemistry, and algal biomass were significantly correlated with metabolism in this study (Table 3). DIN was positively correlated with GPP. PO_4-P was positively correlated with R and negatively correlated with NEP. PAR was positively correlated with both GPP and P/R. GPP and P/R were also positively correlated with degree-days. Like PO_4-P, TSS was correlated positively with R but negatively with NEP. Chl *a* was positively correlated with both GPP and P/R. Epilithic AFDM was also positively correlated with GPP.

Discussion

Land cover trends in the southern Appalachians

Land cover analysis was used to categorize streams based on current and historical agricultural activity in their watersheds. The influence of land-use at different spatial scales on stream biota and ecosystem processes makes interpretation of land cover data difficult (e.g., Allan et al. 1997, Sponseller and Benfield 2001). Adding temporal variation may make spatial scale influences even more complicated to detect because multiple data layers must match geographically for accurate time-series analysis and spatially explicit interpretation of land cover changes. A categorical approach was employed to avoid these complications and to consider the history of human activity in addition to spatial dimensions. This categorization took advantage of spatial and temporal perspectives in order to define sites by the extent of agricultural activity and the changes in land-use over the past 50 years. FOR sites served as a long-term forested reference category, while AG sites were intended to represent a gradient of agriculture from low (AG-L) to high amounts (AG-H). In general, AG sites fit their categories, but forest cover differed among sites within each land-use category at different spatial scales. Agriculture was predominantly found along the stream near sampling locations at most sites. However, some sites had extensive pasture in the uplands with more forested riparian zones. Furthermore, the type of agriculture practice varied among sites within each category but was not distinguished by the land cover estimation technique employed. Despite these quantitative drawbacks, forest and agriculture sites represented long-term land-use patterns common across southern Appalachian watersheds.

Streams of recovering catchments were placed into one of two stages based on the extent of reforestation in their watersheds. REC-1 streams were more heavily influenced by agriculture in 1950 than REC-2 streams, particularly in the riparian zones. As a result, REC-1 watersheds are currently less forested than REC-2 watersheds. However, watersheds in both categories have extensively reforested at all spatial scales, providing the potential for recovery of stream processes from historical disturbance.

Influence of agriculture on physical and chemical stream properties

Chemical and physical properties responded to the gradient of agriculture represented by FOR and AG streams. In addition, several properties of the physical and chemical structure of REC streams were similar to agricultural streams reflecting long-term effects of agriculture despite watershed reforestation. Nutrient concentrations (DIN and PO_4-P) increased with increasing agriculture, and these concentrations remained elevated in streams from both recovering categories. Furthermore, both light (PAR) and temperature (degree-days) responded similarly to the agricultural gradient (higher in more agricultural sites). PAR values from AG-H streams were as high as those recorded in prairie streams of KS but were not quite as high as values reported for desert streams in AZ (Mulholland et al. 2001). PAR and degree-days were not elevated in REC streams suggesting that these variables recover as a result of reforestation. Logging history has similar effects on stream ecosystems in that nutrients remain elevated for decades following logging, but light and temperature return to pre-logging conditions relatively rapidly (Marks and Bormann 1972, Vitousek and Reiners 1975, Webster et al. 1983).

Increased sediment load to receiving streams has been one of the most common influences of agricultural land use (Waters 1995). Suspended material can have important implications for metabolism for several reasons. For example, Young and Huryn (1996) showed that organic material in transport contributed to total reach respiration, while total suspended material reduced primary production by reducing light available to benthic algae. In the present study, baseflow suspended particle concentrations were 3X higher in streams with current and past agricultural activity compared to forested streams. These higher seston concentrations were accompanied with higher % inorganic sediment content. As a result, suspended inorganic sediment was ~ 4X higher in agricultural streams than in forested streams. Organic seston concentrations were relatively similar among categories (< 2X higher in agricultural than in forested streams). Because seston in agricultural streams was primarily inorganic, the primary effect of seston on metabolism in agricultural streams was likely to reduce GPP.

Chl *a* was higher in agricultural than forested streams, presumably resulting from higher nutrients and light. High light intensity and nutrients are associated with high algal productivity in agricultural streams (Corkum 1996), and nutrients have been strongly correlated with algal growth in the absence of light limitation (Lohman et al. 1992, Mosisch et al. 2001). Agricultural streams had ~3X the amount of chl *a* as forested streams in this study, but even the highest chl *a* found in agricultural streams in this study (~ 10 mg/m^2) were much lower than chl *a* reported for some forested streams in the southern Appalachians (Walker Branch, TN 52-93 mg/m^2; White Oak Creek, TN 13-51 mg/m^2, from Hill and Dimick 2002). Surprisingly, chl *a* was abundant in REC-1 streams, despite low light levels. However, AFDM on rock surfaces was low in REC-1 streams relative to AG-H streams. REC-1 streams exhibited the strongest seasonal trend in both chl *a* and AFDM. From April to August, algal biomass (chl *a* and AFDM) declined by two-thirds in REC-1 streams. This corresponds to the transition from open winter foliage to closed summer canopies, and algal biomass may be predicted to decline over this period in forested streams. If light limitation associated with canopy closure causes lower algal biomass in forested streams, then AG-M and AG-H streams should have much higher algal biomass than forested streams, particularly during summer. In general, AG categories did have higher algal biomass than forested streams in each month, but differences were not greatest during summer months. Instead, the largest differences occurred during April. Therefore, seasonal light changes in forested streams may not be great enough to cause light limitation of the algal assemblage particular to forested streams (Hill et al. 2001).

Reaeration coefficients describe the propensity for gas exchange and reflect the physical interaction of flowing water with the stream channel (depth, velocity, slope, turbulence). Reaeration was positively correlated with site elevation and negatively correlated with watershed area. Streams with high elevation and small watershed area tended to have steeper slopes, which likely contributed to higher reaeration rates. However, elevation was not significantly different among land-use categories. Reaeration values were highly variable among sites within land-use categories and thus were not significantly different among land-use categories. Metabolism estimates can be particularly sensitive to reaeration rates and the method used to determine reaeration (Wilcock 1982, McCutchan et al. 1998, Young and Huryn 1999). Streams with high reaeration rates ($k_{2(20°C)} > 100\ d^{-1}$) generally require higher respiration rates in order to make precise metabolism estimates (McCutchan et al. 1998). Reaeration exceeded 100 d^{-1} in only 4 streams, suggesting relatively good quality of metabolism estimates.

Land use effects on ecosystem metabolism

Reductions in forest cover as a result of agriculture affected stream ecosystem metabolism by increasing GPP, but rates of R remained unchanged. GPP was nearly zero in forested streams and was highest in streams with moderate amounts of current agriculture. Streams in catchments with higher amounts of agriculture (AG-H) had higher GPP than forested streams, but GPP rates in these streams were significantly lower than AG-M streams. AG-H streams had the highest nutrient concentrations, PAR values, and algal biomass suggesting that they may support highest GPP rates. In fact, strong correlations between light, chlorophyll, and GPP were evident among all study streams, but lower GPP in AG-H compared to AG-M did not support this trend. Young and Huryn (1999) suggested that GPP could have been light-limited in a tussock grassland stream because channel incision increased canyon shading. Suspended particles reduce light reaching benthic algae in streams and have also been shown to reduce GPP (Wiley et al. 1990, Brown and King 1987, Young and Huryn 1996). Light and TSS data from the present study do not support either of these possibilities as explanations for higher GPP in streams with medium agriculture compared to high agriculture because PAR and TSS from AG-H sites were similar to AG-M sites. Intense agriculture may alter GPP by introducing fine sediment to the stream bottom and changing particle size, as was shown in the Midwest by Brown and King (1987). Small substrates generally support lower algal standing crops and may scour larger particles when moved by storms, which results in lower GPP in streams with shifting benthic substrate (Biggs et al. 1999). Median particle size and the % of fine sediment present on the streambed were higher in AG-H sites than AG-M (unpublished data), which may have limited GPP in AG-H streams despite high PAR.

GPP rates in reforested streams were similar to those in forested and low agriculture streams, most likely due to light limitation from reforestation. GPP was most strongly correlated with light availability (indicated by PAR and degree days) in this study and was only weakly correlated with DIN. While nutrient concentrations in recovering streams were elevated compared to long-term forested streams, canopy closure was evident at all the sites. Primary production in streams has been shown to return rapidly to normally low values as a result of reforestation following clear cutting despite persistent elevated nutrient concentrations (Webster et al. 1983). Furthermore, primary production has been shown to decrease while nutrient concentrations increase during canopy closure from spring to summer in southern, forested streams (Hill et al. 2001). Nutrients have been shown to stimulate GPP in streams but only in conditions where light is not limiting (Lowe et al. 1986, Hill et al. 1992). Furthermore, in a broad survey of streams, PAR explained 72% of the variation in GPP across North American stream ecosystems whereas phosphorus concentration explained only an additional 18% (Mulholland et al. 2001). DIN was weakly correlated with GPP in the present study and did not improve regression models using PAR to predict GPP.

Unlike its influence on GPP, agriculture did not seem to affect ecosystem respiration. It has been suggested that respiration increases with agricultural activity in watersheds (King and Cummins 1989, Bunn et al. 1999). However, others have shown no increase or, conversely, a decrease in respiration with agricultural activity (Young and Huryn 1999). Metabolism of forested southern Appalachian streams is dominated by respiration (e.g., Webster et al. 1997), so high R rates may be the normal condition rather than a response to stress at the ecosystem level. In general, GPP appears to be more sensitive than respiration to differences in light regime

(Mulholland et al. 2001), and removal of riparian vegetation appears to alter GPP more strongly than R rates (Bunn et al. 1999).

For all streams in this study, R was much higher than GPP resulting in negative NEP and P/R values well below 1. Agriculture did not appear to generate significant changes in NEP. Despite little change in NEP, streams with higher GPP had higher P/R values. At broader scales, stream P/R should reflect changing terrestrial-aquatic interactions. Vannote et al. (1980) predicted increases in P/R with distance downstream because increasingly open forest canopy allows light to reach the stream and enhance GPP. Minshall et al. (1985), however, suggested that human activity in watersheds might generate an upstream shift of higher P/R. In the present study, agriculture resulted in higher P/R in small (2nd and 3rd order) streams, thereby supporting the assertion that land clearing alters typical longitudinal patterns in stream metabolism. However, the magnitude of the increase in P/R due to agriculture (i.e., 0.01-0.22) was not as dramatic as that observed in larger rivers (i.e., 0.2 to 1.1 from 4th to 6th order) in the southern Appalachians (McTammany et al. 2003). In addition, all P/R values were much lower than 1, indicating that even agricultural streams were highly heterotrophic despite having open canopies. Several studies have found P/R ratios > 1 in various types of agricultural streams including Midwest U.S. row crop (Wiley et al. 1990), New Zealand pasture streams (Young and Huryn 1999), and Australian agricultural streams (Bunn et al. 1999). Agricultural streams in these studies had GPP values approximately 2-10X higher than those reported in this study but similar rates of R.

What features may be limiting GPP in my agricultural streams relative to other studies? One major difference among agricultural streams in these studies was amount of forested land in watersheds. The most agricultural watershed was approximately 50% forested. In contrast, forest comprised only about 5% of the watershed with the remainder in tussock grassland or pasture in New Zealand (Young and Huryn 1998). In the Midwest U.S., watersheds were over 90% row crop agriculture (Wiley et al. 1990). Bunn et al. (1999) found higher P/R as canopy cover declined from agriculture and suggested a value of 73% canopy cover as the threshold for normal P/R in Australian streams. Obviously, there are major differences in the baseline energetics of undisturbed streams across biomes that affect interpretation of land-use effects on stream metabolism. In addition, the mountainous terrain surrounding the streams may cause shorter photoperiods with subsequently lower GPP and P/R than open-canopy streams in areas with less topographic relief, like the Midwest U.S.

Metabolism was correlated with several factors found to differ among agricultural treatments. In most cases, those factors correlated with GPP and P/R were not correlated with respiration and NEP. Relationships between these chemical and physical variables and metabolism provide insight into factors controlling metabolism in agricultural streams. Light availability seemed to drive GPP in stream ecosystems with only secondary control by other factors. For example, the highest light category (AG-H) did not have the highest GPP, most likely due to substrate unsuitable for algae (Biggs et al. 1999). Nutrient availability may also limit GPP in streams receiving ample light (Lowe et al. 1986), and PO_4-P values were very low in all study streams. Respiration was not related to light or temperature but was related to nutrient and seston concentrations. Therefore, the net result of agriculture on stream metabolism in the southern Appalachians was higher GPP and P/R in streams while net metabolism remained dominated by respiration. Once reforestation occurs on previously agricultural land, stream metabolism returns to pre-agricultural levels. Active management of agricultural streams often entails restoring woody riparian vegetation. Based on the results, such restoration could potentially restore the natural organic matter dynamics of agricultural streams in forested areas by limiting primary production and providing allochthonous detritus inputs.

Acknowledgments

Funding for this project was provided by Sigma Xi, the Graduate Student Assembly and Biology Department of Virginia Tech, and the National Science Foundation grant DEB9632854 to the Coweeta Long-term Ecological Research site. Special thanks to all the landowners who gave me access to their properties and provided many anecdotes about the history of the region and their land. I would also like to thank the Virginia Tech Stream Team for valuable help in data collection and Paul Bolstad and Ned Gardiner for providing GIS data.

Literature Cited

Allan, J. D., D. L. Erickson, and J. Fay. 1997. The influence of catchment land-use on stream integrity across multiple spatial scales. Freshwater Biology 37:149-161.

APHA (American Public Health Association, American Water Works Association, and Water Environment Federation). 1998. Standard methods for the examination of water and wastewater, 20th edition. American Public Health Association, Washington, DC, USA.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology 65:1-13.

Biggs, B. J. F., R. A. Smith, and M. J. Duncan. 1999. Velocity and sediment disturbance of periphyton in headwater streams: biomass and metabolism. Journal of the North American Benthological Society 18:222-241.

Brown, S. S., and D. K. King. 1987. Community metabolism in natural and agriculturally disturbed riffle sections of the Chippewa River, Isabella County, Michigan. Journal of Freshwater Ecology 4:39-51.

Bunn, S. E., P. M. Davies, and T. D. Mosisch. 1999. Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology 41:333-345.

Clark, T. D. 1984. The greening of the South: the recovery of land and forest. University Press of Kentucky, Lexington, Kentucky, USA.

Corkum, L. D. 1996. Responses of chlorophyll-a, organic matter, and macroinvertebrates to nutrient additions in rivers flowing through agricultural and forested land. Archiv fur Hydrobiologie 136:391-411.

Elmore, H. L., and W. F. West. 1961. Effect of water temperature on stream reaeration. Journal of the Sanitary Engineering Division, Proceedings of the American Society of Civil Engineers 87:59-71.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421-439.

Foster, D. R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology 80:753-772.

Genereux, D. P., and H. F. Hemond. 1992. Determination of gas exchange rate constants for a small stream on Walker Branch watershed, Tennessee. Water Resources Research 28:2365-2374.

Granberry, D. M., W. T. Kelley, W. O. Chance, W. McLaurin, K. A. Harrison, and D. Sanders. 1994. Plasticulture for commercial vegetable production. University of Georgia College of Agricultural and Environmental Sciences Cooperative Extension Service, Bulletin 1108. Athens, Georgia.

Gurtz, M. E., J. R. Webster, and J. B. Wallace. 1980. Seston dynamics in southern Appalachian streams: effects of clear-cutting. Canadian Journal of Fisheries and Aquatic Sciences 37:624-631.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones. 1998. Stream biodiversity: the ghost of land-use past. Proceedings of the National Academy of Science 95:14843-14847.

Hill, W. R., H. L. Boston, and A. D. Steinman. 1992. Grazers and nutrients simultaneously limit lotic primary productivity. Canadian Journal of Fisheries and Aquatic Sciences 49:504-512.

Hill, W. R., and S. M. Dimick. 2002. Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. Freshwater Biology 47:1245-1256.

Hill, W. R., P. J. Mulholland, and E. R. Marzolf. 2001. Stream ecosystem responses to forest leaf emergence in spring. Ecology 82:2306-2319.

Holmes, R. M., A. Aminot, R. Kerouel, B. A. Hooker, and B. J. Peterson. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 56:1801-1809.

Honnay, O., M. Hermy, and P. Coppin. 1999. Impact of habitat quality on forest plant species colonization. Forest Ecology and Management 115:157-170.

Horner, R. R., E. B. Welch, M. R. Seeley, and J. M. Jacoby. 1990. Responses of periphyton to change in current velocity, suspended sediment and phosphorus concentration. Freshwater Biology 24:215-232.

Hynes, H. B. N. 1975. The stream and its valley. Verhandlung der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 19:1-15.

Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. Science 201:229-234.

Kilpatrick, F. A., R. E. Rathbun, N. Yotsukura, G. W. Parker, and L. L. DeLong. 1989. Determination of stream reaeration coefficients by use of tracers. Techniques of water-resources investigations 3-A18. U. S. Geological Survey, Denver, Colorado, USA.

King, D. K. and K. W. Cummins. 1989. Factors affecting autotrophic-heterotrophic relationships of a woodland stream. Journal of Freshwater Ecology 5:219-230.

Lohman, K., J. R. Jones, and B. D. Perkins. 1992. Effects of nutrient enrichment and flood frequency on periphyton biomass in northern Ozark streams. Canadian Journal of Fisheries and Aquatic Sciences 49:1198-1205.

Lowe, R. L., S. W. Golladay, and J. R. Webster. 1986. Periphyton response to nutrient manipulation in streams draining clearcut and forested watersheds. Journal of the North American Benthological Society 5:221-229.

Lowrance, R. R., R. A. Leonard, L. E. Asmussen, and R. A. Todd. 1985. Nutrient budgets for agricultural watersheds in the southeastern coastal plain. Ecology 66:287-296.

Marks, P. L., and F. H. Bormann. 1972. Revegetation following forest cutting: mechanisms for return to steady state nutrient cycling. Science 176:914-915.

Marzolf, E. R., P. J. Mulholland, and A. D. Steinman. 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Sciences 51:1591-1599.

McCutchan, J. H., Jr., W. M. Lewis, Jr., and J. F. Saunders, III. 1998. Uncertainty in the estimation of stream metabolism from open-channel oxygen concentrations. Journal of the North American Benthological Society 17:155-164.

McTammany, M. E., J. R. Webster, E. F. Benfield, and M. A. Neatrour. 2003. Longitudinal patterns of metabolism in a southern Appalachian river. Journal of the North American Benthological Society 22:pages?

Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote. 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 42:1045-1055.

Mosisch, T. D., S. E. Bunn, and P. M. Davies. 2001. The relative importance of shading and nutrients on algal production in subtropical streams. Freshwater Biology 46:1269-1278.

Mulholland, P. J., C. S. Fellows, J. L. Tank, N. B. Grimm, J. R. Webster, S. K. Hamilton, E. Marti, L. Ashkenas, W. B. Bowden, W. K. Dodds, W. H. McDowell, M. J. Paul, and B. J. Peterson. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshwater Biology 46:1503-1517.

Myster, R. W., and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr. in 10 contrasting old fields. Ecology 75:387-392.

Neatrour, M. A., J. R. Webster, and E. F. Benfield. 2004. The role of floods in particulate organic matter dynamics of a southern Appalachian river-floodplain ecosystem. Journal of the North American Benthological Society 23:198-213.

Odum, H. T. 1956. Primary production in flowing waters. Limnology and Oceanography 1:102-117.

Otto, J. S. 1983. The decline of forest farming in southern Appalachia. Journal of Forestry 27:18-27.

Simmons, C. E., and R. C. Heath. 1979. Water-quality characteristics of streams in forest and rural areas of North Carolina. Pages B1-B33 *in* Water quality of North Carolina streams. Geological Survey Water-Supply Paper 2185 A-D. North Carolina Department of Natural and Economic Resources, Raleigh, North Carolina, USA.

Sponseller, R. A., and E. F. Benfield. 2001. Influences of land use on leaf breakdown in southern appalachian headwater streams: a multiple-scale analysis. Journal of the North American Benthological Society 20:44-59.

Steinman, A. D., and G. A. Lamberti. 1996. Biomass and pigments of benthic algae. Pages 295-313 *in* Methods in Stream Ecology. F. R. Hauer and G. A. Lamberti, editors. Academic Press, Inc., San Diego, California, USA.

Stover, M. E., and P. L. Marks. 1998. Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. Journal of the Torrey Botanical Society 125:150-164.

Sweeney, B. W. 1980. Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North America. Proceedings of the Academy of Natural Sciences of Philadelphia 144:291-340.

Valett, H. M., C. L. Crenshaw, and P. F. Wagner. 2002. Stream nutrient uptake, forest succession, and biogeochemical theory. Ecology 83:2888–2901.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130-137.

Vitousek, P. M., and W. A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25:376-381.

VRFBP (Virginia Riparian Forest Buffer Panel). 1998. Riparian buffer implementation plan. Commonwealth of Virginia, Richmond, Virginia, USA.

Wanninkhof, R. 1992. Relationship between wind speed and gas exchange over the ocean. Journal of Geophysical Research (Oceans) 97:7373-7382.

Wanninkhof, R., P. J. Mulholland, and J. W. Elwood. 1990. Gas exchange rates for a first-order stream determined with deliberate and natural tracers. Water Resources Research 26:1621-1630.

Waters, T. F. 1995. Sediment in streams; sources, biological effects and control. American Fisheries Society Monograph 7. Bethesda, Maryland, USA.

Wear, D. N. and P. V. Bolstad. 1998. Land-use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Webster, J. R., and B. C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs 49:51-72.

Webster, J. R., J. B. Wallace, and E. F. Benfield. 1995. Organic processes in streams of the eastern United States. Pages 117-187 *in* Ecosystems of the world 22: river and stream ecosystems. C. E. Cushing, K. W. Cummins, and G. W. Minshall, editors. Elsevier, Amsterdam, Netherlands.

Webster, J. R., J. L. Meyer, J. B. Wallace, and E. F. Benfield. 1997. Organic matter dynamics in Hugh White Creek, Coweeta Hydrologic Laboratory, North Carolina, USA. Pages 74-78 *in* J. R. Webster and J. L. Meyer, editors. Stream organic matter budgets. Journal of the North American Benthological Society 16:3-161.

Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. 1983. Stability of stream ecosystems. Pages 355-395 *in* J. R. Barnes and G. W. Minshall, editors. Stream ecology. Plenum Press, New York, New York, USA.

Webster, J. R., S. W. Golladay, E. F. Benfield, J. L. Meyer, W. T. Swank, and J. B. Wallace. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory. Pages 231-253 *in* P. J. Boon, P. Calow, and G. E. Petts, editors. River conservation and management. John Wiley and Sons, Ltd., Chichester, England.

Wenger, S. J. and L. Fowler. 2000. Protecting stream and river corridors: creating effective local riparian buffer ordinances. Carl Vinson Institute of Government, University of Georgia. Athens, GA.

Wetzel, R. G., and G. E. Likens. 2000. Limnological analyses, 3rd edition. Springer-Verlag, New York, New York, USA.

Wilcock, R. J. 1982. Simple predictive equations for calculating stream reaeration rate coefficients. New Zealand Journal of Science 25:53-56.

Wiley, M. J., L. L. Osborne, and R. W. Larimore. 1990. Longitudinal structure of an agricultural prairie river system and its relationship to current stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 47:373-384.

Young, R. G., and A. D. Huryn. 1996. Internannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Canadian Journal of Fisheries and Aquatic Sciences 53:2199-2211.

Young, R. G., and A. D. Huryn. 1998. Comment: Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Sciences 55:1784-1785.

Young, R. G., and A. D. Huryn. 1999. Effects of land use on stream metabolism and organic matter turnover. Ecological Applications 9:1359-137.

Table 1. Historical and current forest cover (%) at different spatial scales for streams in each forest cover category. Percent forest cover of sites in "extant" categories has remained constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Lateral spatial scale is indicated by WS (whole watershed) or RIP (100-m riparian corridor). Extent refers to longitudinal spatial scale. Values are means for each category (n=3 streams) ± 1 SE.

Spatial scale			Extant				Recovering	
Lateral	Extent	Year	FOR	AG-L	AG-M	AG-H	REC-1	REC-2
WS	Whole catchment	1950	99.8 ± 0.2	87.8 ± 5.4	64.8 ± 9.8	58.1 ± 9.9	83.2 ± 5.3	73.2 ± 13.1
WS	Whole catchment	1993	99.8 ± 0.1	94.6 ± 3.4	86.4 ± 3.9	81.1 ± 4.5	95.7 ± 0.9	93.7 ± 1.3
RIP	Whole stream	1950	100.0 ± 0.0	87.4 ± 4.3	52.1 ± 9.1	34.2 ± 1.6	60.8 ± 11.0	69.6 ± 10.7
RIP	Whole stream	1993	99.8 ± 0.2	97.1 ± 1.2	78.8 ± 5.1	63.1 ± 0.8	85.4 ± 4.3	93.2 ± 3.3
RIP	2 km corridor	1950	100.0 ± 0.0	73.9 ± 6.3	19.6 ± 5.2	10.8 ± 10.4	41.8 ± 16.3	66.5 ± 9.2
RIP	2 km corridor	1993	95.4 ± 3.7	87.5 ± 5.2	53.9 ± 3.2	27.4 ± 13.3	75.0 ± 6.6	90.1 ± 2.2
RIP	1 km corridor	1950	100.0 ± 0.0	43.2 ± 12.2	18.7 ± 1.2	7.6 ± 6.1	29.5 ± 16.5	58.2 ± 10.5
RIP	1 km corridor	1993	96.1 ± 2.1	68.9 ± 19.0	43.0 ± 6.2	17.6 ± 12.9	64.0 ± 6.1	83.6 ± 6.6

Table 2. Physical and chemical characteristics of streams in each forest cover category. Values are means (n = 3 streams) with limits in parentheses. Discharge and conductivity were measured semi-monthly at each site, and the value reported is the mean of each site mean with overall range. Reaeration (oxygen exchange) coefficients ($K_{2(20ºC)}$) of streams by category derived from injection of volatile gas (SF_6) and conservative tracer (Cl^{-1} or Br^{-1}) standardized to 20ºC from ambient stream temperature for comparison.

	Extant				Recovering	
	FOR	AG-L	AG-M	AG-H	REC-1	REC-2
Elevation (m)	776 (693-832)	722 (588-861)	652 (576-762)	719 (671-762)	732 (646-838)	829 (766-861)
WS area (ha)	514 (241-922)	1231 (809-1539)	1815 (1551-2033)	1064 (925-1222)	731 (340-982)	333 (321-342)
Discharge (L/s)	73 (59-81)	90 (82-99)	66 (56-86)	70 (49-99)	62 (45-82)	59 (39-73)
Spec. cond. (µS/cm)	20.8 (11.9-28.3)	75.0 (45.2-98.4)	31.5 (22.6-36.8)	43.0 (40.8-45.7)	50.0 (32.1-63.3)	65.2 (43.8-82.0)
Alkalinity (mg $CaCO_3$/L)	5.3 (4.9-6.1)	6.7 (4.8-8.3)	11.0 (9.2-12.5)	11.7 (8.4-15.9)	11.7 (8.7-16.2)	9.7 (9.1-10.3)
$K_{2(20ºC)}$ (d^{-1})	113.5 (17.7-204.1)	48.2 (23.6-82.5)	46.9 (14.7-88.7)	29.5 (16.0-38.1)	69.8 (25.5-146.2)	86.9 (75.5-108.6)

Table 3. Pearson product moment correlations relating physical and chemical parameters and algal biomass to metabolism. Values are correlation coefficients (*P* values) from significant relationships (n = 18); NS denotes non-significant relationships.

