Long-term effects of riparian forest harvest on light in Pacific Northwest (USA) streams

Matthew J. Kaylor[1,4], **Dana R. Warren**[1,2,5], **and Peter M. Kiffney**[3,6]

[1]Oregon State University, Department of Fisheries and Wildlife, Corvallis, Oregon 97331 USA
[2]Oregon State University, Department of Forest Ecosystems and Society, Corvallis, Oregon 97331 USA
[3]National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Fish Ecology Division, Seattle, Washington 98112 USA

Abstract: Riparian forests exert strong influence on abiotic and biotic processes in adjacent streams by regulating light. Harvesting of riparian forests was once common practice, and consequently, many streamside forests across North America are in varying stages of development as they regenerate, thereby affecting stream light regimes. We used 2 approaches to evaluate the influence of riparian forest harvest and stand recovery on light availability in small mountain streams. We estimated light and canopy cover every 25 m along 11.5 km of a 4th-order stream network dominated by late-successional riparian forests that included 7 streamside harvest units 50 to 60 y old. Estimates of stream light fluxes were lower in harvest units than in up- and downstream sections bordered by old-growth forests even though only 1 stream bank was harvested in 5 of 7 units. Differences in stream light between harvested reaches and adjacent old-growth sections were greater when both banks had been logged. We also conducted a space-for-time analysis based on a literature review of Douglas fir-dominated forests of the US Pacific Northwest. Canopy closure generally occurred within 30 y of harvest and was followed by a period of maximum canopy cover (minimum light) that lasted from 30 to 100 y. Data were limited for stands ranging from 100 to 300 y old, but mean canopy openness and variability in openness along the stream were greater in late-successional forests (dominant canopy trees >300 y old) than in stands that were 30 to 100 y old (18 vs 8.7%), a result consistent with the network analysis. Overall results from our study suggest that streams with mid-successional riparian forests probably are in a period of minimal summer light fluxes.

Key words: stream light, stand development, forest succession, Douglas fir, canopy cover, H. J. Andrews

Most North American forests have been cleared at least once within the last 2 centuries for timber harvesting, agriculture, or land development (Pan et al. 2011). Land clearing historically included streamside (riparian) forests with little consideration of potential negative effects on adjacent aquatic environments (Richardson et al. 2012). However, recognition of the ecological linkages between riparian forests and aquatic ecosystems led to increased regulatory protection to maintain key riparian functions, such as recruitment of large wood to streams, nutrient and sediment retention, bank stability, and regulation of shade and stream temperature (FEMAT 1993, Lee et al. 2004, Reeves et al. 2006, Richardson et al. 2012). In the Pacific Northwest region of North America, widespread implementation of riparian regulations did not occur until the late 20th century. By that time, most riparian forests had been harvested once (e.g. FEMAT 1993, British Columbia Ministry of Forests 1995). Therefore, most streamside forests today are still in the early stages of stand development. Forest development processes occur over long time scales, so the recovery of riparian forests will be an important consideration in stream ecosystems for decades and centuries to come. A number of investigators have explored how stand age/development affect key riparian functions including stream wood loading (Hedman et al. 1996, Benda et al. 2002, Warren et al. 2009), stream geomorphology (Fetherston et al. 1995), and stream nutrient processing (Valett et al. 2002, McClain et al. 2003, Cairns and Lajtha 2005). We focused on how stand development in the riparian forest affects stream light dynamics.

Light is an important driver of chemical, physical, and biological processes in streams. It is essential for stream primary production (Gregory 1980, Julian et al. 2011) and is a key component of stream thermal budgets (Caissie 2006, Moore et al. 2006). When light flux to streams is low, such as beneath closed riparian canopies, primary production is often low, and secondary production in the system depends largely on terrestrially derived (allochthonous) C sources (leaves, needles, invertebrates) (Fisher and Likens 1973, Wal-

E-mail addresses: [4]matthew.kaylor@oregonstate.edu; [5]dana.warren@oregonstate.edu; [6]peter.kiffney@noaa.gov

DOI: 10.1086/690624. Received 18 July 2016; Accepted 29 October 2016; Published online 22 December 2016.
Freshwater Science. 2017. 36(1):000–000. © 2017 by The Society for Freshwater Science.

lace et al. 1999). Therefore, reduced canopy cover and greater light fluxes can lead to elevated rates of in-stream primary production (Gregory 1980, Bilby and Bisson 1992, Hill et al. 1995, Clapcott and Barmuta 2010), nutrient demand (Sabater et al. 2000, Warren et al. 2016a), and autochthonous (produced in-stream) C contributions to stream food webs (McCutchan and Lewis 2002, Lau et al. 2009, Wootton 2012). Increased primary production commonly is accompanied by increased reach-scale invertebrate biomass (Stone and Wallace 1998) and enhanced invertebrate predator abundance (Aho 1976, Murphy and Hall 1981, Bilby and Bisson 1992, Wootton 2012). Drastic increases in light after canopy removal elevate stream temperatures (reviewed by Moore et al. 2006), but the magnitude and duration of temperature changes are influenced by local conditions and geomorphology (Johnson 2004, Pollock et al. 2009). Increased temperatures can negatively affect thermally sensitive species, and management of riparian shading has been a focus in assessments of stream warming (Groom et al. 2011). Considerable research has been done on the effects of canopy removal, but given the long-term dynamics of stand regeneration, changes in light associated with recovery may have greater collective effects than harvest on streams.

Stand development and successional processes can influence riparian canopy structure and stream light availability (Keeton et al. 2007, Stovall et al. 2009, Warren et al. 2016b). In riparian zones, fluvial disturbances and hydrologic conditions (e.g., soil moisture) often lead to forest communities and overall successional trajectories that differ from upland forests (Decamps et al. 1988, Cordes et al. 1997, Van Pelt et al. 2006). However, in small streams, differences in vegetation may be apparent only directly adjacent to streams (Villarin et al. 2009) where stand development processes in the upland and riparian zone interact to influence canopy structure and stream light over time. For example, in Douglas fir-dominated regions of the Pacific Northwest (PNW), deciduous alder (*Alnus* spp.) commonly becomes established directly adjacent to streams after riparian harvest and other disturbances. These alder stands can provide the majority of stream shade during summer (Summers 1982) until senescence shifts the canopy to upland coniferous species 40 to 60 y post-harvest (Van Pelt et al. 2006). Conceptual models of stream light following riparian harvest produced for the PNW region predict that light will decrease to preharvest levels within 25 y and then remain at minimal levels until late in stand development (>100 y) when canopy gaps increase insolation (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009).

This trajectory may be common in PNW forests, but stands can develop along alternative trajectories that can alter temporal dynamics of stream light (Warren et al. 2016b). For example, in the PNW, fluvial disturbances (Johnson and Jones 2000) and biological disturbance agents, such as beavers (Naiman et al. 1988), can limit canopy closure and establish new cohorts of trees. Alternatively, lack of conifer recruitment or the establishment of shrub species may result in different successional trajectories (Henderson 1978, Minore and Weatherly 1994, Hibbs and Giordano 1996). Empirical data evaluating stream light as it relates to stand age and stage of development are critically needed to assess the long-term influences of riparian forest stand removal on associated biological and physical characteristics of the system.

We used 2 approaches to evaluate relationships between riparian forest stand age and stream light availability in Douglas fir-dominated forests of the PNW. First, we quantified light and canopy cover throughout a 4th-order stream network that encompasses reaches bordered by old-growth (>300 y old) and mid-successional (50–60 y old) riparian forests. The goals of this sampling effort were to evaluate: 1) characteristics of old-growth light regimes throughout the stream network, and 2) whether canopy openness and light (photosynthetically active radiation [PAR]) differed between stream sections flowing through harvested units and old-growth forest. We hypothesized that stream light and canopy openness would increase with stream size and that mean light and canopy openness would be lower in harvest units relative to up- and downstream old-growth sections. Second, we evaluated canopy cover across a wider range of stand ages by conducting a space-for-time analysis based on a literature review of published studies in which both stand age and canopy cover over the stream were reported. We expected mean canopy openness to decline sharply within 20 y post-harvest, remain low in stands 30 to 100 y old, and then increase in later stages of stand development (>100 y), reflecting proposed conceptual models for this region (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009). We predicted that most data points would follow this trend, but we expected outliers that reflected alternative stand-development trajectories (Warren et al. 2016b). We predicted that both approaches would show variability in canopy openness (and light) that would be lower in streams in mid-successional than in old-growth forests.

