Seasonal Variation in Whole Stream Metabolism across Varying Land Use Types

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ABSTRACT

Historically, whole stream open channel metabolism has been measured over short periods in conjunction with nutrient injections to assess nutrient dynamics within streams. The purpose of my study was to understand the seasonal changes in metabolism within and among streams as well as the impacts of different land use. This was addressed by monitoring nine different watersheds in the Little Tennessee River watershed in southwestern North Carolina. The nine study watersheds were selected to represent a gradient of forested, agricultural, and developed land use / land cover types. Data loggers were deployed to collect continuous oxygen, temperature, conductivity, and stage height data from 2010-2011. I used these data to estimate gross primary production (GPP) and ecosystem respiration (ER). GPP and ER were compared to stream chemistry, light, land cover, and storms. I found that there is greater influence of local riparian land cover than watershed land cover on GPP and ER. Streams had varying annual GPP, but generally the peak in GPP occurred in late winter- early spring with lows in fall. GPP was most strongly influenced by the amount of available light, which is directly related to the amount of canopy cover. ER was much more variable than GPP within and among streams but generally peaked in summer and was lowest in the winter. ER was most strongly related to the proportion of agricultural land cover in the local riparian area. My results suggest that local riparian vegetation may have a greater impact on metabolism than mountainside development.
ACKNOWLEDGEMENTS

First and foremost, I would like to thank my wife, Ariel, for supporting me throughout this program. Despite the frequent trips to Coweeta and strange hours in the lab while conducting the research, and the long hours of data processing/writing after work and on weekends the past year, she has always stood beside me and encouraged me to succeed when morale was low.

Secondly, I would not have been able to do this project without my advisor Dr. Jack Webster. I met Jack at Coweeta during an internship as an undergraduate, which is where he sparked my interest in stream ecology. Over the next few years as an undergraduate, he taught me many lessons in and out of the classroom. During my senior year, I worked on an undergraduate research project with Jack as an advisor where we discussed graduate school to pursue my fascination with stream ecology. He had a very active “open-door” policy as an advisor. If I had a question about anything from classes, to research issues, to general life questions, I could ask him and get a straightforward response on how to proceed. I did a project in his Stream Ecology class that essentially compared metabolism across different land use types and my questions with that project eventually lead to my pursuing the long-term study addressing metabolism. Outside of academia, Jack is also a friend. We would often discuss fishing, hunting, and working on vehicles, all of which I did at or near his property.

Thirdly, I would like to thank my committee. Fred Benfield and Andy Dolloff were very supportive throughout my pursuit of this degree. They would always look critically at what I was doing and help me expand or narrow the scope of work to make it more meaningful and productive. They are a wealth of knowledge and have greatly changed my outlook by getting me to look beyond what I am used to. Also, the most powerful discussion that I had with them was
when I asked for their support in leaving school to pursue a job in West Virginia. They cautioned me that it would be very challenging to finish the degree after leaving, but supported my decision to take an incredible opportunity. I can safely say that they were not kidding when they said it would be a struggle to motivate myself to work on schoolwork at night after a 70 hour week.

I would also like to thank the Stream Team. I got to know many of the graduate students as an undergraduate and it made the shift to being a graduate student seamless. Friday meetings/discussions were always enlightening because there are so many people with different backgrounds that you learn something new every week. The setup of Stream Team is what gives it such success, in that it is a collaborative effort between students and professors to address a myriad of issues regarding ecology. I would like to specifically thank Robert Northington and Bobbie Neiderlehner for their help along the way. Although at some point every member of Stream Team helped with the field work for my project, Robert was with me every step along the way and was a good sounding board for ideas and concepts. Bobbie helped me with just about any question that I had over the years that was related to science and data management/manipulation and was always willing to help me succeed.

And Lastly, I thank the Coweeta Hydrologic Lab staff, US Forest Service staff, and University of Georgia for on the ground support, data access, and data analysis help along the way. It was always reassuring knowing that there was such a diverse and dedicated group of scientists that were willing to help out for the greater good of ecology as a whole.
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Introduction

Historically, people in the southern Appalachians generally have lived in metropolitan areas with suburban areas on the periphery and low population density in rural areas. Beyond these urban and suburban centers lie vast expanses of relatively undeveloped mountains. Residents in the rural mountains generally live in the valleys where agriculture is practical. In recent years, due to socio-economic factors, people have begun to build retirement or second homes on the mountainsides (Webster et al., 2012). This recent transition raises the questions of how the impacts of development and land use change impact southern Appalachian streams, specifically the effect on ecosystem metabolism.

Ecosystem metabolism is a function of photosynthesis by autotrophs (gross primary production, GPP) and the combination of respiration by autotrophs and heterotrophs (ecosystem respiration, ER). In streams, GPP is the amount of organic matter produced by photosynthetic organisms whereas ER results from the decomposition of organic matter produced both within (autochthonous) and from outside streams (allochthonous) (Mulholland et al., 2001). Ecosystem respiration is a combination of microbial, algal, and faunal respiration and is typically dominated by microbes in streams in the eastern United States (Webster et al., 1995). Net ecosystem production (NEP) is the difference between GPP and ER; for streams NEP is often negative, signifying that ER > GPP. The coupling of GPP and ER drives carbon cycling in streams and can be indicative of ecosystem processes, including rates of nutrient processing and secondary production (Meyers et al., 2007).