	GPP	R	NEP	P/R
DIN	0.47 (0.048)	NS	NS	NS
PO_4-P	NS	0.50 (0.034)	-0.52 (0.029)	NS
PAR	0.66 (0.003)	NS	NS	0.73 (0.001)
Degree-days	0.59 (0.009)	NS	NS	0.63 (0.005)
TSS	NS	0.57 (0.014)	-0.52 (0.027)	NS
Chl *a*	0.74 (0.001)	NS	NS	0.62 (0.007)
Epilithic AFDM	0.60 (0.008)	NS	NS	0.58 (0.012)

Figure Captions

Figure 1. Map showing locations of study sites in the southern Appalachian region (gray area on inset). Sites are coded by category (● FOR, ■ AG-L, ○ AG-M, Δ AG-H, □ REC-1, ▲ REC-2).

Figure 2. Nutrient concentrations (DIN and PO_4-P), light (PAR), and cumulative degree-days (above 0 ºC from November 2000 to August 2001) of streams shown by forest cover category. Percent forest cover of sites in “extant” categories has remained constant since 1950, and sites in “recovering” categories are in different stages of reforestation. Bars are means + 1 SE (n=3 streams for each category). DIN and PO_4-P values for each site were based on samples collected bi-monthly from November 2000 to August 2001. Bars with different letters are significantly different (RM ANOVA for DIN and PO_4-P, one-way ANOVA for PAR and degree-days, $P < 0.05$).

Figure 3. Concentration (a-total suspended solids, b-inorganic suspended solids, c-organic suspended solids) and composition (d-% inorganic seston) of seston in streams shown by forest cover category. Percent forest cover of sites in “extant” categories has remained constant since 1950, and sites in “recovering” categories are in different stages of reforestation. Values are means + 1 SE (n=3 streams for each category) over the entire study period. Bars with different letters are significantly different (RM ANOVA, $P < 0.05$).

Figure 4. Algal biomass (chl *a* and AFDM) on rocks collected from each stream by forest cover category. Percent forest cover of sites in “extant” categories has remained constant since 1950, and sites in “recovering” categories are in different stages of reforestation. Categories with significant differences are marked with different letters (RM ANOVA, $P < 0.05$).

Figure 5. Daily rates of gross primary production (GPP), ecosystem respiration (R), and net metabolism by forest cover category. Percent forest cover of sites in “extant” categories has remained constant since 1950, and sites in “recovering” categories are in different stages of reforestation. Values are means + 1 SE (n=3 streams for each category). Bars with different letters are significantly different (one-way ANOVA, $P < 0.05$).

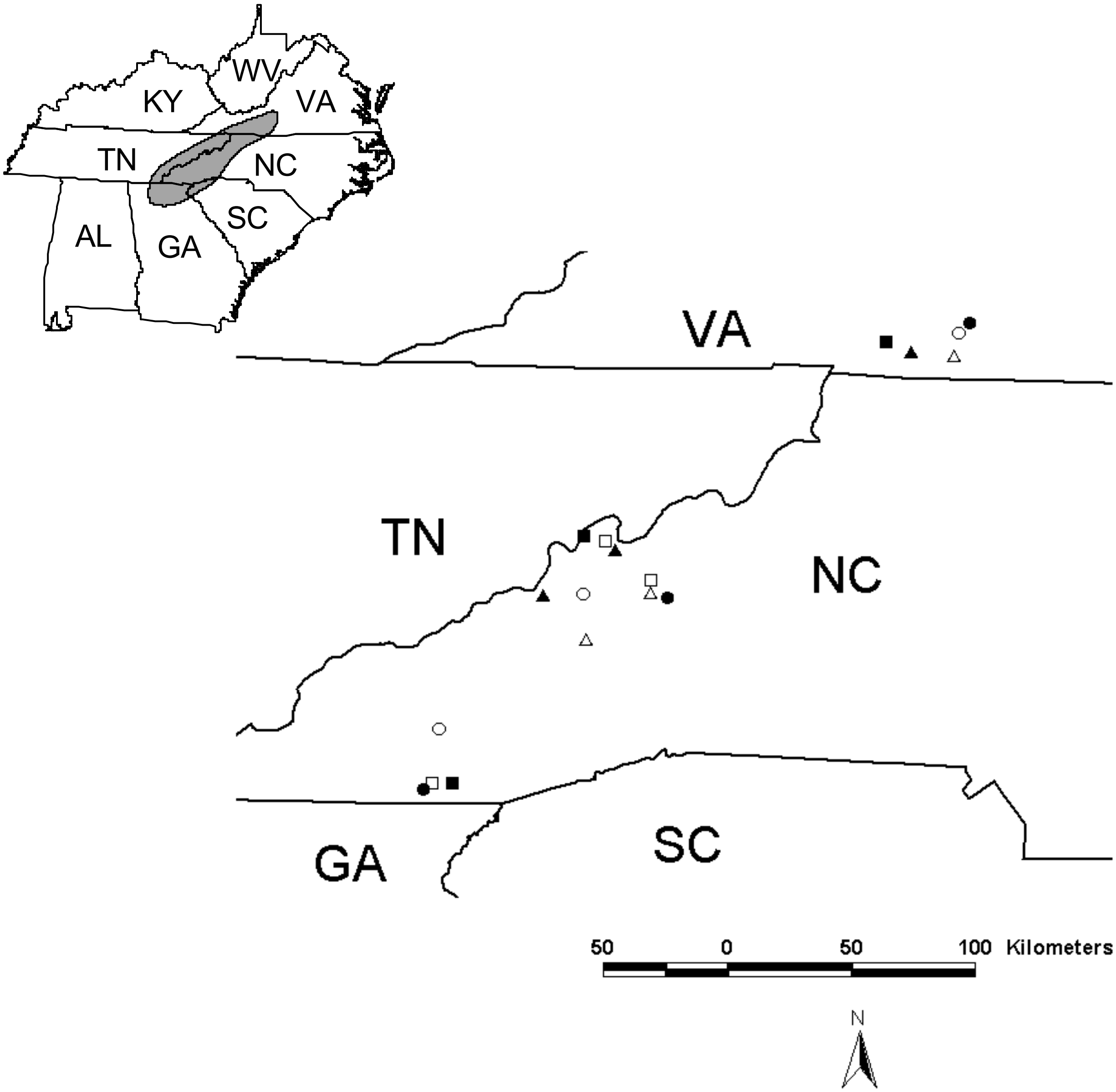


FIGURE 1

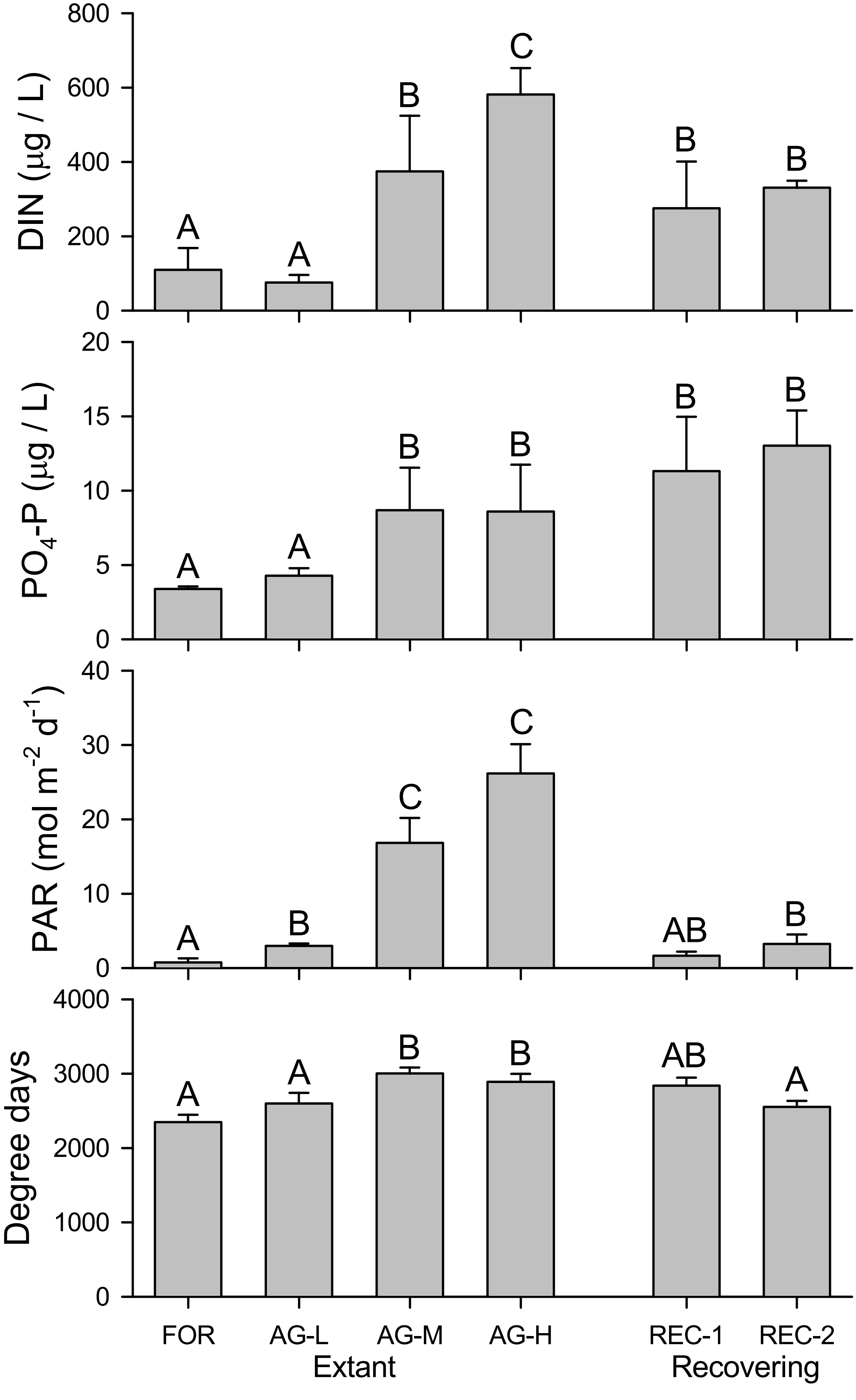

DIN (μg / L)
800
600
400
200
0
A
A
B
C
B
B
PO4-P (μg / L)
20
15
10
5
0
A
A
B
B
B
B
PAR (mol m-2 d-1)
40
30
20
10
0
A
B
C
C
AB
B
Degree days
4000
3000
2000
1000
0
A
A
B
B
AB
A
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 2

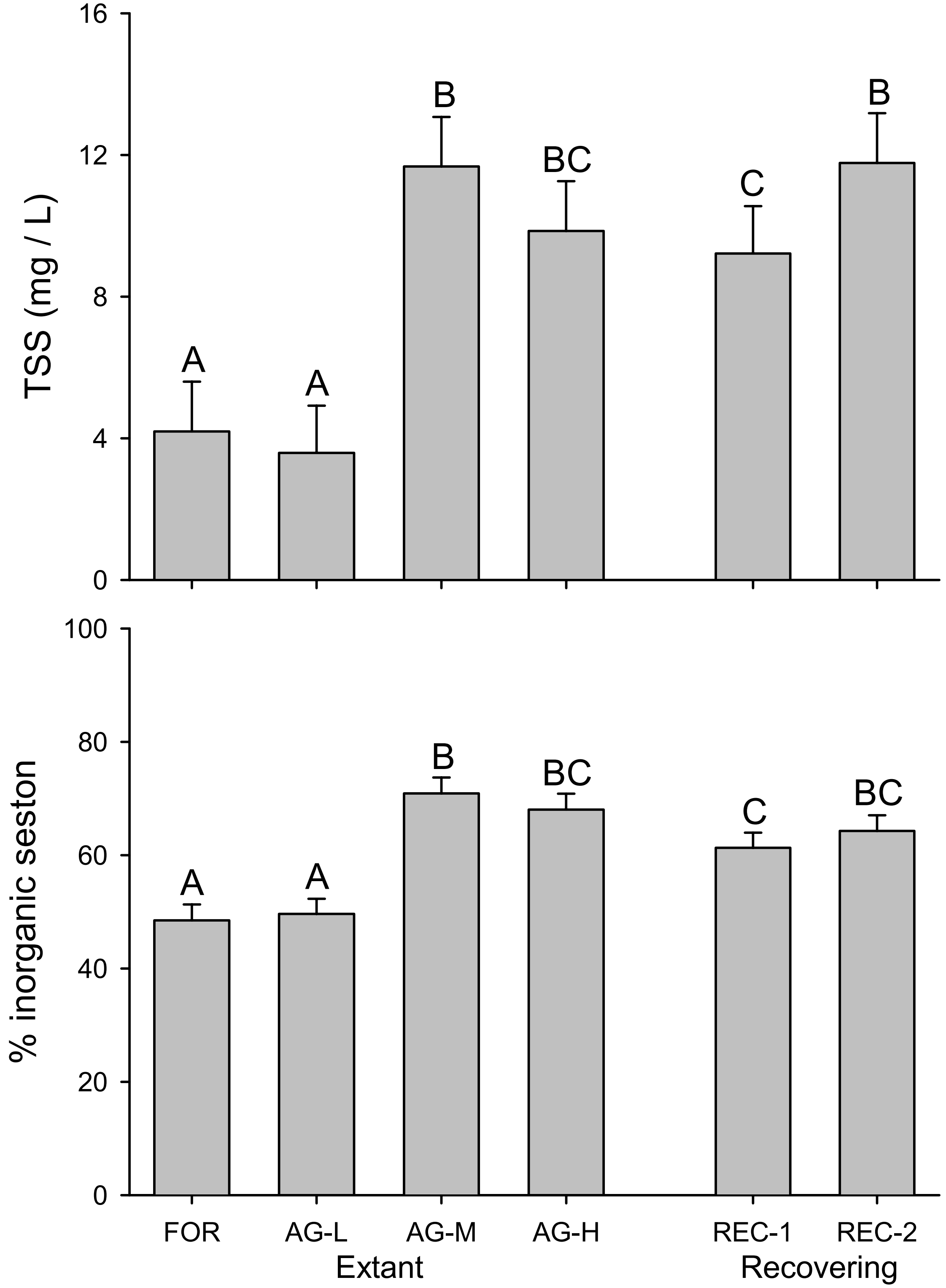

16
12
8
4
0
TSS (mg / L)
A
A
B
BC
C
B
100
80
60
40
20
0
% inorganic seston
A
A
B
BC
C
BC
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 3

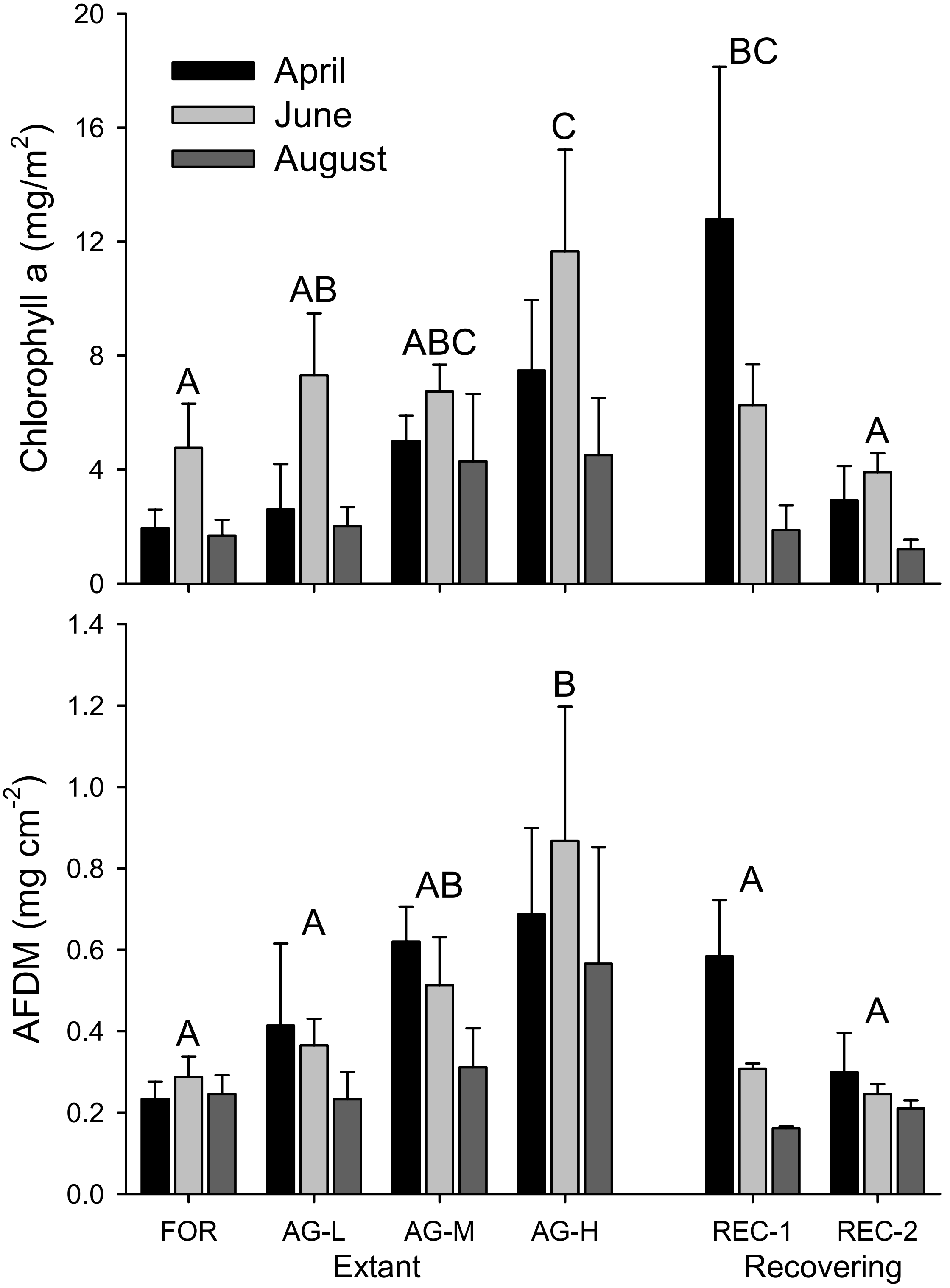

20
16
12
8
4
0
Chlorophyll a (mg/m2)
April
June
August
A
AB
ABC
C
BC
A
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
AFDM (mg cm-2)
A
A
AB
B
A
A
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 4

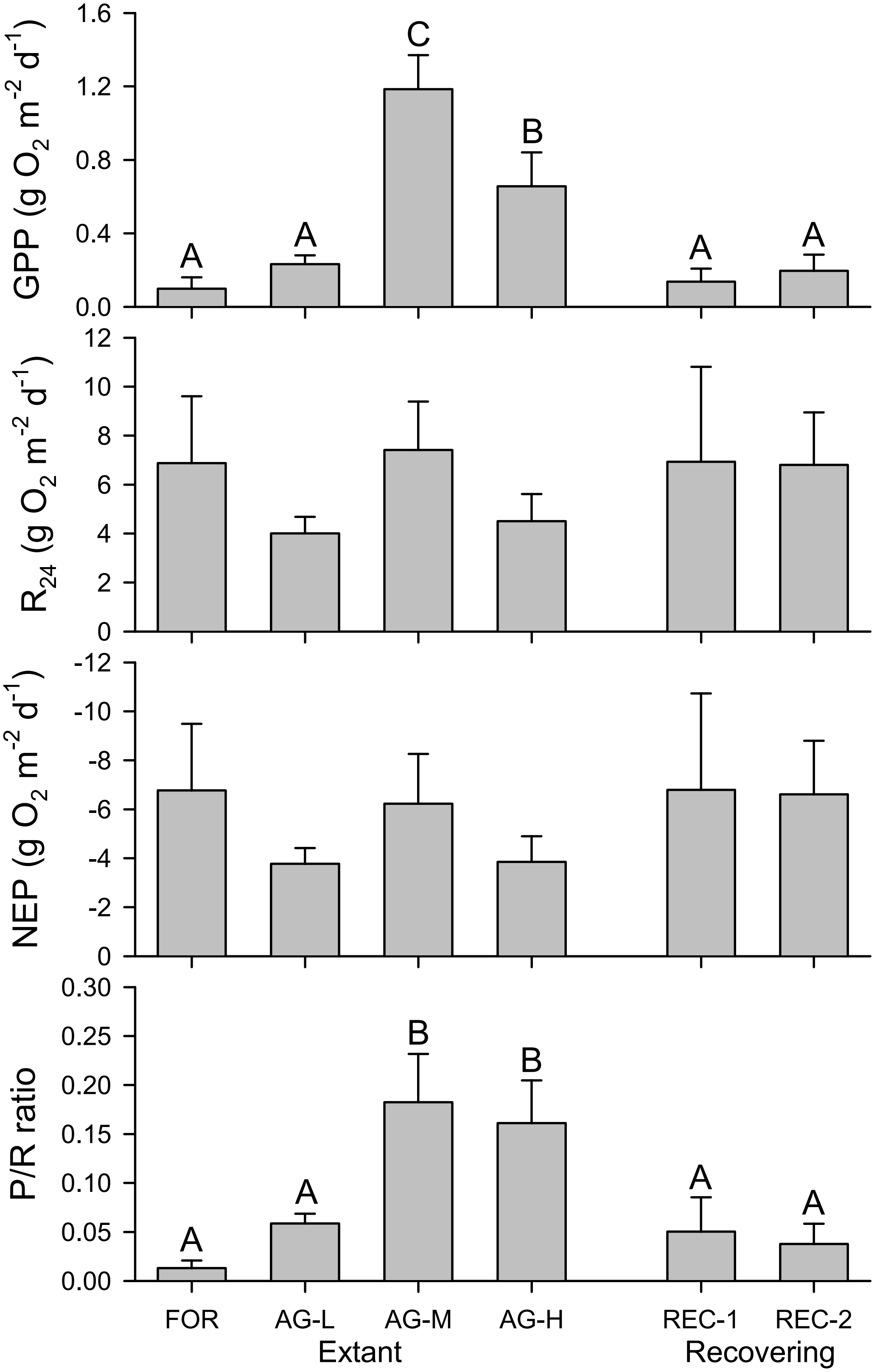

GPP (g O_2 m^{-2} d^{-1})
1.6
1.2
0.8
0.4
0.0
C
B
A
A
A
A
R_{24} (g O_2 m^{-2} d^{-1})
12
10
8
6
4
2
0
NEP (g O_2 m^{-2} d^{-1})
-12
-10
-8
-6
-4
-2
0
P/R ratio
0.30
0.25
0.20
0.15
0.10
0.05
0.00
B
B
A
A
A
A
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 5

CHAPTER 4

Organic matter breakdown and microbial biofilm activity in agricultural streams

Abstract

Agriculture in forested regions causes high sediment, nutrient, and light input to streams, and these inputs may affect rates of ecosystem processes such as organic matter decay. In general, higher nutrients and temperature have been associated with faster organic matter breakdown, but increased sediment may bury organic matter making it unavailable to consumers subsequently slowing decay. In order for stream ecosystems to recover from historical land uses, forests must be allowed to re-grow in their watersheds through either natural succession or human intervention. In the southern Appalachians, socioeconomic trends over the past 50 years have caused widespread abandonment of farmland with subsequent reforestation. Physical and chemical properties of streams in these reforested areas may be returning to pre-agriculture levels thereby creating the potential for recovery of ecosystem processes. I examined wood breakdown and microbial biofilm development in streams with different historical and current agricultural activity in their watersheds. I used a GIS to analyze the amount of historical (1950) and recent (1993) forested land cover in watersheds and riparian zones from large sections of the southern Appalachians. I categorized streams based on the percent forested land cover in their watersheds and riparian zones in these two time periods. Categories included 4 levels of agriculture with no change in % forest over the past 50 years and 2 levels of reforestation from agriculture due to land abandonment. I chose 5 streams from each category and compared microbial biofilm respiration on wood veneer substrates and breakdown of wood veneers among these land-use categories. I also measured nitrogen and phosphorus concentration in the water along with temperature because these factors are thought to be important determinants of biofilm activity and organic matter breakdown. Streams with current agriculture had higher concentrations of dissolved inorganic nitrogen than forested streams. Despite reforestation from agriculture, nitrogen concentrations were also elevated in streams with agricultural histories relative to forested streams. Temperature was also higher in agricultural streams but appeared to recover from historical agriculture through reforestation and stream shading. Wood breakdown rates ranged from 0.0015 to 0.0076 d^{-1} and were similar to other studies using wood veneers to determine breakdown rate. Microbial biofilm respiration increased with incubation time in streams up to approximately 150 days after which it remained constant. Neither wood breakdown nor biofilm respiration was significantly different among categories, despite the observed physical and chemical differences in streams based on land-use. Wood breakdown rates could be predicted from biofilm respiration indicating microbial control of wood breakdown in these streams. Both breakdown and biofilm respiration were negatively correlated to the amount of inorganic sediment accumulated on wood veneers. Higher nutrients and temperature led me to expect faster breakdown and higher microbial respiration in agricultural streams, but sediment in these streams may be limiting microbial activity and breakdown of organic material resulting in no net effect of agriculture on wood breakdown. Stream ecologists have been exploring the potential incorporation of ecosystem functions into biomonitoring programs, which typically use biological structure to indicate influences of humans on ecosystem integrity. In addition, restoration efforts are beginning to include ecosystem processes as indicators of impairment and recovery in previously influenceed streams. Clearly, the influence of agriculture on wood dynamics in streams must be better understood before they can be useful as part of biomonitoring programs.

Keywords: sediment, nutrients, temperature, land-use, history, decomposition, recovery, disturbance, organic matter dynamics, bioassessment, agriculture, biofilm, stream

Introduction

Streams in forested regions rely heavily on the supply of allochthonous organic material for secondary production (Wallace et al. 1997) and nutrient retention (Webster et al. 2000). This organic matter is subject to a variety of processes including microbial colonization, transport, burial, and ingestion. Leaf material is the bulk of allochthonous material reaching small streams (Webster and Meyer 1997), and many organisms are particularly adapted for processing autumnal input of leaves (Anderson and Sedell 1979). However, wood is an important structural component of many streams (e.g., Harmon et al. 1986), and it acts as a long-lasting food resource after the rapid breakdown of leaf material (Webster and Benfield 1986). Wood may be an extremely important resource in streams that do not receive large annual supplies of leaves, such as agricultural streams with altered riparian vegetation or in streams that rapidly process leaf material during winter (Rabeni and Hoel 2000).

Wood decomposition in streams is primarily achieved through microbial activity, mainly fungal and bacterial digestion (Sinsabaugh et al. 1992), and active biofilms develop on the surfaces of wood substrates in streams (Golladay and Sinsabaugh 1991, Tank and Winterbourn 1995). Substrate quality (i.e., tissue chemistry) can be particularly important in determining microbial activity and breakdown rate of organic matter in streams (Melillo et al. 1983, Gessner and Chauvet 1994). However, concentration of nutrients, primarily nitrogen (N) and phosphorus (P), in the water column can also influence microbial biofilm activity (Howarth and Fisher 1976, Tank and Webster 1998) and organic matter breakdown rates (Howarth and Fisher 1976, Benfield et al. 1977, Meyer and Johnson 1983, Elwood et al. 1981, Suberkropp and Chauvet 1995, Diez et al. 2002). In addition, elevated temperature can stimulate higher microbial activity (Tank et al. 1993) and may result in faster decomposition of organic material in streams (Paul et al. 1978). Watershed disturbances that alter these controlling features may influence decomposition of wood in streams (Golladay and Webster 1988).