METHODS

Study system

We collected data for the longitudinal stream light assessment at the HJ Andrews Experimental Forest (HJA) in the Cascade Mountains, Oregon, USA. This region has a Mediterranean climate (wet, cool winters and warm, dry summers). We sampled ~11.5 km of stream length in the McRae Creek basin, a tributary to Lookout Creek, during summer low-flow conditions. This network included 8 km of the 4th-order (Strahler 1957) mainstem McRae Creek, ~3 km of a 3rd-order unnamed tributary on the west side of McRae Creek (MCTW), and 500 m of a 2nd-order unnamed tributary on the east side of McRae Creek (MCTE) (Fig. 1). We sampled MCTE in 2014 and McRae Creek and MCTW in 2015.

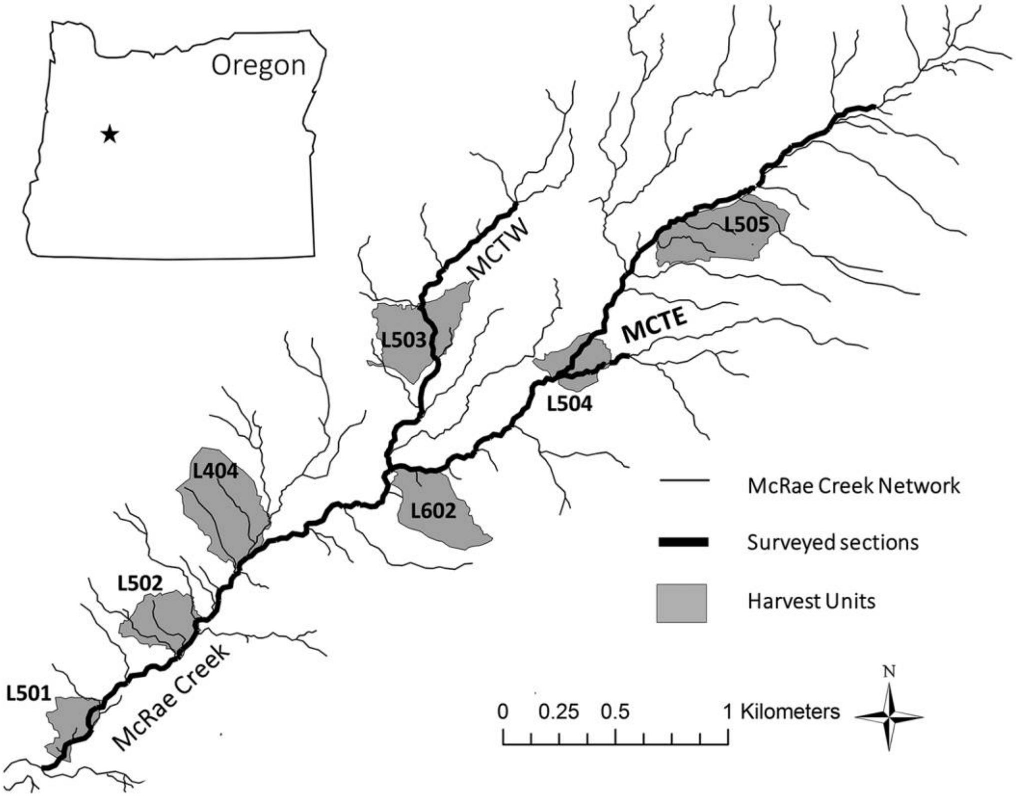

Figure 1. Map of the McRae Creek basin and surveyed sections of the stream network (bold) within the HJ Andrews Forest, Oregon, USA. Gray polygons represent previously harvested, now secondary growth forests (Table 1). The remainder of the stream network was bordered by unharvested forest.

The McRae basin is mostly old-growth forest mixed with small-patch clear-cuts (<30 ha), 7 of which were included in our sampling area. All 7 harvest units were cut within a relatively short time frame 50 to 60 y before our study (Table 1). Clearing on both stream banks occurred in units L503 and L504, whereas clearing on only 1 bank occurred in all other units (Fig. 1). Trees were harvested to the stream bank with no riparian buffers, but in unit L505, a limited number of trees was left for bank stability because of steep slopes. Except unit L503, which was left to regenerate naturally, units were planted with Douglas fir (*Pseudotsuga menziesii*) within 3 y of harvest, a practice typical of managed forests across Oregon and Washington at the time.

We characterized broad patterns of PAR and canopy openness with regard to landscape position by dividing McRae Creek and MCTW into 2 reaches based on distinctive geomorphic and network features that coincided with differences in gradient and bankfull width. The lower reach

Table 1. Characteristics of harvest units and the stream surveyed in harvest units along McRae Creek, McRae Creek Tributary West (MCTW), and McRae Creek Tributary East (MCTE).

Stream	Harvest unit	Stand age (y)	Banks harvested	Stand area (ha)	Stream bankfull width (m)	Reach distance (m)
McRae	L501	59	1	7.4	10.12	425
	L502	52	1	11.5	8.47	375
	L404	58	1	22.8	8.84	325
	L602	52	1	15.9	7.81	375
	L504	55	2	8.7	8.02	300
	L505	56	1	20.2	6.95	550
MCTW	L503	60	2	18.4	3.6	225
MCTE	L504	55	2	8.7	2.80	375

of McRae Creek (4100 m long) began on the downstream end at the confluence with Lookout Creek and extended upstream to a series of steep waterfalls just downstream of harvest unit L504. The waterfalls prevented assessment of a 200-m reach directly downstream of unit L504. The upper reach of McRae Creek (2900 m long) began just upstream of the waterfall section and extended to a distance of 7200 m from the confluence. The waterfall section marked a change in gradient, and the upstream section was steeper and more confined than the downstream reach. At MCTW, the lower reach (950 m long) began at the confluence of MCTW and McRae Creek and continued upstream to unit L503, which was the only harvest unit in MCTW and a logical place to split the stream. The upper reach of MCTW (1250 m long) began at the upstream edge of unit L503 and ended at the crossing with road 320. We surveyed only one 500-m reach in MCTE.

Stream-network light dynamics

To evaluate relationships between channel and riparian characteristics and stream light, we quantified stream bankfull width, wetted width, canopy openness, % red alder (*Alnus rubra*) and estimated PAR. At McRae Creek and MCTW, we collected these data at 25-m intervals. At MCTE, we estimated PAR at 5-m intervals (in concurrence with a study by DRW, unpublished data) and canopy openness at 10-m intervals in the 120-m old-growth section and 120 m of the 380-m second-growth section. We measured all other variables at the standard 25-m intervals.

Canopy openness was quantified by 2 individuals with a convex spherical densiometer (Model A; Forestry Suppliers, Jackson, Mississippi) and reported values are the means of 4 measurements, one in each cardinal direction. We evaluated user bias before the network surveys to ensure that estimates by the 2 individuals were comparable (<5%) at each point. Small light gaps, such as those between branches and leaves, may not be detected as well with a spherical densiometer as with other methods (e.g., hemispherical photos) (Julian et al. 2008a). Therefore, our sampling was focused on detecting relatively large canopy gaps (>1 m).

We assessed light flux to the stream bottom every 25 m throughout the sampling network with the aid of photodegrading fluorescein dye (Bechtold et al. 2012). Fluorescein degrades at a predictable rate when exposed to light and can be used to quantify relative light availability in streams (Bechtold et al. 2012, Warren et al. 2013). We mixed concentrated fluorescein with deionized water to a concentration of 400 μg/L and added 36 g/L of commercial aquarium salt (Instant Ocean®) to buffer the solution. We filled 3.7-mL clear glass vials with the premixed solution and used zip ties to attach 3 vials to a single wire flag at each sampling location. Every 4th flag had a vial wrapped in aluminum foil to serve as a 'field-dark' control to correct for drift in concentration. In McRae Creek and MCTW, we placed fluorescein flags (n = 360) over two 2-d periods in early summer 2015 (6–7 and 8–9 July). In MCTE, we placed fluorescein flags (n = 101) in early summer 2014 (30 June–1 July). All sampling days were sunny and cloudless. We placed the vials in the stream between 0500 and 0800 h, when light levels reaching the stream were still very low, and retrieved them at approximately the same time after 24 h. We placed flags with fluorescein vials attached in the thalweg and secured them by placing a small rock on top of the flag.