There are numerous factors that affect stream metabolism including light availability for photosynthetically active radiation (PAR) (e.g., Mulholland et al., 2001), nutrient concentrations and availability (e.g., Gausch et al., 1995), the quantity and quality of organic matter (e.g.,
Webster *et al.*, 1997), and temperature (e.g., Uehlinger, 2006). One of the most important factors influencing stream metabolism is light. Streams with high proportion of canopy cover often have low PAR leading to low GPP (Mulholland *et al.*, 2001). Headwater streams often have extensive canopy cover and rely on allochthonous inputs, which leads to negative NEP due to high ER. With increasing stream order, canopy cover diminishes causing a transition from allochthonous to autochthonous inputs (Vannote *et al.*, 1980).

Stream metabolism varies both among and within regions. The Lotic Intersite Nitrogen Experiment (LINX) examined numerous streams throughout the United States and showed that regional factors such as PAR, nutrients, and temperature have a significant bearing on stream metabolism (Mulholland *et al.*, 2001). Metabolism is affected by general land use, specifically anthropogenic modification. Land use can change flow regimes by increasing the proportion of impervious surfaces in the watershed and can increase nutrients and contaminants from agriculture and urban areas (Walsh *et al.*, 2005). When land use was assessed within the regions studied in LINX, it was shown that land use has more bearing on metabolism than regional characteristics (Bernot *et al.*, 2010).

Land use has been variably characterized but can be separated into four general categories: Forested, Developed, Agricultural, and Other (e.g., Webster *et al.*, 2012). Development (urbanization/exurbanization) has been shown to be negatively correlated with GPP as well as ER (Bott *et al.*, 2006). Mulholland *et al.* (2005) found that as watershed disturbance increases, there are minor differences in GPP and significant differences in ER. Increased agriculture and development within watersheds affect watersheds by altering flow regimes and sediment dynamics leading to erosion (Burcher and Benfield, 2006).
Seasonal variation in stream metabolism is due to changes in light availability and intensity as well as temperature change (Uehlinger, 2006). Streams in deciduous forests often have highest rates of GPP in early spring when the canopy is open and day length begins to increase, but open streams often have highest rates of GPP in spring/early summer (Fig. 1) (Roberts et al., 2007). Similarly, in forested streams ER often peaks in the late fall due to allochthonous inputs during leaf fall, whereas open streams often have highest rates of ER in the summer due to autotrophic respiration (Fig. 2).

Various methods have been used to measure stream metabolism, beginning with Odum (1956), who measured the rate of change of oxygen using an upstream-downstream method. Because this is an open-channel oxygen change approach, oxygen data must be corrected for reaeration (Odum, 1956), the exchange of O$_2$ with the atmosphere.

In the years following the development and implementation of Odum’s method of measuring stream metabolism, more automated ways to measure oxygen change were developed. Kelly et al. (1974) employed an upstream-downstream approach using a galvanic cell oxygen probe and thermistor. This equipment allowed them to measure oxygen and temperature at each station at 15-second intervals and record them on a cartridge tape recorder (Kelly et al., 1974). To assess the reaeration and calculate GPP and ER, they used Fourier coefficients in an oxygen mass balance equation. This method allowed generation of NEP curves with considerably less noise and more usable data than previous methods (Kelly et al., 1974).

In the following decade, several more methods were developed and can be divided into daytime and nighttime methods. One method used a regression for post-sunset rates of change of dissolved oxygen (DO) over time to assess deficit (Owens, 1974). Another nighttime method
Figure 1. Expected annual gross primary production for forested and open streams.
Figure 2. Expected annual ecosystem respiration for forested and open streams.
involved estimating respiration and reaeration using DO as a predictor (Hornberger and Kelly, 1975). Young and Huryn (1996) calculated daytime ER using the rate of change of DO as a function of light and oxygen deficit. Another daytime method that was developed estimated reaeration by measuring the lag time between peak sunlight and peak DO concentration. Comparison of these methods shows that daytime methods are generally more precise than the nighttime methods (Kosinski, 1984). Each method has strengths and weaknesses, but these developments have been very useful to in the field of stream ecology.

More recently, there have been extensive improvements in monitoring equipment and methods, although the underlying concepts have not changed. The two most common measures of open water metabolism are the one-station method and the two station method. The one-station method measures oxygen change over time at the end of a stream reach. The two-station method measures the change over distance (upstream-downstream method). Both of these methods employ automated recording systems, most often sondes, which allow for continuous measurements of DO and temperature. Sondes can be deployed for extended periods, set at a constant recording interval, and periodically calibrated to allow continuous DO data collection (Roberts et al., 2007). Reaeration is now commonly assessed in the field using the injection of an inert gas such as sulfur hexafluoride (SF$_6$) to calculate the reaeration coefficient (e.g., Grace and Imberger, 2006).