Streams in agricultural areas have elevated temperature and nutrients along with altered organic matter supply (Karr and Schlosser 1978). Altered physicochemical conditions in agricultural streams may cause dramatically different organic matter processing, but studies involving organic matter dynamics in agricultural streams are few (but see Benfield et al. 1977). Agricultural streams do not receive the same amount or type of organic material from their catchments, and wood is often the only remaining allochthonous detritus in the system (Rabeni and Hoel 2000). Therefore, the breakdown of wood in agricultural streams may be crucial to energy pathways that rely on allochthonous organic material. In addition to current agricultural activity, historical agriculture has been linked to current properties of stream ecosystems (Harding et al. 1998). Recovery of ecosystem function from historical influences requires that factors affecting these processes return to pre-disturbance conditions. If physical and chemical properties bestowed by past agricultural activity persist following reforestation, stream ecosystem processes moderated by these properties may remain altered.

Streams in the southern Appalachians have suffered from many anthropogenic insults over the past several centuries including mining, logging, and agriculture (Yarnell 1998). Agriculture in the region is now primarily pasture with small row-crop activities, primarily in bottomlands. Because of recent changes in the socioeconomic and political landscape of the southern Appalachians, large areas are converting from agriculture to forested land cover (Wear and Bolstad 1998). Many of these areas are undergoing suburban development along with reforestation on historically agricultural land (Wear and Bolstad 1998). Benthic communities in southern Appalachian streams have been related to current and historical agriculture (Harding et al. 1998), but the effects of reforestation on other properties of streams have not been studied. I used spatial and temporal patterns of reforestation of agricultural land to determine the influence of historical and current agriculture on wood decomposition and microbial biofilm activity on wood in southern Appalachian streams.

The objectives of this study were 1) to determine the effects of agriculture on stream physical and chemical conditions and to determine if streams in reforested areas show a legacy of historical agriculture, and 2) to compare wood breakdown and biofilm development in streams with different land-uses (current and historical) to assess the role of physical and chemical parameters in organic matter processes. Elevated nutrients and temperature in agricultural streams should cause higher microbial activity on wood substrates, which should result in faster breakdown rates of wood in agricultural streams. Furthermore, the legacy of historical agriculture might result in altered physical and chemical conditions in forested streams, which might affect organic matter processes despite catchment-scale reforestation.

Methods

Study sites

Study streams (2^{nd} and 3^{rd} order) were located in the southern Appalachian Mountains of western North Carolina and southwestern Virginia, USA (Figure 1). Headwater streams in the Blue Ridge physiographic province of the southern Appalachians are typically slightly acidic and have low conductivity and dissolved ion concentration reflecting granitic and micaceous parent lithology (Simmons and Heath 1979). Forests in the region are maturing second-growth (logged ~ 75-100 years ago) and are dominated by oak (*Quercus* spp.), yellow poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and white pine (*Pinus strobus*) with an understory of *Rhododendron*, mountain laurel (*Kalmia latifolia*), and dogwood (*Cornus florida*). Agricultural activity across the region is mainly cattle pasture with isolated row crop (primarily tobacco and corn). Agriculture occurs primarily in bottomland along streams, but many farmers have upland pastures. Riparian zones along agricultural streams frequently lack woody vegetation entirely or are vegetated with a narrow strip of trees, particularly black walnut (*Juglans nigra*), river sycamore (*Platanus occidentalis*), black locust (*Robinia pseudoacacia*), red maple, and oak (Neatrour et al. 2004).

Site selection and categorization

A total of 30 streams from select regions of the southern Appalachians of North Carolina and Virginia were used following a specific site selection procedure. I created a database of past land cover (% forest in 1950) and more recent land cover (1993) for watersheds in the southern Appalachians using a geographic information system (GIS). Land cover data and watershed boundaries were obtained from Coweeta Hydrologic Laboratory for 4 counties: Grayson County, Virginia; Buncombe, Macon, and Madison Counties, North Carolina. Land cover plots of 100 m width delineated riparian corridors for streams in each watershed with stream vectors centered in the plot (i.e., 50 m to each side of the stream) for the entire stream length. Forest cover was determined for each watershed and associated riparian corridor by overlaying these spatial zones on a land cover map from each year and quantifying % forest cover.

Site eligibility was restricted to watersheds with areas between 500 and 3000 ha and stream outlet elevations between 600 and 1000 m to help standardize for confounding factors (Resh et al. 1988). I categorized these 500 watersheds into 6 groups based on the historical and current amount of forest in their watersheds. Four categories were chosen to represent a gradient of extant agriculture with no change over time (FOR >98 % forest; AG-L 90-95 % forest; AG-M 70-80 % forest; AG-H < 60 % forest). Two categories were used to represent different stages of watershed recovery from agriculture by reforestation (REC-1 < 60 % forest in 1950 to > 80 % forest in 1993; REC-2 < 75 % forest in 1950 to > 90 % forest in 1993). Streams of the REC-1 category have undergone considerable reforestation (> 20 %) over the past 50 years, but they have less current forest cover than REC-2 streams. Forest cover in riparian corridors was used to verify category assignment, and streams with riparian forest cover that was dramatically different than watershed category designations were not considered for our study. Each category initially included 5 study streams based on site access, landowner cooperation, and on-site validation of category assignment. For each chosen stream, final catchment characterization was calculated for portions of the watershed up gradient of the specified study site. These spatial zones were whole watershed, 100-m riparian corridor, and 100-m riparian corridors 1 and 2 km upstream of each sampling site. Spatial restriction of land cover analysis to areas upstream of my study sites resulted in 2 sites having incorrect categories (see chapter 2 for more detailed explanation). I changed the categories of one REC-1 site to AG-M and one AG-M site to AG-H. This re-categorization resulted in an unbalanced design (REC-1, $n = 4$ and AG-H, $n = 6$). Figure 1 shows the appropriate categories for each site based on principle component analysis.

Physical and chemical characteristics

Physical and chemical characteristics were measured for each stream from November 2000 to October 2001. Most parameters (discharge, specific conductance, and water chemistry) were measured 6 times. Triplicate water samples were collected semi-monthly from each site, filtered in the field using pre-soaked membrane filters (Whatman nylon, 0.45-µm pore size), and frozen before analysis. Samples were analyzed for nitrate-nitrogen (NO_3-N) and ortho-phosphate (PO_4-P) using a Dionex DX500 Ion Chromatograph (Dionex Corporation, Sunnydale, California) and ammonium-nitrogen (NH_4-N) using the OPA fluorometric method (Holmes et al. 1999). Total dissolved inorganic nitrogen (DIN) was determined as the sum of NO_3-N and NH_4-N. Specific conductance was measured bi-monthly using a field probe (YSI Model 30/50 conductivity meter). Alkalinity was measured once at the beginning of the study using acid titration (APHA 1998). Discharge was measured semi-monthly at each site using average velocity determined with an electronic flow meter (FLOW-MATE, Marsh-McBirney, Inc., Frederick, Maryland) and cross-sectional area. Temperature was recorded every 6 hours during wood incubation (November 2000 through August 2001) using data loggers (HOBO Temp, Onset Corporation, Bourne, Massachusetts). Temperature data were converted to daily means, which were then used to calculate cumulative degree-days (above 0ºC). Physical variables measured once (watershed area, degree-days) were compared among forest cover categories using one-way ANOVA and sequential Bonferroni pair-wise comparisons. Variables measured repeatedly were compared among forest cover categories using one-way repeated measures ANOVA and sequential Bonferroni pair-wise comparisons. Variables not meeting assumptions of normality or homogeneity of variance were compared using ANOVA on Ranks with Dunn's pair-wise comparisons. All statistical analyses were performed in SAS version 8.0 (SAS Institute, Cary, NC).

Wood breakdown and microbial biofilm respiration

I cut white oak wood veneer into strips (2.5 cm x 15 cm, henceforth called sticks) and mounted 5 sticks onto plastic mesh (i.e., one set = 5 sticks) using cable ties (Tank and Webster 1998). Seven sets of sticks were anchored in each stream during autumn 2000 using a cable secured to a stake on the stream bank. Sets were spaced approximately 0.5 m apart along the cable in each stream. Twenty-five sticks were transported to each site and returned to the lab to serve as controls for handling losses and to determine initial ash-free dry mass (AFDM) and microbial respiration rates. Sets of 5 sticks were retrieved periodically over the next 9 months from each stream. Stick sets were collected and placed into sealed containers filled with stream water, which were placed on ice for transport to the laboratory.

The center section (4 cm x 2.5 cm) of each stick was removed for determination of respiration by the microbial biofilm. The remainder of each stick was dried (50°C) to constant weight and ashed at 500°C to determine AFDM. Following the respiration assay, AFDM was determined for the center section each stick and added to AFDM values from the respective stick ends to determine total AFDM remaining for each stick. Breakdown rate (*k*) was calculated for each stream by regressing the natural log of percent AFDM remaining against incubation time (Petersen and Cummins 1974). Breakdown rates were calculated using days and degree-days to correct rates for potential temperature differences among the sites (Webster and Benfield 1986). Using degree-days did not improve the fit of decay models (no significant increase in r^2), so I reported breakdown rates calculated by days. Differences in *k* among land-use categories were determined using one-way ANOVA and sequential Bonferroni pair-wise comparisons.

Microbial respiration was measured on sticks using a carbon dioxide production assay in the laboratory. Each assay used 5 sticks per site along with a control for each stream (20 mL of filtered stream water with no wood). Each stick was placed into a 40-mL EPA vial with 20 mL of filtered stream water from its respective stream. Samples were equilibrated to incubation temperature (average ambient stream temperature on the retrieval date) in the dark prior to sealing the vials with Teflon-coated silicon caps. Samples were then incubated in the dark for 18 hours. After incubation, a 1-mL gas sample was collected from the headspace of each vial and saved in pre-vacuumed borosilicate glass containers. Gas samples were then analyzed for CO_2 using a gas chromatograph equipped with a thermal conductivity detector. Headspace CO_2 concentrations were converted to water CO_2 using Henry's law and the depth and surface area of gas exchange in the vial. CO_2 concentrations were then corrected for filtered stream water controls. Sticks used in the respiration assay were oven dried and ashed to determine AFDM. I calculated microbial respiration rate by dividing control-adjusted CO_2 production by stick surface area and AFDM. Respiration values were compared using two-way ANOVA with time and land-use category as factors and streams as replicates. I used linear regression to explore relationships between stream physicochemistry, breakdown rates, and biofilm respiration. In addition, I quantified inorganic material on wood by subtracting AFDM from total dry weight and used this measurement as another possible factor affecting breakdown and biofilm respiration.

Results

Land cover

Percent forest cover was higher in 1993 than in 1950 in all categories, and % forest was lower in riparian corridors 1 and 2 km upstream of sampling sites than at a whole-watershed scale (Table 1). Forest cover in the riparian corridor 1 km of the heavily forested (FOR) sites was > 95% in both 1950 and 1993, but riparian forest cover was < 30% both in 1950 and 1993 for AG-H sites. Forest cover increased from 1950 to 1993 in watersheds and riparian zones of both classes of recovering catchments (REC-1 and REC-2). By 1993, % forest in the 100-m wide riparian corridor of the recovering catchments was 85.4% in REC-1 sites and 94.6% in REC-2 sites. REC-1 sites also had lower % forest cover (66.4%) than REC-2 sites (84.4%) within the riparian area 1 km upstream of the study sites in 1993. In 1950, riparian forest cover 1 km upstream of REC-1 sites was only 29%, while REC-2 sites had 62.4% forest cover in the same zone, which suggests that REC-1 sites were historically more heavily influenced by agriculture than REC-2 sites.

Physical and chemical characteristics

Elevation among sites varied from 576 to 861 m and was not significantly different among categories (Table 2). Watershed area varied from 320.5 to 2130.5 ha. AG-L and AG-M watersheds were significantly ($P < 0.05$) larger than FOR and REC-2 watersheds. Discharge was not significantly different among categories. Mean discharge for each forest cover category was typically around 65 L / s but varied from 29 to 102 L / s among study sites. Specific conductance varied from 11.9 to 98.4 µS / cm and was highest in AG-L streams. Alkalinity varied from 4 to 21 mg $CaCO_3$ / L among sites and was significantly lower in FOR streams compared with AG-M and AG-H streams.

DIN varied from 21 to 1118 µg / L among sites and was significantly higher in AG-H streams than in FOR, AG-L, and REC-2 streams (Table 2). DIN values for AG-M and REC-1 streams fell between values for AG-H and REC-2 streams. PO_4-P varied from 3 µg / L to 25 µg / L among sites and did not differ significantly among categories. Cumulative degree-days above 0ºC from November 2000 to August 2001 varied from 2172 to 3218 among sites. Degree-days were significantly higher in high agriculture (AG-H) and medium agriculture (AG-M) streams compared to long-term forested (FOR), low agriculture (AG-L), and reforested (REC-2) streams. Degree-days were significantly higher in slightly reforested (REC-1) streams than FOR streams, but the differences among REC-1 streams and other categories was not significant.

Wood breakdown and microbial biofilm respiration

Wood breakdown rate varied from 0.0015 to 0.0076 d^{-1} among all sites. Breakdown rates were slowest in FOR streams and fastest in REC-1 streams, but there were no significant differences among categories (Figure 2; ANOVA, $P = 0.341$). Biofilm respiration increased with time in the stream on all wood substrates (Figure 3; two-way ANOVA, $P < 0.001$), but respiration did not differ among land-use categories, either overall or within months. Respiration on wood not incubated in the streams was negligible (0.000001 mg CO_2 g $AFDM^{-1}$ h^{-1}), and respiration in all months was higher than initial conditions. Respiration was significantly higher in April, June, and August compared to January and was significantly higher than April in June only (Figure 3; two-way ANOVA, $P < 0.05$). Within categories, respiration was significantly lower in January than in April, June, and August for all categories except AG-H. Mean respiration in AG-H streams more than doubled from January (0.0439 mg CO_2 g $AFDM^{-1}$ h^{-1}) to August (0.0975 mg CO_2 g $AFDM^{-1}$ h^{-1}), but this difference was not significant.

Neither breakdown rates nor respiration rates were correlated with land-use at any time or spatial scale. Furthermore, breakdown rates and respiration rates were not significantly related to nutrients or temperature. However, biofilm respiration activity could be used to predict breakdown rate (Figure 4; $r^2 = 0.504$, $P < 0.001$), suggesting that microbes play a critical role in determining rate of wood breakdown. The amount of inorganic material accumulated on wood substrates was not significantly different among land-use categories but was negatively correlated with both breakdown rate (Figure 5; $r^2 = 0.317$, $P = 0.001$) and biofilm respiration (Figure 5; $r^2 = 0.347$, $P < 0.001$).

Discussion

Physical and chemical responses to land use

Streams showed elevated nutrients and temperature in response to historical and current agriculture. Streams in different categories were not significantly different in elevation or discharge making land use the factor likely to have caused physical and chemical differences in streams. Other studies have demonstrated elevated nutrients and temperature in agricultural streams (e.g., Karr and Schlosser 1978, Peterjohn and Correll 1984, Lowrance et al. 1985). Historical agriculture had a persistent effect on water chemistry but not on water thermal regime. DIN concentrations in recovering streams were between values for streams with medium and low amounts of agriculture in their catchments, which suggests that nutrient concentrations might be declining in reforesting streams. However, elevated nutrients in streams have been observed decades following logging in the southern Appalachians (Swank and Vose 1997). Forest development in historically agricultural watersheds was likely dense enough to shade streams resulting in lower stream temperatures than agricultural streams. Swift (1983) showed that stream temperature recovers quickly (within 5 years) during reforestation from clear-cutting. However, reforestation on abandoned agriculture generally takes longer than reforestation from logging because soils are compacted by livestock or farm machinery (Myster and Pickett 1994). Fifty years appears to be enough time for streams to establish a pre-agriculture temperature regime as a result of reforestation.

Wood breakdown and microbial biofilm respiration

Breakdown rates in this study (0.0015-0.0076 d^{-1}) were similar to other studies using wood veneer to assess breakdown in streams of the southern Appalachians (Tank and Webster 1998, Simon and Benfield 2001) but were much faster than breakdown of natural sticks (Golladay and Webster 1988, Webster et al. 1999). Accelerated breakdown of wood veneers has been attributed to the high surface area: volume ratio compared with natural sticks or larger wood pieces (Tank and Webster 1998). Other studies have found that wood size affects breakdown rate (e.g., Melillo et al. 1983, Sinsabaugh et al. 1992, Diez et al. 2002). The wood veneer breakdown rates reported here were much faster than those found using small sticks in southern Appalachian streams (e.g., Webster et al. 1999) but serve as a comparison of organic matter dynamics among land-use categories. Furthermore, microbial biofilm respiration in my study (1 - 4 $\mu g\ CO_2\ cm^{-2}\ h^{-1}$) was similar to values reported for other studies using veneers (~ 4 $\mu g\ CO_2\ cm^{-2}\ h^{-1}$; Tank and Webster 1998) but was higher than natural wood substrates (~ 0.35 $\mu g\ CO_2\ cm^{-2}\ h^{-1}$; Tank et al. 1993). At the same time, biofilm respiration reported from wood veneers in cave streams was approximately 2x higher than values reported here (Simon and Benfield 2001).

Factors controlling breakdown rate and microbial respiration

Higher nutrient concentrations and temperature were expected to stimulate microbial activity and hence increase breakdown rate because microbes are primarily responsible for wood breakdown in streams (Sinsabaugh et al. 1992). Agricultural streams did have higher DIN concentrations and accumulated more degree-days during wood incubation than forested streams. However, neither wood breakdown nor biofilm respiration was correlated with nutrient concentration or temperature. Increased microbial activity on organic matter has been linked to higher ambient nutrient concentrations (Howarth and Fisher 1976, Tank and Webster 1998), and nutrient concentration has been linked to organic matter breakdown rates (Elwood et al. 1981, Suberkropp and Chauvet 1995, Diez et al. 2002). Meyer and Johnson (1983) found faster leaf breakdown due to increased nitrate concentrations in a stream reforested from experimental agriculture. Other studies have documented that increasing temperature can result in higher microbial activity on organic matter (Tank et al. 1993) and faster organic matter breakdown (Paul et al. 1978, Short and Ward 1980). Data from the present study do not support the role of nutrient availability or temperature in biofilm activity or organic matter breakdown because agricultural streams had higher nutrients and temperature but similar biofilm respiration and wood breakdown rates.

While little evidence linked organic matter dynamics to extrinsic features like nutrient concentration or temperature, there was a strong relationship between wood breakdown rate and biofilm respiration suggesting that microbial activity determines breakdown rate. Many of the sticks collected, especially from agricultural streams, were covered in silt and fine sand, and this material did not wash off prior to the respiration assay. In fact, amount of inorganic material accumulated on wood was the only physical or chemical variable correlated with breakdown rate and biofilm respiration. Increased sediment transport and deposition is one of the primary influences of agriculture on streams (Waters 1995), and research has shown reduced breakdown rates of organic matter as a result of burial in sediment (Herbst 1980, Rounick and Winterbourn 1983). Webster and Waide (1982) blamed sedimentation from road construction for slower breakdown of leaves in logged watersheds at Coweeta Hydrological Laboratory. In addition, leaf breakdown was slower in streams with smaller substrate particle size as a result of human-influence (Sponseller and Benfield 2001). My findings of slower microbial respiration and wood breakdown associated with accumulations of fine sediment on wood agree with these studies and suggest that sediment deposition may have more influence on organic matter dynamics in streams severely influenced by agriculture.

From this observation, agriculture may have two potential, and conflicting, influences on organic matter processing in streams. Agriculture can increase nutrients and temperature in streams, which can cause higher microbial biofilm activity and faster breakdown. Conversely, agricultural streams can carry a high sediment load, which may accumulate on biofilms, reduce microbial activity, and slow breakdown. Sediment accumulation on biofilms is likely to reduce of eliminate the supply of water, dissolved nutrients, and oxygen (Herbst 1980). Indeed, many sticks retrieved from streams were blackened and smelled of hydrogen sulfide indicating the presence of anoxic conditions on the wood surface. Biofilms typically exist within a polysaccharide matrix that protects microbes, facilitates intercellular communication, and allows for extracellular enzyme activity (Lock 1993, Ben-Ari 1999). This matrix may create a sticky surface on wood that facilitates the trapping of sediment particles in transport in streams (see Peterson 1986), thereby degrading conditions for wood breakdown. In addition to physical and chemical effects of agriculture, agricultural streams may have reduced abundance of shredder invertebrates (Benfield et al. 1977), which could potentially slow breakdown of organic matter if shredders play in important role (e.g., leaves). However, microbial biofilm activity was fast enough to facilitate leaf breakdown in an agricultural stream despite low shredder abundance

(Benfield et al. 1977). Shredder abundance was much lower in agricultural streams than forested streams (see chapter 2), but shredder abundance was not related to breakdown rate (data not shown), and shredder activity was not evident from inspection of sticks upon retrieval.

Utility of wood breakdown to assess stream ecosystem integrity

In recent years, investigations of human influence on ecosystems have gone beyond assessing the structure of communities and are now considering process rates as integral components of ecosystem integrity (Bunn and Davies 2000, Gessner and Chauvet 2002). While ecosystem processes are critical for defining a "healthy" ecosystem, incorporating them into assessment protocols relies on several factors. In order for a metric to be useful to bioassessment, it must have 1) a predictable directional response to human disturbance; 2) a gradient response (i.e., larger disturbance, larger response); 3) low variability within reference conditions; 4) sensitivity to different types of stresses; and 5) simple measurement and interpretation (Karr and Chu 1997, Smith and Voshell 1997). Leaf breakdown in streams has been extensively studied and may be suitable to incorporate into bioassessment protocols (Gessner and Chauvet 2002). Studies of wood in human-influenceed streams may integrate influences over longer periods than leaves because wood is a longer-lasting organic component in streams. Further, wood may be a more appropriate component to address given the potential for land use to alter the supply of more ephemeral resources, such as leaves.

Gessner and Chauvet (2002) recommended incorporating leaf breakdown into bioassessment protocols and suggested ranges of acceptable breakdown rates to indicate healthy or impaired systems. Leaf breakdown has been the subject of extensive study (see reviews by Anderson and Sedell 1979, Webster and Benfield 1986, Boulton and Boon 1991). Leaf breakdown and the factors controlling it are understood well enough for scientists to begin recognizing rates that deviate dramatically from "normal." On the other hand, wood breakdown is not as well understood. Do wood dynamics show similar promise as useful for bioassessment in streams? Much previous research about wood in streams focused on the role it plays as a structural feature (e.g., Bilby and Likens 1980, Harmon et al. 1986), but fewer studies have explored wood breakdown, particularly in anthropogenically-altered systems. Based on the present study, agricultural streams had higher nutrients and temperature suggesting higher microbial biofilm activity and faster breakdown. However, agricultural streams also have high sediment loads, which may inhibit microbial activity on wood substrates. With these offsetting influences, agriculture showed no net influence on wood breakdown because the stimulation from temperature and nutrients is offset by the accumulation of fine inorganic material on the wood. Organic matter dynamics in human altered systems might include a mosaic of rapidly processed material (i.e., leaves), which relies more heavily on macroinvertebrate activity for breakdown, and slowly processed material (i.e., wood), which relies on microbial processes for breakdown. Considering decomposition of different types of organic matter along this processing spectrum might provide insight into how different factors that control organic matter processes are influenced by land use and ultimately how humans influence organic matter processes.

Acknowledgments

Funding for this project was provided by Sigma Xi, the Graduate Student Assembly and Biology Department of Virginia Tech, and the National Science Foundation grant DEB9632854 to the Coweeta Long-term Ecological Research site. Special thanks to all the landowners who gave me access to their properties and provided many anecdotes about the history of the region and their land. I would also like to thank the Virginia Tech Stream Team for valuable help in data collection and Paul Bolstad and Ned Gardiner for providing GIS data.

Literature Cited

Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351-377.

APHA (American Public Health Association, American Water Works Association, and Water Environment Federation). 1998. Standard methods for the examination of water and wastewater, 20th edition. American Public Health Association, Washington, DC.

Ben-Ari, E. T. 1999. Not just slime. Bioscience 49:689-695.

Benfield, E. F., D. S. Jones, and M. F. Patterson. 1977. Leaf pack processing in a pastureland stream. Oikos 29:99-103.

Boulton, A. J., and P. I. Boon. 1991. Review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf? Australian Journal of Marine and Freshwater Research 42:1-43.

Bunn, S. E., and P. M. Davies. 2000. Biological processes in running waters and their implications for the assessment of ecological integrity. Hydrobiologia 422/423:61-70.

Diez, J., A. Elosegi, E. Chauvet, and J. Pozo. 2002. Breakdown of wood in the Aguera stream. Freshwater Biology 47:2205-2215.

Elwood, J. W., J. D. Newbold, A. F. Trimble, and R. W. Stark. 1981. The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. Ecology 62:146-158.

Gessner, M. O., and E. Chauvet. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75:1807-1817.

Gessner, M. O., and E. Chauvet. 2002. A case for using litter breakdown to assess functional stream integrity. Ecological Applications 12:498-510.

Golladay, S. W., and R. L. Sinsabaugh. 1991. Biofilm development on leaf and wood surfaces in a boreal river. Freshwater Biology 25:437-450.

Golladay, S. W., and J. R. Webster. 1988. Effects of clearcut logging on wood breakdown in Appalachian mountain streams. American Midland Naturalist 119:143-155.

Harding, J. S., E. F. Benfield, P. V. Bolstad, G. S. Helfman, and E. B. D. Jones, III. 1998. Stream biodiversity: the ghost of land use past. Proceedings of the National Academy of Science 95:14843-14847.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302.

Herbst, G. N. 1980. Effects of burial on food value and consumption by aquatic invertebrates in a lowland forest stream. Oikos 35:411-424.

Holmes, R. M., A. Aminot, R. Kerouel, B. A. Hooker, and B. J. Peterson. 1999. A simple and precise method for measuring ammonium in marine and freshwater ecosystems. Canadian Journal of Fisheries and Aquatic Sciences 56:1801-1809.

Howarth, R. W., and S. G. Fisher. 1976. Carbon, nitrogen, and phosphorus dynamics during leaf decay in nutrient enriched stream microecosystems. Freshwater Biology 6:221-228.

Isphording, W. C., and J. F. Fitzpatrick, Jr. 1992. Geologic and evolutionary history of drainage systems in the southeastern United States. Pages 19-56 *in* C. T. Hackney and S. M. Adams, editors. Biodiversity of the southeastern United States, aquatic communities. John Wiley & Sons, New York, New York, USA.

Karr, J. R., and E. W. Chu. 1997. Biological monitoring and assessment: using multimetric indexes effectively. EPA 235-R97-001. University of Washington, Seattle, Washington, USA.

Karr, J. R., and I. J. Schlosser. 1978. Water resources and the land-water interface. Science 201:229-234.

Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. Applied regression analyses and other multivariate methods. Kent Publishing Company, Boston, Massachusetts, USA.

Lock, M. A. 1993. Attached microbial communities in rivers. Pages 113-138 *in* T. E. Ford, editor. Aquatic microbiology: an ecological approach. Blackwell Scientific Publications, Oxford, United Kingdom.

Lowrance, R. R., R. A. Leonard, L. E. Asmussen, and R. L. Todd. 1985. Nutrient budgets for agricultural watersheds in the southeastern coastal plain. Ecology 66:287-296.

Melillo, J. M., R. J. Naiman, J. D. Aber, and K. N. Eshleman. 1983. The influence of substrate quality and stream size on wood decomposition dynamics. Oecologia 58:281-285.

Meyer, J. L., and C. Johnson. 1983. The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. Freshwater Biology 13:177-183.

Myster, R. W., and S. T. A. Pickett. 1994. A comparison of rate of succession over 18 yr. in 10 contrasting old fields. Ecology 75:387-392.

Neatrour, M. A., J. R. Webster, and E. F. Benfield. 2004. The role of floods in particulate organic matter dynamics of a southern Appalachian river-floodplain ecosystem. Journal of the North American Benthological Society 23:198-213.

Paul, R. W., Jr., E. F. Benfield, and J. Cairns, Jr. 1978. Effects of thermal discharge on leaf decomposition in a river ecosystem. Verhandlung der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 20:1759-1766.

Peterjohn, W. T., and D. L. Correll. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology 65:1466-1475.

Peterson, C. G. 1986. Influences of flow regime on development and desiccation response of lotic diatom communities. Ecology 68:946-954.

Rabeni, C. F., and S. M. Hoel. 2000. The importance of woody debris to benthic invertebrates in two Missouri prairie streams. Verhandlung der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 27:1499-1502.

Rounick, J. S., and M. J. Winterbourn. 1983. Leaf processing in two contrasting beech forest streams: effects of physical and biotic factors on litter breakdown. Archiv fur Hydrobiologie 96:448-474.

Short, R. A., and J. V. Ward. 1980. Leaf litter processing in a regulated rocky mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 37:123-127.

Simmons, C. E., and R. C. Heath. 1979. Water-quality characteristics of streams in forest and rural areas of North Carolina. Pages B1-B33 *in* Water quality of North Carolina streams. Geological Survey Water-Supply Paper 2185 A-D. North Carolina Department of Natural and Economic Resources, Raleigh, North Carolina, USA.

Simon, K. S., and E. F. Benfield. 2001. Leaf and wood breakdown in cave streams. Journal of the North American Benthological Society 20:550-563.

Sinsabaugh, R. L., R. K. Antibus, A. E. Linkins, C. A. McClaughtery, L. Rayburn, D. Repert, and T. Weiland. 1992. Wood decomposition over a first order watershed: mass loss as a function of lignocellulase activity. Soil Biology and Biochemistry. 24:743-749.

Smith, E. P., and J. R. Voshell, Jr. 1997. Studies of benthic macroinvertebrates and fish in streams within EPA Region 3 for development of biological indicators of ecological condition, part 1: benthic macroinvertebrates. EPA Report No. CF821462010. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Sponseller, R. A., and E. F. Benfield. 2001. Influences of land use on leaf breakdown in southern Appalachian headwater streams: a multiple-scale analysis. Journal of the North American Benthological Society 20:44-59.

Suberkropp, K., and E. Chauvet. 1995. Regulation of leaf breakdown by fungi in streams: influences of water chemistry. Ecology 76:1433-1445.

Swank, W. T., and J. M. Vose. 1997. Long-term nitrogen dynamics of Coweeta forested watersheds in the southeastern United States of America. Global Biogeochemical Cycles 11:657-671.

Swift, L. W., Jr. 1983. Duration of stream temperature increases following forest cutting in the southern Appalachian mountains. Pages 273-275 *in* A. I. Johnson and R. A. Clark, editors. International Symposium on Hydrometeorology. American Water Resources Association, Bethesda, Maryland, USA.

Tank, J. T., and J. R. Webster. 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. Ecology 79:2168-2179.

Tank, J. L., and M. J. Winterbourn. 1995. Biofilm development and invertebrate colonization of wood in four New Zealand streams of contrasting pH. Freshwater Biol. 34:303-315.

Tank, J. L., J. R. Webster, and E. F. Benfield. 1993. Microbial respiration on decaying leaves and sticks in a southern Appalachian stream. Journal of the North American Benthological Society 12:394-405.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102-104.

Waters, T. F. 1995. Sediment in streams; sources, biological effects and control. American Fisheries Society Monograph 7. Bethesda, Maryland, USA.

Wear, D. N., and P. Bolstad. 1998. Land-use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567-594.

Webster, J. R., and J. L. Meyer. 1997. Stream organic matter budgets. Journal of the North American Benthological Society 16:3-161.

Webster, J. R., and J. B. Waide. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. Freshwater Biology 12:331-344.

Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens, and D. J. D'angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41:687-705.

Webster, J. R., J. L. Tank, J. B. Wallace, J. L. Meyer, S. L. Eggert, T. P. Ehrman, B. R. Ward, B. L. Bennett, P. F. Wagner, and M. E. McTammany. 2000. Effects of litter exclusion and wood removal on phosphorus and nitrogen retention in a forest stream. Verhandlungen der Internationalen Vereinigung fur theoretische und angewandte Limnologie 27:1337-1340.

Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens, and D. J. D'angelo. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41:687-705.

Yarnell, S. L. 1998. The southern Appalachians: a history of the landscape. General Technical Report SRS-18. U. S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA.

Table 1. Historical and current forest cover (%) at different spatial scales for streams in each forest cover category. Percent forest cover of sites in "extant" categories has remained constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Lateral spatial scale is indicated by WS (whole watershed) or RIP (100-m riparian corridor). Extent refers to longitudinal spatial scale. Values are means for each category ± 1 SE.

Spatial scale			Extant				Recovering	
Lateral	Extent	Year	FOR	AG-L	AG-M	AG-H	REC-1	REC-2
WS	Whole catchment	1950	99.9 ± 0.1	87.5 ± 3.0	60.0 ± 6.3	52.7 ± 6.5	79.6 ± 5.2	77.6 ± 7.8
WS	Whole catchment	1993	99.3 ± 0.3	94.9 ± 1.9	83.6 ± 2.8	74.1 ± 4.8	94.9 ± 1.0	94.8 ± 1.1
RIP	Whole stream	1950	99.8 ± 0.2	84.2 ± 3.1	42.0 ± 8.0	29.3 ± 3.8	57.5 ± 8.4	75.5 ± 6.9
RIP	Whole stream	1993	99.9 ± 0.1	96.3 ± 0.9	72.2 ± 5.2	58.4 ± 2.3	85.4 ± 3.0	94.6 ± 2.0
RIP	2 km corridor	1950	99.7 ± 0.3	74.6 ± 3.8	13.7 ± 4.7	11.3 ± 5.1	40.4 ± 11.6	71.7 ± 6.1
RIP	2 km corridor	1993	96.8 ± 1.2	89.2 ± 3.0	47.7 ± 5.2	32.2 ± 6.6	76.7 ± 4.9	91.2 ± 1.4
RIP	1 km corridor	1950	99.1 ± 0.9	58.6 ± 12.2	12.6 ± 3.8	9.6 ± 3.5	29.0 ± 11.7	62.4 ± 6.3
RIP	1 km corridor	1993	96.6 ± 1.3	78.1 ± 12.1	43.8 ± 4.2	25.5 ± 7.5	66.4 ± 4.9	84.4 ± 3.7

Table 2. Physical and chemical characteristics of study sites by forest cover category. Values are means with standard errors in parentheses. Means with different superscripts are significantly different ($P < 0.05$). Discharge, specific conductance, dissolved inorganic nitrogen (DIN), and phosphorus (PO_4-P) were measured semi-monthly at each site from November 2000 to August 2001.

	Extant				Recovering	
	FOR ($n = 5$)	AG-L ($n = 5$)	AG-M ($n = 5$)	AG-H ($n = 6$)	REC-1 ($n = 4$)	REC-2 ($n = 5$)
Elevation (m)	767 (25)	710 (44)	641 (32)	676 (24)	754 (45)	776 (37)
Watershed area[1] (ha)	617.6^{a} (149.1)	1403.2^{bc} (175.0)	1842.5^{c} (92.0)	1311.8^{abc} (247.4)	667.0^{ab} (154.2)	599.8^{a} (166.5)
Discharge (L / s)	69.6 (4.2)	91.7 (3.9)	63.6 (7.6)	62.1 (10.4)	66.6 (9.1)	62.9 (6.2)
Specific conductance[2] (µS / cm)	20.1^{a} (2.8)	72.1^{c} (9.0)	31.6^{ab} (4.8)	38.0^{ab} (4.0)	58.7^{bc} (10.9)	52.9^{bc} (10.0)
Alkalinity[3] (mg $CaCO_3$ / L)	5.4^{a} (0.5)	7.4^{ab} (1.3)	13.0^{b} (1.5)	13.7^{b} (2.4)	11.5^{ab} (1.6)	10.6^{ab} (1.1)
DIN[2] (µg / L)	93^{a} (34)	109^{a} (37)	420^{ab} (127)	643^{b} (111)	287^{ab} (90)	244^{a} (55)
PO_4-P (µg / L)	4 (1)	8 (4)	11 (4)	8 (2)	11 (3)	10 (3)
Degree-days[1]	2543^{a} (62)	2600^{ab} (109)	3013^{c} (88)	3158^{c} (117)	2844^{bc} (88)	2546^{ab} (49)

[1] Differences determined with ANOVA and sequential Bonferroni pair-wise comparisons.
[2] Differences determined with RM ANOVA and sequential Bonferroni pair-wise comparisons
[3] Differences determined with ANOVA on ranks and Dunn's pair-wise comparisons.

Figure captions

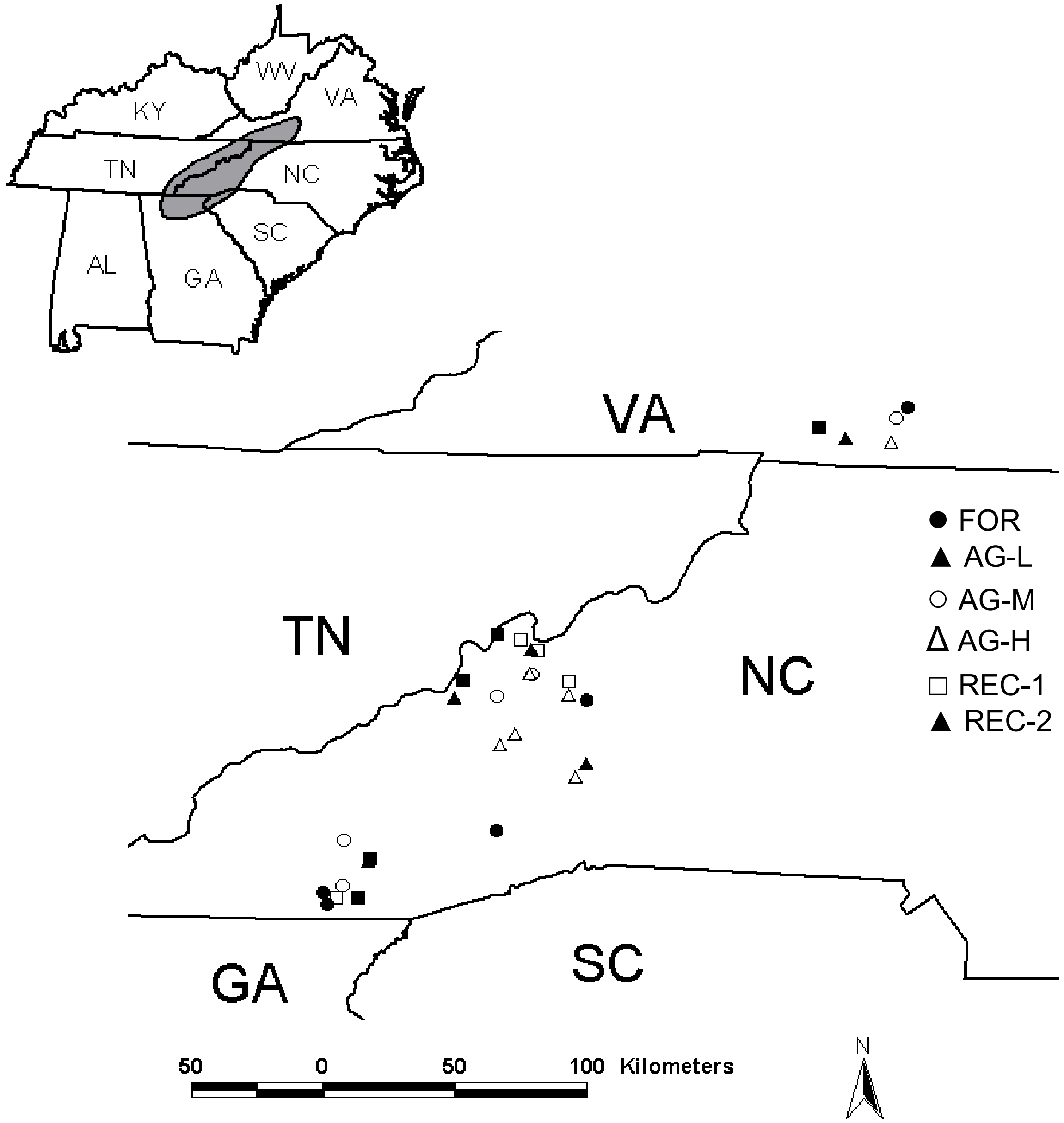
Figure 1. Map showing study sites in relation to the area of the southern Appalachian portion of the Blue Ridge physiographic province (inset). Study sites are categorized according to historical and current forest cover.

Figure 2. Mean breakdown rates of wood in each forest cover category (+ 1 SE). Forest cover of sites in "extant" categories has remained relatively constant since 1950, and sites in "recovering" categories are in different stages of reforestation. Breakdown rates were not significantly different among categories (one-way ANOVA, $P > 0.05$).

Figure 3. Respiration rates of microbial biofilm on wood after incubation in streams expressed per unit mass of wood (mg CO_2 AFDM^{-1} h^{-1}). Day 0 corresponded to date wood was deployed in the streams (1-4 December 2000). Retrievals were made in January, April, June, and August 2001. Respiration rates for day 0 were determined using handling loss controls, and other values are means ± 1 SE for each category on each sampling date.

Figure 4. Breakdown rates (d^{-1}) as a function of microbial biofilm respiration (mg CO_2 g AFDM^{-1} h^{-1}) on the last wood retrieval. Relationships were analyzed using simple linear regression.

Figure 5. Breakdown rates (d^{-1}) and microbial biofilm respiration (mg CO_2 g AFDM^{-1} h^{-1}) as a function of the amount of inorganic sediment (mg / cm^2) accumulated on wood substrates during incubation in streams.



KY
WV
VA
TN
NC
SC
AL
GA
VA
TN
NC
GA
SC
● FOR
▲ AG-L
○ AG-M
Δ AG-H
□ REC-1
▲ REC-2
50
0
50
100 Kilometers
N

FIGURE 1

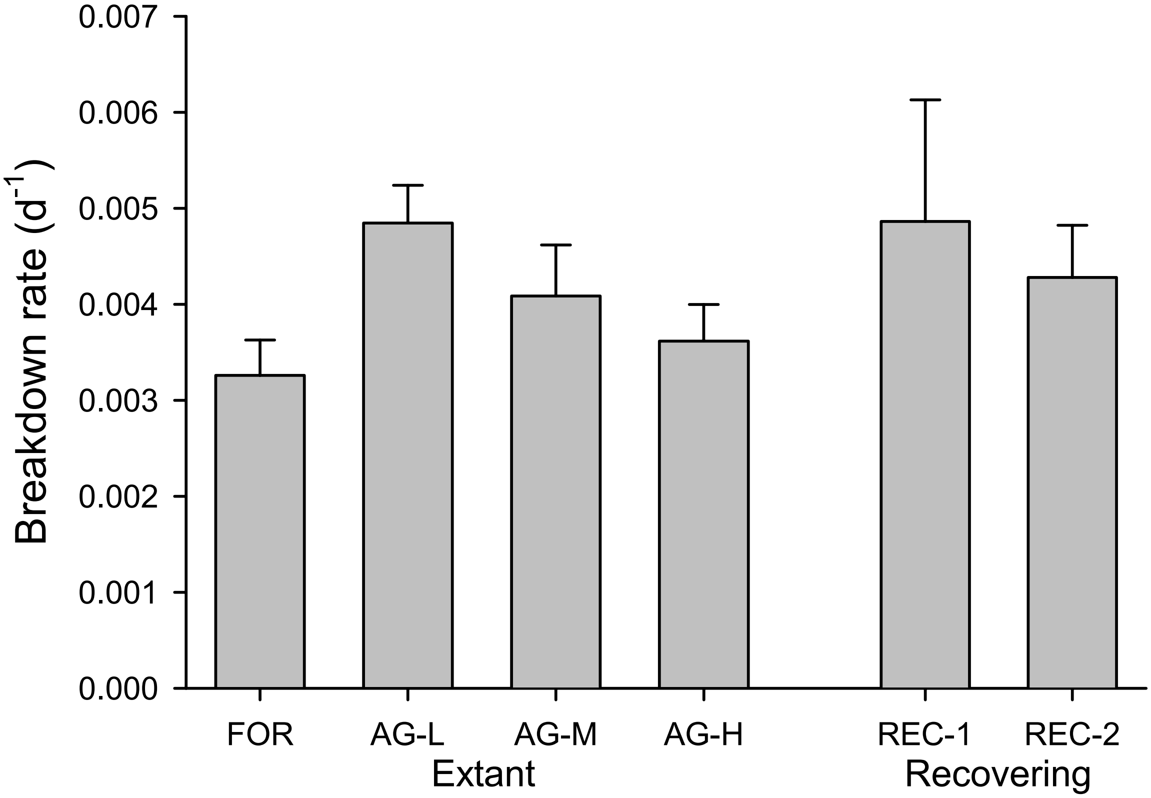

0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
Breakdown rate (d^{-1})
FOR
AG-L
AG-M
AG-H
REC-1
REC-2
Extant
Recovering

FIGURE 2

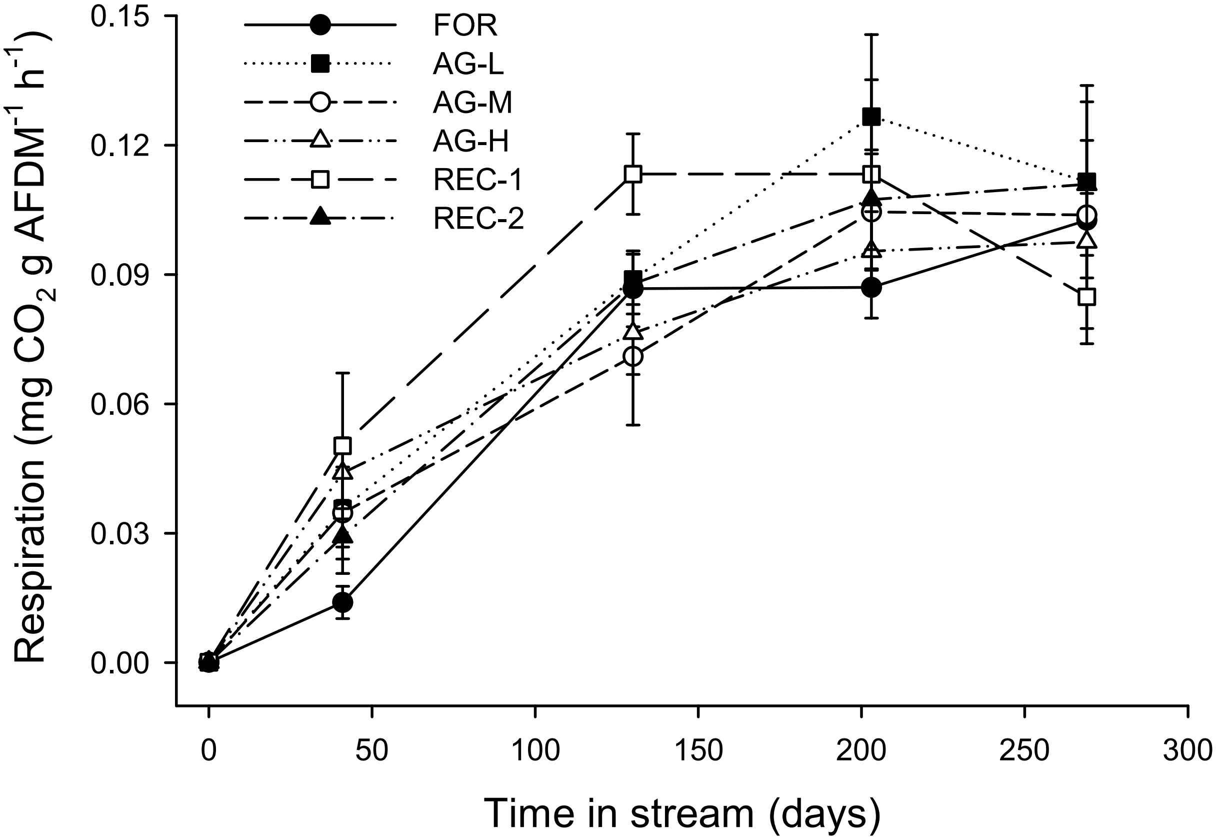

Respiration (mg CO2 g AFDM-1 h-1)
0.15
0.12
0.09
0.06
0.03
0.00
0
50
100
150
200
250
300
Time in stream (days)
FOR
AG-L
AG-M
AG-H
REC-1
REC-2

FIGURE 3

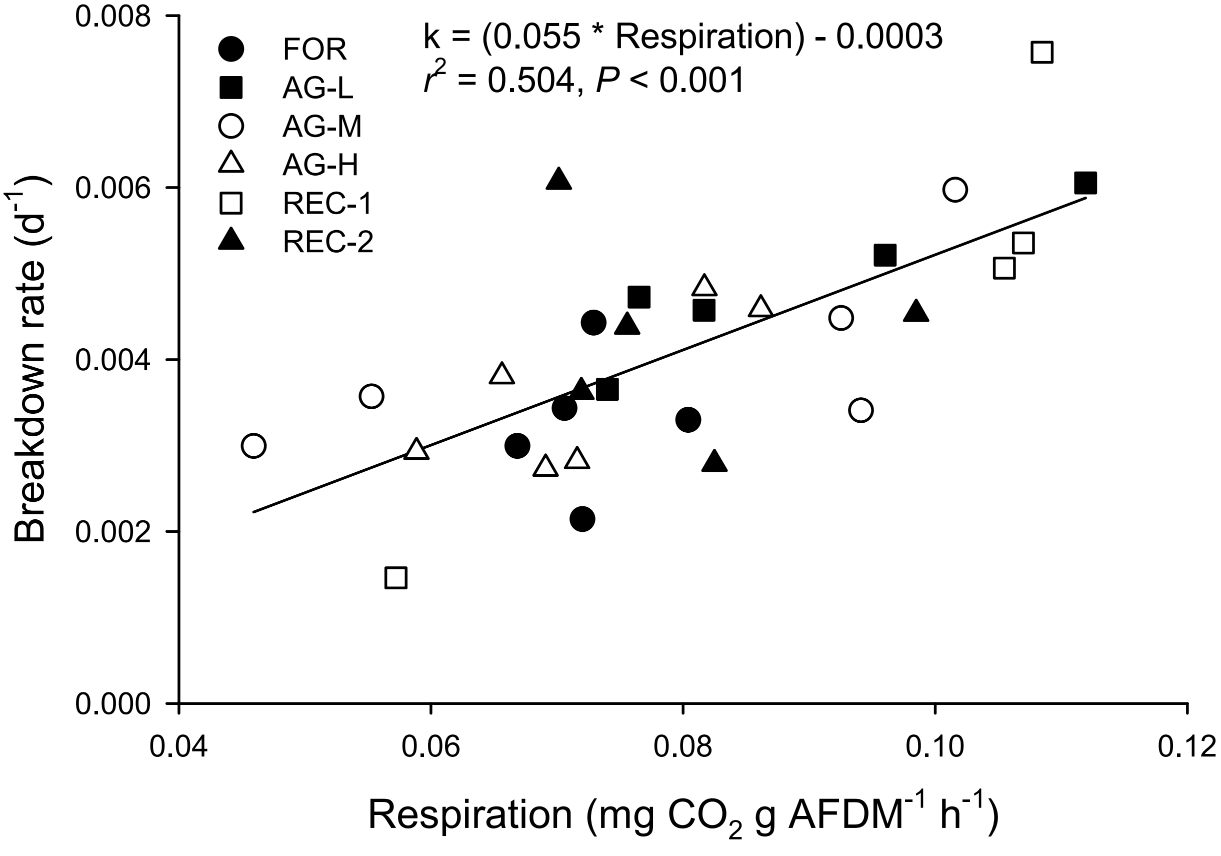

0.008
0.006
0.004
0.002
0.000
0.04
0.06
0.08
0.10
0.12
● FOR
■ AG-L
○ AG-M
△ AG-H
□ REC-1
▲ REC-2
k = (0.055 * Respiration) - 0.0003
r^2 = 0.504, P < 0.001
Breakdown rate (d^{-1})
Respiration (mg CO_2 g $AFDM^{-1}$ h^{-1})

FIGURE 4

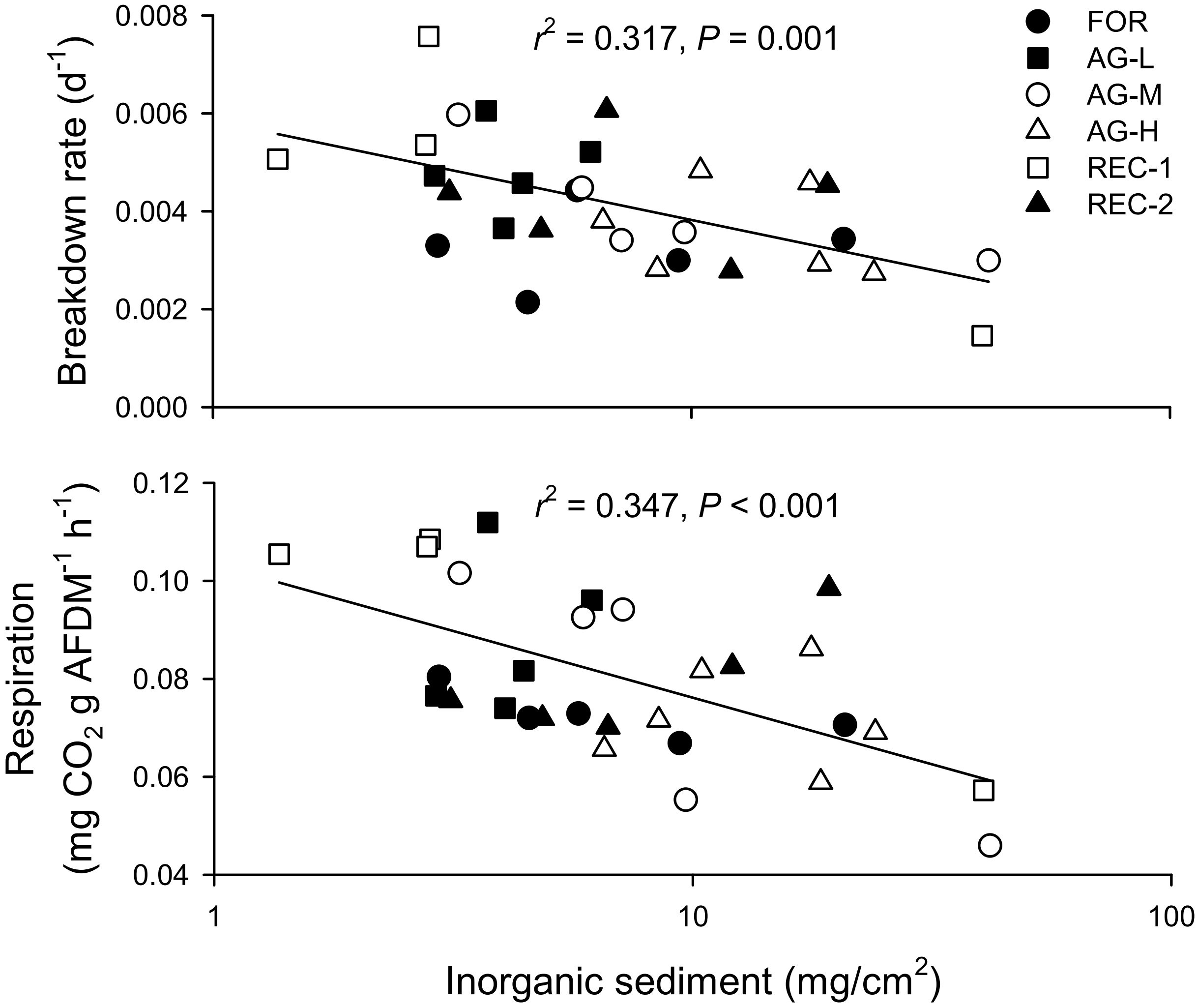

0.008
0.006
0.004
0.002
0.000
Breakdown rate (d^{-1})
r^2 = 0.317, P = 0.001
● FOR
■ AG-L
○ AG-M
△ AG-H
□ REC-1
▲ REC-2
0.12
0.10
0.08
0.06
0.04
Respiration (mg CO$_2$ g AFDM^{-1} h^{-1})
r^2 = 0.347, P < 0.001
1
10
100
Inorganic sediment (mg/cm^2)

FIGURE 5

CHAPTER 5

Synthesis

Resistance and resilience determine how stable an ecosystem will be when confronted with a disturbance (Holling 1973, Webster et al. 1975). Stream ecosystems are generally thought to have low resistance but high resilience to disturbances (Webster et al. 1983, Fisher 1990). However, different properties of streams might be more resistant or resilient than others, and the nature of the disturbance might affect the stability of different properties of streams. Agriculture is a disturbance at broad spatial and temporal scales and impacts streams through several different pathways. Therefore, it seems reasonable to think that different stream properties will respond to agricultural disturbance more or less severely (be more or less resistant) and that these different impacts from agriculture will recovery at different rates (be more or less resilient).