Upon retrieval, we returned the flags to the laboratory and allowed them to warm to room temperature because fluorescence readings are affected by solution temperature (Bechtold et al. 2012). We measured fluorescence with an AquaFluor handheld fluorometer (Turner Designs, San Jose, California). Fluorescence readings for each flag/location were averaged across the 3 replicates and subtracted from the mean fluorescence value of the field-dark controls to produce a single, corrected photodegradation value for each location. We noted in the field those vials covered by leaves or rocks and removed them from analysis.

We used Odyssey PAR sensors (Dataflow Systems, Christchurch, New Zealand) to collect the PAR data needed to build a relationship between fluorescein-dye photodegradation and measured PAR for the 2 field seasons (2014–2015). We attached PAR sensors to rebar pounded into the stream substrate within 0.25 m of a set of flags containing fluorescein vials and left them in place for 24 h to measure total daily accumulated PAR. Total daily accumulated PAR (mol m^{-2} d^{-1}) was compared to mean fluorescein decay for each location at 56 locations and a curve was fitted using a 3-factor polynomial function (Fig. S1). Measured PAR and fluorescein-converted PAR estimates were calculated as % full sun based on accumulated PAR measured at the HJ Andrews CENMET meteorological station. Flags with attached fluorescein-filled vials were situated directly on the stream bottom, whereas PAR sensors were situated directly above the water surface. Water depth, water clarity, and reflection from the water surface can affect light penetration in the water column (Julian et al. 2008b). However, during mid-summer, water in the study streams was clear with little turbidity and all fluorescein vials were in shallow water (0.1–0.25 m) where turbulence was minimal. Julian et al. (2008a) found that ~10% of PAR was reflected by water in a stream. Thus, PAR reaching the stream bottom (and fluorescein vials) probably was reduced even in clear, shallow water. Nevertheless, we found a strong relationship between PAR and fluorescein decay (Fig. S1).

We visually estimated and scored the abundance of alder as % riparian trees within 10 m up- and downstream of the sampling location and 5 m into the riparian zone on each bank as: 0 = not present, 1 = 1–20, 2 = 20–40, 3 = 40–60, 4 = 60–80, and 5 = >80% (Fig. S2).

We used 2 approaches to analyze PAR and canopy openness data. First, we characterized PAR and canopy openness in each of the 5 stream sections (Lower McRae, Upper McRae, Lower MCTW, Upper MCTW, and MCTE) and evaluated trends based on channel characteristics. Second, we compared PAR and canopy openness values in each harvest unit to values in old-growth reaches directly up- and downstream of each unit. We used the same linear distance in up- and downstream old-growth reaches as the linear distance in the harvest unit (e.g., if the harvest unit bordered 300 m of stream, we used the 300 m down- and 300 m upstream of the unit) unless the distance overlapped with another harvest unit, in which case we used the maximum length of the old-growth reach. We examined data in each reach for normality and ln(x)-transformed data if needed. We used a t-test in R (version 3.1.3; R Project for Statistical Computing, Vienna, Austria) for each comparison. We evaluated variance by examining the standard deviations (SDs) for PAR and canopy cover in each harvest unit and associated up- and downstream sections and used F-tests of homogeneity of variance to compare SDs between reaches. We used linear regression to evaluate the relationships between PAR and canopy openness and PAR/canopy openness and bankfull width.

Literature review of canopy cover-to-riparian forest stand age relationships

We used the Web of Science® (Thomson Reuter, Philadelphia, Pennsylvania) to initiate our literature review with the goal of identifying studies that contained estimates of riparian forest stand age (or mean age of dominant canopy trees) and canopy cover over the stream in the Pacific Northwest of North America. Forest development and recovery from harvest is a process occurring across much of North America, but the PNW is the best place to conduct this analysis because of the large number of studies in which influences of forest practices on stream ecosystems were evaluated.

To account for potential stream size and forest community effects, we restricted our search to studies pertaining to small mountain streams (<10 m bankfull) of the Coast and Cascade mountain ranges of Oregon, Washington, and British Columbia where the dominant tree species is Douglas fir. We conducted 3 primary searches based on the following criteria: 1) stream, canopy, Oregon; 2) stream, canopy, Washington; and 3) stream, canopy, British Columbia. We searched the methods, results, and appendices of the resultant 201 papers to find studies in which stand age and an estimate of canopy cover were both reported. We excluded sites where buffer strips were present because buffer strips can affect stream light (Kiffney et al. 2003). When means were reported, we searched citations in those papers and other established references (including appendices and theses) to see whether data were available on individual streams rather than in aggregate. If no data on the individual streams could be found, we used the reported mean values (Table S1). If a relatively narrow range of stand ages were provided for the mean estimate of cover, we used the average of the range of ages reported.

We focused on canopy openness as a proxy for stream light (per Lamberti and Steinman 1997) because direct quantification of stream light flux (e.g., use of PAR sensors) is relatively uncommon, and we could not find enough studies with light and stand age to build a comprehensive synthesis. Canopy cover is quantified much more regularly in stream studies, and canopy architecture strongly influences stream shading and, by proxy, PAR exposure (McTammany et al. 2007). The most common method used to characterize canopy cover in streams is a spherical densiometer. Other methods to estimate cover include hemispherical photography, the line-intercept method, and the use of a moosehorn (a gridded mirror aimed upwards but with a narrower view than a densiometer). In a comparison of these methods, hemispherical photography and densiometer estimates were similar but moosehorn and line-intercept methods were substantially different from densiometer and hemispherical photography estimates, especially when cover was limited (Fiala et al. 2006). Therefore, we included only studies in which spherical densiometer estimates or hemispherical photography was used and excluded studies in which the moosehorn (e.g., Romero et al. 2005) or line-intercept method was used (e.g., De Groot et al. 2007).

We plotted canopy openness vs stand age of the riparian forest as reported in each study. We placed all studies characterized as old-growth or late-successional into a single group (old-growth; >300 y) because the time since a stand-replacing event or the average age of dominant trees is difficult to measure and usually is not reported for forests >200 y old. Canopy closure rates and stand development processes may differ among Douglas fir-dominated regions of the Coast Range and Cascade Range (Summers 1982), so we classified each point as either Coast or Cascade Range. We grouped studies from the Coast Mountains, British Columbia, with those from the Coast Range. We fit a negative exponential decay curve to data from 0 to 100 y to examine rates of canopy closure and to estimate when canopy openness values returned to preharvest conditions (SigmaPlot, version 13.0.0; SYSTAT Software, San Jose, California).

RESULTS

Stream network light dynamics

Within the McRae network, streams bordered by old-growth riparian forests exhibited a wide range of PAR and canopy openness values (Figs 2A, B, 3A–D). Individual measurements of PAR ranged from 0.6 to 26.3 mol m^{-2} d^{-1} (1–58% of full sun values) and canopy openness values ranged from 0 to 69%. Across all sites, canopy openness explained 36% of the variation in PAR estimates (n = 377). When streams were evaluated separately, canopy openness ex-

