

Stream ecosystem responses to the 2007 spring freeze in the southeastern United States: unexpected effects of climate change

PATRICK J. MULHOLLAND*, BRIAN J. ROBERTS*[†], WALTER R. HILL[‡] and JOHN G. SMITH*

*Oak Ridge National Laboratory, Environmental Sciences Division, PO Box 2008, Oak Ridge, TN 37831-6036, USA,

[†]Louisiana Universities Marine Consortium, 8124 Highway 56, Chauvin, LA 70344, USA, [‡]Institute of Natural Resource

Sustainability, University of Illinois, 1816 S. Oak Street, Champaign, IL 61820, USA

Abstract

Some expected changes in climate resulting from human greenhouse gas emissions are clear and well documented, but others may be harder to predict because they involve extreme weather events or heretofore unusual combinations of weather patterns. One recent example of unusual weather that may become more frequent with climate change occurred in early spring 2007 when a large Arctic air mass moved into the eastern United States following a very warm late winter. In this paper, we document effects of this freeze event on Walker Branch, a well-studied stream ecosystem in eastern Tennessee. The 2007 spring freeze killed newly grown leaf tissues in the forest canopy, dramatically increasing the amount of light reaching the stream. Light levels at the stream surface were sustained at levels considerably above those normal for the late spring and summer months due to the incomplete recovery of canopy leaf area. Increased light levels caused a cascade of ecological effects in the stream beginning with considerably higher (two–three times) rates of gross primary production (GPP) during the late spring and summer months when normally low light levels severely limit stream GPP. Higher rates of stream GPP in turn resulted in higher rates of nitrate (NO_3^-) uptake by the autotrophic community and lower NO_3^- concentrations in stream water. Higher rates of stream GPP in summer also resulted in higher growth rates of a dominant herbivore, the snail *Elimia clavaeformis*. Typically, during summer months net NO_3^- uptake and snail growth rates are zero to negative; however, in 2007 uptake and growth were maintained at moderate levels. These results show how changes in forest vegetation phenology can have dramatic effects on stream productivity at multiple trophic levels and on nutrient cycling as a result of tight coupling of forest and stream ecosystems. Thus, climate change-induced changes in canopy structure and phenology may lead to large effects on stream ecosystems in the future.

Keywords: climate change, ecosystem respiration, freeze damage, light, nutrient uptake, plant phenology, primary production, riparian vegetation disturbance, snail growth, stream

Received 27 June 2008; revised version received 19 November 2008 and accepted 15 December 2008

Introduction

Many climate changes resulting from human greenhouse gas emissions are clear and well documented, such as increases in temperature and intensification of the hydrologic cycle (IPCC, 2007). Some changes are

harder to predict, however, because they involve extreme weather events or heretofore unusual combinations of weather patterns. These unpredictable events may produce large, threshold-type responses in ecosystems of greater long-term consequence than responses to more gradual climate changes (Scheffer *et al.*, 2001).

One recent example of the type of unusual weather patterns that may become more frequent with climate change occurred in early spring 2007 when a large

Correspondence: Patrick J. Mulholland, tel. +1 865 574 7304, fax +1 865 576 3989, e-mail: mulhollandpj@ornl.gov

Arctic air mass moved into the eastern United States (Gu *et al.*, 2008). This severe freeze event, which occurred on April 5–9, 2007, killed or delayed the normal phenological development of new tissues on many tree species for a month or more across a broad region of the southeast and south central United States. This region included large sections of northern Arkansas and southern Missouri, Oklahoma, Tennessee, Kentucky, western North Carolina, and northern sections of Mississippi, Alabama and Georgia (Gu *et al.*, 2008). An early April freeze is not in itself an unusual occurrence, but this particular event was preceded by an extended period of unusually warm weather that caused plants to break dormancy considerably earlier than normal. Warmer winters and earlier budbreak have been observed in recent years across the Northern Hemisphere and are consistent with climate change projections (Schwartz *et al.*, 2006).

Using satellite imagery and data from several AmeriFlux sites in the region, Gu *et al.* (2008) showed how the combination of late-winter warmth and early spring freeze resulted in extensive damage to newly grown tissues of crops, horticultural plants and native forest species throughout a wide swath of the central and southeastern United States. Gu *et al.* (2008) also reported that the spring freeze resulted in a prolonged period of lower than normal leaf area throughout spring and early summer leading to reduced canopy cover throughout the summer in Walker Branch Watershed, a forested catchment in eastern Tennessee.