The capacity to continuously measure DO and temperature is now possible, but it is often not implemented across long temporal scales. Typically, metabolism is measured on the order of one to several days often with large gaps between measurements (Roberts et al., 2007). These short term point measurements of metabolism are usually on days that give optimal changes in dissolved oxygen DO and may not reflect true patterns of metabolism. Patterns that do not
appear in these point measurements, such as seasonal variability and land use influences, may emerge with long-term monitoring.

In this study, I assessed stream metabolism in nine southern Appalachian watersheds over the course of one year to evaluate seasonal variability within and among streams draining different land cover types. Land cover data was used to address changes in metabolism among land cover types. I predicted that streams that drain forested watersheds would be heterotrophic year round and have highest GPP during early spring. I also predicted that streams that have a higher proportion of open area in the watershed, which is typical of agriculture or development, would have higher rates of GPP and be relatively less heterotrophic.

Methods

Study Sites

The nine study streams are located within the Little Tennessee River basin in the southern Appalachian Mountains of western North Carolina (Fig. 3). Sites range in watershed size from 218 to 2,913 hectares with variable land cover and hydrologic metrics (Table 1). Land cover data from 2001 and 2006 NASA Landsat Thematic Mapper Imagery were classified by Jeff Hepinstall and Hunter Allen (Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602) (Table 2,3). The watersheds were all primarily forested, but some contained developed and agricultural areas. Ball Creek, Cowee Creek, Jones Creek, and Ray Branch all had over 90% watershed forested land cover. Crawford Branch and Bates Branch had the highest agricultural land cover. Crawford Branch, Watauga Creek, and Bates Creek also had the highest percent of developed land (Table 2).
Figure 3: Location of the nine study watersheds within the Little Tennessee Watershed.
Table 1: Site Descriptions for nine study watersheds in the Little Tennessee watershed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Abbreviated name</th>
<th>Watershed Size (ha)</th>
<th>Average Discharge (L s(^{-1}))</th>
<th>Average Width (m)</th>
<th>Average Depth (cm)</th>
<th>Summer Open Light (%)</th>
<th>Slope (km/m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ball Creek</td>
<td>BCW9</td>
<td>716</td>
<td>213</td>
<td>4.6</td>
<td>12.6</td>
<td>84.3</td>
<td>0.0222</td>
</tr>
<tr>
<td>Bates Creek</td>
<td>BUPP</td>
<td>218</td>
<td>109</td>
<td>2.9</td>
<td>16.0</td>
<td>69.8</td>
<td>0.0041</td>
</tr>
<tr>
<td>Caler Main</td>
<td>CALR</td>
<td>1867</td>
<td>180</td>
<td>4.3</td>
<td>14.4</td>
<td>72.9</td>
<td>0.0111</td>
</tr>
<tr>
<td>Cowee Creek</td>
<td>COCR</td>
<td>2913</td>
<td>321</td>
<td>5.5</td>
<td>15.6</td>
<td>64.2</td>
<td>0.0124</td>
</tr>
<tr>
<td>Crawford Branch</td>
<td>FROG</td>
<td>527</td>
<td>76</td>
<td>2.4</td>
<td>13.3</td>
<td>68.1</td>
<td>0.0067</td>
</tr>
<tr>
<td>Jones Creek</td>
<td>JCKP</td>
<td>1531</td>
<td>321</td>
<td>7.3</td>
<td>16.2</td>
<td>73.7</td>
<td>0.0108</td>
</tr>
<tr>
<td>Ray Branch</td>
<td>RAYB</td>
<td>1438</td>
<td>180</td>
<td>4.8</td>
<td>16.9</td>
<td>83.0</td>
<td>0.0160</td>
</tr>
<tr>
<td>Skeenah Creek</td>
<td>SSKP</td>
<td>602</td>
<td>101</td>
<td>3.0</td>
<td>11.5</td>
<td>57.5</td>
<td>0.0169</td>
</tr>
<tr>
<td>Watauga Creek</td>
<td>WAHZ</td>
<td>1670</td>
<td>196</td>
<td>4.0</td>
<td>19.0</td>
<td>67.9</td>
<td>0.0087</td>
</tr>
</tbody>
</table>
Table 2: Watershed land cover for nine study watersheds in the Little Tennessee watershed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Agricultural</th>
<th>Percent of Land Cover</th>
<th>Forest</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ball Creek</td>
<td>0.0</td>
<td>2.2</td>
<td>97.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Bates Creek</td>
<td>15</td>
<td>13.0</td>
<td>62.6</td>
<td>10.7</td>
</tr>
<tr>
<td>Caler Main</td>
<td>5.5</td>
<td>3.6</td>
<td>82.9</td>
<td>6.3</td>
</tr>
<tr>
<td>Cowee Creek</td>
<td>3.4</td>
<td>2.6</td>
<td>91.9</td>
<td>2.0</td>
</tr>
<tr>
<td>Crawford Branch</td>
<td>14.0</td>
<td>47.8</td>
<td>29.7</td>
<td>8.1</td>
</tr>
<tr>
<td>Jones Creek</td>
<td>2.7</td>
<td>2.4</td>
<td>92.3</td>
<td>2.2</td>
</tr>
<tr>
<td>Ray Branch</td>
<td>0.6</td>
<td>1.1</td>
<td>94.7</td>
<td>2.1</td>
</tr>
<tr>
<td>Skeenah Creek</td>
<td>3.3</td>
<td>4.7</td>
<td>85.3</td>
<td>6.2</td>
</tr>
<tr>
<td>Watauga Creek</td>
<td>6.0</td>
<td>14.4</td>
<td>73.4</td>
<td>5.5</td>
</tr>
</tbody>
</table>
Table 3: Riparian land cover for nine study watersheds in the Little Tennessee watershed.

