Late-successional riparian forest structure results in heterogeneous periphyton distributions in low-order streams

Jeremy P. Stovall, William S. Keeton, and Clifford E. Kraft

Abstract: Late-successional riparian forests often regulate autotrophic microhabitats in low-order streams through shading provided by canopies. However, few studies have linked forest structure with periphyton microhabitat in adjoining streams. Our hypotheses were that (1) the heterogeneous horizontal structure in old-growth forests creates more spatially variable below-canopy light environments compared with mature forests and (2) site-specific light availability over streams correlates with spatial distributions of periphyton microhabitat. We surveyed 15 low-order stream reaches in late-successional northern hardwood–hemlock forests in the Adirondack Mountains of New York, USA. We measured forest structure and the below-canopy light environment at all reaches and the periphyton chlorophyll *a* concentration on artificial substrates in eight reaches. While stand age was not statistically significant, multivariate models of horizontal forest structure (e.g., gap distribution) and topography showed strong relationships ($R^2 > 0.70$) with the below-canopy light environment across all late-successional forests. Furthermore, metrics of below-canopy light availability explained a small but statistically significant proportion of the variation in chlorophyll *a* concentration. This variation in chlorophyll *a* indicates that complex late-successional riparian forests, both mature and old-growth, create a mosaic of heterotrophic (shaded) and autotrophic (lighted) microhabitats along low-order streams. These results reveal important and previously unrecognized links between stream habitat heterogeneity and the horizontal heterogeneous late-successional forest structure.

Résumé : Les forêts riveraines au dernier stade de succession régissent souvent les microhabitats autotrophes dans les cours d'eau secondaires via l'ombre produit par le couvert. Cependant, peu d'études ont relié la structure de la forêt et les microhabitats du périphyton dans les cours d'eau voisins. Nous avons émis les hypothèses suivantes : (1) la structure horizontale hétérogène dans les vieilles forêts crée des conditions de luminosité sous couvert plus variables dans l'espace comparativement aux forêts matures et (2) la disponibilité de la lumière propre à un site au-dessus d'un cours d'eau est corrélée à la distribution spatiale des microhabitats du périphyton. Nous avons réalisé un inventaire de 15 tronçons de cours d'eau secondaires dans les forêts de feuillus nordiques et de pruche au dernier stade de succession dans les monts Adirondacks de l'État de New York, aux États-Unis. Nous avons mesuré la structure de la forêt et les conditions de luminosité sous couvert dans tous les tronçons ainsi que la concentration de la chlorophylle *a* du périphyton sur des substrats artificiels dans huit tronçons. Même si l'âge du peuplement n'était pas statistiquement significatif, des modèles multivariés de la structure horizontale de la forêt (p. ex., la distribution des trouées) et la topographie étaient étroitement reliés ($R^2 > 0,70$) aux conditions de luminosité sous couvert dans toutes les forêts au dernier stade de succession. De plus, des métriques de la disponibilité de la lumière sous couvert expliquent une proportion statistiquement significative, bien que faible, de la variation de la concentration de chlorophylle *a*. Cela indique que les forêts riveraines complexes au dernier stade de succession, matures et surannées, créent une mosaïque de microhabitats hétérotrophes (ombragés) et autotrophes (éclairés) le long des cours d'eau secondaires. Ces résultats révèlent des liens importants et jusqu'ici inconnus entre l'hétérogénéité des habitats des cours d'eau et l'hétérogénéité de la structure des forêts au dernier stade de succession.

[Traduit par la Rédaction]

Introduction

Although the importance of patch dynamics in stream ecosystems has recently gained recognition (Townsend 1989; Montgomery 1999; Thorp et al. 2006), links between stream habitat heterogeneity and heterogeneous forest structure are only beginning to receive attention (Keeton et al. 2007). This awareness of the importance of stream habitat heterogeneity expands upon an earlier view — encompassed within a prevailing framework provided by the "river continuum concept" (Vannote et al. 1980) — of lotic systems as dominated by continuous gradients. The river continuum concept explicitly recognizes the influence of overhanging forest canopies on light availability in streams. It postulates that shading by riparian canopies will decline along a gradient of increasingly stream order and size, which will, in turn, influence the proportion of autotrophic versus heterotrophic production. One common representation of the river continuum concept is that low-order streams are largely

J.P. Stovall[1,2] and W.S. Keeton. University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05405, USA.
C.E. Kraft. Cornell University, Department of Natural Resources, Ithaca, NY 14853, USA.

[1]Corresponding author (e-mail: jstovall@vt.edu).
[2]Present address: Virginia Tech, Department of Forestry, 228 Cheatham Hall (0324), Blacksburg, VA 24061, USA.

viewed as heterotrophic because forest canopies are closed across relatively narrow stream channels.

Forest–stream interactions are better understood by recognizing the forest dynamics that strongly influence forest canopy structure, which subsequently controls light availability over low-order streams. Canopy structure is not constant but rather changes with forest development, age, and interactions with natural disturbances (Franklin et al. 2002). Previous studies of stream ecosystem patch dynamics have not sufficiently described the influence of riparian forest patch dynamics upon heterogeneous in-stream processes. In this paper, we build on the idea that natural disturbances must be incorporated into conceptual frameworks for describing stream ecosystems by focusing specifically on gap dynamics (or fine-scale forest canopy disturbances) that are tightly correlated with forest stand development processes (Runkle 1982; Van Pelt and Franklin 2000).

Late-successional northern hardwood–hemlock forests have structural characteristics distinct from forests in earlier stages of development, including increased gap frequency and size, higher densities of large trees, and a larger average diameter of canopy trees (Tyrrell and Crow 1994; Dahir and Lorimer 1996; Ziegler 2000). Gap-phase dynamics in late-successional forests, caused by fine-scale canopy tree mortality, result in a horizontally heterogeneous stand structure (Pickett and White 1985). The vertical foliage distribution, horizontal structure (e.g., patchiness), and species composition of a forest collectively influence the below-canopy light environment (Canham et al. 1994; Van Pelt and Franklin 2000; Montgomery and Chazdon 2001). The light environment below the canopy of riparian stands influences ecological processes in adjacent streams. For example, shading provided by forest canopies over and adjacent to low-order streams reduces the frequency of favorable microhabitats for periphyton, resulting in reduced autotrophic abundance (Feminella et al. 1989; Kiffney et al. 2004). As a consequence, low-order streams flowing through mature and older forests, both presumed to have closed canopies, are thought to have primarily heterotrophic food webs (Naiman et al. 1998). Despite low algal standing biomass, recent work has cast doubt on this assumption, revealing that invertebrate communities in some forested headwater streams are disproportionately reliant on algal C inputs (McNeely et al. 2007). But how exactly do complex, old riparian forest canopies influence light availability over streams and, thus, in-stream autotrophic microhabitat availability? Our study addresses this and related questions, focusing on late-successional riparian forest systems in the northern hardwood region of eastern North America. We followed Gregory et al.'s (1991, p. 540) definition of riparian areas as "three-dimensional zones of direct interaction between terrestrial and aquatic ecosystems" and "comprised of mosaics of landforms, communities, and environments".
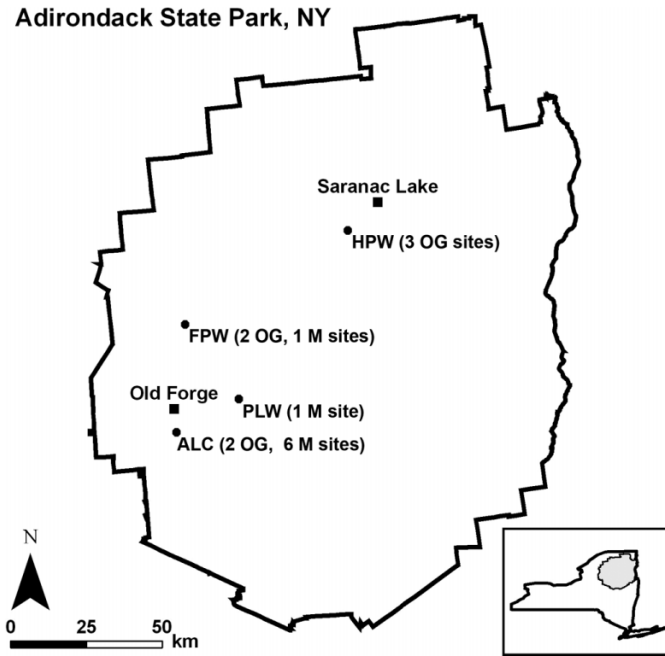
Our first research objective was to explore the relationships between the heterogeneous horizontal forest structure and spatial variability in light availability over low-order streams at a fine, within-reach scale. Studies exploring the relationships between forest structure and the below-canopy terrestrial light environment have typically found that old-growth forest canopies transmit little light (<5% of above-canopy light) compared with mature stands (Canham et al.