Stream ecosystems are strongly influenced by the vegetation in their catchments, especially by characteristics of riparian plants. Riparian vegetation has a strong influence on the light regime, organic matter and nutrient inputs, and other factors that control important processes in stream ecosystems such as metabolism and nutrient cycling (Hill *et al.*, 2001; Strayer *et al.*, 2003; Roberts & Mulholland, 2007; Roberts *et al.*, 2007; Valett *et al.*, 2008). Disturbances to riparian vegetation can have large effects on metabolism, nutrient cycling and export, and biotic structure of streams (Eshleman *et al.*, 1998; Wallace *et al.*, 1999; Bernhardt *et al.*, 2003).

Effects of climate change on stream ecosystems are expected to be direct, due to increases in temperature and changes in runoff and hydrologic regimes, and indirect, via changes in riparian and catchment vegetation (Carpenter *et al.*, 1992; Poff, 1992; Grimm, 1993; Meyer *et al.*, 1999). There are a number of studies documenting the effects of projected or observed changes in stream temperatures and flow regimes resulting from climate change (Clark *et al.*, 2001; Gibson *et al.*, 2005; Hari *et al.*, 2006; Durance & Ormerod, 2007; San-Jensen *et al.*, 2007). There are also many reports

showing the strong linkage between riparian vegetation and disturbance and stream ecosystem dynamics (Sheath *et al.*, 1986; Steinman, 1992; Hill *et al.*, 2001; Roberts & Mulholland, 2007). Linkage between climate variability and nitrate loss in streams draining forested catchments has also been demonstrated (Mitchell *et al.*, 1996). However, there are few empirical studies documenting a connection between climate variability or change and stream ecosystem functions.

Here, we present effects of the 2007 spring freeze on Walker Branch, a well-studied stream ecosystem in eastern Tennessee. Ongoing and historical studies in Walker Branch provided a unique opportunity to observe and compare the response to the 2007 event with data from previous years. We show how the 2007 freeze had important effects on stream metabolism, nutrient concentrations, and growth rate of a dominant herbivore.

Materials and methods

Site description

This study was conducted in a 120 m reach of the West Fork of Walker Branch (hereafter referred to as Walker Branch), a first order, forested stream in the Ridge and Valley province of eastern Tennessee. It drains a 38.4 ha catchment on the US Department of Energy's Oak Ridge National Environmental Research Park (35°58'N, 84°17'W). The catchment is underlain by siliceous dolomite that has weathered to develop deep soils abundant in chert (McMaster, 1963). Watershed vegetation consists of a second-growth deciduous forest dominated by chestnut oak (*Quercus prinus*), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), white oak (*Quercus alba*), and American beech (*Fagus granifolia*) (Johnson & Van Hook, 1989). The climate is typical of the humid Appalachian region of the southeastern United States, with a mean annual temperature of ~14.5 °C and mean annual precipitation of ~135 cm distributed relatively evenly throughout the year (Mulholland, 2004).

Stream discharge is highly seasonal with higher baseflows and more frequent spates (high storm flows) during winter and early spring when evapotranspiration rates are low (Mulholland, 2004). Summer baseflows are generally about 5 L s⁻¹, and spates only occur after large storms at this time of year. Stream water chemistry is dominated by calcium, magnesium, and bicarbonate, and the pH is moderately basic (usually 8.0–8.3) (Mulholland, 1992). The channel gradient is relatively gentle (~0.035 m m⁻¹). The streambed in the study reach is composed of bedrock outcrops, gravel and cobble in a series of shallow (<10 cm deep) riffle-run sections. The forest canopy over the stream is

complete due to the relatively narrow channel width (average of 3.1 m). The light regime at the stream surface is highly dependent on forest phenology, with highest levels in late winter and early spring before leaf emergence declining to very low levels later in spring and throughout the summer (Hill *et al.*, 2001; Roberts *et al.*, 2007).

Walker Branch has been the site of numerous past studies of stream ecosystem structure and function. Periphyton growth is light-limited for much of the year (Steinman, 1992), but can be limited by both nitrogen and phosphorus during spring when light levels are highest (Rosemond *et al.*, 2000). Periphyton photosynthesis rates increase during the open-canopy spring period (Hill *et al.*, 2001), but biomass is maintained at low levels due to intense grazing by the snail *Elimia clavaeformis* (Rosemond *et al.*, 2000). *Elimia* accounts for 90–95% of total invertebrate biomass (Newbold *et al.*, 1983; Mulholland *et al.*, 2000). Bryophytes are common year-round (Steinman & Boston, 1993), and blooms of filamentous algae are commonly observed in late winter and early spring, leading to a sharp peak in reach-scale gross primary production (GPP) during March and April (Hill *et al.*, 2001; Roberts *et al.*, 2007). The late winter–early spring peak in primary production is accompanied by high rates of nutrient uptake (Mulholland *et al.*, 2000; Roberts & Mulholland, 2007) and growth of *Elimia* (Hill *et al.*, 2001). After leaf-out of the deciduous vegetation in mid-late April, stream gross primary productivity, nutrient uptake, and herbivore growth all drop sharply and remain low throughout the summer (Rosemond *et al.*, 2000; Hill *et al.*, 2001; Roberts & Mulholland, 2007; Roberts *et al.*, 2007).