<table>
<thead>
<tr>
<th>Site</th>
<th>Agricultural</th>
<th>Developed</th>
<th>Forest</th>
<th>Shrub/Scrub</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ball Creek</td>
<td>0</td>
<td>4.6</td>
<td>95.1</td>
<td>0.3</td>
<td>0</td>
</tr>
<tr>
<td>Bates Creek</td>
<td>41.5</td>
<td>9.6</td>
<td>36.0</td>
<td>12.2</td>
<td>0.7</td>
</tr>
<tr>
<td>Caler Main</td>
<td>8.7</td>
<td>10.0</td>
<td>68.1</td>
<td>9.0</td>
<td>4.1</td>
</tr>
<tr>
<td>Cowee Creek</td>
<td>12.1</td>
<td>9.7</td>
<td>74.8</td>
<td>3.3</td>
<td>0.1</td>
</tr>
<tr>
<td>Crawford Branch</td>
<td>18.2</td>
<td>62.2</td>
<td>14.0</td>
<td>5.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Jones Creek</td>
<td>12.4</td>
<td>7.9</td>
<td>75.5</td>
<td>3.9</td>
<td>0</td>
</tr>
<tr>
<td>Ray Branch</td>
<td>0</td>
<td>0.4</td>
<td>99.6</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Skeenah Creek</td>
<td>13.5</td>
<td>12.9</td>
<td>57.4</td>
<td>15.0</td>
<td>1.2</td>
</tr>
<tr>
<td>Watauga Creek</td>
<td>16.4</td>
<td>21.2</td>
<td>56.1</td>
<td>3.8</td>
<td>2.5</td>
</tr>
</tbody>
</table>
Land cover in the 100 m riparian buffer on each side of the stream for 1000 m upstream of each of the study sites. Within the corridor, Ball Creek and Ray Branch had over 90% forested land cover, whereas Cowee Creek and Jones Creek had the most agricultural areas in the watershed, but Cowee Creek, Jones Creek, and Watauga Creek also had greater than 10% agricultural land cover in the riparian area (Table 3). Crawford Branch, Watauga Creek, Skeenah Creek had the most developed riparian land cover (Table 3).

Metabolism

A single-station, diel oxygen curve technique was used to measure GPP and ER. Dissolved Oxygen (DO), temperature, and conductivity were measured continuously from September 2010 through August 2011 using Hydrolab Minisonde 5 sondes (Hydrolab-Hach Company, Loveland, Colorado). The sondes recorded DO, temperature, and conductivity at a 60 minute interval 24 hours a day. Oxygen sensors were calibrated for drift every three weeks in water saturated air.

By correcting for changes in oxygen caused by physical reaeration, I was able to estimate metabolism from diel oxygen curves. To estimate the reaeration coefficient (k_{O2}), I evaluated three methods: sulfur hexafluoride (SF$_6$) injection, energy dissipation method, and the surface renewal method. SF$_6$ injection was used to directly measure gas exchange and calculate a rate of O$_2$ exchange as k$_{O2}$ (d$^{-1}$) (Marzolf et al, 1994). Concurrently with the SF$_6$ injection, I measured stream velocity and discharge using a NaCl slug to determine travel time of each 200-m reach. After the NaCl slug completely passed the downstream site, I collected triplicate gas samples every 25 m along the study reach for a total of 7 sampling sites. Gas samples were collected by withdrawing 10 mL of stream water and injecting into a 20-mL air-sealed glass vials and removing 10 mL of air from the headspace. I quantified SF$_6$ in the headspace using a SRI-8610
Gas Chromatograph (SRI Instruments, Torrance, California) with electron capture detector. Once quantified, the peak SF₆ injection was used to calculate a rate of O₂ exchange as kₒ₂ (d⁻¹) (Marzolf et al., 1994). To convert SF₆ to O₂, I multiplied the k₂ value by 1.345 (Grace and Imberger, 2006) which gives kₒ₂. The seasonal variation required the reaeration values to be temperature corrected (kₒ₂(20)) by the equation:

\[ kₒ₂(20) = kₒ₂(\text{temp}) \times 1.0241^{(20-\text{temp})} \]

Where kₒ₂(\text{Temp}) is the reaeration at a measured temperature (Grace and Imberger, 2006).