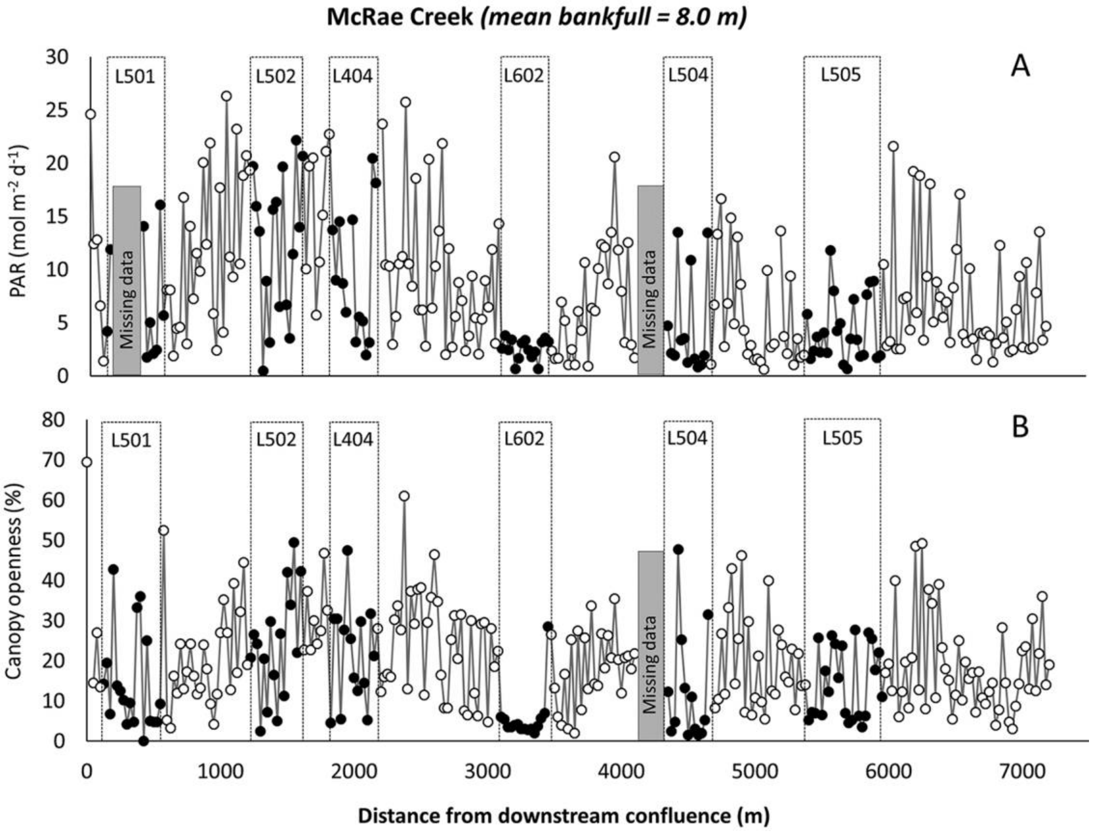

Figure 2. Photosynthetically active radiation (PAR) (A) and canopy openness (B) measured every 25 m for 7400 m on McRae Creek. Filled dots represent areas bordered by previously harvested riparian forest on ≥1 stream bank, whereas open dots represent areas bordered by old-growth riparian forest on both banks. Dashed lines indicate harvest units.

plained more variation of PAR estimates in McRae ($R^2 = 0.44$, $n = 266$) than in MCTW ($R^2 = 0.23$, $n = 90$) and MCTE ($R^2 = 0.02$, $n = 21$).

When the stream network was broken up into 5 larger sections, mean PAR in streams bordered by old-growth forest was greatest in the lower section of McRae (9.9 mol m^{-2} d^{-1}), followed by the upper section of McRae (6.4 mol m^{-2} d^{-1}), the lower section of MCTW (4.7 mol m^{-2} d^{-1}), MCTE (3.3 mol m^{-2} d^{-1}), and the upper section of MCTW (2.0 mol m^{-2} d^{-1}) (Table 2). Mean canopy openness was greatest in lower McRae (22.4%), followed by upper McRae (18.4%), lower MCTW (10.2%), MCTE (10.1%), and upper MCTW (6.5%) (Table 2). The larger mainstem McRae had greater mean PAR and canopy openness than the smaller tributaries, but bankfull width explained <5% of the variation in PAR and canopy openness values across all data points within the stream network.

Mean estimated PAR was lower in the harvest unit than in adjacent up- and downstream reaches bordered by old-growth forests for all comparisons ($n = 14$), but only 6 comparisons were significant at $p < 0.05$ (Fig. 4A). Estimated PAR was, on average, 2.78 mol m^{-2} d^{-1} lower in harvest units than in up- and downstream old-growth sections (range: 0.55–6.16 mol m^{-2} d^{-1}). Thus, PAR values in old-growth reaches averaged 1.70× greater than PAR values in adjacent harvest units (range: 1.14–2.54× greater). The contrast between harvest units and adjacent old-growth sections was most pronounced when harvesting occurred on both banks (e.g., L503, L504) or when a dense and uniform alder canopy was established (e.g., L602). The SD of PAR estimates was lower in the harvest unit in 13 of 14 comparisons (Fig. 4A), but only 5 of these comparisons had $p < 0.05$ (comparison of variances *F*-test).

Mean differences in canopy openness were largely comparable to the PAR results. Openness was lower in the harvest unit in 12 of 14 comparisons and 6 comparisons were significantly different ($p < 0.05$; Fig. 4B). Percent canopy openness was 6.1% greater on average (range: –2.2–14.5%) in old-growth sections than in adjacent harvest units. The SD of canopy openness estimates was lower in harvest units in 8 of 14 comparisons and 5 of these had $p < 0.05$ (comparisons of variances *F*-test).

The relationship between canopy openness and PAR was much stronger at the reach-scale than at individual locations. Mean canopy openness explained 78% of the variation in mean PAR estimates for the 22 reaches used to evaluate differences in canopy openness and PAR between harvest units and old-growth forests.

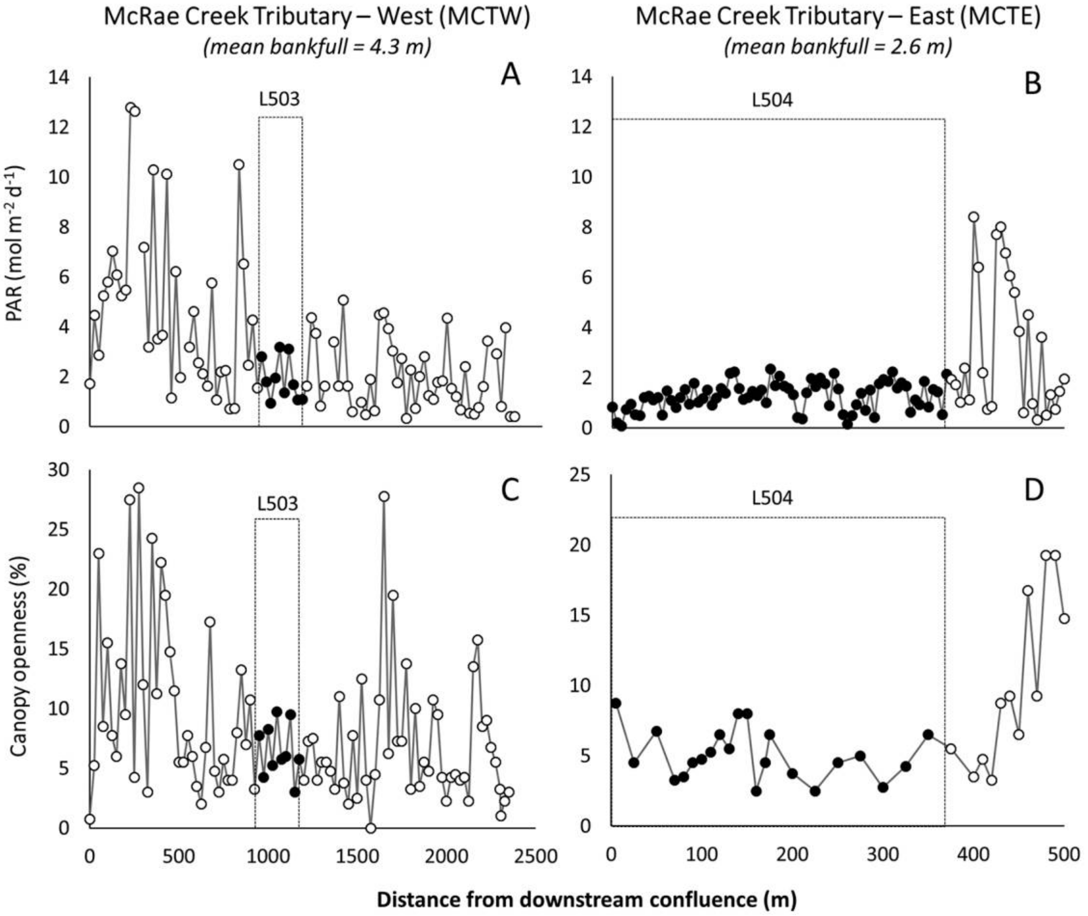

Figure 3. Photosynthetically active radiation (PAR) (A, B) and canopy openness (C, D) on McRae Creek Tributary West (MCTW) (A, C) and McRae Creek Tributary East (MCTE) (B, D). PAR was measured every 5 m for MCTE. See Fig. 2 for explanation of details.

Literature review of canopy cover-to-riparian forest stand age relationships

Despite an extensive literature search, we found relatively few studies in which authors reported both stand age and canopy openness and that met our other criteria (e.g., Douglas fir dominated, no riparian buffers, densiometer or hemispherical photography). We identified 10 studies encompassing a total of 92 individual points: 54 from the Coast Range or Coast Mountains and 37 from the Cascade Range. Of these, 72 sites had been previously harvested and ranged in age from 0 to 100 y, 2 sites were 100 to 300 y old, and 17 sites were old-growth where a stand-replacing disturbance had not occurred within 300 y.