1990; Van Pelt and Franklin 2000). Although below-canopy light transmission is more spatially variable in tropical primary forest systems (Montgomery and Chazdon 2001), this relationship has not been established in the northern hardwood region of eastern North America.

In this paper, we hypothesize that spatial variability in light availability over streams at a fine, within-reach scale is greater in old-growth (e.g., dominant trees >150 years of age) stands than in mature (e.g., dominant trees 80–150 years of age) stands, resulting from the increasing frequency and average size of canopy gaps in late-successional forests. Gaps are most commonly caused by single-tree mortality; trees in old-growth stands tend to be larger, resulting in larger gaps than that in younger late-successional stages (Dahir and Lorimer 1996). Gaps created by density-independent mortality processes, such as natural disturbances, become increasingly prevalent in the very latest stage of stand development (Ziegler 2000; Franklin et al. 2002; Keeton et al. 2007). At any given time, canopy openings cover an average of 9.5% of old-growth forests while new gaps are formed at an average rate of 1% of total land area per year (Runkle 1982). In a prior study, we found preliminary evidence suggesting that fine, within-reach scale light availability over streams may be influenced by gap-related variability in canopy structure (Keeton et al. 2007) but were not able to support this inference directly. In this study, we test that hypothesis using direct empirical evidence.

The second research objective explored in this paper is the relationship between fine-scale below-canopy light availability and periphyton microhabitat availability. We hypothesized that spatial variability in light transmission in structurally complex late-successional forests would correlate with the location-specific pattern of periphyton microhabitat in low-order streams, as assessed by chlorophyll a concentration. Because many periphyton communities in shaded low-order reaches are not nutrient limited, even during periods of high light in spring before leaf-out (Bourassa and Cattaneo 2000; Bernhardt and Likens 2004; Greenwood and Rosemond 2005), it is reasonable to assume that light may remain as the primary limiting resource. Periphyton abundance in small headwater reaches has frequently been evaluated in riparian forests subjected to intensive silvicultural practices (e.g., clear-cutting), with late-successional stands employed as controls (Boothroyd et al. 2004; England and Rosemond 2004; Kiffney et al. 2004). While between-reach (i.e., macrohabitat) variability in periphyton biomass as a function of light limitation has also been studied (Larned and Santos 2000), no studies have addressed the spatial variability of periphyton microhabitat as a function of within-reach variability in the light environment. While algal photosynthetic rates have been shown to vary under temporally heterogeneous light environments (Wellnitz and Rinne 1999), there is less information available pertaining to fine-scale spatial variability. Thus our research adds to previous work by examining the roles of specific stand structural elements in the spatial patterning of periphyton across a range of late-successional forest structural conditions. Understanding the relationships between forest stand development and forest–stream interactions is vital for promoting riparian forest management along headwater streams

Fig. 1. Map of study sites in the 2.5×10^6 ha Adirondack State Park in upstate New York, USA. The location of the park in New York State is shown in the inset, and the towns of Old Forge and Saranac Lake are included on the main map for reference. Site labels are locations (ALC, Adirondack League Club private reserve; FPW, Five Ponds state wilderness area; HPW, High Peaks state wilderness area; and PLW, Pigeon Lakes state wilderness area) followed by stand age class (M, mature; OG, old-growth).

(Gregory 1997; Naiman et al. 2005) because of the controlling influence of riparian forests on in-stream habitat conditions (Gregory et al. 1991; Keeton et al. 2007).

Methods

Study site

Our study was conducted in the Adirondack Mountains of upstate New York, USA ($44°N$, $74°W$; see Fig. 1). We evaluated 15 riparian sites representing a range of mature to old-growth forest structural conditions along low-order streams (bank-full width <10 m). In the southwestern Adirondacks, eight sites (six mature, two old-growth) were located on the 20 200 ha Adirondack League Club private reserve (ALC), one (mature) in the Pigeon Lakes state wilderness area (PLW), and three (one mature, two old-growth) in the Five Ponds state wilderness area (FPW). In the northern Adirondacks, three sites (all old-growth) were located in the High Peaks state wilderness area (HPW). The sites are described in Table 1. The mature, secondary forest sites were initiated following windthrow events or logging and, in some cases, slash-fueled fires in the late 19th and early 20th centuries (Ziegler 2000; Latty et al. 2004). We controlled for variability in management history by selecting mature sites with little or no logging since establishment. Old-growth sites were primary forests, having never been logged or burnt by historical fires. The dominant canopy species at these old-growth sites included *Betula alleghaniensis* Britton (yellow birch), *Fagus grandifolia* Ehrh. (American beech), *Picea rubens* Sarg. (red spruce), and *Tsuga canadensis* (L.) Carrière

Table 1. Descriptive information for the 15 sites in Adirondack State Park, New York, USA.

Site ID	Dominant tree age (years)	Basal area (m²/ha)	Stem density (no./ha)	Relative density	Biomass above ground (Mg/ha)	% of conifers†	ITDS	ISF	DSF
ALC-M-1*	81	22.6 (6.4)	586 (348)	4.42	140.4	18	0.74	0.12 (0.02)	0.08 (0.02)
ALC-M-2	106	26.3 (9.6)	680 (584)	4.64	146.9	13	1.37	0.15 (0.04)	0.11 (0.05)
ALC-M-3	114	28.7 (5.6)	674 (265)	4.74	145.0	19	0.65	0.12 (0.03)	0.09 (0.04)
ALC-M-5*	124	31.7 (5.3)	905 (597)	6.07	175.9	29	0.92	0.09 (0.03)	0.06 (0.02)
ALC-M-4*	132	34.8 (3.4)	850 (303)	6.50	194.0	32	1.24	0.13 (0.04)	0.09 (0.04)
PLW-M-1	144	31.8 (3.4)	826 (564)	5.16	134.4	61	0.66	0.21 (0.06)	0.14 (0.07)
FPW-M-1	145	33.3 (10.6)	1196 (922)	6.37	162.2	45	0.61	0.10 (0.05)	0.09 (0.05)
ALC-M-6*	148	27.9 (7.2)	1307 (819)	5.85	145.2	7	1.95	0.12 (0.03)	0.10 (0.02)
ALC-OG-1*	345	36.4 (9.9)	744 (409)	5.95	190.3	34	0.59	0.12 (0.06)	0.10 (0.05)
FPW-OG-2	254	33.7 (2.2)	1105 (676)	6.71	164.1	68	1.29	0.17 (0.07)	0.15 (0.08)
ALC-OG-2	270	39.2 (12.9)	976 (186)	6.68	190.9	50	0.54	0.10 (0.01)	0.09 (0.03)
HPW-OG-2*	280	36.7 (10.9)	974 (458)	6.95	200.3	75	1.09	0.09 (0.02)	0.06 (0.03)
HPW-OG-3*	280	40.6 (11.5)	844 (503)	7.12	202.3	69	1.16	0.12 (0.05)	0.10 (0.05)
HPW-OG-1*	300	46.2 (14.3)	680 (557)	8.01	247.3	29	0.93	0.13 (0.05)	0.10 (0.04)
FPW-OG-1	315	41.7 (5.3)	1919 (400)	5.89	198.0	44	1.13	0.08 (0.04)	0.07 (0.03)

Note: Variables are described in Table 2 and in the text. Standard deviations are shown in parentheses. Biomass includes only live trees, while other metrics include live and dead trees. Site labels are location (ALC, Adirondack League Club private reserve; FPW, Five Ponds state wilderness area; HPW, High Peaks state wilderness area; and PLW, Pigeon Lakes state wilderness area) followed by stand age class (M, mature; and OG, old-growth). ITDS, Index of Topography and Disturbance Susceptibility; ISF, proportion of indirect light transmitted through the canopy; DSF, proportion of direct light transmitted through the canopy.