The energy dissipation method uses water velocity and stream gradient to determine kₒ₂ (Tsivoglou and Neal, 1976). Stream gradient was measured over each 200-m reach in 2011 with a transit and stadia rod. Reaeration was estimated using these measurements in the equation:

\[ kₒ₂ (20ºC) = K' (S) v \]

where K' is a constant dictated by stream velocity, S is slope (m/km), and v is velocity in m s⁻² (Tsivoglou and Neal, 1976).

The surface renewal method estimates kₒ₂ using stream velocity and mean depth. The reaeration coefficient is calculated by the equation:

\[ kₒ₂ (20ºC) = 50.8 (v^{0.67}) (z^{-0.85}) \]

Where v is velocity in cm s⁻¹ and z is mean depth in centimeters (Elmore and West, 1961). This method is accurate between 3-150 cm s⁻¹ and depths of 12-355 cm (Elmore and West, 1961).

Each of these methods was evaluated to compare to established literature as well as validate field methods vs empirical methods. I also tried the Nighttime Regression method (Young et al, 2004), but it gave very inconsistent results. The Surface Renewal method was used to calculate reaeration values, but comparison with other methods showed inconclusive or contradictory results. The hydrologic parameters were commonly outside of the established
range of accuracy (Elmore and West, 1961). As discharge increased, the depth often increased, which when raised to a negative exponent gave a lower reaeration. SF\textsubscript{6} injection and Energy Dissipation gave similar results for reaeration, for this reason I used SF\textsubscript{6} measured reaeration rates. The absolute values did not always agree, but the regressions generally had similar slope (Fig. 4).

In order to extrapolate reaeration measurements, stage was continuously measured in each of the study streams using a 720 Submerged Probe Flow Module (Teledyne Isco Inc., Lincoln, Nebraska). Field measures of discharge were conducted throughout the year over variable flows to develop rating curves (Table 4). Reaeration was measured concurrently with the discharge measurements, allowing me to establish a relationship between discharge and reaeration to develop a regression for each site (Fig. 4). Once discharge rating curves were established for each site, regressions were developed between discharge and reaeration. These regressions allowed me to calculate reaeration for each stream for each recording interval.

Gross Primary Production (GPP) and Ecosystem Respiration (ER) were calculated using the single station method. The single station method calculates GPP and ER by reaeration corrected change in DO:

\[
\Delta DO \ (gO_2 \ m^{-2} \ min^{-1}) = \left(\frac{C_t - C_0}{\Delta t} - k_{O_2} \ D \right) z
\]

Where \(C_t - C_0\) is change in O\textsubscript{2} concentration between recording intervals (mg/L), \(k_{O_2}\) is the temperature corrected oxygen reaeration coefficient (day\textsuperscript{-1}), \(D\) is the oxygen deficit (calculated saturation concentration minus measured concentration for recording interval), \(\Delta t\) is change in time (min) between recording intervals, and \(z\) is stream depth (m) (Bernot et al., 2010). Depth for
Figure 4. Comparison of reaeration methods in nine study streams in Little Tennessee watershed.
Table 4. Rating curves were used to estimate discharge (Q, L/s) from stage (X, mm) for each of the nine study sites.

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Rating Curve</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ball Creek</td>
<td>$Q = 19.38e^{0.0067X}$</td>
</tr>
<tr>
<td>Bates Creek</td>
<td>$Q = 21.161e^{0.0065X}$</td>
</tr>
<tr>
<td>Caler Fork</td>
<td>$Q = 40.231e^{0.0044X}$</td>
</tr>
<tr>
<td>Cowee Creek</td>
<td>$Q = 68.046e^{0.006X}$</td>
</tr>
<tr>
<td>Crawford Branch</td>
<td>$Q = 17.426e^{0.0026X}$</td>
</tr>
<tr>
<td>Jones Creek</td>
<td>$Q = 61.54e^{0.0056X}$</td>
</tr>
<tr>
<td>Ray Branch</td>
<td>$Q = e^{(3.7598\ln(X) - 15.003)}$</td>
</tr>
<tr>
<td>Skeenah Creek</td>
<td>$Q = e^{(1.5591\ln(X) - 3.5299)}$</td>
</tr>
<tr>
<td>Watauga Creek</td>
<td>$Q = e^{(1.7805\ln(X) - 3.5648)}$</td>
</tr>
</tbody>
</table>
each recording interval was calculated from regressions of measured depth and discharge at each site. Nighttime ER was calculated as the oxygen change rate (corrected for reaeration) during the night. Daytime ER was determined by linear extrapolation between ER for the hour before dawn and the hour after dusk. Dusk and dawn were established based off of known sunrise/sunset times for the area. A given sunrise and sunset time were assigned to each month, with the assumption that it remained the within a reasonable margin. Daily GPP was calculated by integrating the diel ΔDO curve minus ER from dawn to dusk using reaeration-corrected ΔDO values. GPP and ER were calculated on a per time basis and converted to area estimates by multiplying by depth. Net Ecosystem Production (NEP) was calculated by the equation: NEP = GPP – ER, where positive NEP values indicate a more autotrophic system and negative NEP values indicate a more heterotrophic system (Allan and Castillo, 2007).