I attempted to measure a number of variables in streams that are likely to be impacted by agriculture activity and that may or may not have recovered from historical agriculture through watershed reforestation. I have summarized the responses (positive or negative) to and recovery from (yes or no) agriculture of these variables in Table 1. In addition, I have designated how each variable imparts stability of stream ecosystems to agricultural disturbance by stating whether each variable is resistant or resilient to agriculture based on data from my study. Variables that responded to the gradient of agriculture represented by the study sites are considered to be low in resistance. Variables that are not resistant but that showed recovery (i.e., similar among long-term forested and reforested categories) are considered resilient. Variables that responded to the gradient of agriculture and did not demonstrate recovery were considered to be neither resistant nor resilient.

Agriculture impacted stream chemistry and physical structure. Agricultural streams had higher cumulative degree-days, higher PAR, higher nutrient and seston concentrations, more suspended sediment, and smaller median substrate particle size (with more sand and silt) when compared to long-term forested streams. Of these variables, only temperature and light recovered from historical agriculture while the other variables reflected the agricultural histories of their watersheds despite reforestation. Some biological parameters were also affected by agricultural land use. Agricultural streams had higher chlorophyll *a* concentrations, slightly lower macroinvertebrate diversity (measured by diversity indices), fewer detritivorous invertebrates, and more pollution-tolerant invertebrates than long-term forested streams. Agriculture did not seem to affect macroinvertebrate density in our study. All of the measured properties of biological community structure were similar between reforested and long-term forested streams indicating that these variables recovered from historical agriculture. Agriculture had variable impacts on ecosystem processes. Agricultural streams had higher primary production and P/R ratios than long-term forested streams, but both of these properties appear to have recovered from historical agriculture. Ecosystem respiration was not affected by agriculture. Wood breakdown and microbial biofilm respiration were highly variable among sites and, as a result, were inconclusive in their response to agriculture. Interestingly, these two parameters were strongly related to each other leading me to think that microbial biofilm activity controls wood breakdown. Microbial biofilm activity was strongly correlated with sediment accumulations on wood substrates, but these sediment accumulations showed little pattern related to agricultural activity, despite strong links between agriculture and suspended sediment, substrate size, and fine substrate amounts. Based on the wood breakdown and biofilm activity results, I think agriculture might stimulate wood breakdown through higher temperature and nutrients but that this effect only holds if biofilms on wood remain free of sediment accumulations.

Therefore, my study showed that agriculture impacts a multitude of variables in streams but that these impacts are not permanent with respect to biological community structure or ecosystem processes. The longest lasting effects of agriculture on streams in the southern Appalachians were higher sediment transport, changes in stream substrate, and altered water chemistry. Properties of streams related to shading by vegetation (water temperature, light, chlorophyll concentrations, GPP) all were higher in agricultural streams but returned to pre-disturbance levels. Biological communities likely recovered from historical agriculture because their food resources returned to pre-agricultural conditions (i.e., allochthonous detritus instead of algal production). The impacts of agriculture on organic matter dynamics were unclear, but the link between microbial activity and organic matter decay was supported. In addition, most properties in the stream affected by agriculture were most strongly related to riparian-scale land use. Coupled with the recovery of shade-related stream properties and subsequent recovery of biological community structure, this suggests that development and maintenance of streamside forests might be an extremely effective mechanism for mitigating the effects of agriculture on streams in the southern Appalachians.

Literature Cited

Fisher, S. G. 1990. Recovery processes in lotic ecosystems: limits of successional theory. Environmental Management 14:725-736.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1-24.

Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. 1983. Stability of stream ecosystems. Pages 355-395 *in* J. R. Barnes and G. W. Minshall, editors. Stream Ecology. Plenum Publishing Corp., New York.

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient cycling and stability of ecosystems. Pages 1-27 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral Cycling in Southeastern Ecosystems. ERDA Symposium Series, Washington, DC.

Table 1. Summary of variables measured in my study (physicochemical variables, components of biological structure, and ecosystem processes), their response to agriculture, whether they recovered from agriculture, and how these patterns indicate ecosystem stability parameters.

Variable	Response to agriculture?	Recovery?	Stability
Temperature	Y, higher degree days	Y	Resilient
Light	Y, higher PAR	Y	Resilient
Nutrients	Y, higher N concentration	N	Neither
Seston quantity	Y, higher seston concentration	N	Neither
Seston quality	Y, more inorganic sediment	N	Neither
Substrate size	Y, smaller substrate size	N	Neither
In-stream habitat	Y, more sand and silt	N	Neither
Chlorophyll	Y, higher chl *a* concentration	Y	Resilient
Invertebrate density	N	--	Resistant
Invertebrate diversity	Y/N, depends on metric	Y	Both
Invertebrate trophic structure	Y, fewer shredders	Y	Resilient
Invertebrate pollution tolerance	Y, more tolerant	Y	Resilient
Primary production	Y, higher GPP and P/R	Y	Resilient
Ecosystem respiration	N	--	Resistant
Wood breakdown	?	?	?
Microbial biofilm respiration	?	?	?

APPENDIX A

General site information

This appendix contains a table with geographic information for each study site including site code, stream name, major river basin, county, state, latitude, longitude, and landownership. Landowners listed with names were contacted and informed about the study as it progressed. Public access was inferred if I could not contact someone for a site or if the site was along a road outside of fences.

Site Code	Stream Name	Basin	County	State	Latitude	Longitude
FOR 1	Bournes Branch	New	Grayson	VA	36º46’07”N	81º00’34”W
FOR 2	Corner Rock Creek	FB	Madison	NC	35º45’23”N	82º22’49”W
FOR 3	Avery Creek	FB	Transylvania	NC	35º18’36”N	82º44’47”W
FOR 4	Jones Creek	LT	Macon	NC	35º05’03”N	83º27’43”W
FOR 5	Ball Creek	LT	Macon	NC	35º02’43”N	83º26’48”W
AG-L 1	Ripshin Creek	New	Grayson	VA	36º41’46”N	81º24’29”W
AG-L 2	Little Laurel Creek	FB	Madison	NC	35º58’35”N	82º45’17”W
AG-L 3	Roaring Fork, NWM	FB	Madison	NC	35º48’56”N	82º53’46”W
AG-L 4	North Prong Ellijay Creek	LT	Macon	NC	35º12’19”N	83º16’04”W
AG-L 5	Tessentee Creek	LT	Macon	NC	35º04’17”N	83º19’11”W
AG-M 1	Knob Fork	New	Grayson	VA	36º43’51”N	81º05’10”W
AG-M 2	East Fork Bull Creek	FB	Madison	NC	35º50’22”N	82º36’49”W
AG-M 3	Little Pine Creek	FB	Madison	NC	35º45’45”N	82º45’26”W
AG-M 4	Caler Creek	LT	Macon	NC	35º16’06”N	83º23’26”W
AG-M 5	Skeenah Creek	LT	Macon	NC	35º06’41”N	83º23’22”W
AG-H 1	Rock Creek	New	Grayson	VA	36º39’03”N	81º06’21”W
AG-H 2	West Fork Bull Creek	FB	Madison	NC	35º50’35”N	82º36’54”W
AG-H 3	Paint Fork	FB	Buncombe	NC	35º46’09”N	82º27’26”W
AG-H 4	Newfound Creek	FB	Buncombe	NC	35º36’03”N	82º44’15”W
AG-H 5	Gouches Branch	FB	Buncombe	NC	35º38’22”N	82º40’31”W
AG-H 6	Gap Creek	FB	Buncombe	NC	35º29’51”N	82º25’30”W
REC-1 1	Terry Fork	FB	Madison	NC	35º49’11”N	82º27’21”W
REC-1 2	Roaring Fork, BLA	FB	Madison	NC	35º55’16”N	82º34’59”W
REC-1 3	Lisenbee Creek	FB	Madison	NC	35º57’46”N	82º39’31”W
REC-1 4	Shope Creek	LT	Macon	NC	35º03’59”N	83º24’22”W
REC-2 1	Little Fox Creek	New	Grayson	VA	36º39’31”N	81º17’42”W
REC-2 2	Little Foster Creek	FB	Madison	NC	35º55’44”N	82º36’49”W
REC-2 3	Meadow Fork	FB	Madison	NC	35º45’39”N	82º55’51”W
REC-2 4	Rocky Fork	FB	Buncombe	NC	35º32’38”N	82º22’57”W
REC-2 5	Little Ellijay Creek	LT	Macon	NC	35º11’42”N	83º16’27”W

Site Code	Stream Name	Landowner
FOR 1	Bournes Branch	Washington-Jefferson National Forest, Mount Rogers National Recreation Area
FOR 2	Corner Rock Creek	Pisgah National Forest, Pisgah Ranger District
FOR 3	Avery Creek	Pisgah National Forest, Highlands Ranger District
FOR 4	Jones Creek	Nantahala National Forest, Wayah Ranger District
FOR 5	Ball Creek	Nantahala National Forest, Coweeta Hydrologic Laboratory
AG-L 1	Ripshin Creek	Public access along road
AG-L 2	Little Laurel Creek	Dorothy Cook and Fred Shelton, Belva, North Carolina
AG-L 3	Roaring Fork, NWM	Public access along road
AG-L 4	North Prong Ellijay Creek	Public access along road
AG-L 5	Tessentee Creek	Public access along road
AG-M 1	Knob Fork	David Snow, Spring Valley, Virginia
AG-M 2	East Fork Bull Creek	Public access along road
AG-M 3	Little Pine Creek	Public access along road
AG-M 4	Caler Creek	Eula Holbrook, Cowee, North Carolina
AG-M 5	Skeenah Creek	Public access along road
AG-H 1	Rock Creek	Rebecca Bullock, Independence, Virginia
AG-H 2	West Fork Bull Creek	Jim Clark, Petersburg, North Carolina
AG-H 3	Paint Fork	Ed Maney, Democrat, North Carolina
AG-H 4	Newfound Creek	Barry Bowlin, Newfound, North Carolina
AG-H 5	Gouches Branch	Public access along road
AG-H 6	Gap Creek	Paul Blevius, Fairview, North Carolina
REC-1 1	Terry Fork	Public access along road
REC-1 2	Roaring Fork, BLA	Public access along road
REC-1 3	Lisenbee Creek	Public access along road
REC-1 4	Shope Creek	Public access along road
REC-2 1	Little Fox Creek	David C. Parsons, Independence, Virginia
REC-2 2	Little Foster Creek	Adele Riddle, Easley, South Carolina
REC-2 3	Meadow Fork	Tony Plemmons, Trust, North Carolina
REC-2 4	Rocky Fork	Public access along road
REC-2 5	Little Ellijay Creek	Public access along road

APPENDIX B

Benthic macroinvertebrate data

This appendix contains densities (no./m^2) for each macroinvertebrate taxon collected at each site. The appendix is separated by land cover categories in the following order: FOR, AG-L, AG-M, AG-H, REC-1, REC-2. Insect taxa are arranged phylogenetically followed by non-insect taxa. In most cases, family is in the first column with genus in the second, but non-insect taxa are shown with the appropriate taxon in the first and columns (phylum, class, or order).

		Forested (FOR) Streams				
		1	2	3	4	5
Order Collembola						
Isotomidae		0.0	0.0	0.0	3.9	0.0
Order Ephemeroptera						
Ameletidae	*Ameletus*	3.9	3.9	1.0	0.0	2.9
Baetidae	*Acentrella*	11.8	482.4	84.5	702.0	2.0
Baetidae	*Baetis*	34.3	3.9	12.5	0.0	89.2
Baetiscidae	*Baetisca*	0.0	0.0	0.0	0.0	0.0
Ephemerellidae	*Drunella*	0.0	15.7	85.7	17.6	12.7
Ephemerellidae	*Ephemerella*	202.0	102.0	363.1	186.3	104.9
Ephemerellidae	*Eurylophella*	0.0	0.0	0.0	0.0	0.0
Ephemerellidae	*Serratella*	54.9	0.0	19.8	14.7	0.0
Ephemeridae	*Ephemera*	2.9	0.0	0.0	3.9	0.0
Heptageniidae	*Cinygmula*	379.4	128.4	462.9	146.1	14.7
Heptageniidae	*Epeorus*	162.7	113.7	143.1	108.8	64.7
Heptageniidae	*Leucrocuta*	69.6	0.0	41.6	0.0	2.9
Heptageniidae	*Rhithrogena*	0.0	0.0	0.0	0.0	0.0
Heptageniidae	*Stenacron*	10.8	8.8	2.0	7.8	1.0
Heptageniidae	*Stenonema*	71.6	21.6	52.0	14.7	7.8
Isonychiidae	*Isonychia*	0.0	0.0	0.0	0.0	0.0
Leptophlebiidae	*Paraleptophlebia*	176.5	79.4	112.2	44.1	11.8
Order Odonata						
Calopterygidae	*Hataerina*	0.0	0.0	0.0	0.0	0.0
Gomphidae	*Lanthus*	3.9	5.9	6.3	5.9	11.8
Gomphidae	*Ophiogomphus*	0.0	0.0	0.0	0.0	0.0
Gomphidae	*Stylogomphus*	0.0	0.0	0.0	0.0	0.0
Order Plecoptera						
Capniidae		0.0	1.0	0.0	0.0	0.0
Chloroperlidae	*Alloperla*	0.0	0.0	0.0	0.0	0.0
Chloroperlidae	*Haploperla*	37.3	4.9	4.3	0.0	8.8
Chloroperlidae	*Sweltsa*	61.8	0.0	10.6	0.0	0.0
Leuctridae	*Leuctra*	69.6	177.5	181.8	192.2	115.7
Nemouridae	*Amphinemura*	60.8	5.9	12.7	34.3	27.5
Nemouridae	*Prostoia*	0.0	0.0	0.0	0.0	0.0
Peltoperlidae	*Tallaperla*	0.0	2.0	3.9	52.0	76.5
Perlidae	*Acroneuria*	16.7	13.7	4.3	3.9	8.8
Perlidae	*Agnetina*	0.0	0.0	0.0	0.0	0.0
Perlidae	*Beloneuria*	0.0	0.0	15.1	0.0	0.0
Perlidae	*Paragnetina*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Cultus*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Diploperla*	0.0	0.0	0.0	13.7	0.0
Perlodidae	*Isogenoides*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Isoperla*	19.6	10.8	58.8	50.0	15.7
Perlodidae	*Malirekus*	0.0	0.0	0.0	2.9	0.0
Perlodidae	*Remenus*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Yugus*	0.0	3.9	3.9	0.0	1.0

Pteronarcyidae	*Pteronarcys*	7.8	12.7	75.5	85.3	10.8
Order Hemiptera						
Hebridae	*Merragata*	0.0	0.0	0.0	0.0	0.0
Order Megaloptera						
Corydalidae	*Corydalus*	0.0	0.0	0.0	0.0	0.0
Corydalidae	*Nigronia*	1.0	0.0	0.0	0.0	0.0
Order Trichoptera						
Brachycentridae	*Brachycentrus*	0.0	0.0	0.0	0.0	0.0
Brachycentridae	*Micrasema*	12.7	0.0	11.2	0.0	0.0
Glossosomatidae	*Agapetus*	0.0	42.2	22.7	5.9	0.0
Glossosomatidae	*Glossosoma*	0.0	0.0	3.9	0.0	0.0
Glossosomatidae	*Matrioptila*	0.0	0.0	0.0	0.0	0.0
Goeridae	*Goera*	2.9	4.9	0.0	0.0	0.0
Goeridae	*Goerita*	1.0	0.0	0.0	0.0	0.0
Hydropsychidae	*Cheumatopsyche*	7.8	2.9	2.4	0.0	0.0
Hydropsychidae	*Diplectrona*	20.6	31.4	19.8	69.6	45.1
Hydropsychidae	*Hydropsyche*	3.9	5.9	0.0	0.0	3.9
Hydropsychidae	*Parapsyche*	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Hydroptila*	0.0	0.0	2.4	0.0	0.0
Hydroptilidae	*Leucotrichia*	0.0	0.0	0.0	0.0	0.0
Lepidostomatidae	*Lepidostoma*	0.0	0.0	0.0	3.9	7.8
Leptoceridae	*Oecetis*	0.0	0.0	0.0	0.0	0.0
Leptoceridae	*Setodes*	0.0	0.0	0.0	0.0	0.0
Limnephilidae	*Hydatophylax*	0.0	1.0	0.0	0.0	0.0
Limnephilidae	*Pycnopsyche*	0.0	0.0	0.0	0.0	0.0
Odontoceridae	*Psilotreta*	1.0	0.0	0.0	0.0	0.0
Philopotamidae	*Dolophilodes*	0.0	0.0	0.0	11.8	0.0
Polycentropodidae	*Polycentropus*	2.9	19.6	15.5	19.6	32.4
Polycentropodidae	*Neureclipsis*	6.9	0.0	2.4	0.0	0.0
Psychomyiidae	*Lype*	0.0	0.0	0.0	7.8	0.0
Psychomyiidae	*Psychomyia*	0.0	0.0	6.3	0.0	0.0
Rhyacophilidae	*Rhyacophila*	3.9	13.7	272.2	29.4	8.8
Uenoidae	*Neophylax*	0.0	15.7	12.5	6.9	4.9
Order Lepidoptera						
Noctuidae		0.0	0.0	0.0	0.0	1.0
Order Coleoptera						
Dryopidae	*Helichus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Ancyronyx*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Dubiraphia*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Macronychus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Optioservus*	13.7	237.3	314.9	21.6	48.0
Elmidae	*Oulimnius*	194.1	273.5	353.7	273.5	121.6
Elmidae	*Promoresia*	0.0	0.0	8.8	0.0	4.9
Elmidae	*Stenelmis*	0.0	0.0	0.0	0.0	1.0
Psephenidae	*Ectopria*	11.8	0.0	4.9	15.7	5.9
Psephenidae	*Psephenus*	27.5	3.9	0.0	0.0	0.0

Ptilodactylidae	*Anchytarsus*	0.0	0.0	0.0	0.0	0.0
Staphylinidae	*Thinobius*	0.0	1.0	0.0	0.0	0.0
Order Diptera						
Athericidae	*Atherix*	0.0	0.0	0.0	14.7	0.0
Blephariceridae	*Blepharicera*	27.5	4.9	55.3	0.0	0.0
Cecidomyiidae		0.0	0.0	2.4	0.0	0.0
Ceratopogonidae	*Atrichopogon*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Ceratopogon*	2.9	0.0	0.0	0.0	0.0
Ceratopogonidae	*Culicoides*	0.0	2.9	0.0	0.0	3.9
Ceratopogonidae	*Dasyhelea*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Monohelea*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Palpomyia*	0.0	42.2	25.7	15.7	33.3
Ceratopogonidae	*Stilobezzia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Brillia*	35.7	0.0	18.6	0.0	0.0
Chironomidae	*Chernovskiia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Chironomus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Conchapelopia*	22.3	25.4	55.7	23.4	24.4
Chironomidae	*Constempellina*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Corynoneura*	0.0	12.7	18.6	0.0	36.6
Chironomidae	*Cryptochironomus*	4.5	0.0	0.0	0.0	6.1
Chironomidae	*Demicryptochironomus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Diamesa*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Epoicocladius*	0.0	0.0	0.0	7.8	0.0
Chironomidae	*Eukiefferiella*	13.4	0.0	0.0	0.0	0.0
Chironomidae	*Harnischia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Lopescladius*	13.4	76.1	111.5	15.6	18.3
Chironomidae	*Micropsectra*	49.1	215.5	445.8	93.5	128.2
Chironomidae	*Microtendipes*	13.4	0.0	241.5	39.0	30.5
Chironomidae	*Nilotanypus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Orthocladius*	8.9	0.0	0.0	31.2	0.0
Chironomidae	*Parachaetocladius*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parakiefferiella*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parametriocnemus*	31.2	19.0	18.6	101.3	97.7
Chironomidae	*Polypedilum*	26.8	19.0	18.6	7.8	0.0
Chironomidae	*Potthastia*	0.0	19.0	18.6	0.0	0.0
Chironomidae	*Rheocricotopus*	22.3	0.0	18.6	101.3	6.1
Chironomidae	*Rheotanytarsus*	13.4	31.7	18.6	23.4	24.4
Chironomidae	*Robackia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Stempellina*	4.5	44.4	390.1	0.0	0.0
Chironomidae	*Stempellinella*	0.0	0.0	55.7	0.0	6.1
Chironomidae	*Thienemanniella*	0.0	0.0	0.0	0.0	79.4
Dixidae	*Dixa*	0.0	0.0	0.0	0.0	0.0
Dolichopodidae		0.0	0.0	0.0	0.0	0.0
Empididae	*Chelifera*	0.0	0.0	1.0	10.8	1.0
Empididae	*Clinocera*	0.0	0.0	0.0	3.9	0.0
Empididae	*Hemerodromia*	0.0	2.9	8.0	0.0	2.0
Ephydridae		0.0	0.0	0.0	0.0	0.0
Phoridae		1.0	0.0	0.0	0.0	0.0
Psychodidae	*Pericoma*	0.0	0.0	0.0	0.0	0.0
Scathophagidae		0.0	0.0	0.0	0.0	0.0

Simuliidae	*Prosimulium*	55.9	12.7	150.4	143.1	9.8
Simuliidae	*Simulium*	0.0	0.0	26.5	3.9	0.0
Stratiomyidae	*Caloparyphus*	0.0	0.0	0.0	0.0	0.0
Stratiomyidae	*Odontomyia*	0.0	0.0	0.0	0.0	2.0
Stratiomyidae	*Stratiomys*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Chrysops*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Tabanus*	0.0	0.0	0.0	2.9	0.0
Tanyderidae	*Protoplasa*	0.0	0.0	4.7	0.0	0.0
Tipulidae	*Antocha*	4.9	0.0	15.9	0.0	1.0
Tipulidae	*Brachyprenna*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Cryptolabis*	0.0	0.0	304.3	0.0	0.0
Tipulidae	*Dactylolabis*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Dicranota*	0.0	2.9	9.8	2.9	12.7
Tipulidae	*Hexatoma*	30.4	7.8	10.6	5.9	9.8
Tipulidae	*Limonia*	19.6	0.0	0.0	0.0	0.0
Tipulidae	*Lipsothrix*	3.9	0.0	0.0	0.0	0.0
Tipulidae	*Molophilus*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Pseudolimnophila*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Rhabdomastix*	9.8	0.0	1.0	3.9	0.0
Tipulidae	*Tipula*	3.9	2.9	0.0	10.8	0.0
Unknown	Genus A	0.0	0.0	0.0	0.0	0.0
Unknown	Genus B	0.0	0.0	5.9	0.0	0.0
Class Crustacea						
Acari	Hydracarina	14.7	53.9	117.3	77.5	23.5
Copepoda		0.0	2.9	1.0	3.9	2.0
Decapoda		0.0	0.0	1.0	3.9	0.0
Phylum Mollusca						
Gastropoda	Ancylidae	0.0	2.0	125.3	0.0	0.0
Gastropoda	Prosobranchia	9.8	72.5	0.0	6.9	0.0
Gastropoda	Pulmonata	0.0	0.0	0.0	0.0	0.0
Bivalvia	Corbicula	7.8	0.0	0.0	0.0	0.0
Phylum Annelida						
Oligochaeta		141.2	213.7	265.5	64.7	156.9
Phylum Platyhelminthes						
Platyhelminthes		0.0	4.9	29.2	11.8	5.9
Phylum Nematoda						
Nematoda		2.9	5.9	20.4	0.0	2.0