Climate

To evaluate the historical context of the 2007 spring freeze in Walker Branch, daily average air temperatures for the period 1950–2007 (the period of available record) were obtained from the NOAA climate station in Oak Ridge, TN, approximately 5 km from Walker Branch (<http://www.atdd/noaa.gov>). The date of the last hard freeze, defined as daily minimum air temperature $\leq -2.2^\circ\text{C}$ (28°F), was determined for each year.

Light

Photosynthetically active radiation (PAR) at the stream surface was monitored throughout the study with a quantum sensor (LiCor 190SA, LiCor Biosciences, Lincoln, NE, USA) and data logger (LiCor 1400, USA) at stream level [quantum sensor attached to a fallen tree that spanned Walker Branch within the study reach ~ 1 m above the stream surface (Hill *et al.*,

2001)]. Instantaneous PAR was measured by the quantum sensor every 5 s, averaged, and recorded by the datalogger every 15 min. Daily PAR was determined by integrating the 15 min readings for each day.

Streamwater chemistry

Streamwater chemistry has been measured at a station 60 m upstream from the weir (~ 60 m below the study reach) weekly since 1991 on filtered samples as described in Mulholland (2004). Concentrations of nitrite (NO_2^-) + nitrate (NO_3^-) were determined by Cu–Cd reduction followed by azo dye colorimetry (American Public Health Association, 1992) using an autoanalyzer (Seal Analytical Model AA3, Seal Analytical Inc., Mequon, WI, USA). Hereafter, concentrations of $\text{NO}_2^- + \text{NO}_3^-$ are referred to as NO_3^- because NO_2^- concentrations are generally below detection limits in the well-oxygenated stream water (Mulholland, 2004). Concentrations of Ca^{2+} were determined by inductively coupled plasma (American Public Health Association, 1992).

Previous research in Walker Branch Watershed has shown that the relative importance of deep groundwater flowpaths for streamflow generation increases as stream discharge declines, and deeper flowpaths have considerably higher NO_3^- concentrations as well as higher base cation concentrations from weathering of the dolomitic bedrock (Mulholland, 1992; Mulholland & Hill, 1997). To normalize for the effect of increased deep groundwater flow, we calculated $\text{NO}_3^-/\text{Ca}^{2+}$ ratio which provides a clearer indication of effects of in-stream processes on streamwater NO_3^- concentration (Mulholland & Hill, 1997).

Metabolism

GPP and ecosystem respiration (ER) rates were calculated from measurements of dissolved oxygen (DO) concentration and water temperature using the open-system, single station diel approach (Odum, 1956; Roberts *et al.*, 2007). DO concentration and temperature were measured and recorded using a YSI Model 6920 sonde equipped with a YSI model 6562 (YSI Inc., Yellow Springs, OH, USA) DO sensor at 15 min intervals. Between July 2006 and July 2007, DO was simultaneously measured using a YSI model 6150 ROX optical oxygen sensor, and after July 2007 only the optical oxygen sensor was used. The YSI sonde was deployed at the same well-mixed site (~ 120 m upstream from the weir) used in previous metabolism studies in Walker Branch (e.g. Marzolf *et al.*, 1994, Roberts *et al.*, 2007). The DO sensor was calibrated in water-saturated air every 7–14 days, DO data were corrected for barometric pressure recorded during calibration and consecutive

calibrations were used to detect instrument drift over deployment. Percent saturation was determined from the measured DO concentration, water temperature, and barometric pressure. Instantaneous barometric pressure readings were measured with a Vaisala Model PTB101B analog barometer (Vaisala Oyj, Vantaa, Finland) and recorded every 15 min with a Campbell Scientific Model CR10WP datalogger (Campbell Scientific Inc., Logan, UT, USA) at a streamside site located ~ 10 m upstream from the DO sonde. During periods when on-site barometric pressure readings were not available, we obtained readings from a NOAA monitoring site (T. Meyers, unpublished data; NOAA, Oak Ridge, TN, USA) located in the Walker Branch watershed and applied an elevation-based correction (based on >8000 comparisons between the two sites) to estimate the barometric pressure at our study reach.

Reaeration rate coefficient (k_{O_2}) and average water velocity were measured for a 62 m study reach immediately upstream from the sonde deployment site using simultaneous, continuous injections of propane gas (volatile tracer) and a concentrated NaCl solution (conservative tracer) as described in Roberts *et al.* (2007). These injections were performed over a range of stream discharges to develop relationships between discharge and k_{O_2} and between discharge and average stream depth and width. Daily rates of GPP and ER were calculated from the diel DO and temperature data and stream reaeration rates as described by Roberts *et al.* (2007).