Light

Canopy cover was measured using a concave spherical densiometer (Model C - Forest Densiometers, Bartlesville, OK, USA). The densiometer was read at 10 meter intervals along each stream. The number of locations on the densiometer that showed presence of an object in the canopy above allowed me to calculate canopy cover. Direct light intensity measurements were collected at each site at peak sunlight during summer 2011. Light intensity was measured by two sets of Onset HOBO light intensity data loggers (ONSET Computer Corp., Pocasset, MA, USA). Three data loggers were carried above my head and recorded light intensity in 10 second intervals as I walked along each stream reach for a period of fifteen minutes. A second set of three data loggers were placed in a clearing and recorded direct sunlight every 10 seconds as a
baseline. Light intensity for the stream reach was divided by the measurements in the clearing to calculate the percent open light available in the stream channel.

**Results**

**Seasonal Variation Within Sites**

*Gross Primary Production*

Seasonal variation in Gross Primary Production (GPP) was observed in most of the study sites (Fig. 5). Bates Creek, Crawford Branch, and Watauga Creek all showed a similar pattern with the lowest GPP in December and January and a peak in late June to early August. Cowee Creek and Caler Fork had lowest GPP in January and the peaks were earlier in the year, during April and May. GPP in Ball Creek, the most forested stream (Table 2), peaked in late February through early March and had low periods in both May through June and October through November. Jones Creek and Skeenah Creek both had peak GPP in March. While Skeenah Creek, the most open stream (Table 2), had lowest production in late August through early September, Jones Creek GPP declined through May and peaked again in late June through early July with a yearly low December. Ray Branch showed a similar peak to Cowee Creek and Caler Fork in April and May but had a low in the fall with a slow increase from November through April.

*Ecosystem Respiration*

Seasonal variation and seasonal trends in Ecosystem Respiration (ER) were also noted in most of the study sites (Fig. 6). In general, ER was more variable than GPP. Bates Creek, Caler Fork, Cowee Creek, Crawford Branch, and Watauga Creek all showed lowest ER in December and highest ER in May through June. Skeenah Creek, the most open stream peaked in October and again in April with the lowest ER in August and September. Jones Creek showed similar
Figure 5: Daily Gross Primary Production in the nine study sites taken from 1 Sep 2010 through 31 Aug 2011. Lines are best fit to a 3, or 4-parameter sine wave equation or to a 5-parameter damped sine wave equation and are shown for visual reference only.
double peaks as Skeenah, with highs in October and again in late March and early April but with
the low occurring in June. Ball Creek, the most forested stream, also had double peaks, but the
highs occurred in late January through early February and again in late June through early July.
Ray Branch had no clear pattern of high and low respiration.

Annual Gross Primary Production and Ecosystem Respiration Among Sites

Gross Primary Production

There was a large amount of variability in annual GPP (Fig. 7, Table 5). The sites with
lowest GPP were Ball Creek and Bates Creek, both of which had GPP less than 150 gO₂ m⁻² y⁻¹
(Table 5). Watauga Creek, Ray Branch, and Cowee Creek all had slightly higher GPP, between
150 and 300 gO₂ m⁻² y⁻¹. Caler Fork and Jones Creek had annual GPP slightly higher than the
aforementioned sites. The sites with the highest GPP were Crawford Branch and Skeenah Creek.

Ecosystem Respiration

There was considerable variation in annual ER (Fig. 7, Table 5). Similarly to GPP, Bates Creek
had the lowest ER. Watauga Creek and Ball Creek had similar values that were comparatively
low. Jones Creek and Cowee Creek had similar values, which were slightly higher than Ball
Creek, Bates Creek, and Watauga. Skeenah Creek, Crawford Branch, Caler Fork and Ray Branch
all had values greater than 1000 gO₂ m⁻² y⁻¹.

There was a significant relationship between the GPP and ER (Fig. 8). Generally sites fell
close to the line of best fit with the exception of Ball Creek, Ray Branch, and Skeenah Creek.
Ball Creek and Ray Branch fell below the line, which indicates that there was considerably more
respiration than production making them relatively more heterotrophic. Skeenah Creek fell above
the line, which indicated that there was more production relative to the amount of respiration
measured, making it relatively less heterotrophic.
Figure 6: Daily Ecosystem Respiration in the nine study sites taken from 1 Sep 2010 through 31 Aug 2011. Lines are best fit to a 3, or 4-parameter sine wave equation or to a 5-parameter damped sine wave equation and are shown for visual reference only.
Figure 7: Comparison of GPP and ER among sites, grouped from highest to lowest watershed forest land cover. Percent forest land cover is indicated after each stream name.
Table 5: Metabolism parameters for nine study streams in Little Tennessee watershed.