Across the full data set, maximum canopy openness occurred shortly after a stand-replacing event but rapidly declined over a 40-y period, eventually reaching minimum

Table 2. Mean (±SD) canopy openness (%) and photosynthetically active radiation (PAR) for streams in old-growth riparian forests of the McRae Creek network (upper and lower reaches of McRae Creek and McRae Creek Tributary West [MCTW], and McRae Creek Tributary East [MCTE]).

Stream	Bankfull width (m)	Gradient (%)	Canopy openness (%)	PAR (mol m^{-2} d^{-1})	*n*
McRae (Lower)	10.0 (3.4)	5.4	22.4 (12.6)	9.9 (6.8)	100
McRae (Upper)	6.6 (2.3)	10.6	18.4 (10.8)	6.4 (5.0)	86
MCTW (Lower)	5.7 (2.7)	9.8	10.2 (7.4)	4.7 (3.3)	38
MCTW (Upper)	3.1 (0.9)	8	6.5 (5.1)	2.0 (1.4)	51
MCTE[a]	3.5 (0.7)	6.8	10.1 (5.9)	3.3 (2.6)	27 (12)

[a] PAR was estimated at 5-m intervals ($n = 26$), whereas canopy openness was measured at 10-m intervals ($n = 12$).

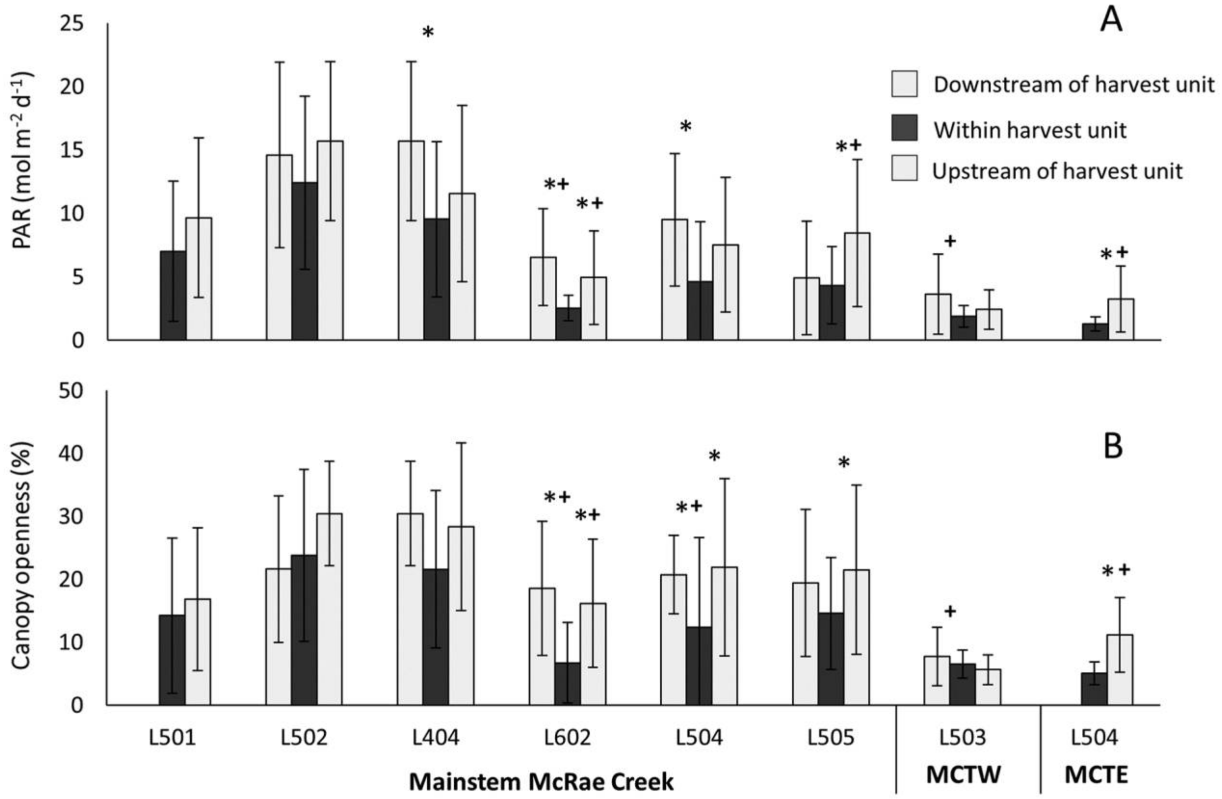

Figure 4. Mean (±SD) photosynthetically active radiation (PAR) (A) and canopy openness (B) in harvest units and unharvested up- and downstream sections of equal linear stream distance along McRae Creek, McRae Creek Tributary West (MCTW), and McRae Creek Tributary East (MCTE). Asterisks indicate significant difference ($p < 0.05$) between harvest unit and unharvested section and plus signs indicate significantly different standard deviations.

levels between 30 and 100 y (Fig. 5A). Based on a fitted negative exponential decay curve, canopy openness reached preharvest, old-growth levels (see below) ~28 y after harvest (Fig. 5B). Canopy openness over streams in old-growth forests averaged 18.0% but was highly variable and ranged from 3.4 to 34.0% (SD = 7.9). Mean canopy openness in stands between 30 and 100 y old was 8.7% and ranged from 1.2 to 32.0% (SD = 5.7), but canopy openness was >15% at 1 site (SD = 3.7 with outlier removed). Variance between old-growth and stands 30 to 100 y old were significantly different when this outlier was removed (*F*-test; $p = 0.001$) but not when the outlier was included (*F*-test, $p = 0.14$). Data on stream size, aspect, elevation and gradient, were not available for all studies, so we could not examine relationships between these covariates and changes in canopy cover over time; Fig. S2).

DISCUSSION

Stand recovery from timber harvest is widespread in stream riparian zones across North America. Our results indicate that stream light regimes are affected by both initial canopy removal and recovery. Light regimes continue to shift as conditions change through stand development and forest successional processes. Network sampling indicated that stream light availability and canopy openness were lower in harvest units where the forest ages ranged from 50 to 60 y than in old-growth forests (>300 y). These results are consistent with those of other studies in which investigators found greater mean canopy openness in streams of late-successional forests than in second-growth forests (Murphy and Hall 1981, Keeton et al. 2007, Stovall et al. 2009, Warren et al. 2013). We observed this difference in light regimes even in the 5 harvest units where the clearing had been done on only 1 stream bank, but the contrast in light between harvest units and adjacent stream reaches with old-growth riparian forests was generally greater in units where harvesting occurred on both stream banks. Data from the literature review were relatively consistent with conceptual models of summer light availability over time for Douglas fir-dominated forests of the PNW region (Sedell and Swanson 1984, Gregory et al. 1987). Canopy openness values decreased rapidly after harvest, reflecting a negative exponential decay curve, and returned to preharvest (old-growth) levels after ~30 y. Between 30 and 100 y later, mean canopy openness was less than the mean values for streams bor-

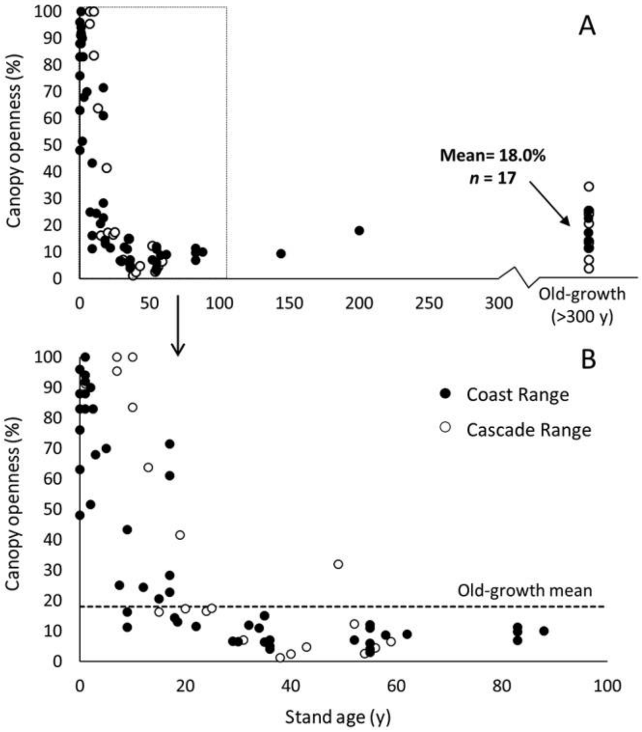

Figure 5. Stand age (years since a stand-replacing event) vs canopy openness for 92 sites in Coastal and Cascade Mountains (A) and expanded view of the first 100 y (B). Stands >300 y old were grouped. Coast = sites in the Coast Range, Oregon, and the Coast Mountains, British Columbia.

dered by forests where stand-replacing disturbances had been absent for ≥300 y. Consistent with other studies evaluating light in streams bordered by second-growth vs old-growth riparian forests (Keeton et al. 2007, Stovall et al. 2009, Warren et al. 2013), canopy openness values were far less variable along the stream when stands were between 30 and 100 y old compared to streams with old-growth riparian forests. Data were limited for stands between 100 and 300 y old, and we were not able to assess canopy patterns for this time frame.