Nutrient uptake rate

Net rates of NO_3^- uptake were measured by collecting streamwater samples at the upstream and downstream ends of a 62 m study reach between 12:00 and 14:00 hours EST approximately two to three times per week from March to July 2005 and 2006 and on 11 dates between April 2 and July 14, 2007. On each date, stream water was collected with a 30 mL plastic syringe and immediately filtered (Whatman GF/F glass fiber filters, 0.7 μ m nominal pore size) into acid-washed and streamwater rinsed Nalgene bottles. Filtered samples were stored frozen before NO_3^- analysis at Oak Ridge National Laboratory or LUMCON (2007 samples). Net NO_3^- uptake rate, expressed as net mass removal rate per unit streambed area (U , μ g N m⁻² min⁻¹), was calculated from the change in NO_3^- concentration between upstream and downstream ends of the reach and stream discharge under nonstorm conditions (<50 L s⁻¹) as described by Roberts & Mulholland (2007). Uptake rates were corrected for groundwater input of NO_3^- based on estimates of groundwater inflow and groundwater NO_3^- concentrations as described in Roberts & Mulholland (2007).

Snail growth

Growth of the herbivorous snail *E. clavaeformis* in Walker Branch was measured at a site ~ 20 m downstream of the light and dissolved oxygen sensors. Snail growth was measured over 2-month periods in 2005–2007 beginning in the third week of June each year. Approximately 100 snails were collected from the reach and transported back to the laboratory in plastic containers filled with stream water and secured with a lid. Snails were blotted dry and then numbered bee tags were attached dorsally to the anterior end of the shells with Duro® Quick gel super glue (Loctite Corp., Cleveland, OH, USA). A representative size range of snails (approximately 15–120 mg) was tagged on each date. The glue was allowed to dry for 30 min, after which the snails were returned to the containers with stream water and held overnight. The snails were blotted dry the next morning, weighed to the nearest 0.1 mg, and released at the study site. After 2 months, the tagged snails were located visually and returned to the laboratory in water-filled containers for reweighing. The mean percentage of tagged snails recovered at the end of the 2-month deployment period was 54% (range = 19–74%). Growth rates (μ) for individual snails were calculated as $\mu = \ln(B_2) - \ln(B_1)$ per days of deployment, where B_2 and B_1 are the blotted wet mass of snails at the end and beginning of the 2-month period, respectively.

Statistical analysis

Climate variables were evaluated for long-term trends by simple linear regression with year as the independent variable. To identify effects of the 2007 spring freeze, mean monthly values of daily PAR, GPP, NO_3^- concentration, NO_3^-/Ca^{2+} ratio, and net NO_3^- uptake for 2007 were compared with the 95% confidence intervals from mean monthly values during 2004–2006 or 1991–2006 (NO_3^- concentration and NO_3^-/Ca^{2+} ratio). Snail growth rate differences between 2007 and the preceding 2 years were tested with Kruskal–Wallis nonparametric analysis of variance, and Dunn's multiple comparison test was used to compare individual years. Tests were performed with SIGMASTAT software.

Results

Historical air temperatures indicate that the late winter period has become warmer over the past half century, with significant positive trends in both average (not shown) and median values of March daily average air temperature since 1950 (Fig. 1a). March 2007 was unusually warm, however, with a median average daily air temperature of 13.8 °C which was 0.9 °C higher than the

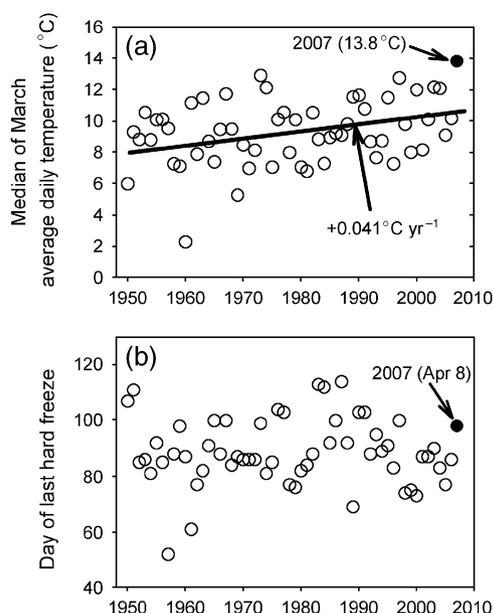


Fig. 1 (a) Median values of March daily average air temperatures for the Oak Ridge area from 1950 through 2007, and (b) day of year of last hard freeze (minimum daily air temperature $\leq -2.2^\circ\text{C}$). Regression line and slope are shown in (a) ($P = 0.012$, $r^2 = 0.091$). The trend over time was not significant in (b) ($P = 0.933$).

next highest year (12.9°C in 1973). In contrast, the latest date of hard freeze (daily minimum air temperature $\leq -2.2^\circ\text{C}$) shows no significant trend over time (Fig. 1b), and the date of the freeze in 2007 (8 April) was not unusually late.