*Sites were sampled for periphyton.
†By basal area.

(eastern hemlock), with minor components of *Acer rubrum* L. (red maple), *Acer saccharum* Marsh. (sugar maple), and *Abies balsamea* (L.) Mill. (balsam fir). At each site, we chose one 200–300 m stream reach for evaluating adjoining riparian forest structure and the associated in-stream light environment. These reaches were selected based on several criteria, including consistent and representative forest structure, minimal anthropogenic disturbances, such as roads or structures, and minimal inclusion of open or forested wetlands, tributaries, or cascades.

Data collection

Forest structural attributes for living and dead trees (>5 cm diameter at breast height (DBH)) were inventoried in 6 to 10 variable-radius (2.3 metric basal area factor) prism plots. These plots were evenly distributed between right and left banks and were randomly located within 30 m (i.e., approx. one site potential tree height) of the nearest stream channel edge. We used Impulse 200 laser rangefinders (Laser Technology, Englewood, Colorado, USA) to measure the height of trees in 50% of the plots. Increment borers were used to determine age at breast height for four to six of the larger canopy trees of either *B. alleghaniensis*, *P. rubens*, or *T. canadensis* at each site. Therefore, stand ages used in this study are weighted towards the maximum achieved in the dominant cohort. Age and field error estimation protocol are described in Keeton et al. (2007).

We used both categorical and continuous variables of age to assess our first hypothesis. Sites were classified into two age or structural classes: mature forest (eight sites) and old-growth (seven sites). Classification systems for late stand development stages in northern hardwood and mixed northern hardwood–conifer forests vary but generally rely on a combination of age, human-disturbance history, and structure (Dunwiddie et al. 1996; Hunter and White 1997). Our classifications incorporated (*i*) structural criteria, such as the density of live trees >50 cm DBH, which is a "large tree" threshold based on previous studies of old-growth northern hardwoods (e.g., McGee et al. 1999), and (*ii*) the average age of dominant trees. Our age criteria defined "mature" sites as dominated by canopy trees 80–150 years of age and "old-growth" sites as dominated by trees >150 years of age.

To measure the light environment over streams, we used digital hemispheric canopy photography. Hemispherical canopy photography is a well-established technique for developing long-term estimates of the ground level, below-canopy light environment using a single or several permanent records of the canopy (Canham et al. 1990; Easter and Spies 1994). Estimates produced by hemispheric canopy photography are typically reported either as site factors or as the proportion of direct (DSF), indirect (ISF), or global (GSF) light transmitted through the canopy. Additionally, an open-canopy metric describes the proportion of total pixels not occupied by canopy elements. Hemispherical photographs were taken over the center of the stream channel at 25 m intervals beginning from a random point of origin, using a digital camera with a fisheye lens. The camera was mounted on a tripod set as low (<1 m) over the water surface as possible. Photographs were taken on each reach between 28 June 2006 and 17 July 2006 during partially to fully overcast days at times when the sun was fully obscured

by cloud cover; however, it was not possible to photograph all sites under uniform overcast conditions because of their remote location. The photographs were automatically thresholded on the gray channel using Sidelook version 1.1 (Nobis 2005) and were visually inspected to ensure accuracy. The photographs were further post-processed with Hemiview canopy analysis software (Delta-T_Devices 1999) to calculate below-canopy light metrics (ISF, DSF, GSF).

Chlorophyll *a* concentration was chosen as an indicator of periphyton microhabitat distribution and was measured in 8 of 15 reaches. These eight reaches (four old-growth, four mature) were selected based on accessibility to ensure that chlorophyll *a* samples could be properly transported to the laboratory on ice. These reaches were representative of the full set of 15 reaches sampled for forest structure and light. On 5–6 July 2006 we placed unglazed clay disks (6.7 and 10.4 cm diameter for streams with lower discharge and higher discharge, respectively) at the center of the channel within these eight stream reaches at 25 m intervals, i.e., the same points at which hemispheric canopy photographs were taken. Channel class (pool, riffle, run) and substrate (gravel, cobble, boulder, organic debris) were recorded for each disk and included in later analyses to account for geomorphic variability in a microhabitat. Disks were not placed in water deeper than 35 cm. Disks remained in situ for 50 days and were removed on 24 August 2006. Of the 9–13 disks placed per stream (number dependant upon reach length), an average of 76% were successfully recovered and analyzed. Before removal, the water depth above each disk and the bank-full width at each disk were measured. The proportion of each disk's area covered in sediment or debris was visually estimated by dividing the disk's surface into quadrants, estimating the area covered by sediment, and averaging these estimates. The estimates of sedimentation were included as a variable in analyses of chlorophyll *a* concentration but were not used to adjust the chlorophyll *a* density on an aerial basis. Using a brush, the sediment covering each disk was scraped into a known volume of water and then filtered onto a glass microfiber filter, which was immediately frozen. The samples were later analyzed for chlorophyll *a* concentration using the procedure described in Lorenzen (1967).

Data analysis

We developed an Index of Topography and Disturbance Susceptibility (ITDS) that allowed us to assess the potential for physical blocking of light by the landscape and to incorporate some measure of relative wind disturbance susceptibility among our sites. Although the relationship between topography and small-scale (i.e., single tree) windthrow disturbance susceptibility has not been clearly established in the literature (Boose et al. 2001; Kramer et al. 2001), the various disturbance histories of late-successional forests play an important role in regulating stand-development rates and pathways (Franklin et al. 2002). We used ArcMap (ESRI, Redlands, California) to calculate the mean slope, standard deviation of slope, and percentage of the area that was convergent (i.e., concave) within a 50 m radius of each 200–300 m reach. Mean bank-full width was also included in the index. Because the relationship between topography and windthrow disturbance is not well established, the index

Table 2. Description of variables of riparian stand structure and below-canopy light environment used in Tables 3 and 4.

Variable	Short	Description
Indirect site factor	ISF	Proportion of diffuse light penetrating the canopy
Direct site factor	DSF	Ratio of direct light below the canopy to direct light above
Global site factor	GSF	Ratio of total light below the canopy to total light above
Open canopy	OC	Proportion of sky not obscured by canopy
Basal area	ba	Basal area of living and dead trees (m^2/ha)
SD of basal area	basd	Standard deviation of basal area of all trees (m^2/ha)
Biomass	bm	Aboveground biomass of live trees only (Mg/ha)
Stem density	d	Stem density of living and dead trees (no./ha)
SD of stem density	dsd	Standard deviation of stem density of all trees (no./ha)
Relative density	rd	Basal area / (Quadratic mean diameter)$^{1/2}$
Percent conifer	pc	Percentage of coniferous species by basal area (%)
Canopy height	ch	Mean height of dominant canopy trees (m)
Big tree density	bt	Density of living trees >50 cm DBH (no./ha)
Age (continuous)	age	Mean age of dominant canopy trees (years)
Age (categorical)	age	Old-growth or mature
ITDS	itds	Index of Topography and Disturbance Susceptibility

Note: The variables annotated with capital letters were derived from analysis of hemispherical canopy photographs taken over the stream center, while those annotated with lowercase letters were gathered from 6 to 10 sample plots per site located within 30 m of the stream bank.

was calculated by standardizing each of the four variables across all sites and then averaging them to yield a relative comparison of our sites. A higher score (>1) indicates a relatively steep, hilly site with a wider stream and a higher percentage of convergent, seep-prone area, which may be factors that may increase susceptibility to windthrow (Kramer et al. 2001). A lower score (<1) indicates the converse of all these trends and may correspond to a decreased susceptibility to windthrow.