		Low Agriculture (AG-L) Streams				
		1	2	3	4	5
Order Collembola						
Isotomidae		0.0	0.0	0.0	0.0	2.9
Order Ephemeroptera						
Ameletidae	*Ameletus*	0.0	0.0	0.0	0.0	0.0
Baetidae	*Acentrella*	12.7	86.3	121.6	278.4	308.8
Baetidae	*Baetis*	12.7	18.6	2.0	49.0	156.9
Baetiscidae	*Baetisca*	0.0	0.0	0.0	0.0	0.0
Ephemerellidae	*Drunella*	2.9	5.9	73.5	162.7	422.5
Ephemerellidae	*Ephemerella*	764.7	96.1	275.5	595.1	750.0
Ephemerellidae	*Eurylophella*	0.0	14.7	0.0	0.0	3.9
Ephemerellidae	*Serratella*	258.8	20.6	0.0	6.9	109.8
Ephemeridae	*Ephemera*	0.0	3.9	0.0	0.0	0.0
Heptageniidae	*Cinygmula*	47.1	499.0	33.3	253.9	162.7
Heptageniidae	*Epeorus*	251.0	129.4	21.6	132.4	233.3
Heptageniidae	*Leucrocuta*	79.4	20.6	0.0	0.0	7.8
Heptageniidae	*Rhithrogena*	40.2	3.9	2.0	12.7	18.6
Heptageniidae	*Stenacron*	15.7	0.0	0.0	1.0	0.0
Heptageniidae	*Stenonema*	38.2	52.0	2.0	14.7	158.8
Isonychiidae	*Isonychia*	0.0	2.0	0.0	0.0	3.9
Leptophlebiidae	*Paraleptophlebia*	360.8	46.1	1.0	16.7	183.3
Order Odonata						
Calopterygidae	*Hataerina*	0.0	0.0	0.0	0.0	0.0
Gomphidae	*Lanthus*	0.0	13.7	0.0	3.9	14.7
Gomphidae	*Ophiogomphus*	0.0	5.9	0.0	0.0	0.0
Gomphidae	*Stylogomphus*	0.0	0.0	0.0	0.0	0.0
Order Plecoptera						
Capniidae		0.0	0.0	0.0	0.0	0.0
Chloroperlidae	*Alloperla*	0.0	0.0	0.0	0.0	0.0
Chloroperlidae	*Haploperla*	7.8	9.8	0.0	3.9	0.0
Chloroperlidae	*Sweltsa*	7.8	4.9	0.0	0.0	0.0
Leuctridae	*Leuctra*	125.5	175.5	75.5	85.3	337.3
Nemouridae	*Amphinemura*	13.7	9.8	4.9	4.9	0.0
Nemouridae	*Prostoia*	0.0	0.0	0.0	0.0	0.0
Peltoperlidae	*Tallaperla*	27.5	2.0	7.8	2.9	15.7
Perlidae	*Acroneuria*	21.6	3.9	0.0	2.9	30.4
Perlidae	*Agnetina*	0.0	0.0	0.0	0.0	0.0
Perlidae	*Beloneuria*	0.0	0.0	0.0	3.9	0.0
Perlidae	*Paragnetina*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Cultus*	2.9	0.0	0.0	1.0	0.0
Perlodidae	*Diploperla*	0.0	0.0	0.0	0.0	2.9
Perlodidae	*Isogenoides*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Isoperla*	40.2	31.4	22.5	35.3	83.3
Perlodidae	*Malirekus*	2.9	0.0	7.8	0.0	0.0
Perlodidae	*Remenus*	0.0	0.0	3.9	0.0	3.9
Perlodidae	*Yugus*	0.0	0.0	3.9	2.9	0.0

Pteronarcyidae	*Pteronarcys*	31.4	0.0	7.8	20.6	0.0
Order Hemiptera						
Hebridae	*Merragata*	0.0	0.0	0.0	0.0	0.0
Order Megaloptera						
Corydalidae	*Corydalus*	0.0	0.0	0.0	0.0	0.0
Corydalidae	*Nigronia*	2.9	3.9	0.0	0.0	3.9
Order Trichoptera						
Brachycentridae	*Brachycentrus*	0.0	0.0	0.0	0.0	0.0
Brachycentridae	*Micrasema*	0.0	0.0	0.0	0.0	52.0
Glossosomatidae	*Agapetus*	0.0	3.9	0.0	2.9	0.0
Glossosomatidae	*Glossosoma*	7.8	2.9	0.0	12.7	11.8
Glossosomatidae	*Matrioptila*	0.0	0.0	0.0	2.9	0.0
Goeridae	*Goera*	0.0	0.0	0.0	0.0	3.9
Goeridae	*Goerita*	0.0	0.0	0.0	0.0	2.9
Hydropsychidae	*Cheumatopsyche*	52.0	102.0	0.0	5.9	44.1
Hydropsychidae	*Diplectrona*	17.6	0.0	23.5	52.9	35.3
Hydropsychidae	*Hydropsyche*	62.7	56.9	0.0	0.0	6.9
Hydropsychidae	*Parapsyche*	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Hydroptila*	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Leucotrichia*	0.0	0.0	0.0	0.0	0.0
Lepidostomatidae	*Lepidostoma*	0.0	0.0	1.0	0.0	3.9
Leptoceridae	*Oecetis*	0.0	0.0	0.0	0.0	0.0
Leptoceridae	*Setodes*	0.0	0.0	0.0	0.0	8.8
Limnephilidae	*Hydatophylax*	0.0	0.0	0.0	0.0	0.0
Limnephilidae	*Pycnopsyche*	0.0	0.0	0.0	0.0	0.0
Odontoceridae	*Psilotreta*	0.0	0.0	0.0	0.0	0.0
Philopotamidae	*Dolophilodes*	0.0	8.8	0.0	3.9	139.2
Polycentropodidae	*Polycentropus*	44.1	60.8	0.0	12.7	49.0
Polycentropodidae	*Neureclipsis*	0.0	0.0	0.0	0.0	0.0
Psychomyiidae	*Lype*	0.0	0.0	0.0	0.0	6.9
Psychomyiidae	*Psychomyia*	18.6	0.0	0.0	0.0	8.8
Rhyacophilidae	*Rhyacophila*	26.5	3.9	1.0	24.5	146.1
Uenoidae	*Neophylax*	64.7	0.0	3.9	4.9	0.0
Order Lepidoptera						
Noctuidae		0.0	0.0	0.0	0.0	0.0
Order Coleoptera						
Dryopidae	*Helichus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Ancyronyx*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Dubiraphia*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Macronychus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Optioservus*	208.8	62.7	1.0	112.7	260.8
Elmidae	*Oulimnius*	567.6	235.3	54.9	195.1	447.1
Elmidae	*Promoresia*	0.0	0.0	0.0	0.0	113.7
Elmidae	*Stenelmis*	0.0	0.0	0.0	0.0	0.0
Psephenidae	*Ectopria*	2.9	0.0	0.0	0.0	0.0
Psephenidae	*Psephenus*	68.6	41.2	0.0	0.0	2.9

Ptilodactylidae	*Anchytarsus*	0.0	0.0	0.0	0.0	0.0
Staphylinidae	*Thinobius*	0.0	0.0	0.0	0.0	0.0
Order Diptera						
Athericidae	*Atherix*	0.0	0.0	3.9	13.7	0.0
Blephariceridae	*Blephariceras*	42.2	2.9	0.0	71.6	70.6
Cecidomyiidae		0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Atrichopogon*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Ceratopogon*	0.0	0.0	11.8	0.0	0.0
Ceratopogonidae	*Culicoides*	3.9	0.0	0.0	0.0	0.0
Ceratopogonidae	*Dasyhelea*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Monohelea*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Palpomyia*	3.9	4.9	0.0	8.8	7.8
Ceratopogonidae	*Stilobezzia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Brillia*	48.8	0.0	0.0	21.2	136.0
Chironomidae	*Chernovskiia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Chironomus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Conchapelopia*	56.9	50.7	2.8	0.0	45.3
Chironomidae	*Constempellina*	0.0	0.0	2.8	0.0	0.0
Chironomidae	*Corynoneura*	32.5	10.1	0.0	0.0	15.1
Chironomidae	*Cryptochironomus*	0.0	10.1	0.0	0.0	0.0
Chironomidae	*Demicryptochironomus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Diamesa*	0.0	5.1	57.0	0.0	0.0
Chironomidae	*Epoicocladius*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Eukiefferiella*	40.6	10.1	51.3	0.0	151.1
Chironomidae	*Harnischia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Lopescladius*	0.0	25.3	2.8	0.0	30.2
Chironomidae	*Micropsectra*	187.0	121.7	14.2	76.2	362.7
Chironomidae	*Microtendipes*	32.5	0.0	2.8	21.2	60.5
Chironomidae	*Nilotanypus*	8.1	0.0	0.0	0.0	0.0
Chironomidae	*Orthocladius*	16.3	0.0	79.8	12.7	30.2
Chironomidae	*Parachaetocladius*	32.5	0.0	0.0	0.0	0.0
Chironomidae	*Parakiefferiella*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parametriocnemus*	48.8	45.6	22.8	4.2	15.1
Chironomidae	*Polypedilum*	8.1	20.3	8.5	12.7	15.1
Chironomidae	*Potthastia*	0.0	0.0	0.0	4.2	0.0
Chironomidae	*Rheocricotopus*	16.3	20.3	5.7	8.5	15.1
Chironomidae	*Rheotanytarsus*	8.1	25.3	0.0	33.9	45.3
Chironomidae	*Robackia*	0.0	0.0	0.0	0.0	15.1
Chironomidae	*Stempellina*	81.3	10.1	8.5	29.6	15.1
Chironomidae	*Stempellinella*	16.3	30.4	0.0	59.3	136.0
Chironomidae	*Thienemanniella*	8.1	0.0	14.2	33.9	0.0
Dixidae	*Dixa*	3.9	0.0	1.0	0.0	0.0
Dolichopodidae		3.9	0.0	0.0	0.0	0.0
Empididae	*Chelifera*	6.9	0.0	1.0	2.9	6.9
Empididae	*Clinocera*	0.0	0.0	0.0	3.9	0.0
Empididae	*Hemerodromia*	0.0	8.8	0.0	0.0	6.9
Ephydridae		0.0	0.0	0.0	0.0	0.0
Phoridae		0.0	0.0	0.0	0.0	0.0
Psychodidae	*Pericoma*	0.0	0.0	0.0	0.0	0.0
Scathophagidae		0.0	0.0	0.0	0.0	0.0

Simuliidae	*Prosimulium*	94.1	14.7	5.9	51.0	203.9
Simuliidae	*Simulium*	0.0	0.0	7.8	35.3	0.0
Stratiomyidae	*Caloparyphus*	0.0	0.0	0.0	0.0	0.0
Stratiomyidae	*Odontomyia*	0.0	0.0	0.0	2.0	9.8
Stratiomyidae	*Stratiomys*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Chrysops*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Tabanus*	0.0	0.0	0.0	0.0	0.0
Tanyderidae	*Protoplasa*	0.0	0.0	0.0	2.0	0.0
Tipulidae	*Antocha*	35.3	69.6	11.8	3.9	23.5
Tipulidae	*Brachyprenna*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Cryptolabis*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Dactylolabis*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Dicranota*	17.6	3.9	0.0	11.8	20.6
Tipulidae	*Hexatoma*	26.5	17.6	0.0	0.0	23.5
Tipulidae	*Limonia*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Lipsothrix*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Molophilus*	0.0	0.0	3.9	1.0	0.0
Tipulidae	*Pseudolimnophila*	2.9	0.0	0.0	0.0	0.0
Tipulidae	*Rhabdomastix*	0.0	0.0	1.0	0.0	0.0
Tipulidae	*Tipula*	2.9	0.0	8.8	2.9	0.0
Unknown	Genus A	0.0	0.0	0.0	0.0	0.0
Unknown	Genus B	0.0	0.0	0.0	0.0	0.0
Class Crustacea						
Acari	Hydracarina	42.2	56.9	8.8	24.5	124.5
Copepoda		6.9	0.0	0.0	0.0	0.0
Decapoda		3.9	0.0	0.0	3.9	1.0
Phylum Mollusca						
Gastropoda	Ancylidae	56.9	34.3	0.0	0.0	0.0
Gastropoda	Prosobranchia	0.0	1.0	0.0	0.0	0.0
Gastropoda	Pulmonata	0.0	2.9	0.0	0.0	0.0
Bivalvia	Corbicula	17.6	0.0	0.0	0.0	7.8
Phylum Annelida						
Oligochaeta		273.5	276.5	123.5	115.7	440.2
Phylum Platyhelminthes						
Platyhelminthes		0.0	34.3	0.0	0.0	26.5
Phylum Nematoda						
Nematoda		0.0	2.0	3.9	0.0	17.6

		Medium Agriculture (AG-M) Streams				
		1	2	3	4	5
Order Collembola						
Isotomidae		0.0	1.2	0.0	0.0	0.0
Order Ephemeroptera						
Ameletidae	*Ameletus*	0.0	0.0	0.0	0.0	0.0
Baetidae	*Acentrella*	3.9	57.1	396.5	17.6	3.9
Baetidae	*Baetis*	39.2	0.0	16.1	0.0	5.9
Baetiscidae	*Baetisca*	17.6	14.7	0.0	0.0	0.0
Ephemerellidae	*Drunella*	9.8	3.5	99.8	3.9	9.8
Ephemerellidae	*Ephemerella*	929.4	485.9	557.6	353.9	20.6
Ephemerellidae	*Eurylophella*	11.8	7.1	4.7	3.9	0.0
Ephemerellidae	*Serratella*	31.4	59.4	10.6	25.5	22.5
Ephemeridae	*Ephemera*	0.0	0.0	0.0	0.0	1.0
Heptageniidae	*Cinygmula*	7.8	0.0	203.5	0.0	0.0
Heptageniidae	*Epeorus*	84.3	112.4	96.5	9.8	9.8
Heptageniidae	*Leucrocuta*	0.0	42.9	14.7	0.0	0.0
Heptageniidae	*Rhithrogena*	58.8	1.8	36.5	3.9	0.0
Heptageniidae	*Stenacron*	0.0	31.2	0.0	0.0	22.5
Heptageniidae	*Stenonema*	13.7	45.3	5.3	10.8	10.8
Isonychiidae	*Isonychia*	11.8	0.0	0.0	0.0	0.0
Leptophlebiidae	*Paraleptophlebia*	92.2	38.2	40.6	0.0	0.0
Order Odonata						
Calopterygidae	*Hataerina*	0.0	0.0	0.0	0.0	0.0
Gomphidae	*Lanthus*	0.0	4.7	0.0	0.0	0.0
Gomphidae	*Ophiogomphus*	0.0	3.5	3.9	2.9	0.0
Gomphidae	*Stylogomphus*	0.0	0.0	0.0	0.0	0.0
Order Plecoptera						
Capniidae		0.0	62.4	0.0	0.0	0.0
Chloroperlidae	*Alloperla*	0.0	2.4	0.0	0.0	2.9
Chloroperlidae	*Haploperla*	3.9	11.8	6.3	0.0	0.0
Chloroperlidae	*Sweltsa*	0.0	0.0	0.0	0.0	0.0
Leuctridae	*Leuctra*	147.1	30.0	41.8	37.3	10.8
Nemouridae	*Amphinemura*	0.0	1.8	5.3	3.9	0.0
Nemouridae	*Prostoia*	3.9	0.0	0.0	0.0	0.0
Peltoperlidae	*Tallaperla*	0.0	0.0	0.0	0.0	0.0
Perlidae	*Acroneuria*	0.0	7.6	10.6	2.9	0.0
Perlidae	*Agnetina*	3.9	31.2	0.0	0.0	0.0
Perlidae	*Beloneuria*	0.0	4.7	0.0	0.0	2.9
Perlidae	*Paragnetina*	0.0	1.2	0.0	0.0	0.0
Perlodidae	*Cultus*	0.0	37.1	11.2	0.0	2.0
Perlodidae	*Diploperla*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Isogenoides*	0.0	1.8	0.0	0.0	0.0
Perlodidae	*Isoperla*	229.4	57.6	90.2	78.4	1.0
Perlodidae	*Malirekus*	3.9	0.0	0.0	0.0	0.0
Perlodidae	*Remenus*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Yugus*	0.0	0.0	1.0	0.0	0.0

Pteronarcyidae	*Pteronarcys*	0.0	5.9	2.9	18.6	0.0
Order Hemiptera						
Hebridae	*Merragata*	0.0	0.0	0.0	0.0	0.0
Order Megaloptera						
Corydalidae	*Corydalus*	0.0	1.2	0.0	0.0	0.0
Corydalidae	*Nigronia*	0.0	1.8	0.0	2.9	4.9
Order Trichoptera						
Brachycentridae	*Brachycentrus*	0.0	0.0	0.0	0.0	0.0
Brachycentridae	*Micrasema*	0.0	0.0	0.0	0.0	8.8
Glossosomatidae	*Agapetus*	0.0	0.0	0.0	0.0	2.0
Glossosomatidae	*Glossosoma*	0.0	12.9	0.0	3.9	0.0
Glossosomatidae	*Matrioptila*	0.0	0.0	0.0	0.0	0.0
Goeridae	*Goera*	17.6	1.2	0.0	5.9	0.0
Goeridae	*Goerita*	0.0	0.0	0.0	0.0	0.0
Hydropsychidae	*Cheumatopsyche*	51.0	114.1	56.7	13.7	88.2
Hydropsychidae	*Diplectrona*	0.0	0.0	0.0	0.0	4.9
Hydropsychidae	*Hydropsyche*	137.3	94.1	27.5	20.6	1.0
Hydropsychidae	*Parapsyche*	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Hydroptila*	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Leucotrichia*	0.0	0.0	7.6	0.0	0.0
Lepidostomatidae	*Lepidostoma*	0.0	0.0	0.0	3.9	0.0
Leptoceridae	*Oecetis*	0.0	0.0	0.0	0.0	2.0
Leptoceridae	*Setodes*	0.0	0.0	0.0	2.9	0.0
Limnephilidae	*Hydatophylax*	0.0	0.0	0.0	0.0	0.0
Limnephilidae	*Pycnopsyche*	0.0	0.0	0.0	0.0	0.0
Odontoceridae	*Psilotreta*	0.0	0.0	0.0	0.0	0.0
Philopotamidae	*Dolophilodes*	3.9	3.5	0.0	0.0	0.0
Polycentropodidae	*Polycentropus*	19.6	30.6	32.7	2.9	3.9
Polycentropodidae	*Neureclipsis*	0.0	0.0	0.0	0.0	0.0
Psychomyiidae	*Lype*	3.9	0.0	2.4	0.0	0.0
Psychomyiidae	*Psychomyia*	13.7	16.5	26.7	0.0	0.0
Rhyacophilidae	*Rhyacophila*	5.9	3.5	1.0	3.9	2.0
Uenoidae	*Neophylax*	13.7	0.0	0.0	0.0	0.0
Order Lepidoptera						
Noctuidae		0.0	0.0	0.0	0.0	0.0
Order Coleoptera						
Dryopidae	*Helichus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Ancyronyx*	0.0	0.0	0.0	3.9	0.0
Elmidae	*Dubiraphia*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Macronychus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Optioservus*	174.5	137.1	448.0	104.9	41.2
Elmidae	*Oulimnius*	56.9	37.1	130.4	91.2	1.0
Elmidae	*Promoresia*	0.0	3.5	0.0	2.9	23.5
Elmidae	*Stenelmis*	0.0	0.0	0.0	53.9	2.0
Psephenidae	*Ectopria*	3.9	0.0	0.0	0.0	0.0
Psephenidae	*Psephenus*	366.7	419.4	112.0	14.7	25.5

Ptilodactylidae	*Anchytarsus*	0.0	0.0	0.0	0.0	0.0
Staphylinidae	*Thinobius*	0.0	0.0	1.0	0.0	0.0
Order Diptera						
Athericidae	*Atherix*	0.0	0.0	0.0	0.0	0.0
Blephariceridae	*Blephericera*	31.4	62.4	32.0	0.0	2.0
Cecidomyiidae		0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Atrichopogon*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Ceratopogon*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Culicoides*	3.9	2.4	0.0	0.0	1.0
Ceratopogonidae	*Dasyhelea*	0.0	0.0	0.0	0.0	2.0
Ceratopogonidae	*Monohelea*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Palpomyia*	7.8	1.2	18.2	9.8	3.9
Ceratopogonidae	*Stilobezzia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Brillia*	0.0	20.6	0.0	0.0	0.0
Chironomidae	*Chernovskiia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Chironomus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Conchapelopia*	11.3	41.3	13.9	0.0	19.6
Chironomidae	*Constempellina*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Corynoneura*	22.5	41.3	55.7	0.0	0.0
Chironomidae	*Cryptochironomus*	0.0	0.0	0.0	29.1	0.0
Chironomidae	*Demicryptochironomus*	0.0	0.0	13.9	0.0	0.0
Chironomidae	*Diamesa*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Epoicocladius*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Eukiefferiella*	33.8	82.6	0.0	0.0	0.0
Chironomidae	*Harnischia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Lopescladius*	202.7	144.5	139.3	0.0	0.0
Chironomidae	*Micropsectra*	56.3	144.5	320.4	29.1	58.8
Chironomidae	*Microtendipes*	135.1	123.9	167.2	96.8	0.0
Chironomidae	*Nilotanypus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Orthocladius*	33.8	1094.4	209.0	154.9	431.4
Chironomidae	*Parachaetocladius*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parakiefferiella*	0.0	0.0	0.0	9.7	0.0
Chironomidae	*Parametriocnemus*	67.6	247.8	0.0	9.7	29.4
Chironomidae	*Polypedilum*	45.0	82.6	97.5	29.1	117.6
Chironomidae	*Potthastia*	56.3	0.0	41.8	0.0	0.0
Chironomidae	*Rheocricotopus*	0.0	185.8	0.0	0.0	137.3
Chironomidae	*Rheotanytarsus*	45.0	206.5	97.5	87.2	0.0
Chironomidae	*Robackia*	0.0	0.0	0.0	9.7	0.0
Chironomidae	*Stempellina*	11.3	0.0	41.8	38.7	0.0
Chironomidae	*Stempellinella*	0.0	0.0	0.0	48.4	0.0
Chironomidae	*Thienemanniella*	67.6	0.0	0.0	9.7	0.0
Dixidae	*Dixa*	3.9	0.0	0.0	0.0	0.0
Dolichopodidae		0.0	0.0	0.0	0.0	0.0
Empididae	*Chelifera*	0.0	4.1	2.0	10.8	10.8
Empididae	*Clinocera*	0.0	25.9	6.9	0.0	0.0
Empididae	*Hemerodromia*	9.8	50.0	3.9	21.6	9.8
Ephydridae		0.0	0.0	0.0	0.0	0.0
Phoridae		0.0	0.0	0.0	0.0	0.0
Psychodidae	*Pericoma*	0.0	0.0	0.0	0.0	0.0
Scathophagidae		0.0	0.0	0.0	0.0	0.0

Simuliidae	*Prosimulium*	31.4	1.8	1.0	29.4	3.9
Simuliidae	*Simulium*	0.0	0.0	0.0	17.6	0.0
Stratiomyidae	*Caloparyphus*	0.0	0.0	0.0	0.0	0.0
Stratiomyidae	*Odontomyia*	0.0	0.0	0.0	3.9	0.0
Stratiomyidae	*Stratiomys*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Chrysops*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Tabanus*	0.0	0.0	0.0	0.0	0.0
Tanyderidae	*Protoplasa*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Antocha*	117.6	208.2	43.9	5.9	9.8
Tipulidae	*Brachyprenna*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Cryptolabis*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Dactylolabis*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Dicranota*	0.0	0.0	7.1	10.8	1.0
Tipulidae	*Hexatoma*	86.3	0.0	6.3	5.9	1.0
Tipulidae	*Limonia*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Lipsothrix*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Molophilus*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Pseudolimnophila*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Rhabdomastix*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Tipula*	10.8	3.5	0.0	3.9	0.0
Unknown	Genus A	5.9	0.0	0.0	0.0	0.0
Unknown	Genus B	0.0	0.0	0.0	0.0	0.0
Class Crustacea						
Acari	Hydracarina	70.6	90.6	168.4	51.0	151.0
Copepoda		0.0	17.1	1.0	0.0	2.9
Decapoda		0.0	0.0	0.0	0.0	1.0
Phylum Mollusca						
Gastropoda	Ancylidae	49.0	41.8	182.9	0.0	24.5
Gastropoda	Prosobranchia	21.6	17.1	80.6	0.0	37.3
Gastropoda	Pulmonata	0.0	0.0	0.0	0.0	0.0
Bivalvia	Corbicula	3.9	3.5	2.9	2.9	0.0
Phylum Annelida						
Oligochaeta		337.3	1518.8	362.2	598.0	1290.2
Phylum Platyhelminthes						
Platyhelminthes		0.0	22.4	0.0	0.0	4.9
Phylum Nematoda						
Nematoda		21.6	30.0	44.9	11.8	13.7

		High Agriculture (AG-H) Streams					
		1	2	3	4	5	6
Order Collembola							
Isotomidae		0.0	1.8	2.9	6.3	0.0	0.0
Order Ephemeroptera							
Ameletidae	*Ameletus*	0.0	0.0	0.0	0.0	0.0	0.0
Baetidae	*Acentrella*	17.7	2.9	20.6	36.1	62.7	0.0
Baetidae	*Baetis*	0.0	1.2	0.0	0.0	15.7	0.0
Baetiscidae	*Baetisca*	0.6	5.3	17.6	4.7	11.8	0.6
Ephemerellidae	*Drunella*	0.0	7.6	6.9	7.1	113.7	0.6
Ephemerellidae	*Ephemerella*	398.1	499.4	193.1	542.0	202.9	6.5
Ephemerellidae	*Eurylophella*	46.0	0.0	0.0	11.8	0.0	0.0
Ephemerellidae	*Serratella*	24.7	64.1	9.8	76.1	39.2	0.0
Ephemeridae	*Ephemera*	0.0	0.0	2.9	2.4	0.0	0.0
Heptageniidae	*Cinygmula*	0.0	0.6	0.0	13.3	66.7	0.0
Heptageniidae	*Epeorus*	16.5	84.7	5.9	112.9	31.4	0.6
Heptageniidae	*Leucrocuta*	0.0	4.7	15.7	58.0	17.6	0.0
Heptageniidae	*Rhithrogena*	0.0	12.9	0.0	12.5	0.0	0.0
Heptageniidae	*Stenacron*	11.8	11.8	27.5	0.0	5.9	0.0
Heptageniidae	*Stenonema*	17.1	32.9	44.1	24.3	126.5	0.0
Isonychiidae	*Isonychia*	0.0	0.0	0.0	0.0	0.0	0.0
Leptophlebiidae	*Paraleptophlebia*	8.2	55.3	200.0	36.1	27.5	0.0
Order Odonata							
Calopterygidae	*Hataerina*	0.0	0.0	0.0	2.4	0.0	0.0
Gomphidae	*Lanthus*	0.0	8.2	2.9	3.9	0.0	2.4
Gomphidae	*Ophiogomphus*	4.2	5.3	6.9	60.4	59.8	0.0
Gomphidae	*Stylogomphus*	0.0	0.0	2.9	0.0	0.0	0.0
Order Plecoptera							
Capniidae		0.0	9.4	0.0	0.0	0.0	0.0
Chloroperlidae	*Alloperla*	0.0	12.9	0.0	0.0	0.0	0.0
Chloroperlidae	*Haploperla*	1.6	9.4	3.9	12.5	0.0	0.6
Chloroperlidae	*Sweltsa*	0.0	0.0	0.0	0.0	0.0	0.0
Leuctridae	*Leuctra*	22.1	23.5	117.6	36.9	35.3	0.0
Nemouridae	*Amphinemura*	0.0	0.0	0.0	0.0	3.9	0.0
Nemouridae	*Prostoia*	0.0	0.0	0.0	0.0	0.0	0.0
Peltoperlidae	*Tallaperla*	0.0	0.0	0.0	0.0	0.0	0.0
Perlidae	*Acroneuria*	4.5	0.0	0.0	7.8	3.9	0.6
Perlidae	*Agnetina*	3.5	44.1	0.0	0.0	0.0	0.0
Perlidae	*Beloneuria*	0.0	0.0	0.0	0.0	0.0	0.0
Perlidae	*Paragnetina*	0.0	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Cultus*	5.1	7.1	17.6	3.9	0.0	0.0
Perlodidae	*Diploperla*	0.0	0.0	2.9	0.0	0.0	0.0
Perlodidae	*Isogenoides*	0.0	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Isoperla*	107.7	48.2	28.4	77.6	25.5	0.0
Perlodidae	*Malirekus*	0.0	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Remenus*	0.0	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Yugus*	0.0	0.0	0.0	0.0	0.0	0.0