Light levels reaching the stream were considerably higher in 2007 during the spring and summer following the April freeze than for the same months in the previous year (Fig. 2a). Average daily PAR in May to August 2007 was 2.5 (July and August) to five times higher (May) than average daily PAR for these months from 2004 to 2006 (Fig. 2b).

The higher light levels resulted in considerably higher rates of instream daily GPP in 2007 compared with 2006 (Fig. 3a). The sharp declines in daily PAR and GPP shown for 2006 in early to mid-April represent the typical pattern resulting from leaf emergence. In 2007, there was a brief sharp decline in GPP just after the spring freeze that was due to a large storm and low PAR on 14–15 April (peak discharge of 64 L s^{-1}), but GPP recovered rapidly under the unusually high PAR resulting from leaf-fall following the freeze a week earlier. Average monthly values of daily GPP rates in 2007 were about three times higher in May and June, and two times higher in July and August than average values for the same months in the previous 3 years (Fig. 3b).

Stream nutrient concentrations in the late spring and summer of 2007 also were affected by the April freeze.

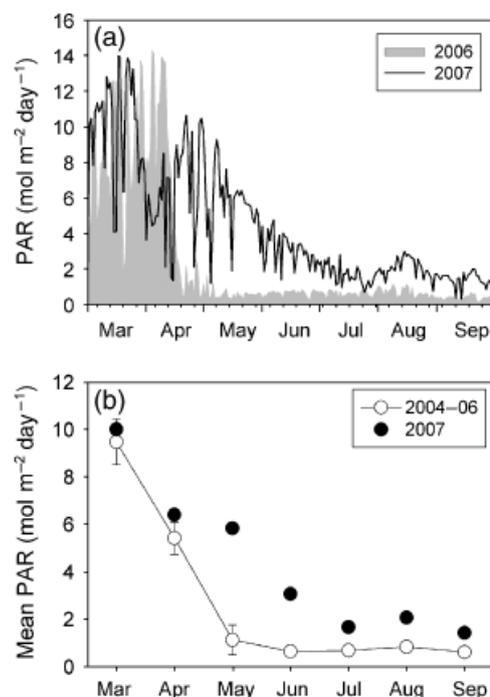


Fig. 2 (a) Daily photosynthetically active radiation (PAR) at the stream surface in Walker Branch for the months of March through September in 2006 and 2007, and (b) mean monthly values of daily PAR for the months of March through September in 2004–2006 and in 2007. Error bars represent the 95% confidence interval of the mean monthly values for 2004–2006.

NO_3^- concentrations were slightly lower during most of the months between April and September 2007 compared with monthly average concentrations during 1991–2006 (Fig. 4a). Stream discharge in 2007 was considerably lower than during previous years due to an extended drought (Fig. 4b). Streamwater $\text{NO}_3^-/\text{Ca}^{2+}$ ratios in 2007 from April through September were significantly lower than the average ratios for these months during the preceding 16-year period (Fig. 4c).

Net NO_3^- uptake rates in April 2007 were comparable with those observed in 2005 and 2006 (Fig. 5). Net NO_3^- uptake rate was three times greater in May 2007 than in previous years, and net NO_3^- uptake persisted through July. This was in contrast to 2005 and 2006 when NO_3^- uptake was negative (i.e. net release of NO_3^- to stream water due to remineralization and nitrification) in June and July (Fig. 5).

Snail growth in summer 2007 was significantly greater ($H = 32.5$, $P < 0.001$) than during the same period in 2005 and 2006 (Fig. 6). Growth rates in 2007 (median growth rate across all snail sizes of 0.00036 day^{-1}) were significantly higher than growth rates in 2005 (median of 0 day^{-1}) and 2006 (median of -0.00015 day^{-1}) (Dunn's multiple comparison test, $P < 0.05$).