Forest structure metrics (see Table 2) were generated in the Northeast Ecosystem Management Decision Model (NED-2, Twery et al. 2005), which included an estimate of aboveground biomass based on species-specific allometric equations. Relative density calculations followed Curtis (1982). Forest structure metrics and the ITDS were used as independent variables in multivariate analyses of the effects of forest structure and site characteristics on light availability over streams ($n = 15$). We examined 10 independent variables, including nine forest structure metrics representing a range of structural attributes plus the ITDS (Table 2).

Akaike information criteria for small sample sizes (AIC_c) was used to select models of site factor means and standard deviations as a function of forest structure and the ITDS. AIC allows for all models in a model set to be objectively ranked and compared based on their maximized log-likelihood and a bias correction applied as a function of the number of model parameters (Burnham and Anderson 2002). This bias correction will account for correlated variables by penalizing a model with additional variables added that contribute little new information (i.e., are highly correlated to terms already in the model). AIC_c models were compared against the best model using Δ_i scores ($\Delta_i = AIC_{c,i} - AIC_{c,min}$); model weights and adjusted R^2 values were also calculated for interpretation. We used a threshold of $\Delta_i < 4$ to select best model sets. While AIC is most often used to compare an a priori set of models developed from hypotheses, we employed it as a technique to compare the

full possible set of model combinations for our 10 independent variables. Although this technique is inappropriate if used to generate predictive models (e.g., overfitting to sample population), we employed it strictly to explore which variables of stand structure might have the greatest influence on the below-canopy light environment.
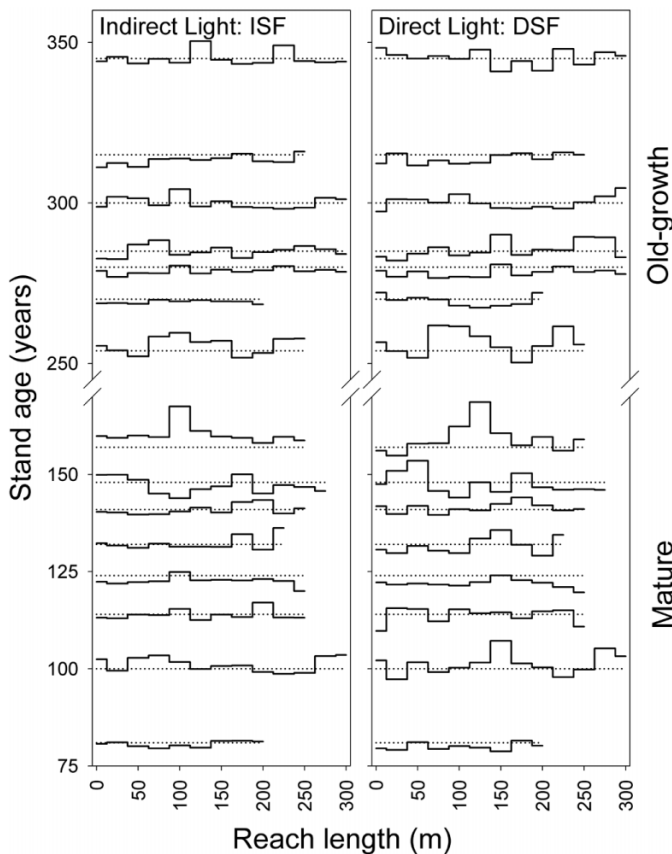
Analyses of the relationship between paired hemispherical photographs and chlorophyll a density were performed in SAS 9.2 (SAS Institute Inc. 2008), using PROC GLIMMIX with stream included as a random effect. The sample size for this portion of the analysis was 72 paired light and chlorophyll measurements from eight streams. The same procedure was employed to test the effect of stand age on the below-canopy light environment means and standard deviations ($n = 15$) and chlorophyll a density ($n = 72$) using both categorical (old-growth, mature) and continuous (age in years) independent variables.

Results

Age, light, and periphyton

Results did not support the first research hypothesis that mature and old-growth forests differ in their below-canopy light environments, which could create different distributions of periphyton microhabitat. No statistically significant relationships were found between stand age (as either a categorical or continuous variable) and any metric of the below-canopy light environment or chlorophyll a density. However, a large degree of spatial variability was found in the below-canopy light environment among all of these late-successional reaches. Figure 2 clearly shows the variability in the below-canopy light environment along each reach relative to the mean of all reaches, with no clear trend in variability due to age. Both mature and old-growth stands created a spatially variable below-canopy light environment over the stream, although the extent of variability differed from stream to stream.

Fig. 2. Indirect (ISF) and direct (DSF) light variability along streams in late-successional stands with a range of ages in Adirondack State Park (New York, USA). Each solid line represents the light environment varying spatially along the length of a reach. For comparison, the dotted line located along the *y* axis at the mean age of each reach represents the mean light level for all 15 reaches (ISF = 0.124, DSF = 0.095). The solid line falling above the corresponding dotted line indicates more light transmitted through the canopy, while the solid line falling below the dotted line shows an area along the reach were less light was transmitted. Note that both mature and old-growth stands produce variable below-canopy light environments over low-order streams and that there is substantial variability between reaches. Some reach ages have been adjusted ±5% for clarity of the figure, although age rank is correct.

Forest structure and light

Whereas age among late-successional stands does not predict light availability over streams at our sites, multivariate models of stand structure metrics were highly predictive of both the mean and variability of the below-canopy light environment at a reach scale. Tables 3 and 4 show the best models of both standard deviations and means of four different below-canopy light metrics as ranked by AIC$_c$. Adjusted R^2 statistics for these models all exceed 0.71 for the standard deviation of the four light metrics and 0.59 for the means, indicating that a large proportion of the variance in both mean intensity and variability of below-canopy light is explained by the structural characteristics of these late-successional riparian stands.

Basal area, relative density, and the ITDS appeared in most of the best models predicting mean below-canopy light over these streams based on stand structure. While the per-

centage of coniferous basal area and the standard deviation of basal area were included in most models of diffuse light (ISF) and open canopy (OC), aboveground biomass was included in models of direct light (DSF) and total light (GSF). Total biomass appears to be more important in the transmittance of direct light, while conifers and variability in basal area seem to be more important in regulating the transmittance of diffuse light. Overall, these models reveal that when data are aggregated by site, a large proportion of variance in the mean transmitted light is explained by measures of horizontal forest structure (i.e., patchiness or gapiness), topography, and possibly by windthrow susceptibility, based on inclusion of the ITDS.

Variability in stand structure, specifically basal area standard deviation and stem density standard deviation, was included in all models of variability in below-canopy light as shown in Table 3. This variability indicates that the heterogeneous stand structure created a heterogeneous below-canopy light environment. While standard deviations typically exhibit a positive correlation to the magnitude of the mean, in this instance, the standard deviation of stem density was not correlated ($R^2 = 0.07$, $p = 0.35$) to stem density. Basal area displayed only a weak relationship to its standard deviation ($R^2 = 0.21$, $p = 0.08$). Thus, these models appear to represent a true horizontal stand structural heterogeneity and are not merely a by-product of the magnitude of mean stem density and basal area in each stand.

Light and periphyton

Our second hypothesis, i.e., that the site-specific light distribution over streams correlates with periphyton microhabitat distribution, was supported by the data depicted in Fig. 3. While no clear relationship was evident between stand age and chlorophyll *a* density (see Fig. 4), all four light metrics significantly ($p < 0.10$; Fig. 3) explained a small proportion of variance in chlorophyll *a* density. Chlorophyll *a* was positively correlated with all four metrics of light, indicating that high-light locations within these stream reaches are more favorable periphyton microhabitats than low-light locations. The models and *p* values depicted in Fig. 3 were derived using a mixed model method, with stream included as a random variable. However, no consistently applied and agreed upon R^2 statistics are currently available for mixed models, so those presented were calculated using a generalized linear model (PROC GLM) without stream included as a random effect. Thus, these R^2 values do not account for the full error structure or variance that may be associated with between-stream rather than within-stream effects.