Pteronarcyidae	*Pteronarcys*	3.5	2.4	3.9	0.0	7.8	0.0
Order Hemiptera							
Hebridae	*Merragata*	0.0	1.8	0.0	0.0	0.0	0.0
Order Megaloptera							
Corydalidae	*Corydalus*	0.0	1.2	0.0	0.0	0.0	0.0
Corydalidae	*Nigronia*	0.0	0.6	2.9	0.0	2.9	4.7
Order Trichoptera							
Brachycentridae	*Brachycentrus*	0.0	0.0	0.0	0.0	0.0	0.0
Brachycentridae	*Micrasema*	0.0	0.0	0.0	0.0	0.0	0.0
Glossosomatidae	*Agapetus*	0.0	0.0	8.8	0.0	0.0	0.0
Glossosomatidae	*Glossosoma*	0.0	11.8	11.8	0.0	0.0	0.0
Glossosomatidae	*Matrioptila*	0.0	0.0	0.0	0.0	0.0	0.0
Goeridae	*Goera*	0.0	0.0	0.0	2.4	0.0	0.0
Goeridae	*Goerita*	0.6	0.0	0.0	2.4	0.0	0.0
Hydropsychidae	*Cheumatopsyche*	48.7	168.8	274.5	18.0	176.5	12.4
Hydropsychidae	*Diplectrona*	17.6	2.4	0.0	14.1	3.9	0.0
Hydropsychidae	*Hydropsyche*	164.6	41.8	25.5	12.5	0.0	0.0
Hydropsychidae	*Parapsyche*	0.0	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Hydroptila*	0.0	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Leucotrichia*	0.0	34.7	0.0	3.9	0.0	0.0
Lepidostomatidae	*Lepidostoma*	0.0	0.0	0.0	3.9	3.9	0.0
Leptoceridae	*Oecetis*	0.0	0.0	0.0	0.0	0.0	0.0
Leptoceridae	*Setodes*	0.0	0.0	0.0	0.0	0.0	0.0
Limnephilidae	*Hydatophylax*	0.0	0.0	0.0	0.0	0.0	0.0
Limnephilidae	*Pycnopsyche*	1.0	0.0	0.0	0.0	0.0	0.0
Odontoceridae	*Psilotreta*	0.0	0.0	0.0	0.0	0.0	0.0
Philopotamidae	*Dolophilodes*	4.1	1.8	3.9	4.7	11.8	0.0
Polycentropodidae	*Polycentropus*	2.4	11.2	16.7	0.0	11.8	0.0
Polycentropodidae	*Neureclipsis*	0.0	0.0	0.0	0.0	0.0	0.0
Psychomyiidae	*Lype*	0.0	0.0	11.8	0.0	5.9	0.0
Psychomyiidae	*Psychomyia*	0.0	0.0	0.0	0.0	0.0	0.0
Rhyacophilidae	*Rhyacophila*	0.0	0.0	0.0	7.8	27.5	0.0
Uenoidae	*Neophylax*	0.0	7.1	0.0	6.3	3.9	0.0
Order Lepidoptera							
Noctuidae		0.0	0.0	0.0	0.0	0.0	0.0
Order Coleoptera							
Dryopidae	*Helichus*	0.0	2.4	0.0	3.9	5.9	0.0
Elmidae	*Ancyronyx*	0.0	24.7	0.0	0.0	0.0	1.2
Elmidae	*Dubiraphia*	9.1	0.0	0.0	0.0	0.0	0.0
Elmidae	*Macronychus*	3.5	0.0	0.0	0.0	0.0	0.6
Elmidae	*Optioservus*	843.4	120.6	546.1	282.4	71.6	13.5
Elmidae	*Oulimnius*	311.3	86.5	86.3	31.4	110.8	59.4
Elmidae	*Promoresia*	0.6	0.0	2.9	0.0	0.0	0.6
Elmidae	*Stenelmis*	6.3	0.0	0.0	57.3	42.2	4.1
Psephenidae	*Ectopria*	0.0	0.0	0.0	0.0	17.6	0.0
Psephenidae	*Psephenus*	26.5	358.2	264.7	135.7	56.9	48.2

Ptilodactylidae	*Anchytarsus*	0.0	0.0	0.0	0.0	2.9	0.0
Staphylinidae	*Thinobius*	0.0	0.0	0.0	0.0	0.0	0.0
Order Diptera							
Athericidae	*Atherix*	0.0	0.0	19.6	0.0	3.9	0.0
Blephariceridae	*Blephariceria*	1.2	15.3	6.9	18.0	3.9	0.6
Cecidomyiidae		0.0	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Atrichopogon*	0.0	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Ceratopogon*	0.0	0.0	0.0	3.9	12.7	0.0
Ceratopogonidae	*Culicoides*	0.0	0.0	0.0	0.0	5.9	0.0
Ceratopogonidae	*Dasyhelea*	0.0	0.0	0.0	0.0	8.8	0.0
Ceratopogonidae	*Monohelea*	0.0	1.8	0.0	0.0	0.0	0.0
Ceratopogonidae	*Palpomyia*	6.2	1.8	2.9	64.3	0.0	0.6
Ceratopogonidae	*Stilobezzia*	0.6	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Brillia*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Chernovskiia*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Chironomus*	0.0	0.0	0.0	0.0	0.0	9.8
Chironomidae	*Conchapelopia*	20.8	51.3	107.4	18.6	255.5	0.0
Chironomidae	*Constempellina*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Corynoneura*	20.8	20.5	26.8	43.4	0.0	0.0
Chironomidae	*Cryptochironomus*	41.7	10.3	0.0	18.6	0.0	39.3
Chironomidae	*Demicryptochironomus*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Diamesa*	0.0	0.0	0.0	0.0	0.0	29.5
Chironomidae	*Epoicocladius*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Eukiefferiella*	0.0	51.3	0.0	0.0	0.0	0.0
Chironomidae	*Harnischia*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Lopescladius*	0.0	113.0	0.0	0.0	0.0	0.0
Chironomidae	*Micropsectra*	166.7	51.3	402.6	80.5	204.4	49.1
Chironomidae	*Microtendipes*	62.5	51.3	26.8	24.8	51.1	9.8
Chironomidae	*Nilotanypus*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Orthocladius*	708.4	20.5	0.0	105.3	766.5	737.2
Chironomidae	*Parachaetocladius*	83.3	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parakiefferiella*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parametriocnemus*	62.5	277.3	187.9	31.0	408.8	0.0
Chironomidae	*Polypedilum*	312.5	51.3	751.6	86.7	1226.4	314.5
Chironomidae	*Potthastia*	0.0	0.0	0.0	0.0	51.1	98.3
Chironomidae	*Rheocricotopus*	145.8	10.3	53.7	0.0	357.7	0.0
Chironomidae	*Rheotanytarsus*	166.7	30.8	26.8	0.0	1022.0	0.0
Chironomidae	*Robackia*	0.0	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Stempellina*	0.0	0.0	161.0	12.4	306.6	0.0
Chironomidae	*Stempellinella*	0.0	0.0	241.6	6.2	0.0	0.0
Chironomidae	*Thienemanniella*	0.0	0.0	0.0	0.0	0.0	0.0
Dixidae	*Dixa*	0.0	0.0	0.0	0.0	0.0	0.0
Dolichopodidae		0.0	0.0	0.0	0.0	0.0	0.0
Empididae	*Chelifera*	2.0	0.0	3.9	0.0	15.7	0.6
Empididae	*Clinocera*	15.5	7.1	12.7	2.4	0.0	0.6
Empididae	*Hemerodromia*	22.4	57.1	20.6	11.8	549.0	63.5
Ephydridae		0.0	0.0	0.0	0.0	0.0	0.0
Phoridae		1.0	0.0	0.0	0.0	0.0	0.6
Psychodidae	*Pericoma*	0.0	0.0	0.0	0.0	0.0	0.0
Scathophagidae		0.6	0.0	0.0	0.0	0.0	0.0

Simuliidae	*Prosimulium*	11.6	2.9	3.9	0.0	58.8	3.5
Simuliidae	*Simulium*	0.0	0.0	0.0	0.0	7.8	0.0
Stratiomyidae	*Caloparyphus*	0.0	0.0	0.0	0.0	0.0	0.0
Stratiomyidae	*Odontomyia*	0.0	0.0	0.0	0.0	0.0	0.0
Stratiomyidae	*Stratiomys*	0.0	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Chrysops*	0.0	0.0	3.9	0.0	0.0	0.0
Tabanidae	*Tabanus*	0.0	0.0	0.0	0.0	0.0	0.0
Tanyderidae	*Protoplasa*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Antocha*	366.0	102.4	98.0	3.9	25.5	1.2
Tipulidae	*Brachyprenna*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Cryptolabis*	0.0	0.0	0.0	0.0	7.8	0.0
Tipulidae	*Dactylolabis*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Dicranota*	0.0	0.0	0.0	3.9	0.0	0.0
Tipulidae	*Hexatoma*	8.4	0.0	19.6	0.0	15.7	9.4
Tipulidae	*Limonia*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Lipsothrix*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Molophilus*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Pseudolimnophila*	2.4	0.6	9.8	22.0	0.0	0.0
Tipulidae	*Rhabdomastix*	0.0	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Tipula*	2.4	7.6	18.6	3.9	5.9	0.0
Unknown	Genus A	0.0	0.0	0.0	0.0	0.0	0.0
Unknown	Genus B	0.0	0.0	0.0	0.0	0.0	0.0
Class Crustacea							
Acari	Hydracarina	82.7	17.1	39.2	23.5	302.0	55.9
Copepoda		20.0	3.5	2.9	0.0	60.8	0.0
Decapoda		0.6	0.0	0.0	0.0	0.0	0.0
Phylum Mollusca							
Gastropoda	Ancylidae	47.4	15.3	99.0	3.9	35.3	0.6
Gastropoda	Prosobranchia	62.1	0.0	49.0	242.4	54.9	0.6
Gastropoda	Pulmonata	0.6	2.9	0.0	0.0	0.0	0.0
Bivalvia	Corbicula	30.3	0.6	8.8	49.4	0.0	0.0
Phylum Annelida							
Oligochaeta		726.8	984.7	775.5	609.4	4049.0	784.7
Phylum Platyhelminthes							
Platyhelminthes		9.4	1.2	41.2	11.8	9.8	8.2
Phylum Nematoda							
Nematoda		33.6	37.6	10.8	16.5	39.2	19.4

		Recovery 1 (REC-1) Streams			
		1	2	3	4
Order Collembola					
Isotomidae		0.0	2.9	0.0	0.0
Order Ephemeroptera					
Ameletidae	*Ameletus*	3.9	0.0	0.0	0.0
Baetidae	*Acentrella*	172.5	735.3	18.6	67.6
Baetidae	*Baetis*	9.8	142.2	45.1	7.8
Baetiscidae	*Baetisca*	8.8	0.0	0.0	2.0
Ephemerellidae	*Drunella*	12.7	381.4	115.7	27.5
Ephemerellidae	*Ephemerella*	970.6	580.4	305.9	467.6
Ephemerellidae	*Eurylophella*	37.3	0.0	0.0	9.8
Ephemerellidae	*Serratella*	62.7	15.7	5.9	22.5
Ephemeridae	*Ephemera*	0.0	0.0	0.0	5.9
Heptageniidae	*Cinygmula*	0.0	24.5	13.7	2.0
Heptageniidae	*Epeorus*	55.9	122.5	88.2	20.6
Heptageniidae	*Leucrocuta*	1.0	0.0	0.0	1.0
Heptageniidae	*Rhithrogena*	2.9	182.4	9.8	7.8
Heptageniidae	*Stenacron*	2.9	2.9	15.7	2.9
Heptageniidae	*Stenonema*	13.7	9.8	7.8	55.9
Isonychiidae	*Isonychia*	0.0	0.0	0.0	1.0
Leptophlebiidae	*Paraleptophlebia*	54.9	23.5	35.3	64.7
Order Odonata					
Calopterygidae	*Hataerina*	0.0	0.0	0.0	0.0
Gomphidae	*Lanthus*	0.0	2.9	8.8	0.0
Gomphidae	*Ophiogomphus*	37.3	0.0	0.0	0.0
Gomphidae	*Stylogomphus*	11.8	0.0	0.0	0.0
Order Plecoptera					
Capniidae		0.0	0.0	0.0	0.0
Chloroperlidae	*Alloperla*	0.0	0.0	0.0	0.0
Chloroperlidae	*Haploperla*	2.0	6.9	36.3	1.0
Chloroperlidae	*Sweltsa*	0.0	0.0	0.0	0.0
Leuctridae	*Leuctra*	171.6	11.8	499.0	94.1
Nemouridae	*Amphinemura*	13.7	0.0	11.8	2.0
Nemouridae	*Prostoia*	0.0	0.0	0.0	0.0
Peltoperlidae	*Tallaperla*	0.0	8.8	7.8	11.8
Perlidae	*Acroneuria*	33.3	2.9	12.7	5.9
Perlidae	*Agnetina*	0.0	0.0	0.0	0.0
Perlidae	*Beloneuria*	2.9	0.0	0.0	0.0
Perlidae	*Paragnetina*	0.0	0.0	0.0	0.0
Perlodidae	*Cultus*	0.0	2.9	0.0	1.0
Perlodidae	*Diploperla*	0.0	0.0	0.0	0.0
Perlodidae	*Isogenoides*	0.0	0.0	0.0	0.0
Perlodidae	*Isoperla*	50.0	35.3	25.5	25.5
Perlodidae	*Malirekus*	0.0	0.0	2.0	0.0
Perlodidae	*Remenus*	0.0	0.0	0.0	0.0
Perlodidae	*Yugus*	0.0	0.0	11.8	0.0

Pteronarcyidae	*Pteronarcys*	14.7	8.8	7.8	8.8
Order Hemiptera					
Hebridae	*Merragata*	0.0	0.0	0.0	0.0
Order Megaloptera					
Corydalidae	*Corydalus*	0.0	0.0	0.0	0.0
Corydalidae	*Nigronia*	0.0	0.0	0.0	0.0
Order Trichoptera					
Brachycentridae	*Brachycentrus*	0.0	0.0	0.0	0.0
Brachycentridae	*Micrasema*	0.0	0.0	0.0	0.0
Glossosomatidae	*Agapetus*	17.6	66.7	28.4	82.4
Glossosomatidae	*Glossosoma*	1.0	0.0	0.0	1.0
Glossosomatidae	*Matrioptila*	0.0	0.0	0.0	63.7
Goeridae	*Goera*	2.9	5.9	0.0	0.0
Goeridae	*Goerita*	0.0	0.0	0.0	0.0
Hydropsychidae	*Cheumatopsyche*	71.6	0.0	6.9	17.6
Hydropsychidae	*Diplectrona*	62.7	20.6	54.9	0.0
Hydropsychidae	*Hydropsyche*	8.8	0.0	4.9	5.9
Hydropsychidae	*Parapsyche*	0.0	0.0	0.0	0.0
Hydroptilidae	*Hydroptila*	0.0	0.0	0.0	1.0
Hydroptilidae	*Leucotrichia*	0.0	0.0	0.0	0.0
Lepidostomatidae	*Lepidostoma*	0.0	5.9	2.9	4.9
Leptoceridae	*Oecetis*	0.0	0.0	0.0	0.0
Leptoceridae	*Setodes*	0.0	0.0	0.0	0.0
Limnephilidae	*Hydatophylax*	0.0	0.0	0.0	0.0
Limnephilidae	*Pycnopsyche*	0.0	0.0	0.0	0.0
Odontoceridae	*Psilotreta*	0.0	0.0	0.0	0.0
Philopotamidae	*Dolophilodes*	2.9	0.0	1.0	81.4
Polycentropodidae	*Polycentropus*	28.4	0.0	30.4	25.5
Polycentropodidae	*Neureclipsis*	0.0	0.0	0.0	0.0
Psychomyiidae	*Lype*	0.0	0.0	2.0	7.8
Psychomyiidae	*Psychomyia*	7.8	0.0	0.0	29.4
Rhyacophilidae	*Rhyacophila*	3.9	18.6	65.7	31.4
Uenoidae	*Neophylax*	10.8	8.8	2.0	1.0
Order Lepidoptera					
Noctuidae		0.0	0.0	0.0	0.0
Order Coleoptera					
Dryopidae	*Helichus*	11.8	0.0	0.0	0.0
Elmidae	*Ancyronyx*	0.0	0.0	0.0	0.0
Elmidae	*Dubiraphia*	0.0	0.0	0.0	0.0
Elmidae	*Macronychus*	3.9	0.0	0.0	0.0
Elmidae	*Optioservus*	218.6	253.9	70.6	70.6
Elmidae	*Oulimnius*	193.1	657.8	86.3	13.7
Elmidae	*Promoresia*	7.8	15.7	3.9	0.0
Elmidae	*Stenelmis*	0.0	0.0	0.0	0.0
Psephenidae	*Ectopria*	3.9	0.0	2.9	1.0
Psephenidae	*Psephenus*	102.9	8.8	3.9	30.4

Ptilodactylidae	*Anchytarsus*	0.0	0.0	0.0	0.0
Staphylinidae	*Thinobius*	0.0	0.0	1.0	0.0
Order Diptera					
Athericidae	*Atherix*	9.8	0.0	0.0	11.8
Blephariceridae	*Blephariceria*	93.1	114.7	20.6	83.3
Cecidomyiidae		0.0	0.0	0.0	0.0
Ceratopogonidae	*Atrichopogon*	1.0	0.0	0.0	0.0
Ceratopogonidae	*Ceratopogon*	5.9	0.0	0.0	0.0
Ceratopogonidae	*Culicoides*	0.0	0.0	2.9	3.9
Ceratopogonidae	*Dasyhelea*	13.7	0.0	1.0	0.0
Ceratopogonidae	*Monohelea*	0.0	0.0	0.0	0.0
Ceratopogonidae	*Palpomyia*	25.5	0.0	46.1	4.9
Ceratopogonidae	*Stilobezzia*	0.0	0.0	0.0	0.0
Chironomidae	*Brillia*	0.0	0.0	80.0	0.0
Chironomidae	*Chernovskiia*	0.0	0.0	50.0	0.0
Chironomidae	*Chironomus*	0.0	0.0	0.0	0.0
Chironomidae	*Conchapelopia*	17.4	6.7	10.0	18.1
Chironomidae	*Constempellina*	0.0	0.0	0.0	0.0
Chironomidae	*Corynoneura*	34.8	6.7	0.0	18.1
Chironomidae	*Cryptochironomus*	0.0	6.7	0.0	0.0
Chironomidae	*Demicryptochironomus*	0.0	0.0	60.0	0.0
Chironomidae	*Diamesa*	0.0	0.0	20.0	0.0
Chironomidae	*Epoicocladius*	0.0	0.0	0.0	0.0
Chironomidae	*Eukiefferiella*	52.2	66.7	70.0	18.1
Chironomidae	*Harnischia*	0.0	0.0	0.0	0.0
Chironomidae	*Lopescladius*	0.0	0.0	10.0	9.0
Chironomidae	*Micropsectra*	243.5	240.1	130.0	108.4
Chironomidae	*Microtendipes*	0.0	0.0	50.0	0.0
Chironomidae	*Nilotanypus*	0.0	0.0	0.0	0.0
Chironomidae	*Orthocladius*	295.7	126.7	190.0	81.3
Chironomidae	*Parachaetocladius*	0.0	0.0	0.0	0.0
Chironomidae	*Parakiefferiella*	0.0	0.0	0.0	27.1
Chironomidae	*Parametriocnemus*	34.8	53.4	0.0	72.3
Chironomidae	*Polypedilum*	34.8	0.0	20.0	108.4
Chironomidae	*Potthastia*	0.0	0.0	50.0	18.1
Chironomidae	*Rheocricotopus*	104.4	20.0	0.0	18.1
Chironomidae	*Rheotanytarsus*	0.0	0.0	30.0	36.1
Chironomidae	*Robackia*	0.0	0.0	0.0	0.0
Chironomidae	*Stempellina*	17.4	13.3	30.0	36.1
Chironomidae	*Stempellinella*	156.6	33.3	0.0	0.0
Chironomidae	*Thienemanniella*	295.7	0.0	0.0	135.6
Dixidae	*Dixa*	0.0	11.8	4.9	0.0
Dolichopodidae		0.0	0.0	0.0	0.0
Empididae	*Chelifera*	3.9	0.0	14.7	12.7
Empididae	*Clinocera*	3.9	0.0	3.9	1.0
Empididae	*Hemerodromia*	3.9	0.0	0.0	1.0
Ephydridae		0.0	0.0	0.0	0.0
Phoridae		0.0	0.0	0.0	0.0
Psychodidae	*Pericoma*	0.0	3.9	0.0	0.0
Scathophagidae		0.0	0.0	0.0	0.0

Simuliidae	*Prosimulium*	9.8	20.6	10.8	113.7
Simuliidae	*Simulium*	2.9	0.0	0.0	39.2
Stratiomyidae	*Caloparyphus*	0.0	0.0	0.0	0.0
Stratiomyidae	*Odontomyia*	0.0	0.0	4.9	0.0
Stratiomyidae	*Stratiomys*	0.0	0.0	0.0	0.0
Tabanidae	*Chrysops*	0.0	0.0	0.0	0.0
Tabanidae	*Tabanus*	0.0	0.0	0.0	0.0
Tanyderidae	*Protoplasa*	0.0	0.0	0.0	0.0
Tipulidae	*Antocha*	5.9	33.3	33.3	37.3
Tipulidae	*Brachyprenna*	0.0	0.0	0.0	0.0
Tipulidae	*Cryptolabis*	0.0	0.0	0.0	0.0
Tipulidae	*Dactylolabis*	0.0	0.0	0.0	0.0
Tipulidae	*Dicranota*	10.8	48.0	23.5	4.9
Tipulidae	*Hexatoma*	2.9	30.4	39.2	25.5
Tipulidae	*Limonia*	0.0	2.9	0.0	0.0
Tipulidae	*Lipsothrix*	0.0	0.0	0.0	0.0
Tipulidae	*Molophilus*	0.0	0.0	0.0	0.0
Tipulidae	*Pseudolimnophila*	6.9	0.0	0.0	0.0
Tipulidae	*Rhabdomastix*	1.0	3.9	0.0	0.0
Tipulidae	*Tipula*	3.9	5.9	1.0	2.9
Unknown	Genus A	0.0	0.0	0.0	0.0
Unknown	Genus B	0.0	0.0	0.0	5.9
Class Crustacea					
Acari	Hydracarina	24.5	17.6	7.8	74.5
Copepoda		1.0	0.0	9.8	0.0
Decapoda		0.0	0.0	0.0	1.0
Phylum Mollusca					
Gastropoda	Ancylidae	3.9	0.0	0.0	0.0
Gastropoda	Prosobranchia	83.3	40.2	12.7	2.9
Gastropoda	Pulmonata	0.0	0.0	0.0	0.0
Bivalvia	Corbicula	5.9	0.0	2.0	0.0
Phylum Annelida					
Oligochaeta		1300.0	240.2	664.7	199.0
Phylum Platyhelminthes					
Platyhelminthes		30.4	0.0	1.0	5.9
Phylum Nematoda					
Nematoda		3.9	5.9	17.6	0.0

		Recovery 2 (REC-2) Streams				
		1	2	3	4	5
Order Collembola						
Isotomidae		0.0	0.0	0.0	0.0	0.0
Order Ephemeroptera						
Ameletidae	*Ameletus*	1.4	0.0	0.0	0.0	0.0
Baetidae	*Acentrella*	2.6	54.7	29.4	33.9	59.8
Baetidae	*Baetis*	33.2	31.0	27.5	6.3	17.6
Baetiscidae	*Baetisca*	0.0	0.0	0.0	0.0	6.9
Ephemerellidae	*Drunella*	9.4	132.4	11.8	5.9	56.9
Ephemerellidae	*Ephemerella*	265.2	1000.6	172.5	537.5	232.4
Ephemerellidae	*Eurylophella*	4.7	0.0	0.0	0.0	0.0
Ephemerellidae	*Serratella*	3.2	20.2	0.0	11.6	10.8
Ephemeridae	*Ephemera*	50.0	4.3	0.0	0.0	0.0
Heptageniidae	*Cinygmula*	55.1	0.0	2.9	235.3	152.9
Heptageniidae	*Epeorus*	98.4	168.2	110.8	198.2	56.9
Heptageniidae	*Leucrocuta*	23.2	27.5	0.0	0.0	3.9
Heptageniidae	*Rhithrogena*	0.0	0.0	0.0	0.0	0.0
Heptageniidae	*Stenacron*	18.2	2.4	2.9	2.4	0.0
Heptageniidae	*Stenonema*	12.2	18.0	3.9	9.2	32.4
Isonychiidae	*Isonychia*	0.0	0.0	0.0	0.0	0.0
Leptophlebiidae	*Paraleptophlebia*	56.2	25.1	40.2	42.4	10.8
Order Odonata						
Calopterygidae	*Hataerina*	0.0	0.0	0.0	0.0	0.0
Gomphidae	*Lanthus*	2.0	2.9	0.0	2.4	0.0
Gomphidae	*Ophiogomphus*	0.0	0.0	0.0	0.0	0.0
Gomphidae	*Stylogomphus*	0.0	0.0	0.0	0.0	0.0
Order Plecoptera						
Capniidae		0.0	0.0	0.0	0.0	0.0
Chloroperlidae	*Alloperla*	0.0	0.0	0.0	0.0	0.0
Chloroperlidae	*Haploperla*	7.8	83.1	2.9	7.1	0.0
Chloroperlidae	*Sweltsa*	5.4	0.0	3.9	0.0	0.0
Leuctridae	*Leuctra*	89.9	147.1	43.1	144.7	35.3
Nemouridae	*Amphinemura*	63.6	3.3	14.7	19.8	6.9
Nemouridae	*Prostoia*	0.0	0.0	0.0	0.0	0.0
Peltoperlidae	*Tallaperla*	8.1	13.9	14.7	0.0	3.9
Perlidae	*Acroneuria*	7.4	12.5	3.9	10.0	1.0
Perlidae	*Agnetina*	0.0	0.0	0.0	0.0	0.0
Perlidae	*Beloneuria*	3.4	0.0	2.9	9.8	0.0
Perlidae	*Paragnetina*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Cultus*	0.0	0.0	0.0	4.3	3.9
Perlodidae	*Diploperla*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Isogenoides*	0.0	0.0	0.0	0.0	2.9
Perlodidae	*Isoperla*	27.6	54.1	6.9	35.1	21.6
Perlodidae	*Malirekus*	0.0	0.0	0.0	0.0	0.0
Perlodidae	*Remenus*	0.0	2.4	0.0	0.0	0.0
Perlodidae	*Yugus*	2.6	49.8	13.7	0.0	0.0