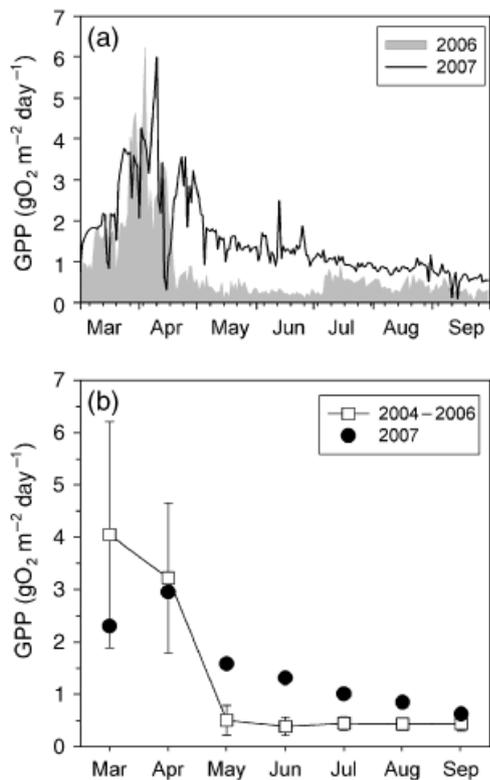


Fig. 3 (a) Daily gross primary production (GPP) in Walker Branch for the months of March through September in 2006 and 2007, and (b) mean monthly values of daily stream GPP for the months of March through September in 2004–2006 and in 2007. Error bars represent the 95% confidence interval of the mean monthly values for 2004–2006.

Discussion

Climate data for Oak Ridge, TN, indicate that the late winter period has become increasingly warmer over the last half century, and that March 2007 was the warmest on record (Fig. 1a). This is consistent with observations of warmer winters and earlier budbreak in recent years across the Northern Hemisphere and with climate change projections (Schwartz *et al.*, 2006). In contrast, the date of the last hard freeze has been highly variable during this period, has shown no temporal trend over time, and in 2007, was not unusually late (Fig. 1b). These analyses suggest that the unusual weather pattern in spring 2007, which resulted in extensive plant tissue mortality, may become more common with future climate change.

Our results showed that the loss of newly grown leaf tissues in the forest canopy following the spring 2007 freeze dramatically increased the amount of light reaching the stream, and light levels remained considerably above normal throughout the remainder of the growing season due to incomplete recovery of canopy leaf area. Increased light levels caused a cascade of ecological

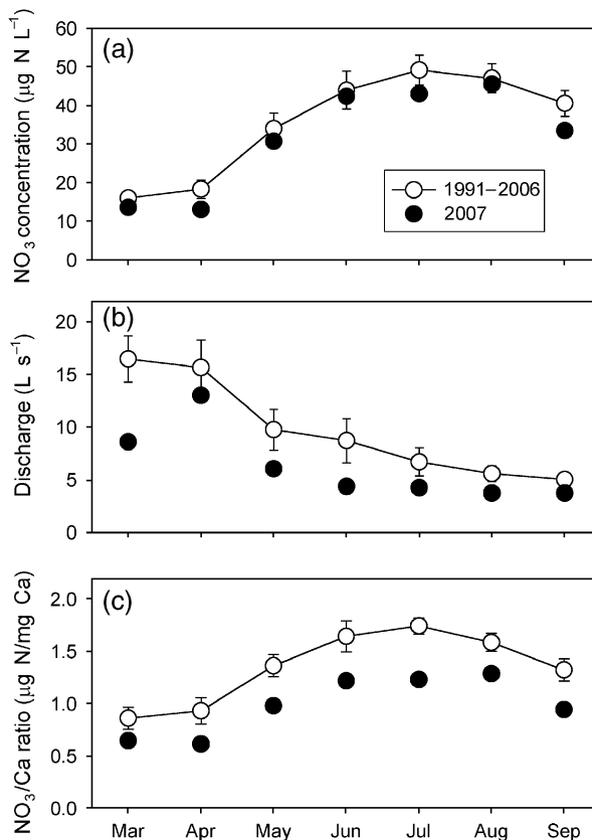


Fig. 4 Mean monthly values of (a) stream NO₃⁻ concentration, (b) stream discharge, and (c) NO₃⁻/Ca²⁺ ratio for March through September in 1991 to 2006 and individual weekly values for the same months in 2007. Samples collected during stormflow (> 50 L s⁻¹) were not included. Error bars represent the 95% confidence interval of the mean monthly values for 1991–2006.

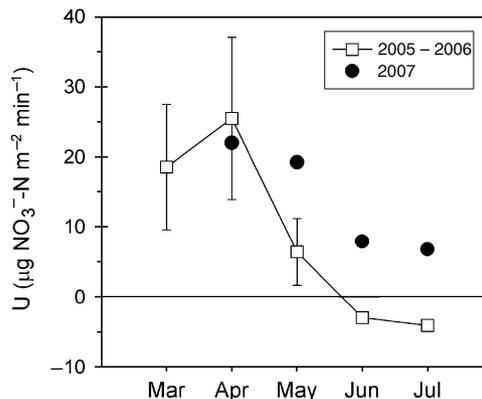


Fig. 5 Mean monthly rates of net NO₃⁻ uptake (U) in Walker Branch for the months of March through July in 2005–2006 and in 2007. Error bars represent the 95% confidence interval of the mean monthly values for 2005–2006.