<table>
<thead>
<tr>
<th>Site</th>
<th>GPP (gO$_2$ m$^{-2}$ y$^{-1}$)</th>
<th>ER (gO$_2$ m$^{-2}$ y$^{-1}$)</th>
<th>NEP (gO$_2$ m$^{-2}$ y$^{-1}$)</th>
<th>P/R</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ball Creek</td>
<td>107</td>
<td>681</td>
<td>-574</td>
<td>0.16</td>
</tr>
<tr>
<td>Bates Creek</td>
<td>127</td>
<td>214</td>
<td>-87</td>
<td>0.59</td>
</tr>
<tr>
<td>Caler Main</td>
<td>358</td>
<td>1242</td>
<td>-884</td>
<td>0.29</td>
</tr>
<tr>
<td>Cowee Creek</td>
<td>296</td>
<td>790</td>
<td>-494</td>
<td>0.37</td>
</tr>
<tr>
<td>Crawford Branch</td>
<td>377</td>
<td>1170</td>
<td>-793</td>
<td>0.32</td>
</tr>
<tr>
<td>Jones Creek</td>
<td>326</td>
<td>855</td>
<td>-529</td>
<td>0.38</td>
</tr>
<tr>
<td>Ray Branch</td>
<td>224</td>
<td>1259</td>
<td>-1035</td>
<td>0.18</td>
</tr>
<tr>
<td>Skeenah Creek</td>
<td>532</td>
<td>1129</td>
<td>-597</td>
<td>0.47</td>
</tr>
<tr>
<td>Watauga Creek</td>
<td>252</td>
<td>695</td>
<td>-443</td>
<td>0.36</td>
</tr>
</tbody>
</table>
**Light**

Integrated light measurements indicated highest canopy light interception at Ball Creek and Ray Branch, the most forested sites and the lowest canopy light interception was at Skeenah Creek, which had a higher proportion of developed and agricultural areas. Cowee Creek, Crawford Branch, Watauga Creek, Bates Creek, Caler Fork, and Jones all showed similar ranges in light interception along the study reaches (Fig. 9). Densiometer readings showed that Ball Creek and Bates Creek were the sites with highest canopy cover. Cowee exhibited the lowest canopy cover. There was a minimal range among the sites with the highest and lowest canopy cover using the densiometer readings (93 to 99%). The remaining sites all fell closely together within that range (Fig. 10). Integrated canopy light interception and canopy cover were highly correlated (Fig. 11). Overall, canopy light interception and canopy cover followed a consistent trend with the exception of Skeenah Creek. Skeenah Creek has the highest shrub/scrub in the riparian area and relatively high agriculture and developed land uses. There was an abundance of Multiflora Rose (*Rosa multiflora*) along the immediate riparian buffer, which accounted for a majority of the shrub/scrub. This shrub/scrub species may have caused the densiometer readings taken at chest height to indicate high canopy cover, whereas the integrated canopy light measurements, taken at head height, were relatively lower. Another potential influence on light availability is the aspect of the stream. Skeenah Creek had higher light than Bates Creek, which had a higher agricultural and developed watershed and local riparian zone. One explanation of this could be that in Skeenah Creek, the south bank is exposed due to clearing, whereas in Bates it is the north bank that is exposed.
Figure 8: Comparison of ecosystem respiration and gross primary production.
Figure 9: Integrated canopy light interception for each site represented as percent.
Figure 10: Canopy cover for each site represented as percent from densiometer.
Figure 11: Integrated canopy light interception vs densiometer canopy cover for each site represented as percent.
Discussion

Gross Primary Production

Average annual gross primary production ranged from 0.29 to 1.46 g O₂ m⁻² d⁻¹ in the nine streams in this study. These values fall in line with numerous other studies showing ranges of <0.01 to 1.75, 0.1-1.8, 0.2-1.7, and 0.05-1.9 g O₂ m⁻² d⁻¹ (Houser *et al.*; 2005, Mulholland *et al.*, 2001; Fellows *et al.*, 2001; and Acuna *et al.*, 2004).

The primary control on GPP in this study appears to be light (Fig. 7, 8). Other studies have shown that riparian zone vegetation (Bott *et al.*, 2006) and canopy cover influence primary production (Bott *et al.*, 1985, Young and Huryn, 1999). Streams with little to no canopy cover have higher photosynthetically active radiation (PAR) and often have higher rates of GPP. Similarly, streams with higher canopy cover had lower PAR and lower rates of GPP (Mulholland *et al.*, 2001). Forested streams generally have highest rates of GPP in the early spring when there is more PAR, but the deciduous forest canopy has not emerged (Roberts *et al.*, 2007) (Fig. 1), and the closed canopy in the summer often lowers GPP (Young and Huryn, 1999) (Fig. 1). The most forested sites, Ball Creek and Ray Branch, showed this trend, and in most cases, with the exception of Bates Creek and Cowee Creek, the other sites I monitored also had spring peaks (Fig. 5). However, in Bates Creek, Watauga Creek, and Crawford Branch there was also a strong summer peak in GPP (Fig. 5).