Averaged across all study reaches, high diffuse light (ISF $\geq$ 0.15) patches exhibited a 3.0 times higher concentration of chlorophyll *a* compared with low diffuse light (ISF < 0.15) patches. High direct light (DSF $\geq$ 0.15) patches had a 2.3 times higher concentration of chlorophyll *a* than low direct light patches, and high total light (GSF $\geq$ 0.15) patches had a chlorophyll *a* concentration 2.9 times higher than total light patches. More open canopied patches (OC $\geq$ 10%) showed 2.0 times the chlorophyll *a* density versus closed canopied patches (OC < 10%).

The percentage of disk sedimentation, depth to disk, bank-full width, substrate (e.g., gravel, boulder, organic debris), and channel class (e.g., pool, riffle, run) were initially

Table 3. Best models ($\Delta_i < 4.0$) predicting variability in below-canopy light based on stand structure and the Index of Topography and Disturbance Susceptibility.

Rank	Model*	ba	basd	bm	d	dsd	rd	ch	itds	bt	pc	AIC$_c$	Δ_i	w_i	Adj. R^2
1	ISF SD	+	−			+	−	+				−136.54	0.00	0.32	0.78
2	ISF SD	+	−			+	−					−135.39	1.16	0.18	0.71
3	ISF SD	+	−			+	−	+			−	−133.63	2.92	0.07	0.80
4	ISF SD	+	−	−	−	+		+				−133.18	3.37	0.06	0.79
1	DSF SD	+	−	−	−	+		+				−131.30	0.00	0.42	0.81
1	GSF SD	+	−	−	−	+		+				−132.86	0.00	0.46	0.81
1	OC SD	+	−			+	−	+			−	−158.44	0.00	0.32	0.87
2	OC SD	+	−	−	−	+		+				−157.72	0.72	0.23	0.86
3	OC SD	+	−			+	−	+				−156.64	1.79	0.13	0.81
4	OC SD	+	−			+	−					−154.76	3.68	0.05	0.73

*Models are of standard deviations of diffuse light (ISF), direct light (DSF), total light (GSF), and open canopy (OC) measured over the stream center and averaged by reach for 15 streams in Adirondack State Park (New York, USA).

†Correlation is indicated as positive (+) or negative (–) for each variable included in each model. Abbreviations for variables are defined in Table 1.

Table 4. Best models ($\Delta_i < 4.0$) predicting mean below-canopy light based on stand structure and the Index of Topography and Disturbance Susceptibility.

Rank	Model*	ba	basd	bm	d	dsd	rd	ch	itds	bt	pc	AIC$_c$	Δ_i	w_i	Adj. R^2
1	ISF	+	−		+		−		+		+	−114.30	0.00	0.18	0.83
2	ISF	+	−				−		+		+	−112.97	1.33	0.09	0.75
3	ISF	+	−	−			−		+		+	−112.87	1.42	0.09	0.81
4	ISF		−				−		+		+	−111.82	2.47	0.05	0.67
5	ISF	+	−		+		−		+		+	−111.33	2.96	0.04	0.79
6	ISF	+	−	−	−		−		+			−111.16	3.13	0.04	0.72
7	ISF	+	−						+	−	+	−110.96	3.33	0.03	0.78
8	ISF		−				−	+	+		+	−110.94	3.36	0.03	0.71
9	ISF	+	−		+		−		+	−	+	−110.46	3.84	0.03	0.84
1	DSF	+		−			−		+			−120.39	0.00	0.34	0.68
2	DSF	+		−	+		−		+			−116.89	3.50	0.06	0.67
3	DSF	+	−	−			−		+			−116.73	3.66	0.05	0.67
4	DSF	+		−	−				+			−116.63	3.76	0.05	0.59
1	GSF	+		−			−		+			−119.85	0.00	0.30	0.69
2	GSF	+	−	−			−		+			−116.95	2.89	0.07	0.69
3	GSF	+		−	−				+			−116.59	3.26	0.06	0.62
4	GSF	+		−	+		−		+			−116.18	3.67	0.05	0.68
5	GSF	+		−			−		+	−		−115.90	3.95	0.04	0.67
6	GSF	+		−			−		+		+	−115.86	3.98	0.04	0.67
1	OC	+	−		+		−		+		+	−133.73	0.00	0.17	0.83
2	OC	+	−				−		+		+	−132.96	0.78	0.12	0.77
3	OC	+	−	−			−		+		+	−131.98	1.76	0.07	0.81
4	OC	+	−				−		+	−	+	−131.44	2.29	0.05	0.81
5	OC		−				−	+	+		+	−131.22	2.52	0.05	0.74
6	OC		−				−		+		+	−131.15	2.59	0.05	0.68

*Models are of reach-level means of diffuse light (ISF), direct light (DSF), total light (GSF), and open canopy (OC) measured over the stream center for 15 streams in Adirondack State Park (New York, USA).

†Correlation is indicated as positive (+) or negative (–) for each variable included in each model. Abbreviations for variables are defined in Table 1.

included in models of the light environment's effects on chlorophyll *a* density both individually and in all possible combinations, but these features were later removed based upon (1) reduced support for the models based on ΔAIC$_c$ scores, (2) nonsignificant *p* values, and (3) a lack of substantial improvement in *p* values of the light metrics. The lack of significance of these variables was likely due to the relatively narrow range of each variable across all disks (e.g., depth ranged from 1 to 35 cm) and the inclusion of stream as a random effect within all models.

Discussion

Late-successional riparian forests are more structurally complex than younger northern hardwood–conifer forests (Keeton et al. 2007). Our findings suggest that gap mosaics

Fig. 3. Regressions of chlorophyll *a* density versus metrics of below-canopy light from 73 samples distributed across eight streams in Adirondack State Park (New York, USA). Samples are from streams in old-growth stands (●) and mature stands (▲). Models and *p* values include stream as a random effect. Coefficients of determination were calculated without stream as a random effect and, thus, are approximations that do not represent the full model structure or variance.
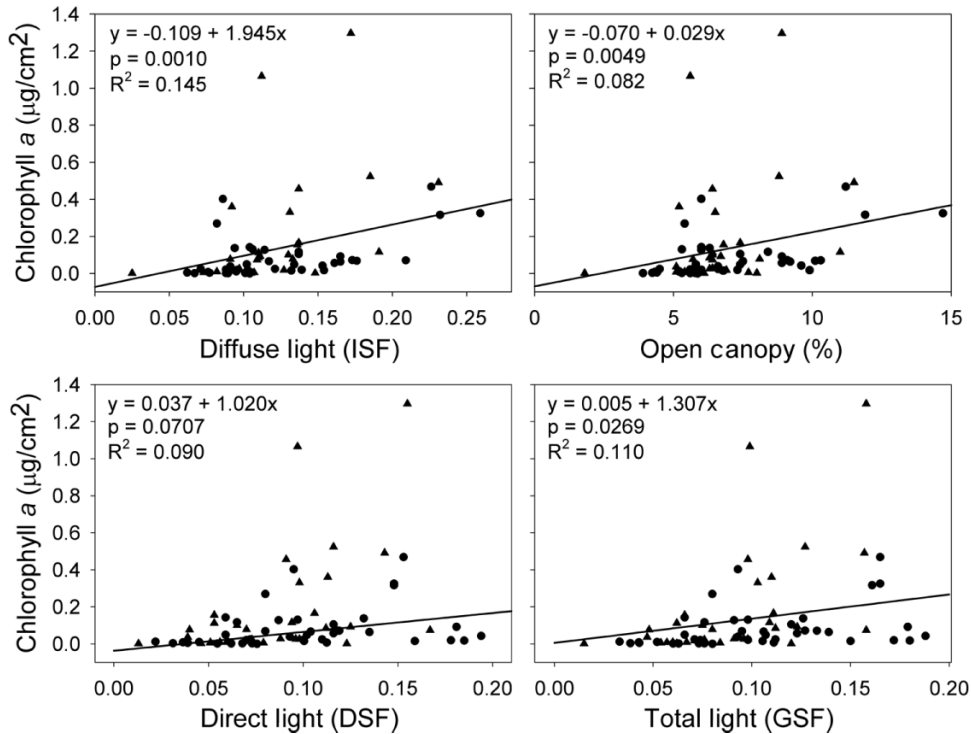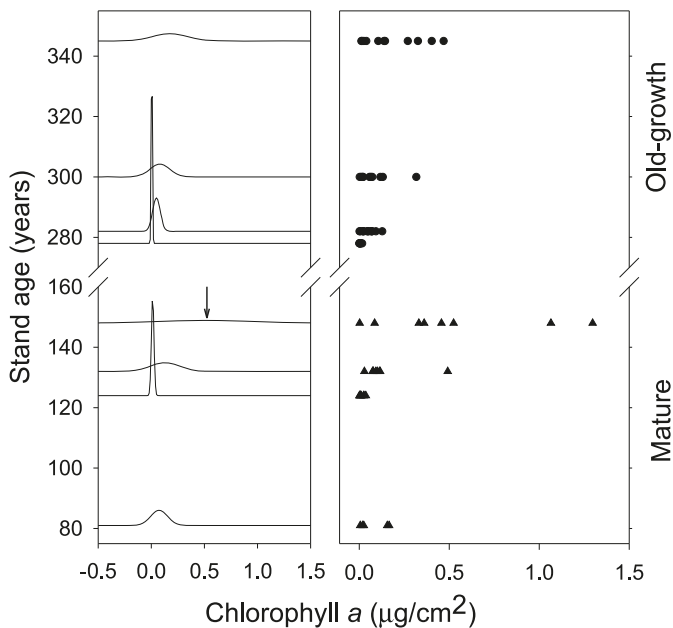