The type of plant community that regenerates after a stand-replacing event can affect how forests influence stream light (Warren et al. 2016b). In the western PNW, red alder commonly occupies riparian zones after harvest and can form a closed canopy relatively quickly—within 12 y for the Coast Range and 25 y for the Cascade Range (Summers 1982). However, alder is a short-lived species, and initial cohorts can senesce after 40 to 60 y, giving way to a coniferous overstory (Van Pelt et al. 2006). Gregory et al. (1987) suggested that light may briefly increase during this transition before canopy closure by coniferous species. Harvested units in the McRae basin were between 50 and 60 y old and, consistent with the prediction of a short period of increased light following alder senescence, we observed signs of alder mortality and associated canopy gaps in some units. However, results from our literature review, in which alder was a dominant canopy species in most early stands, did not indicate any period of elevated canopy openness between 30 and 100 y. Even within the small geographic extent of the McRae Creek basin, alder was not evenly distributed. In the lower sections of the McRae network, alder was typically more abundant in harvest units but still common in old-growth sections. On the other hand, alder was nearly absent from the 3-km upstream section of mainstem McRae Creek above 850 m in elevation. Here, deciduous vine maple (*Acer circinatum*) provided substantial shade in some sections, but overstory canopies were dominated by conifers. The lower reach of McRae Creek is alluvial and less steep than the more confined upper McRae, which may provide more favorable hydrologic and disturbance conditions for alder establishment and maintenance (Villarin et al. 2009). Alternatively, the loss of red alder may be a consequence of elevation change because red alder is typically more common at elevations <750 m (Harrington 2006). These differences in vegetative communities may, in part, explain why bankfull width explained little of the variation in light or canopy cover across the McRae Creek network.

Canopy openness explained far less of the variation in PAR at a given single location than when mean values were compared at the reach scale. This result is consistent with findings by Warren et al. (2013) and suggests that stream light availability is not well correlated with direct overhead canopy cover at a single point. The angle of the sun may cause an offset in light penetration to the understory such that the gap responsible for a local increase in light may not be within the field of view for a spherical densiometer. However, gaps and associated areas of elevated light are more likely to be surveyed during multiple measurements along the length of a reach. Therefore, mean PAR and mean canopy openness are likely to be more strongly correlated at the reach scale than at individual locations. Other factors, such as stream orientation and topographic shading, also may affect relationships between canopy cover and PAR. East–west-oriented streams receive more shading from trees on the south than on the north stream bank because of the sun angle (Julian et al. 2008a). In McRae Creek and MCTW (more north–west oriented streams), canopy openness explained much more of the variation in PAR than in MCTE (east–west oriented), indicating that canopy openness in east–west streams may not be a good metric of light availability. Topographic shading can influence stream light availability substantially in areas with steep valley walls or in areas with minimal shading from the riparian forest (Yard et al. 2005), but we do not think it was a dominant control on light in streams in our study. Hillslopes were generally not steep enough to provide topographical shade except for very early and late in the day when the sun is at a lower angle. Moreover, streams were densely forested and, at these time periods, vegetation typically already shaded streams.

The River Continuum Concept hypothesizes that stream light availability follows an orderly pattern of increasing light with distance downstream as widening channels create larger canopy gaps (Vannote et al. 1980). In our network study, results were consistent with this hypothesis when we evaluated the smallest headwaters down to the largest section of the mainstem. Across this range in stream size, mean PAR and canopy openness in old-growth forests were greater in the larger mainstem than in the narrower tributaries, and in the mainstem, canopy openness and PAR were greater in the larger downstream section than in the narrower upstream section. However, at individual locations across the stream network, bankfull width explained very little (<5%) of the variation in PAR and canopy openness. This finding may be attributable to the high variability in PAR and canopy openness values in all old-growth sections of the stream network. Even the widest stream sections (lower McRae = 9.6 m on average) were narrow enough to allow canopies to close entirely over the stream. At larger spatial scales, increasing channel width will inevitably be a dominant factor influencing light flux to the stream surface, but water depth and water clarity may reduce light reaching the stream bottom (Vannote et al. 1980, Julian et al. 2008a, b).

Our data show that changes in canopy openness associated with canopy closure are large but differences in stream canopy openness and light between previously harvested riparian forests and old-growth forests are relatively small. Most investigators who studied the influence of light on stream biotic processes have evaluated large increases in light associated with clear-cut harvesting. Comparatively few investigators have evaluated small changes in light, but their results suggest these changes can be biologically significant. For example, in a field manipulation (Kiffney et al. 2003) and an experimental study in streamside channels (Kiffney et al. 2004), small increases in light (<25% full sun) resulted in greater periphyton accrual and biomass of some invertebrates. Quinn et al. (1997) observed increasing algal standing stocks and invertebrate biomass when light increased from 2 to 10% ambient sun and again when light increased from 10 to 40%. These studies suggest that small changes in mean canopy cover can alter biological processes, but they are few in number and geographic extent and more research is needed in this area.

Stream light is typically more heterogeneous in old-growth forests than in younger stands because of spatially variable canopy gaps (Stovall et al. 2009, Warren et al. 2013). In our network sampling, the SD of PAR estimates was greater in most old-growth sections than in harvest units, and this difference was most pronounced where harvesting occurred on both banks or where alder formed a closed canopy (e.g., L602). Both Stovall et al. (2009) and Warren et al. (2016a) found significant relationships between local light availability and local periphyton chlorophyll *a* accrual in streams in late-successional forests. Warren et al. (2016a) found that the relationship between light and chlorophyll *a* accrual was much steeper when substrates were augmented with nutrients than where they were not augmented and that spatial variability in light created spatial variability in nutrient limitation and ultimately reach-scale colimitation. However, the influences of spatially variable light on local (patch-scale) and reach-scale primary production, invertebrate communities, temperature, and other ecosystem processes remains largely unexplored (but see Julian et al. 2008b, 2011).

The overall trend in canopy cover from our literature review is consistent with conceptual models for this region that predict temporal changes in stream light (Sedell and Swanson 1984, Gregory et al. 1987, Mellina and Hinch 2009), but our results should be interpreted with some caution. First, most studies were from 4 research forests: the HJ Andrews Experimental Forest, the Hinkle Creek watershed study, the Alsea watershed study, and the Malcolm Knapp Forest. Trajectories of canopy cover over time did not appear to differ among these forests or between Coastal and Cascade Ranges, but we acknowledge that a more spatially balanced distribution of sites would provide a more comprehensive evaluation of stream light dynamics. Second, we were not able to quantify how abiotic and biotic disturbances influence stand trajectories. Fluvial disturbances can alter riparian vegetation, limit riparian canopy closure, and establish new cohorts of alder (Johnson and Jones 2000), which would alter timing of alder senescence. In addition, organisms such as beaver (Naiman et al. 1988, Pollock et al. 1995) and insect defoliators (Obedzinski and Shaw 2001) can substantially alter riparian vegetation and, thus, stream light dynamics over time. Last, our literature review showed that canopy openness was greater in old-growth reaches than in reaches bordered by 30- to 100-y-old forests that were clear-cut harvested. However, we had very limited data from streams bordered by stands 100 to 300 y old, which reduced our ability to assess if, and when, a transition to late-successional gap-dynamic structure may occur. A lack of studies from this age range is not surprising given widespread 20th century harvesting (Pan et al. 2011), but given reduced harvest and the establishment of riparian reserves, progression to these ages probably will become more prevalent, warranting further evaluation of light dynamics.