Gross primary production had a marginally significant positive correlation with ecosystem respiration (p= 0.056, r=0.65) (Fig. 6). A study on streams in New York also showed a relationship between GPP and ER, generally as GPP increased ER also increased (Bott *et al.*, 2006). While some studies have showed this relationship (e.g., Bunn *et al.*, 1999), others have showed that there is only a weak relationship or no relationship at all (Mulholland et al. 2001).
The relationship between GPP and ER was a good indicator of degree of heterotrophy for the nine study streams, i.e., if a site fell below the line of best fit, it was relatively more heterotrophic. Overall, there was a linear relationship between GPP and ER among the sites with the exception of Ball Creek, Ray Branch, and Skeenah Creek. Ball Creek and Bates Creek had the highest canopy light interception and fell below the line indicating they were relatively more heterotrophic. Skeenah Creek had the lowest canopy light interception and fell above the line, which indicated that it was relatively less heterotrophic.

*Ecosystem Respiration*

Average annual ecosystem respiration ranged from 0.58 to 3.4 g O$_2$ m$^{-2}$ d$^{-1}$ in the nine streams in this study. These values were within the range of previous studies 0.3-16.3 and 0.4-23.1 g O$_2$ m$^{-2}$ d$^{-1}$ (Houser et al., 2005; Bernot et al., 2010). While these values agreed with some studies, other studies showed higher ER of 2.41-11.00 and 1.59-5.76 g O$_2$ m$^{-2}$ d$^{-1}$ (Mulholland et al., 2001; Hall and Tank, 2003).

With the exception of GPP, the strongest influence of ER in this study was the amount of agricultural land cover in the riparian buffer (p=0.059, r$^2$=0.42). I found no significant relationships between ER and watershed land cover (Forested p=0.95, Agricultural p=0.37, Developed p=0.83). Previous studies have showed that there is not a substantial difference in ER with different types of disturbance, because the driver may be the influences on autotrophic production rather than the source of organic matter (Bernot et al., 2010). Other studies have also seen a significant relationship between ER and the extent of riparian vegetation (Riley and Dodds, 2012).
Consequences of Land Use Change

The Little Tennessee watershed is convenient to Atlanta, Asheville, and other urban centers. Being in the vicinity of these urban centers enables people to live in the country and work in the city or have second homes in the mountains. Historically, people in this area lived in the valleys, but they are now developing the mountainsides (Webster et al., 2012). As a result of this mountainside development, ecologists need to look at the impacts and consequences of development.

As exurbanization expands, it has the potential to affect stream processes and physical characteristics if not managed properly. Development can affect stream metabolism through reduced GPP resulting in sediment transport and turbidity that reduces light penetration (Walling and Fang, 2003). However, home site development and road construction remove vegetation in areas that were previously forests. By removing riparian vegetation, development reduces shading, increases temperature, and increases GPP (Julian et al., 2008). For example, Riley and Dodds (2012) showed that removing riparian vegetation resulted in changes in primary production and food web structure by changing available resources from allochthonous inputs to production by filamentous algae.

Another way that land-use change may affect stream dynamics is by altering the flow regime. Increased impervious surfaces and open compacted areas generate higher runoff during storms and potentially change stream morphology (Navratil et al., 2013). With an increase in runoff and change in flow regime, there is a potential for changes in stream metabolism. During the course of my study, there were several large storms, the largest of which had a noticeable effect on stream metabolism (Fig. 12). A majority of the streams had a notable decrease in NEP
immediately following the onset of the storm. The most forested watersheds, Ball Creek and Ray Branch, had an initial decrease but had a much more rapid recovery than less forested watersheds. Watauga Creek showed an increase in NEP with the storm, followed by a decline following the storm. Skeenah Creek had a strong relation between storm discharge and NEP; the storm had a bimodal curve and that same pattern appears in the NEP data (Fig. 12). There are numerous factors that could influence the general decrease in NEP following increased discharge from storms: scouring of algae and detritus from stream channels, sedimentation, and increased turbidity. There was no consistent pattern between discharge and NEP throughout the year, only during high flows. Roberts et al. (2007) also found that storms temporarily lowered GPP, and ER initially decreased following storms but reached much higher levels after the storms.

The general trends seen in this study agree with some previous studies, but also suggest some different trends. Roberts et al. (2007) found that GPP peaks in the early spring which agrees with my results, whereas they found that the peak of ER was in the fall following leaffall. Similarly, Uelinger (2006) found GPP to peak in the early spring and that ER was much more variable, as seen in this study.

Land-use change in the southern Appalachians will continue to increase as people develop the exurban landscape. Mountainside development may not have as great of an influence on metabolism compared to agricultural disturbance, due to intact riparian buffers. Mountainside development is not usually adjacent to streams, whereas an increase in agriculture or stream-side development may have greater short and long-term effects on stream metabolism.
Figure 12: Net ecosystem production plotted with discharge during February and March, 2011, which included the largest storm within the study period.
Conclusion

Gross primary production and ecosystem respiration vary seasonally within and among streams as well as across the gradient of land use studied. There were several factors which affected stream metabolism. Seasonal patterns in primary production were generally attributed to light availability. Generally, the peak in GPP occurred in early spring, which agreed with prior studies, and ER peaks were more variable than prior studies. Also, I found that there was a greater land-use influence on streams at the riparian scale than the watershed scale. This study developed a year round picture of in-stream metabolic function and will allow ecologist to assess the impacts of mountainside development in the future.
Literature Cited