Fig. 4. Chlorophyll *a* density as sampled from eight different reaches within a range of late-successional forest ages in Adirondack State Park (New York, USA). The right panel shows individual data points, while the left panel depicts normal distributions parameterized by the same data to better view variability in the data. The arrow indicates the mean of the broad (i.e., highly variable) distribution for site ALC-M-6, age = 148 years (see Table 1 for site description). Note the differences between streams in the variability of apparent periphyton microhabitat distribution.

and horizontal stand structural complexity create a heterogeneous light environment, resulting in fine-scale periphyton spatial dynamics that may differ from younger stands with a more uniform (i.e., fewer gaps) closed canopy over low-order streams. Gap dynamics in late-successional temperate forests are spatially and temporally dynamic (Runkle 1982); and on-going research has found that gaps are abundant, relatively large (e.g., caused by single or multiple tree deaths), and well distributed along the old-growth stream reaches we studied (Curzon and Keeton 2009). Forest influences on light availability and the associated distribution of in-stream periphyton appear to mirror this spatial heterogeneity. This conclusion adds a new layer of complexity to conceptual frameworks describing stream ecosystems, in that some forest–stream interactions in low-order streams should be viewed as dynamic with respect to late-successional forests and interactions with canopy gap disturbances.

Our conclusion is based on several lines of evidence. Late-successional riparian forest structure was strongly correlated with both mean the below-canopy light levels and the spatial variability in light availability over constituent streams. These relationships were established by combining variables of stand structure with the ITDS in models predicting the mean and standard deviation of ISF, DSF, and GSF. A small (8.2%–14.5%) but statistically significant proportion of the variance in chlorophyll *a* concentration was predicted by these same below-canopy light metrics. We recognize, however, that light may not have been the only limiting resource in our streams. Including stream as a random effect in these models incorporated between-stream covariates that

were not evaluated as predictors of chlorophyll *a* concentrations (e.g., differences in grazers, nitrogen, phosphorus, or pH levels). All disks were placed in a similar range of hydrological environments, and variables accounting for differences in hydrological environment (bank-full width, substrate beneath disk, channel class, water depth) were not found to improve model performance.

These results point to a heretofore unrecognized but potentially important forest–stream interaction. Because late-successional forests transmit low levels of light at whole-reach scales (Canham et al. 1990; Easter and Spies 1994), light is likely the primary limiting resource in many low-order streams within these forests (Hill et al. 1995; Bernhardt and Likens 2004; Greenwood and Rosemond 2005). Our results and previous research demonstrate that a complex late-successional, temperate forest canopy structure produces a spatially complex below-canopy light environment at fine (e.g., 25 m) scales (Van Pelt and Franklin 2000; Montgomery and Chazdon 2001). The increased frequency and size of canopy gaps found in late-successional stands is a likely causal mechanism explaining the variable below-canopy light environment (Dahir and Lorimer 1996). Thus, low-order streams within late-successional Adirondack forests provide microhabitats conducive to both high and low autotrophic abundance at fine, within-reach scales.

Forest structure and below-canopy light

Relationships between stand age and structure (Franklin et al. 2002), such as development of complex horizontal structure and patch mosaics (Tyrrell and Crow 1994; Dahir and Lorimer 1996; Ziegler 2000), indicate how riparian forest structure influences the light environment associated with streams. Previous work at our study sites found that although these stands developed distinct structural traits as age increased (e.g., greater basal area and biomass), the relationship between structure and age was variable from site to site and was best considered in the context of multiple independent continuous metrics of forest structure (Keeton et al. 2007). Individual sites may follow different stand development pathways and rates, which in northern temperate forests are commonly mediated by frequent low-intensity wind disturbance events, less frequent high-intensity wind disturbance events, and moderate intensity ice storms (Seymour et al. 2002; Millward and Kraft 2004). This may be one reason why stand age (as assessed using dominant tree age) was not a significant predictor of light, by contrast with the significant influence of stand structure.

Previous research in other forest stands supports our finding of great spatial variability in below-canopy light along stream reaches in late-successional forests. Vertically differentiated canopies, high leaf area index, high aboveground biomass levels, and a predominance of shade-tolerant species all contribute to lower below-canopy light levels relative to younger stands in temperate late-successional forests (Canham et al. 1994; Van Pelt and Franklin 2000). While the total and mean amount of light transmitted below the canopy decreases as stands move into a late-successional condition, spatial variability in below-canopy light increases with gap disturbances and associated horizontal structural diversification typical of late-successional temperate forests (Montgomery and Chazdon 2001; Franklin et al. 2002).

Canopy gaps result not only in higher light levels directly beneath the canopy openings but also in adjacent closed-canopy patches to the north of gaps (in the northern hemisphere) that are illuminated by low angle sunlight common at high latitudes (Canham et al. 1990). The spatial offset of light availability below the canopy as a result of both canopy height and latitude is important when considering the scale of the canopy gap's influence on the spatial patterning of light transmission throughout the stand (Van Pelt and Franklin 2000). We infer that horizontal complexity in stand structure is directly related to spatial variability in the light availability over streams based on our top-ranked AIC_c models of the standard deviations of below-canopy light metrics. These models included covariates, such as the standard deviations of stem density and basal area, which are strongly indicative of horizontal variation in stand structure, including patchiness or gapiness (Franklin and Van Pelt 2004; Keeton et al. 2007).

Other site-level factors besides stand structure, such as topography, are important when predicting below-canopy mean and total light availability or its spatial variability. The inclusion of the ITDS, representing an indirect indicator of site differences reflecting disturbance susceptibility, improved AIC_c model fit when compared with models predicting mean light transmittance only from forest structure. Portions of the Adirondack region, including our study areas, are characterized by steep mountainous terrain. This topography can influence light availability over streams because of the physical obstruction of light by the terrain. Additionally, some sites may be more susceptible to wind disturbances because of steep topography with relatively thinner soils, extensive convergent areas with greater soil moisture content, or valleys that are oriented parallel to the predominant weather patterns (Kramer et al. 2001). This may result in the development of greater structural horizontal heterogeneity, which causes spatial variability in light over streams.