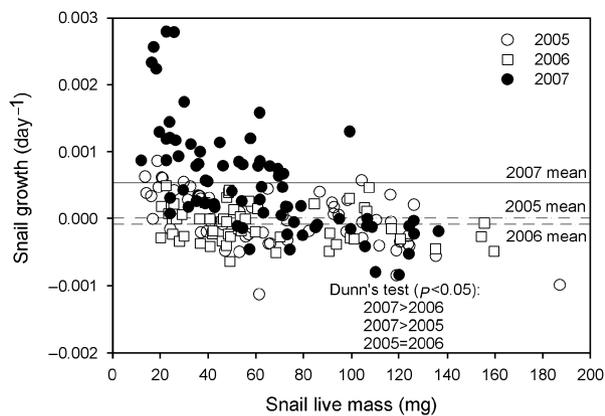


Fig. 6 Individual growth rates of herbivorous snails (*Elimia clavaeformis*) vs. snail size in Walker Branch during 2-month periods beginning in the third week of June in 2005–2007. Also shown are mean growth rates and results of Dunn's multiple comparison test to compare differences in snail growth rates between individual years.

effects beginning with higher rates of GPP by stream autotrophs during the late spring and summer months when low light conditions normally prevail and limit GPP (Roberts *et al.*, 2007). Higher GPP in turn resulted in higher rates of removal and lower concentrations of stream water NO_3^- and higher growth rates of a dominant herbivore in Walker Branch, the snail *E. clavaeformis*.

The large variance in average monthly GPP values observed in March and April (Fig. 3) was the result of interannual variation in the size of the spring bloom of filamentous algae primarily because of interannual differences in winter and early spring discharge (incidence of streambed-scouring spates) (Roberts *et al.*, 2007). Average rates of stream GPP in March and April 2007 (2.3 and $3.0 \text{ gO}_2 \text{ m}^{-2} \text{ day}^{-1}$, respectively) were within the 95% CI of 2004–2006 values; however, from May through August average GPP rates were well above the 95% CI for the previous years. The relatively high rates of stream GPP during late spring and summer in 2007 have considerable ecological importance because this is a period when stream GPP is normally very low because of light limitation (Fig. 3).

Light limitation of primary production during late spring and summer is common in small streams in forested catchments, and is the basis for predictions of low rates of primary productivity in low-order streams in the River Continuum Concept (Vannote *et al.*, 1980). The importance of light limitation has been demonstrated in several studies in which increases in stream algal growth occurred after forest clear-cutting (Holopainen & Huttunen, 1992; Kiffney *et al.*, 2003), insect defoliation of riparian trees (Sheath *et al.*, 1986), and

experimental light addition (Steinman, 1992; Hill *et al.*, 1995). Several cross-site studies have shown that light is the primary driver of autochthonous production in streams (Bott *et al.*, 1985; Mulholland *et al.*, 2001). Therefore, the responses to increases in light observed in Walker Branch after the 2007 spring freeze are likely representative of what could occur in other small forested streams.

The effect of the spring freeze on stream NO_3^- concentrations (Fig. 4a) appeared to be small because it was partially masked by greater importance of deep groundwater flowpaths during an extended drought in 2007 compared with previous years (Fig. 4b). Previous work in Walker Branch has shown that seasonal variation in stream NO_3^- concentration is the result of differences in groundwater flowpath (shallow vs. deep) and instream biotic uptake (Mulholland & Hill, 1997; Mulholland, 2004). In most years increase in the importance of deep groundwater flow for streamflow generation and decline in instream uptake of NO_3^- by algae result in a sharp increase in stream NO_3^- concentrations beginning in May (Mulholland & Hill, 1997; Mulholland, 2004; Roberts & Mulholland, 2007). Highest NO_3^- concentrations are observed during the summer months when discharge and biotic uptake are both low. Although this seasonal pattern was observed in 2007, $\text{NO}_3^-/\text{Ca}^{2+}$ ratios (Fig. 4c) indicate that NO_3^- concentrations were considerably lower than expected given the lower-than-normal flow conditions in summer 2007. Lower NO_3^- concentrations in 2007 were likely caused by increased uptake of NO_3^- by stream autotrophs whose nutrient demand was stimulated by higher rates of GPP under higher light levels. Our measurements of higher rates of in-stream net uptake of NO_3^- during May–July 2007 compared with 2005 and 2006 support this conclusion (Fig. 5).

Previous research in Walker Branch also has shown a tight linkage between snail growth rate and algal productivity with higher snail growth rates in spring when GPP is high, and lowest growth rates in summer when GPP is low due to light limitation (Hill *et al.*, 2001). The 2007 spring freeze resulted in significantly higher snail growth rates the following summer than in previous summers, particularly for the smaller size classes of snails (Fig. 5). Typically, snail growth rates are zero or even negative during summer in undisturbed headwater streams on the Oak Ridge National Environmental Research Park due to low food availability (Hill *et al.*, 1995). In 2007, however, snails grew throughout the summer, further demonstrating the tight coupling of light, primary productivity, herbivore growth, and nutrient cycling in this forest stream, albeit in the opposite direction from the usual spring phenology (i.e. reduction in light, productivity, and nutrient uptake during late spring).