Future conditions may differ substantially from those observed in the last century, and therefore, future developmental trajectories and ultimately stream light also may differ (Warren et al. 2016b). Climate change, in particular, is anticipated to shift tree species distributions (Iverson and Prasad 1998, Hamann and Wang 2006), increase stress-related mortality (Allen et al. 2010), alter growth rates and productivity (Pastor and Post 1988), and affect disturbance processes (Overpeck et al. 1990, Dale et al. 2001). For example, climate change is expected to expand the geographic extent of insect pest species that can cause selective mortality (Carroll et al. 2003, Paradis et al. 2008, Cudmore et al. 2010, Liang and Fei 2013). As noted by Reilly and Spies (2015), disturbance that removes only a portion of dominant trees can substantially alter developmental trajectories, forest structure, and canopy coverage. Moreover, effects of climate change on the frequency, magnitude, and extent of forest disturbance are anticipated to alter forest structure and successional patterns (Dale et al. 2001). The influence of these changes on forest development trajectories, stream light, and light-associated stream processes will be an important area of research as we evaluate stream responses to climate change.

Conclusions

Many riparian areas that historically were old-growth forests are currently dominated by younger stands because of landuse legacies (Pan et al. 2011), and we suggest that as a result, the distribution of stream light availability has shifted. Most PNW second-growth forests are <100 y old (Pan et al. 2011), and our results indicate that streams adjacent to these forests probably are exhibiting either: 1) decreasing light availability as canopies close, or 2) minimum light levels associated with closed canopies and stands in the stem-exclusion phase of development. Stand development is ongoing, and successional processes may be reset by natural or anthropogenic stand-replacement events. In the absence of new stand-replacing disturbances, these forests probably will develop greater complexity and increased stream light as dynamic canopy gaps form. Overall, understanding the interactions among riparian forest stand development, canopy cover, and stream light will enhance our understanding of stream ecosystems and how they may change in the future.

ACKNOWLEDGEMENTS

Author contributions: MJK contributed to the initial study design and field work, and wrote most of the manuscript. DRW contributed to the initial study design, helped frame ideas, produced some of the figures, and wrote some of the manuscript. PMK helped frame and edit the manuscript.

We thank Brian VerWey, Emily Heaston, Graham Takacs, Gavin Jones, and Lauren Still for their field sampling efforts. Comments from Michael Pollock, Ivan Arismendi, Jonathan Armstrong, and 2 anonymous referees substantially improved this manuscript. Results from this study were presented at the 2015 Society for Freshwater Science meeting by MJK, and an award for this presentation has covered publishing costs in *FWS*, which we greatly appreciate. Summer 2015 fieldwork was supported by National Science Foundation grant DEB 1547628 awarded to DRW. Facilities and logistical support at the HJ Andrews Experimental Forest were provided through funding from the National Science Foundation's Long-Term Ecological Research Program (DEB 1440409), the US Forest Service Pacific Northwest Research Station, and Oregon State University.

LITERATURE CITED

Aho, R. S. 1976. A population study of the cutthroat trout in an unshaded and shaded section of stream. MS Thesis, Oregon State University, Corvallis, Oregon.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. H. Hogg, P. Gonzalez, R. Fensham, Z. Zhang, J. Castro, N. Demidova, J. H. Lim, G. Allard, S. W. Running, A. Semerci, and N. Cobb. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660–684.

Bechtold, H. A., E. J. Rosi-Marshall, D. R. Warren, and J. J. Cole. 2012. A practical method for measuring integrated solar radiation reaching streambeds using photodegrading dyes. Freshwater Science 31:1070–1077.

Benda, L. E., P. Bigelow, and T. M. Worsley. 2002. Recruitment of wood to streams in old-growth and second-growth redwood forests, northern California, U.S.A. Canadian Journal of Forest Research 32:1460–1477.

Bilby, R. E., and P. A. Bisson. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. Canadian Journal of Fisheries and Aquatic Sciences 49:540–551.

British Columbia Ministry of Forests. 1995. Riparian management area guidebook. British Columbia, Ministry of Forests, Victoria, British Columbia. (Available from: https://www.for.gov.bc.ca/tasb/legsregs/fpc/fpcguide/riparian/rip-toc.htm)

Cairns, M. A., and K. Lajtha. 2005. Effects of succession on nitrogen export in the west-central Cascades, Oregon. Ecosystems 8: 583–601.

Caissie, D. 2006. The thermal regime of rivers: a review. Freshwater Biology 51:1389–1406.

Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223–232 *in* T. L. Shore, J. E. Brooks, and J. E. Stone (editors). Mountain Pine Beetle Symposium: Challenges and Solutions. Natural Resources Canada, Canadian Forest Service, and Pacific Forestry Centre, Victoria, British Columbia.

Clapcott, J. E., and L. A. Barmuta. 2010. Forest clearance increases metabolism and organic matter processes in small headwater streams. Journal of the North American Benthological Society 29:546–561.

Cordes, L. D., F. M. R. Hughes, and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. Journal of Biogeography 24:675–695.

Cudmore, T. J., N. Björklund, A. L. Carroll, and B. Staffan Lindgren. 2010. Climate change and range expansion of an aggressive bark beetle: evidence of higher beetle reproduction in naïve host tree populations. Journal of Applied Ecology 47:1036–1043.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. H. Hanson, L. C. Irland, A. E. Lugo, C. J. Peterson, D. Simberloff, F. J. Swanson, B. J. Stocks, and M. B. Wotton. 2001. Climate change and forest disturbances. BioScience 51:723–734.

Decamps, H., M. Fortune, F. Gazelle, and G. Pautou. 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecology 1:163–173.

De Groot, J. D., S. G. Hinch, and J. S. Richardson. 2007. Effects of logging second-growth forests on headwater populations of coastal cutthroat trout: a 6-year, multistream, before-and-after field experiment. Transactions of the American Fisheries Society 136:211–226.

FEMAT (Forest Ecosystem Management Assessment Team). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Forest Ecosystem Management Assessment Team, Portland, Oregon. (Available from: http://www.blm.gov/or/plans/nwfpnepa/FEMAT-1993/1993_%20FEMAT_Report.pdf)

Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology 13:133–144.

Fiala, A. C. S., S. L. Garman, and A. N. Gray. 2006. Comparison of five canopy cover estimation techniques in the western Oregon Cascades. Forest Ecology and Management 232:188–197.

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

Gregory, S. V. 1980. Effects of light, nutrients, and grazers on periphyton communities in streams. PhD Dissertation, Oregon State University, Corvallis, Oregon.

Gregory, S. V., G. A. Lamberti, D. C. Erman, K. V. Koski, M. L. Murphy, and J. R. Sedell. 1987. Influences of forest practices on aquatic production. Pages 233–255 *in* E. O. Salo and T. W. Cundy (editors). Streamside management: forestry and fishery interactions. Institute of Forest Resources, University of Washington, Seattle, Washington.

Groom, J. D., L. Dent, L. J. Madsen, and J. Fleuret. 2011. Response of western Oregon (USA) stream temperatures to contemporary forest management. Forest Ecology and Management 262: 1618–1629.

Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786.

Harrington, C. 2006. Biology and ecology of red alder. Red alder—a state of knowledge. General Technical Report PNW-GTR-669. US Department of Agriculture, Forest Service, Portland, Oregon.

Hedman, C. W., D. H. Van Lear, and W. T. Swank. 1996. In-stream large woody debris loading and riparian forest seral stage associations in the southern Appalachian Mountains. Canadian Journal of Forest Research 26:1218–1227.

Henderson, J. A. 1978. Plant succession on the *Alnus rubra*/*Rubus spectabilis* habitat type in western Oregon. Northwest Science 52:156–167.

Hibbs, D. E., and P. A. Giordano. 1996. Vegetation characteristics of alder-dominated riparian buffer strips in the Oregon Coast Range. Northwest Science 70:213–222.

Hill, W. R., M. G. Ryon, and E. M. Schilling. 1995. Light limitation in a stream ecosystem: responses by primary producers and consumers. Ecology 76:1297–1309.

Iverson, L. R., and A. M. Prasad. 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68:465–485.

Johnson, S. L. 2004. Factors influencing stream temperatures in small streams : substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 61:913–923.

Johnson, S. L., and J. A. Jones. 2000. Stream temperature responses to forest harvest and debris flows in western Cascades, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 57:30–39.