Light and periphyton

Our findings demonstrate that horizontal heterogeneity in late-successional riparian forest structure correlates with spatial variability in the distribution of autotrophic microhabitats in low-order streams. We infer this relationship from (1) the strong correlation between multivariate models of below-canopy light metric standard deviations as a function of variability in forest structure and (2) the correlation we found between mixed-effects models of chlorophyll *a* concentration as a function of these light metrics. This inference is similar to results previously reported for artificial stream channels (Bourassa and Cattaneo 2000). Our artificial substrates remained in situ for 50 days, thus our measures of chlorophyll *a* concentration integrate any increases — and any possible losses of chlorophyll — during that period. Increases in chlorophyll *a* density in high light environments (high ISF = 3.0×, high DSF = 2.3×, high GSF = 2.9× relative to low light environments) were similar in magnitude to those observed for periphyton abundance in artificial stream channels subjected to high and low light (4 increase in high light) (Wellnitz and Ward 1998). Our observed chlorophyll *a* values (old-growth mean: 0.083 $\mu g/cm^2$; mature mean: 0.072 $\mu g/cm^2$) were greater than summer chlorophyll *a* val-

ues reported for a stream located in a mature stand in New Hampshire (0.001 µg/cm²) (Bernhardt and Likens 2004) but lower than summer values reported from streams in western North Carolina (0.55 µg/cm²) (Greenwood and Rosemond 2005).

It is important to note that we cannot conclude that these streams were strictly light limited, as we did not measure other factors limiting periphyton biomass production, such as nutrient concentrations or potential losses due to grazing pressure or scouring. Nevertheless, light limitation of periphyton in our streams is consistent with the results of previous studies. Diminished light transmittance limits photosynthesis by periphyton and is common during summer in low-order streams in temperate deciduous forests (Bourassa and Cattaneo 2000). Much of the previous research on this topic involves comparisons between leaf-off and leaf-on conditions (Hill and Dimick 2002), experimental manipulation of the light environment (Bourassa and Cattaneo 2000), or comparisons between clearcut streams and those with riparian forests or buffers (Boothroyd et al. 2004; Kiffney et al. 2004). Our research augments these previous studies by more thoroughly evaluating the influence of forest structure, which is typically ignored in stream studies that simply reflect the presence or absence of riparian forest or leaves. We specifically addressed within-reach variability in microhabitat availability by using many (9–13) paired light and chlorophyll *a* concentration measurements at sites within each reach across a substantial) number (eight) of stream reaches. Additionally, by quantifying riparian forest structure we related specific aspects of late-successional riparian forest structure (i.e., relative density, stem density, standard deviation of stem density) to the relative abundance of periphyton in microhabitat patches.

The inclusion of stream as a random effect in our models, while not a direct measurement of ambient nitrogen and phosphorous concentrations, provides an indirect indicator of ecological variability among our study streams. The literature supports our assumption that autotrophic production in small headwater streams is limited primarily by light (Bourassa and Cattaneo 2000; Rosemond et al. 2000). However, nitrogen or phosphorus limitation can be an important factor constraining autotrophic production, even in heavily shaded streams (Greenwood and Rosemond 2005). While numerous studies have found that the addition of nitrogen or phosphorus does not result in long-term significant increases in periphyton production in low-order reaches (Bernhardt and Likens 2004; Greenwood and Rosemond 2005), these results were not obtained from streams within late-successional temperate forests.

While we did not assess autotrophic production or nutrient availability, based upon our results on microhabitat distribution, we speculate that autotrophic production in late-successional streams may be nutrient limited in high-light patches. This would contrast with heavily shaded locations where productivity may be light limited. It is possible that streams in late-successional temperate forests include locations with greater overall levels of autotrophic production relative to younger riparian forests, although we did not test this. Future research seems warranted to investigate whether microhabitat heterogeneity may result in greater reach-scale productivity in streams flowing through older forests. We are aware of no previous studies that have evaluated the within-reach spatial variability in light availability in streams and the effects on either the fine-scale patterning of autotrophic abundance or the contribution to reach-scale autotrophic production.

Conclusion and management implications

Overall, our results establish the importance of considering light as a spatially variable limiting resource at fine, within-reach scales in late-successional forests. Furthermore, these results suggest that the influence of stand development processes, including fine-scaled canopy gap disturbances, on light availability is an important aspect of forest–stream interactions in low-order streams that has previously received little attention. Conceptual models describing forest–stream interactions would be strengthened through explicit recognition of the dynamic nature of forest stand structure and associated riparian influences. Conclusions derived from our results are applicable to forests that are characterized by fine-scale gap disturbances, such as those of the northeastern United States. However, forests experiencing stand-replacing disturbances (e.g., boreal forests) may display forest–stream interactions unlike those we observed.

Riparian forest management is of great interest to watershed managers (Gregory 1997), yet management standards and practices vary widely (Lee et al. 2004). Riparian areas provide unique habitats for both terrestrial and aquatic biota, have controlling influences on in-stream processes, and are generally sensitive in terms of susceptibility to human disturbance (Naiman et al. 2005). Consequently managers are interested in developing riparian management practices that maintain and even enhance riparian forest functionality. Management approaches promoting the development of late-successional forest structure, including variably sized gaps, could provide a diverse array of in-stream light regimes and associated habitat conditions. Alternatives include establishment of passively managed riparian reserves (or buffers) where late-successional characteristics are allowed to develop (FEMAT 1993). Gap-based (e.g., small group selection, see Seymour et al. 2002) and restorative silvicultural systems (Berg 1995; Keeton 2006) offer additional options for promoting late-successional characteristics where low-impact timber harvesting is deemed appropriate within riparian areas. However, active management options would need to be evaluated very carefully due to the highly sensitive nature of riparian areas, which in many cases leads, appropriately in our view, to delineation of no-harvest areas closest to streams.

References

Berg, D.R. 1995. Riparian silvicultural system-design and assessment in the Pacific-Northwest Cascade Mountains, USA. Ecol. Appl. **5**(1): 87–96. doi:10.2307/1942054.

Bernhardt, E.S., and Likens, G.E. 2004. Controls on periphyton biomass in heterotrophic streams. Freshw. Biol. **49**(1): 14–27. doi:10.1046/j.1365-2426.2003.01161.x.

Boose, E., Chamberlin, K., and Foster, D. 2001. Landscape and regional impacts of hurricanes in New England. Ecol. Monogr. **71**(1): 27–48.

Boothroyd, I.K.G., Quinn, J.M., Langer, E.R.L., Costley, K.J., and Steward, G. 2004. Riparian buffers mitigate effects of pine plantation logging on New Zealand streams: 1. Riparian vegetation structure, stream geomorphology and periphyton. For. Ecol. Manage. **194**(1–3): 199–213. doi:10.1016/j.foreco.2004.02.018.

Bourassa, N., and Cattaneo, A. 2000. Responses of a lake outlet community to light and nutrient manipulation: effects on periphyton and invertebrate biomass and composition. Freshw. Biol. **44**(4): 629–639. doi:10.1046/j.1365-2427.2000.00610.x.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information–theoretic approach. 2nd ed. Springer, New York.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. **20**(5): 620–631. doi:10.1139/x90-084.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**(2): 337–349. doi:10.1139/x94-046.

Curtis, R.O. 1982. A simple index of stand density for Douglas-fir. For. Sci. **28**(1): 92–94.

Curzon, M.T., and Keeton, W.S. 2009. Spatial characteristics of canopy disturbances in riparian old-growth hemlock-northern hardwood forests, Adirondack Mountains, New York, USA. Can. J. For. Res. In press.

Dahir, S.E., and Lorimer, C.G. 1996. Variation in canopy gap formation among developmental stages of northern hardwood stands. Can. J. For. Res. **26**(10): 1875–1892. doi:10.1139/x26-212.

Delta-T_Devices. 1999. HemiView Canopy Analysis Software. Version 2.1 SR1. Cambridge, England.

Dunwiddie, P., Foster, D.R., Leopold, D.J., and Leverett, R.T. 1996. Old-growth forests of southern New England, New York, and Pennsylvania. *In* Eastern old-growth forests: prospects for rediscovery and recovery. *Edited by* M.B. Davis. Island Press, Washington, D.C. pp. 126–143.

Easter, M.J., and Spies, T.A. 1994. Using hemispherical photography for estimating photosynthetic photon flux density under canopies and in gaps in Douglas-fir forests of the Pacific Northwest. Can. J. For. Res. **24**(10): 2050–2058. doi:10.1139/x94-263.

England, L., and Rosemond, A. 2004. Small reductions in forest cover weaken terrestrial–aquatic linkages in headwater streams. Freshw. Biol. **49**(6): 721–734. doi:10.1111/j.1365-2427.2004.01219.x.