The 2007 spring freeze demonstrated that unusual weather events that may become more common with climate change not only produce strong effects on forest ecosystems, but they can have large effects on stream ecosystems draining these forests as well. It has long been known that stream ecosystems are strongly influenced by characteristics of the catchments they drain (Hynes, 1975), particularly the regulation of inputs of organic matter and light by riparian vegetation (Kaushik & Hynes, 1968; Minshall, 1978). Disturbances to riparian vegetation can produce large effects on streamwater chemistry and biota (Sheath *et al.*, 1986; Eshleman *et al.*, 1998; Wallace *et al.*, 1999; Goodale *et al.*, 2000). Therefore, it is not surprising that the 2007 spring freeze, which had such a large effect on forests in the region, also would have a large effect on forested streams. Although our study was limited to effects on only one stream, it is reasonable to conclude that other forested streams in the region were also affected. Strong trophic cascades produced by variations in energy resource inputs have been observed in Walker Branch (Rosemond *et al.*, 1993; Hill *et al.*, 2001) and in other streams as well (Wootton & Power, 1993; Hill *et al.*, 1995; Wallace *et al.*, 1999). Interestingly, the major impact of the freeze was generally opposite for the forest and stream, with a reduction in forest leaf area and presumably in forest primary production but an increase in stream primary production and herbivore growth.

Our results showing the tight coupling of light availability and stream ecosystem processes in spring suggest that the predominant effect of climate change could actually be lower productivity and nutrient retention in streams. Spring freeze events such as that in 2007 may be infrequent while the earlier leaf emergence resulting from climate warming in most years may reduce food supplies to stream herbivores and higher trophic levels dependent on the spring algal productivity pulse. Stream algal productivity is constrained by short day length and steep solar angle in winter and earlier forest leaf emergence will likely shorten the period of high algal productivity in late winter and early spring. Earlier leaf emergence in spring has been documented for much of North America (Schwartz *et al.*, 2006), a trend that is likely to continue with human-induced climate change. Thus, an important effect of climate change for stream ecosystems may be a reduction in ecosystem productivity and nutrient cycling with earlier leaf emergence in spring.

Several recent studies have projected or documented direct effects of climate change on stream ecosystems due to increases in water temperature (Clark *et al.*, 2001; Hari *et al.*, 2006; Durance & Ormerod, 2007) and changes in flow regime, particularly lower flows and longer periods of low flow (Gibson *et al.*, 2005; Xenopoulos *et al.*, 2005).

However, there have been few reports of documented responses of stream ecosystems to the indirect effects of climate change such as effects on riparian vegetation. One notable exception is the study of Tuchman *et al.* (2002) showing that leaves grown under elevated levels of atmospheric CO₂ had decreased nutritional value for aquatic decomposers and detritivores because of higher levels of structural compounds and lower nitrogen content. The strong linkage between the quality and quantity of leaf inputs and the food web of forest streams (Wallace *et al.*, 1997) suggests that climate-induced changes in leaf inputs will have major effects on stream ecosystems. Our results expand the evidence for indirect effects of climate change on stream ecosystems by showing that changes in the seasonal light regime as a result of changes in forest leaf phenology in spring can have strong effects on stream primary productivity, nutrient dynamics, and biota. While the effects of spring freeze events such as those described here may not carry over to subsequent years if forest vegetation recovers, the trend toward warmer late winter periods and earlier leaf emergence in spring may have long-term effects on stream productivity at multiple trophic levels and the magnitude and timing of nutrient export.

Acknowledgements

We thank Deanne Brice and Kitty McCracken for field and laboratory analysis of stream water chemistry. We also thank Tilden Meyers and Lynne Satterfield for providing long-term climate data for Oak Ridge. Dale Kaiser and Garrett Marino provided helpful insights for historical climate analysis. Comments from Lianhong Gu, Paul Hanson, and three anonymous reviewers greatly improved earlier versions of the manuscript. This research was part of the Long-term Walker Branch Watershed project and supported by the US Department of Energy's Program for Ecosystem Research, in the Office of Science, Office of Biological and Environmental Research. Oak Ridge National Laboratory is managed by University of Tennessee-Battelle LLC for the US Department of Energy under contract DE-AC05-00OR22725. Brian Roberts was supported by a post-doctoral fellowship through the ORNL Postdoctoral Research Associates Program administered by Oak Ridge Associated Universities.

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