Julian, J. P., M. W. Doyle, and E. H. Stanley. 2008a. Empirical modeling of light availability in rivers. Journal of Geophysical Research 113:G03022.

Julian, J. P., S. Z. Seegert, S. M. Powers, E. H. Stanley, and M. W. Doyle. 2011. Light as a first-order control on ecosystem structure in a temperate stream. Ecohydrology 4:422–432.

Julian, J. P., E. H. Stanley, and M. W. Doyle. 2008b. Basin-scale consequences of agricultural land use on benthic light availability and primary production along a sixth-order temperate river. Ecosystems 11:1091–1105.

Keeton, W. S., C. E. Kraft, and D. R. Warren. 2007. Mature and old-growth riparian forests: structure, dynamics, and effects on Adirondack stream habitats. Ecological Applications 17: 852–868.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. Journal of Applied Ecology 40:1060–1076.

Kiffney, P. M., J. S. Richardson, and J. P. Bull. 2004. Establishing light as a causal mechanism structuring stream communities in response to experimental manipulation of riparian buffer width. Journal of the North American Benthological Society 23:542–555.

Lamberti, G. A., and A. D. Steinman. 1997. Primary production in stream ecosystems. Journal of the North American Benthological Society 16:95–104.

Lau, D. C. P., K. M. Y. Leung, and D. Dudgeon. 2009. Are autochthonous foods more important than allochthonous resources to benthic consumers in tropical headwater streams? Journal of the North American Benthological Society 28:426–439.

Lee, P., C. Smyth, and S. Boutin. 2004. Quantitative review of riparian buffer width guidelines from Canada and the United States. Journal of Environmental Management 70:165–180.

Liang, L., and S. Fei. 2013. Divergence of the potential invasion range of emerald ash borer and its host distribution in North America under climate change. Climatic Change 122:1–12.

McClain, M. E., E. W. Boyer, C. L. Dent, S. E. Gergel, N. B. Grimm, P. M. Groffman, S. C. Hart, J. W. Harvey, C. A. Johnston, E. Mayorga, W. H. McDowell, and G. Pinay. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312.

McCutchan, J. H., and W. M. Lewis, Jr. 2002. Relative importance of carbon sources for macroinvertebrates in a Rocky Mountain stream. Limnology and Oceanography 47:742–752.

McTammany, M. E., E. F. Benfield, and J. R. Webster. 2007. Recovery of stream ecosystem metabolism from historical agriculture. Journal of the North American Benthological Society. 26:532–545.

Mellina, E., and S. G. Hinch. 2009. Influences of riparian logging and in-stream large wood removal on pool habitat and salmonid density and biomass: a meta-analysis. Canadian Journal of Forest Research 39:1280–1301.

Minore, D., and H. Weatherly. 1994. Riparian trees, shrubs, and forest regeneration in the coastal mountains of Oregon. New Forests 8:249–263.

Moore, R. D., D. L. Spittlehouse, and A. Story. 2006. Riparian microclimate and stream temperature response to forest harvesting: a review. Journal of the American Water Resources Association 41:813–834.

Murphy, M. L., and J. D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Naiman, R. J., C. A. Johnston, and J. C. Kelley. 1988. Alteration of North American streams by beaver. BioScience 38:753–762.

Obedzinski, R. A., and C. G. Shaw. 2001. Declining woody vegetation in riparian ecosystems of the western United States. Western Journal of Applied Forestry 16:169–181.

Overpeck, J., D. Rind, and R. Goldberg. 1990. Climate-induced changes in forest disturbances and vegetation. Nature 343:51–53.

Pan, Y., J. M. Chen, R. Birdsey, K. McCullough, L. He, and F. Deng. 2011. Age structure and disturbance legacy of North American forests. Biogeosciences 8:715–732.

Paradis, A., J. Elkinton, K. Hayhoe, and J. Buonaccorsi. 2008. Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. Mitigation and Adaptation Strategies for Global Change 13:541–554.

Pastor, J., and W. Post. 1988. Response of northern forests to CO_2-induced climate change. Nature 334:55–58.

Pollock, M. M., T. J. Beechie, M. Liermann, and R. E. Bigley. 2009. Stream temperature relationships to forest harvest in Western Washington. Journal of the American Water Resources Association 45:141–156.

Pollock, M. M., R. J. Naiman, H. E. Erickson, C. A. Johnston, J. Pastor, and G. Pinay. 1995. Beaver as engineers: influences on biotic and abiotic characteristics of drainage basins. Pages 117–126 *in* C. G. Jones and J. H. Lawton (editors). Linking species and ecosystems, Springer Science and Business Media, Dordrecht, The Netherlands.

Quinn, J. M., A. B. Cooper, M. J. Stroud, and G. P. Burrell. 1997. Shade effects on stream periphyton and invertebrates: an experiment in streamside channels. New Zealand Journal of Marine and Freshwater Research 31:665–683.

Reeves, G. H., J. E. Williams, K. M. Burnett, and K. Gallo. 2006. The aquatic conservation strategy of the Northwest Forest Plan. Conservation Biology 20:319–329.

Reilly, M. J., and T. A. Spies. 2015. Regional variation in stand structure and development in forests of Oregon, Washington, and inland northern California. Ecosphere 6:1–27.

Richardson, J. S., R. J. Naiman, and P. A. Bisson. 2012. How did fixed-width buffers become standard practice for protecting freshwaters and their riparian areas from forest harvest practices? Freshwater Science 31:232–238.

Romero, N., R. E. Gresswell, and J. L. Li. 2005. Changing patterns in coastal cutthroat trout (*Oncorhynchus clarki clarkii*) diet and prey in a gradient of deciduous canopies. Canadian Journal of Fisheries and Aquatic Sciences 62:1797–1807.

Sabater, F., A. Butturini, E. Martí, and I. Muñoz. 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. Journal of the North American Benthological Society 19:609–620.

Sedell, J. R., and F. J. Swanson. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. Pages 9–16 *in* W. R. Meehan, T. R. Merrell, and T. A. Hanley (editors). Fish and wildlife relationships in old-growth forests. Proceedings of a symposium held in Juneau, Alaska. American Institute of Fisheries Research Biologists, Morehead City, North Carolina.

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

Stovall, J. P., W. S. Keeton, and C. E. Kraft. 2009. Late-successional riparian forest structure results in heterogeneous periphyton distributions in low-order streams. Canadian Journal of Forest Research 39:2343–2354.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions American Geophysical Union 38:913–920.

Summers, R. P. 1982. Trends in riparian vegetation regrowth following timber harvesting in western Oregon watersheds. MS Thesis, Oregon State University, Corvallis, Oregon.

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

Vannote, R. L., W. G. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Van Pelt, R., T. C. O'Keefe, J. J. Latterell, and R. J. Naiman. 2006. Riparian forest stand development along the Queets River in Olympic National Park, Washington. Ecological Monographs 76:277–298.

Villarin, L. A., D. M. Chapin, and J. E. Jones. 2009. Riparian forest structure and succession in second-growth stands of the central Cascade Mountains, Washington, USA. Forest Ecology and Management 257:1375–1385.

Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

Warren, D. R., S. M. Collins, E. M. Purvis, M. J. Kaylor, and H. A. Bechtold. 2016a. Spatial variability in light yields co-limitation of primary production by both light and nutrients in a forested stream ecosystem. Ecosystems. doi:10.1007/s10021-016-0024-9

Warren, D. R., W. S. Keeton, H. A. Bechtold, and E. J. Rosi-Marshall. 2013. Comparing streambed light availability and canopy cover in streams with old-growth versus early-mature riparian forests in western Oregon. Aquatic Sciences 75:547–558.

Warren, D. R., W. S. Keeton, P. M. Kiffney, M. J. Kaylor, H. A. Bechtold, and J. Magee. 2016b. changing forests—changing streams: riparian forest stand development and ecosystem function in temperate headwaters. Ecosphere 7:1–19.

Warren, D. R., C. E. Kraft, W. S. Keeton, J. S. Nunery, and G. E. Likens. 2009. Dynamics of wood recruitment in streams of the northeastern US. Forest Ecology and Management 258:804–813.

Wootton, J. T. 2012. River food web response to large-scale riparian zone manipulations. PLoS ONE 7:e51839.

Yard, M. D., G. E. Bennett, S. N. Mietz, L. G. Coggins, L. E. Stevens, S. Hueftle, and D. W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, AZ. Ecological Modelling 183:157–172.