FEMAT. 1993. Forest ecosystem management: an ecological, economic, and social assessment. USDA Forest Service, USDI Bureau of Land Management, Government Printing Office, Washington, D.C., USA.

Feminella, J.W., Power, M.E., and Resh, V.H. 1989. Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. Freshw. Biol. **22**(3): 445–457. doi:10.1111/j.1365-2427.1989.tb01117.x.

Franklin, J.F., and Van Pelt, R. 2004. Spatial aspects of structural complexity in old-growth forests. J. For. **102**(3): 22–28.

Franklin, J.F., Spies, T.A., Pelt, R.V., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**(1-3): 399–423. doi:10.1016/S0378-1127(01)00575-8.

Greenwood, J.L., and Rosemond, A.D. 2005. Periphyton response to long-term nutrient enrichment in a shaded headwater stream. Can. J. Fish. Aquat. Sci. **62**(9): 2033–2045. doi:10.1139/f05-117.

Gregory, S.V. 1997. Riparian management in the 21st century. *In* Creating a forestry for the 21st century. *Edited by* K.A. Kohm and J.F. Franklin. Island Press, Washington, D.C., USA. pp. 69–86.

Gregory, S.V., Swanson, F.J., McKee, W.A., and Cummins, K.W. 1991. An ecosystem perspective of riparian zones. Bioscience, **41**(8): 540–551. doi:10.2307/1311607.

Hill, W.R., and Dimick, S.M. 2002. Effects of riparian leaf dynamics on periphyton photosynthesis and light utilisation efficiency. Freshw. Biol. **47**(7): 1245–1256. doi:10.1046/j.1365-2427.2002.00837.x.

Hill, W.R., Ryon, M.G., and Schilling, E.M. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology, **76**(4): 1297–1309. doi:10.2307/1940936.

Hunter, M.L., and White, A.S. 1997. Ecological thresholds and the definition of old-growth forest stands. Nat. Areas J. **17**(4): 292–296.

Keeton, W.S. 2006. Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. For. Ecol. Manage. **235**(1–3): 129–142. doi:10.1016/j.foreco.2006.08.005.

Keeton, W.S., Kraft, C.E., and Warren, D.R. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecol. Appl. **17**(3): 852–868. doi:10.1890/06-1172. PMID:17494402.

Kiffney, P.M., Richardson, J.S., and Bull, J.P. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. J.N. Am. Benthol. Soc. **23**(3): 542–555. doi:10.1899/0887-3593(2004)023<0542:ELAACM>2.0.CO;2.

Kramer, M.G., Hansen, A.J., Taper, M.L., and Kissinger, E.J. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology, **82**(10): 2749–2768.

Larned, S.T., and Santos, S.R. 2000. Light- and nutrient-limited periphyton in low order streams of Oahu, Hawaii. Hydrobiologia, **432**(1/3): 101–111. doi:10.1023/A:1004074004416.

Latty, E.F., Canham, C.D., and Marks, P.L. 2004. The effects of land-use history on soil properties and nutrient dynamics in Northern hardwood forests of the Adirondack Mountains. Ecosystems (N.Y., Print), **7**(2): 193–207. doi:10.1007/s10021-003-0157-5.

Lee, P., Smyth, C., and Boutin, S. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. J. Environ. Manage. **70**(2): 165–180. doi:10.1016/j.jenvman.2003.11.009. PMID:15160742.

Lorenzen, C.J. 1967. Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol. Oceanogr. **12**(2): 343–346.

McGee, G.G., Leopold, D.J., and Nyland, R.D. 1999. Structural characteristics of old-growth, maturing, and partially cut northern hardwood forests. Ecol. Appl. **9**(4): 1316–1329. doi:10.1890/1051-0761(1999)009[1316:SCOOGM]2.0.CO;2.

McNeely, C., Finlay, J.C., and Power, M.E. 2007. Grazer traits, competition, and carbon sources to a headwater-stream food web. Ecology, **88**(2): 391–401. doi:10.1890/0012-9658(2007)88[391:GTCACS]2.0.CO;2. PMID:17479757.

Millward, A.A., and Kraft, C.E. 2004. Physical influences of landscape on a large-extent ecological disturbance: the northeastern North American ice storm of 1998. Landsc. Ecol. **19**(1): 99–111. doi:10.1023/B:LAND.0000018369.41798.2f.

Montgomery, D.R. 1999. Process domains and the river continuum. J. Am. Water Resour. Assoc. **35**(2): 397–410. doi:10.1111/j.1752-1688.1999.tb03598.x.

Montgomery, R.A., and Chazdon, R.L. 2001. Forest structure, canopy architecture, and light transmittance in tropical wet forests. Ecology, **82**: 2707–2718.

Naiman, R.J., Fetherston, K.L., McKay, S.J., and Chen, J. 1998. Riparian forests. *In* River ecology and management: lessons from the Pacific costal ecoregion. *Edited by* R.J. Naiman and R.E. Bilby. Springer, New York. pp. 289–323.

Naiman, R.J., Decamps, H., and McClain, M.E. 2005. Riparia: ecology, conservation, and management of streamside communities. Elsevier/Academic Press, San Diego, Calif., USA.

Nobis, M. 2005. Sidelook 1.1 — imaging software for the analysis of vegetation structure with true-colour photographs. Available from www.appleco.ch [accessed 21 August 2006].

Pickett, S.T.A., and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Inc., New York.

Rosemond, A., Mulholland, P., and Brawley, S. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. Can. J. Fish. Aquat. Sci. **57**(1): 66–75. doi:10.1139/cjfas-57-1-66.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of Eastern North America. Ecology, **63**(5): 1533–1546. doi:10.2307/1938878.

SAS Institute Inc. 2008. SAS version 9.2 [computer program]. SAS Institute Inc., Cary, N.C., USA.

Seymour, R.S., White, A.S., and deMaynadier, P.G. 2002. Natural disturbance regimes in northeastern North America — evaluating silvicultural systems using natural scales and frequencies. For. Ecol. Manage. **155**(1-3): 357–367. doi:10.1016/S0378-1127(01)00572-2.

Thorp, J.H., Thoms, M.C., and Delong, M.D. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. River Res. Appl. **22**(2): 123–147. doi:10.1002/rra.901.

Townsend, C.R. 1989. The patch dynamics concept of stream community ecology. J. N. Am. Benthol. Soc. **8**(1): 36–50. doi:10.2307/1467400.

Twery, M.J., Knopp, P.D., Thomasma, S.A., Rauscher, H.M., Nute, D.E., Potter, W.D., Maier, F., Wang, J., Dass, M., Uchiyama, H., Glende, A., and Hoffman, R.E. 2005. NED-2: a decision support system for integrated forest ecosystem management. Comput. Electron. Agric. **49**(1): 24–43. doi:10.1016/j.compag.2005.03.001.

Tyrrell, L.E., and Crow, T.R. 1994. Structural characteristics of old-growth hemlock–hardwood forests in relation to age. Ecology, **75**(2): 370–386. doi:10.2307/1939541.

Van Pelt, R., and Franklin, J.F. 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. Can. J. For. Res. **30**(8): 1231–1245. doi:10.1139/cjfr-30-8-1231.

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., and Cushing, C.E. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. **37**(1): 130–137. doi:10.1139/f80-017.

Wellnitz, T., and Rinne, B. 1999. Photosynthetic response of stream periphyton to fluctuating light regimes. J. Phycol. **35**(4): 667–672. doi:10.1046/j.1529-8817.1999.3540667.x.

Wellnitz, T.A., and Ward, J.V. 1998. Does light intensity modify the effect mayfly grazers have on periphyton? Freshw. Biol. **39**(1): 135–149. doi:10.1046/j.1365-2427.1998.00270.x.

Ziegler, S.S. 2000. A comparison of structural characteristics between old-growth and postfire second-growth hemlock–hardwood forests in Adirondack Park, New York, U.S.A. Glob. Ecol. Biogeogr. **9**(5): 373–389. doi:10.1046/j.1365-2699.2000.00191.x.