Pteronarcyidae	*Pteronarcys*	4.9	5.7	7.8	28.4	23.5
Order Hemiptera						
Hebridae	*Merragata*	0.0	0.0	0.0	0.0	0.0
Order Megaloptera						
Corydalidae	*Corydalus*	0.0	0.0	0.0	0.0	0.0
Corydalidae	*Nigronia*	1.4	0.0	0.0	0.0	0.0
Order Trichoptera						
Brachycentridae	*Brachycentrus*	0.9	0.0	0.0	0.0	0.0
Brachycentridae	*Micrasema*	0.0	0.0	0.0	20.4	0.0
Glossosomatidae	*Agapetus*	0.0	29.4	0.0	2.4	10.8
Glossosomatidae	*Glossosoma*	1.4	39.8	0.0	3.9	4.9
Glossosomatidae	*Matrioptila*	0.0	0.0	0.0	0.0	0.0
Goeridae	*Goera*	1.4	4.9	0.0	0.0	8.8
Goeridae	*Goerita*	0.0	0.0	0.0	0.0	0.0
Hydropsychidae	*Cheumatopsyche*	5.5	0.0	0.0	0.0	11.8
Hydropsychidae	*Diplectrona*	22.2	30.6	20.6	56.5	7.8
Hydropsychidae	*Hydropsyche*	0.6	0.0	8.8	2.0	1.0
Hydropsychidae	*Parapsyche*	0.0	0.0	1.0	0.0	0.0
Hydroptilidae	*Hydroptila*	0.0	0.0	0.0	0.0	0.0
Hydroptilidae	*Leucotrichia*	0.0	0.0	0.0	0.0	0.0
Lepidostomatidae	*Lepidostoma*	0.6	1.0	3.9	4.3	7.8
Leptoceridae	*Oecetis*	0.0	0.0	0.0	0.0	0.0
Leptoceridae	*Setodes*	0.0	0.0	0.0	0.0	1.0
Limnephilidae	*Hydatophylax*	1.2	0.0	0.0	0.0	0.0
Limnephilidae	*Pycnopsyche*	0.0	0.0	0.0	0.0	0.0
Odontoceridae	*Psilotreta*	0.0	0.0	0.0	0.0	0.0
Philopotamidae	*Dolophilodes*	1.8	0.0	0.0	0.0	0.0
Polycentropodidae	*Polycentropus*	12.5	11.2	0.0	10.8	0.0
Polycentropodidae	*Neureclipsis*	0.0	0.0	0.0	0.0	0.0
Psychomyiidae	*Lype*	2.3	0.0	0.0	0.0	0.0
Psychomyiidae	*Psychomyia*	0.0	0.0	0.0	2.0	0.0
Rhyacophilidae	*Rhyacophila*	4.4	15.7	16.7	14.1	9.8
Uenoidae	*Neophylax*	16.4	33.7	0.0	16.9	16.7
Order Lepidoptera						
Noctuidae		0.0	0.0	0.0	0.0	0.0
Order Coleoptera						
Dryopidae	*Helichus*	0.0	0.0	0.0	2.4	0.0
Elmidae	*Ancyronyx*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Dubiraphia*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Macronychus*	0.0	0.0	0.0	0.0	0.0
Elmidae	*Optioservus*	36.8	156.7	1.0	50.8	74.5
Elmidae	*Oulimnius*	162.1	696.9	27.5	76.7	98.0
Elmidae	*Promoresia*	0.0	1.0	0.0	38.8	7.8
Elmidae	*Stenelmis*	0.0	0.0	0.0	0.0	0.0
Psephenidae	*Ectopria*	3.7	5.9	0.0	0.0	1.0
Psephenidae	*Psephenus*	38.6	4.9	0.0	6.7	0.0

Ptilodactylidae	*Anchytarsus*	0.0	0.0	0.0	0.0	0.0
Staphylinidae	*Thinobius*	0.0	0.0	0.0	0.0	0.0
Order Diptera						
Athericidae	*Atherix*	0.0	0.0	0.0	28.8	6.9
Blephariceridae	*Blephāricera*	7.9	187.5	1.0	8.2	37.3
Cecidomyiidae		0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Atrichopogon*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Ceratopogon*	1.4	0.0	0.0	2.0	0.0
Ceratopogonidae	*Culicoides*	0.0	3.3	0.0	0.0	0.0
Ceratopogonidae	*Dasyhelea*	0.0	0.0	0.0	0.0	2.0
Ceratopogonidae	*Monohelea*	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	*Palpomyia*	6.8	35.5	9.8	2.9	2.0
Ceratopogonidae	*Stilobezzia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Brillia*	11.1	0.0	21.8	5.3	0.0
Chironomidae	*Chernovskiia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Chironomus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Conchapelopia*	15.5	11.9	2.7	0.0	11.8
Chironomidae	*Constempellina*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Corynoneura*	13.3	0.0	8.2	0.0	0.0
Chironomidae	*Cryptochironomus*	0.0	0.0	2.7	0.0	5.9
Chironomidae	*Demicryptochironomus*	2.2	0.0	0.0	0.0	0.0
Chironomidae	*Diamesa*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Epoicocladius*	6.6	0.0	0.0	0.0	0.0
Chironomidae	*Eukiefferiella*	0.0	0.0	2.7	16.0	0.0
Chironomidae	*Harnischia*	0.0	5.9	0.0	0.0	0.0
Chironomidae	*Lopescladius*	4.4	53.4	0.0	0.0	0.0
Chironomidae	*Micropsectra*	13.3	136.4	30.0	187.2	41.2
Chironomidae	*Microtendipes*	2.2	5.9	5.5	5.3	5.9
Chironomidae	*Nilotanypus*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Orthocladius*	6.6	23.7	27.3	16.0	47.1
Chironomidae	*Parachaetocladius*	26.5	0.0	2.7	0.0	0.0
Chironomidae	*Parakiefferiella*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Parametriocnemus*	11.1	23.7	90.0	26.7	41.2
Chironomidae	*Polypedilum*	2.2	47.4	0.0	37.4	76.5
Chironomidae	*Potthastia*	6.6	11.9	2.7	5.3	0.0
Chironomidae	*Rheocricotopus*	26.5	17.8	13.6	42.8	17.6
Chironomidae	*Rheotanytarsus*	15.5	29.6	2.7	32.1	0.0
Chironomidae	*Robackia*	0.0	0.0	0.0	0.0	0.0
Chironomidae	*Stempellina*	2.2	0.0	0.0	16.0	0.0
Chironomidae	*Stempellinella*	0.0	0.0	0.0	5.3	82.4
Chironomidae	*Thienemanniella*	0.0	0.0	0.0	16.0	11.8
Dixidae	*Dixa*	1.4	0.0	1.0	0.0	2.9
Dolichopodidae		0.0	0.0	0.0	0.0	0.0
Empididae	*Chelifera*	0.9	0.0	0.0	6.9	8.8
Empididae	*Clinocera*	0.0	0.0	0.0	0.0	0.0
Empididae	*Hemerodromia*	0.0	0.0	3.9	0.0	1.0
Ephydridae		0.9	0.0	0.0	0.0	0.0
Phoridae		2.3	0.0	0.0	0.0	0.0
Psychodidae	*Pericoma*	0.0	0.0	0.0	0.0	0.0
Scathophagidae		0.0	0.0	0.0	0.0	0.0

Simuliidae	*Prosimulium*	55.7	42.2	24.5	82.5	115.7
Simuliidae	*Simulium*	0.0	0.0	0.0	0.0	18.6
Stratiomyidae	*Caloparyphus*	0.9	0.0	0.0	0.0	0.0
Stratiomyidae	*Odontomyia*	0.0	0.0	0.0	0.0	0.0
Stratiomyidae	*Stratiomys*	0.0	7.1	0.0	0.0	0.0
Tabanidae	*Chrysops*	0.0	0.0	0.0	0.0	0.0
Tabanidae	*Tabanus*	0.0	0.0	0.0	0.0	0.0
Tanyderidae	*Protoplasa*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Antocha*	4.6	60.0	8.8	58.0	7.8
Tipulidae	*Brachyprenna*	2.3	0.0	0.0	0.0	0.0
Tipulidae	*Cryptolabis*	0.0	0.0	0.0	0.0	2.0
Tipulidae	*Dactylolabis*	1.4	0.0	0.0	0.0	0.0
Tipulidae	*Dicranota*	2.4	18.8	32.4	34.7	38.2
Tipulidae	*Hexatoma*	2.6	24.9	2.0	13.9	5.9
Tipulidae	*Limonia*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Lipsothrix*	0.0	0.0	0.0	0.0	0.0
Tipulidae	*Molophilus*	1.8	0.0	0.0	0.0	0.0
Tipulidae	*Pseudolimnophila*	0.0	8.8	0.0	0.0	0.0
Tipulidae	*Rhabdomastix*	0.0	1.0	0.0	0.0	2.0
Tipulidae	*Tipula*	0.0	4.9	4.9	2.4	2.0
Unknown	Genus A	0.0	0.0	0.0	0.0	0.0
Unknown	Genus B	0.0	0.0	0.0	0.0	0.0
Class Crustacea						
Acari	Hydracarina	1.4	5.3	0.0	18.4	100.0
Copepoda		0.0	3.9	0.0	0.0	0.0
Decapoda		2.0	0.0	0.0	1.0	1.0
Phylum Mollusca						
Gastropoda	Ancylidae	0.0	0.0	0.0	0.0	0.0
Gastropoda	Prosobranchia	9.2	15.1	4.9	32.4	0.0
Gastropoda	Pulmonata	0.0	0.0	0.0	0.0	0.0
Bivalvia	Corbicula	1.4	0.0	0.0	2.4	0.0
Phylum Annelida						
Oligochaeta		96.2	576.3	78.4	105.3	153.9
Phylum Platyhelminthes						
Platyhelminthes		1.8	13.3	0.0	7.3	5.9
Phylum Nematoda						
Nematoda		4.8	13.1	8.8	14.9	2.9

CURRICULUM VITAE
Matthew E. McTammany
18 March 2004

Birthdate: 1 June 1973 in Reading, Pennsylvania, USA

Home Address:
1131 Market Street
Lewisburg, PA, 17837, USA
Phone: 570-523-4921
Cell: 570-490-8009
E-mail: mmctamma@bucknell.edu
URL: http://www.facstaff.bucknell.edu/mmctamma/

Work Address:
Biology Department
Bucknell University
Lewisburg, PA, 17837, USA
Phone: 570-577-3975
Fax: 570-577-3537

EDUCATION
Ph. D. in Biology, 2004, Virginia Polytechnic Institute and State University, Blacksburg, Virginia
M. S. in Biology, 1998, Virginia Polytechnic Institute and State University, Blacksburg, Virginia
B. S. in Biology, 1995, Bucknell University, Lewisburg, Pennsylvania

CURRENT POSITION
2003-present, Assistant Professor of Biology and Environmental Science, Bucknell University, Lewisburg, Pennsylvania

TEACHING
PHILOSOPHY:
My approach to teaching attempts to engage students through interactions in class facilitated by field and lab exercises. I feel that my role as a teacher is to provide the knowledge and tools required to explore questions with a critical and creative mind and to create an atmosphere where students are challenged to push their knowledge into new areas.

EXPERIENCE:
Assistant professor, 2003-present, Biology Department and Environmental Studies Program, Bucknell University
- Population and Community Biology Lecture and Lab
- Limnology Lecture and Lab
- General Biology Lab

Instructor, Spring 2000, Department of Entomology, Virginia Polytechnic Institute and State University
- Aquatic Entomology Lecture and Lab

Graduate teaching assistant, 1995-2001, Department of Biology, Virginia Polytechnic Institute and State University
- Freshwater Ecology Lab
- Aquatic Entomology Lab
- Field and Lab Ecology
- General Biology Lab

Undergraduate teaching assistant, 1992-1995, Biology Department, Bucknell University

- Population and Community Biology Lab
- Plant and Animal Physiology Lab
- Cellular and Molecular Biology Lab
- Introductory Biology Lab

AWARDS:

Graduate Teaching Excellence Commendation, Spring 2002, Graduate School, Virginia Polytechnic Institute and State University

Outstanding Graduate Teaching Assistant, Spring 2002, Biology Department, Virginia Polytechnic Institute and State University

RESEARCH

RESEARCH INTERESTS:

My research interests include how landscapes affect stream ecosystem structure (biodiversity) and function (metabolism, organic matter processing, and nutrient dynamics). I am interested in stream recovery through passive and active restoration. I plan to use remote sensing and GIS to integrate spatial and temporal models of landscape change with models of stream ecosystems.

CURRENT PROJECTS:

Effects of heavy metals on leaf breakdown in mine-impacted streams of the Anthracite coal region

Role of leaf pack size in determining leaf breakdown rates in streams

Acidification of streams in Tuscarora sandstone geology and the impact on aquatic organisms

INDEPENDENT RESEARCH PROJECTS AS A STUDENT:

Doctoral research, 1998-2004, Virginia Polytechnic Institute and State University, Stream recovery during reforestation of agricultural watersheds, Dr. E. F. Benfield

Master's research, 1995-1998, Virginia Polytechnic Institute and State University, The impact of urbanization on benthic macroinvertebrates in southern Appalachian streams, Dr. E. F. Benfield

Undergraduate research, 1994-1995, Bucknell University, Treating the first flush: artificial wetland stormwater runoff treatment project, Dr. W. F. McDiffett

Undergraduate research, 1994-1995, Bucknell University, Groundwater chemistry and bacteria of the Montandon Marsh, Northumberland Co., Pennsylvania, USA, Dr. W. F. McDiffett

OTHER RESEARCH EXPERIENCE:

Research assistant, 1996-2003, Department of Biology, Virginia Polytechnic Institute and State University

- Lab manager, Virginia Tech Stream Team
- Stream hazard project: watersheds at risk for development, Dr. E. F. Benfield
- Modeling organic matter dynamics in a logged headwater stream, Dr. J. R. Webster
- Ecosystem metabolism in a mid-sized southern Appalachian river, Dr. J. R. Webster
- Effects of leaf litter exclusion and wood removal on phosphorus and nitrogen retention in a first-order forest stream, Dr. J. R. Webster

Research assistant, 1993-1995, Biology Department, Bucknell University

- Water chemistry of streams in different regions of New Zealand, Dr. W. F. McDiffett
- DNA Sequencing of *Drosophila hydei* polytene chromosomes, Dr. J. Tonzetich

Animal care technician, 1991-1995, Biology Department Animal Facility, Bucknell University

GRANTS & FELLOWSHIPS

Sigma Xi Grants in Aid of Research, $800 awarded for proposal entitled "Recovery of stream metabolic properties following reforestation of agricultural watersheds," Spring 2000.

Graduate Research Development Project, Graduate Student Assembly, Virginia Polytechnic Institute and State University, $250 awarded for proposal entitled "Recovery of stream ecosystems from agriculture: temporal and spatial patterns," Summer 1999.

Sigma Xi Grants in Aid of Research, $700 awarded for proposal entitled "Stream ecosystem recovery following reforestation of agricultural watersheds," Spring 1999.

Graduate Research Development Project, Graduate Student Assembly, Virginia Polytechnic Institute and State University, $300 awarded for proposal entitled "Effects of urbanization on biodiversity of streams in the southern Appalachians," Summer 1997.

McKenna Environmental Research Fellowship, funded for project entitled "Treating the first flush: artificial wetland stormwater runoff treatment project," Summer 1994.

McKenna Environmental Research Fellowship, funded for project entitled "Groundwater chemistry and bacteria of the Montandon Marsh, Northumberland Co., Pennsylvania, USA," Summer 1993.

TRAVEL AWARDS:

Simpson Fund Award for applied research, North American Benthological Society, $500 awarded for travel to NABS Meeting in Pittsburgh, PA, Spring 2002.

Travel Fund Project, Graduate Student Assembly, Virginia Polytechnic Institute and State University, $300 awarded for travel to NABS Meeting in LaCrosse, WI, Spring 2001.

Travel Fund Project, Graduate Student Assembly, Virginia Polytechnic Institute and State University, $150 awarded for travel to NABS Meeting in Keystone, CO, Spring 2000.

General Endowment Travel Award, North American Benthological Society, $300 awarded for travel to NABS Meeting in Keystone, CO, Spring 2000.

Travel Fund Project, Graduate Student Assembly, Virginia Polytechnic Institute and State University, $300 awarded for travel to American Society of Limnology and Oceanography/Ecological Society of America Meeting in St. Louis, MO, Spring 1998.

General Endowment Travel Award, North American Benthological Society, $250 awarded for travel to NABS Meeting in Charlottetown, PEI Canada, Spring 1998.

Travel Fund Project, Graduate Student Assembly, Virginia Polytechnic Institute and State University, $300 awarded for travel to NABS Meeting in San Marcos, TX, Spring 1997.

HONORS:

Second Place Student Poster Competition, 13 March 2002, Remote Sensing and GIS Research Symposium

Outstanding Graduate Student Award, Biology Department Nominee, Spring 2001, Virginia Polytechnic Institute and State University

Sigma Xi - General science society, inducted 1998, Virginia Polytechnic Institute and State University.

Phi Kappa Phi - Graduate student honor society, inducted 1996, Virginia Polytechnic Institute and State University.

Phi Sigma - Biological sciences honor society, inducted 1995, Bucknell University.

Alpha Lambda Delta - First-year student honor society, inducted 1992, Bucknell University.

PROFESSIONAL AND SERVICE ACTIVITIES

- Volunteer for the Susquehanna River Ice Observer Program, 2004-present
- Bucknell representative to the Woods Hole Marine Science Consortium, 2004-present
- Representative on the Monitoring Committee and member of the Buffalo Creek Watershed Alliance, 2004-present
- McKenna Foundation Committee, 2004-present
- Bucknell representative to the SEDA-COG Forum for the Future Susquehanna River Research Team, 2003-present
- GIS and remote sensing consultant for Lake of the Woods Association, Locust Grove, VA, 2003-present
- Reviewed sabbatical proposal for Wilkes University, 2003
- Panelist for Virginia Polytechnic Institute and State University GTA Workshop, 2002
- Invited student advisor to North American Benthological Society Naming Committee, 2002-2003
- Poster: Professional profile and programming opinions of the North American Benthological Society. North American Benthological Society 50th Annual Meeting. Pittsburgh, PA. 27 May-1 June 2002.
- Volunteer: Save Our Streams, Virginia Museum of Natural History, 2001-2003
- Manuscript reviewer for Freshwater Biology and the Journal of the North American Benthological Society, 2000-present
- Instructor: Teaching Life Sciences Labs, Virginia Polytechnic Institute and State University GTA Workshop, 2000-2002
- Representative on the International Profile Committee of the North American Benthological Society, 2000-present
- Student representative on the Executive Committee of the North American Benthological Society, 2000-2001
- Representative on the Human Resources Committee of the North American Benthological Society, 1998-present
- Workshop chair and member of the Graduate Resources Committee of the North American Benthological Society, 1998-2002
- Member of Biology Graduate Student Assembly Executive Committee, 1996-2002
- Judge, Virginia Junior Academy of Science, 56th Annual Meeting, Blacksburg, VA, May 1997

SOCIETY MEMBERSHIP:

- American Association for the Advancement of Science, member since 2000
- American Institute of Biological Sciences, member since 2002
- American Society of Limnology and Oceanography, member since 1997
- American Society of Photogrammetry and Remote Sensing, member since 1999
- American Water Resources Association, member since 2002
- Ecological Society of America, member since 1995
- International Association of Theoretical and Applied Limnology, member since 2000
- North American Benthological Society, member since 1995
- Pennsylvania Academy of Science, member 2004

PUBLICATIONS

Burcher, C. L., M. E. McTammany, G. S. Helfman, and E. F. Benfield. In review. Fish assemblage structure along a historical land use gradient. Environmental Monitoring and Assessment.

McTammany, M. E. and E. F. Benfield. In review. Role of spatial scale and stream size in determining urban impact on stream benthic macroinvertebrate communities. Hydrobiologia.

Webster, J. R., E. F. Benfield, S. W. Golladay, and M. E. McTammany. In press. Recovery of particulate organic matter dynamics in a stream draining a logged watershed—a pressing situation. In W. T. Swank (editor). Ecosystem recovery from clear-cutting.

McTammany, M. E., J. R. Webster, E. F. Benfield, and M. A. Neatrour. 2003. Longitudinal patterns of metabolism in a southern Appalachian river. Journal of the North American Benthological Society 22:359-370.

Scott, M. C., G. S. Helfman, M. E. McTammany, E. F. Benfield, and P. V. Bolstad. 2002. Multiscale influences on physical and chemical stream conditions across southern Appalachian landscapes. Journal of the American Water Resources Association 38:1379-1392.

McTammany, M. E. and R. H. Wynne. 2000. Spectral comparison of different age forests in the southern Appalachians. Proceedings of the American Society of Photogrammetry and Remote Sensing. CD-ROM.

Webster, J. R., J. L. Tank, J. B. Wallace, J. L. Meyer, S. L. Eggert, T. P. Ehrman, B. R. Ward, B. L. Bennett, P. F. Wagner, and M. E. McTammany. 2000. Effects of litter exclusion and wood removal on phosphorus and nitrogen retention in a forest stream. Verhandlung Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 27:1337-1340.

Simmons, G. M., J. R. Webster, A. S. Schultheis, and M. E. McTammany. 1998. Methods for use in Freshwater Ecology. Department of Biology, Virginia Polytechnic Institute and State University.

NOTES, REVIEWS:

Webster, J. R. and M. E. McTammany. In press. Review of W. K. Dodds. 2002. “Freshwater ecology: concepts and environmental applications.” Academic Press, San Diego, California. Transactions of the American Fisheries Society.

PRESENTATIONS

INVITED SEMINARS:

Are all forested streams the same? The legacy of agricultural impact on southern Appalachian streams. American Water Resources Association. Blacksburg, VA. 7 October 2002.

Recovery of streams from agriculture: lessons from the southern Appalachians. Biology Department, Bucknell University. Lewisburg, PA. 16 November 2001.

PAPERS AT MEETINGS:

M. E. McTammany and E. F. Benfield. Assessing recovery of streams from agriculture using biological structure and ecosystem function. North American Benthological Society 51st Annual Meeting. Athens, GA. 27 May-1June 2003.

M. E. McTammany and E. F. Benfield. Poster: Wood breakdown and microbial biofilm respiration in southern Appalachian streams draining watershed with different land use histories. North American Benthological Society 50th Annual Meeting. Pittsburgh, PA. 27 May-1June 2002.

C. L. Burcher, M. E. McTammany, E. F. Benfield, and G. S. Helfman. Poster: Effects of land-use on fish assemblages in southern Appalachian streams. North American Benthological Society 50th Annual Meeting. Pittsburgh, PA. 27 May-1June 2002.

M. E. McTammany, E. P. Gardiner, and E. F. Benfield. Poster: The effect of spatial uncertainty in watershed boundaries and stream locations on watershed and riparian zone land cover analysis. Remote Sensing and GIS Research Symposium. Roanoke, VA. 13 March 2002.

M. E. McTammany, C. L. Burcher, and E. F. Benfield. Poster: Recovery of biological structure and ecosystem function in reforesting agricultural streams. Coweeta LTER Meeting. Highlands, NC. 8-9 January 2002.

M. E. McTammany and E. F. Benfield. Recovery of stream ecosystems from agriculture: preliminary results of a region-wide study. Coweeta LTER Meeting. Athens, GA. 26-27 June 2001.

M. E. McTammany, J. R. Webster, E. F. Benfield, and D. J. Sobota. Seasonal and longitudinal trands of metabolism in a southern Appalachian mid-sized river. North American Benthological Society 49th Annual Meeting. LaCrosse, WI. 3-7 June 2001.

E. F. Benfield, B. L. Bennett, J. S. Harding, M. E. McTammany, R. A. Sponseller, and P. F. Wagner. Land-use and invertebrate biodiversity in southern Appalachian streams, USA. International Association of Theoretical and Applied Limnology 28th Congress. Melbourne, Australia. 2-9 February 2001.

M. E. McTammany and E. F. Benfield. Poster: Chemical conditions in streams recovering from long-term agriculture. Coweeta LTER Meeting. Highlands, NC. 6-7 January 2001.

M. E. McTammany and E. F. Benfield. Summary of regional research investigating legacies of historical land use impact on streams. Coweeta LTER Meeting. Athens, GA. 12-14 June 2000.

M. E. McTammany, E. F. Benfield, and J. R. Voshell. Using indices to detect urban impact on streams: a comparison of multimetric, tolerance-based, multivariate, and traditional approaches. North American Benthological Society 48th Annual Meeting. Keystone, CO. 28 May-1 June 2000.

M. E. McTammany and R. H. Wynne. Spectral comparison of different age forests in the southern Appalachians. American Society of Photogrammetry and Remote Sensing Annual Convention. Washington, DC. 23-26 May 2000.

M. E. McTammany, E. F. Benfield, N. Gardiner, and P. V. Bolstad. Poster: Stream selection using spatially and temporally explicit land-use patterns. Coweeta LTER Meeting. Highlands, NC. 2-4 January 2000.

M. E. McTammany, E. F. Benfield, N. Gardiner, and P. V. Bolstad. Poster: Stream recovery from long-term agriculture: using GIS to select sites for a multi-stream experiment. Coweeta LTER Meeting. Franklin, NC. 21-23 June 1999.

M. E. McTammany, J. S. Harding, E. F. Benfield, P. V. Bolstad, and G. A. Edwards. Poster: The impact of urbanization type and degree on benthic macroinvertebrates and stream quality. Coweeta LTER Meeting. Athens, Georgia; 15-16 June 1998.

M. E. McTammany, J. S. Harding, E. F. Benfield, P. V. Bolstad, and G. A. Edwards. The impact of different degrees and types of urbanization on benthic macroinvertebrates in southern Appalachian streams: potential mechanisms for land use impact. American Society of Limnology and Oceanography/Ecological Society of America Joint Meeting; St. Louis, Missouri; 7-12 June 1998.

M. E. McTammany, J. S. Harding, E. F. Benfield, P. V. Bolstad, and G. A. Edwards. Poster: Mechanisms of macroinvertebrate response to urbanization: gradients of degree and type. North American Benthological Society, 46th Annual Meeting; Prince Edward Island, Canada; 2-5 June 1998.

M. E. McTammany, J. S. Harding, and E. F. Benfield. Poster: Biodiversity in southern Appalachian urbanized streams. Coweeta LTER Meeting. Athens, Georgia; 16-17 June 1997.

J. R. Webster, J. L. Tank, J. B. Wallace, J. L. Meyer, S. L. Eggert, T. P. Ehrman, B. R. Ward, B. L. Bennett, P. F. Wagner, and M. E. McTammany. Effects of leaf litter exclusion and wood removal on phosphorus and nitrogen retention in a first-order forest stream. North American Benthological Society, 45th Annual Meeting; San Marcos, Texas; 27-30 May 1997.

M. E. McTammany, J. S. Harding, and E. F. Benfield. Poster: Do stream invertebrate assemblages reflect variations in watershed urbanization? North American Benthological Society, 45th Annual Meeting; San Marcos, Texas; 27-30 May 1997.

M. E. McTammany, J. S. Harding, and E. F. Benfield. Poster: Biodiversity and differential urbanization in southern Appalachian stream ecosystems. Virginia Academy of Science, 75th Annual Meeting; Blacksburg, Virginia; 20-23 May 1997.

REFERENCES

Dr. E. F. Benfield, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Dr. J. R. Voshell, Jr., Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Dr. J. R. Webster, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Dr. R. H. Jones, Department of Biology, Head, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Dr. R. H. Wynne, Department of Forestry, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061

Dr. H. M. Valett, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061