Comparing streambed light availability and canopy cover in streams with old-growth

versus early-mature riparian forests in western Oregon

Dana R. Warren[1]*, William S. Keeton[2], Heather A. Bechtold[3], Emma J. Rosi-Marshall[3]

[1] Oregon State University,
  Department of Fisheries and Wildlife,
  109 Nash Hall
  Corvallis, Oregon 97330

[2] University of Vermont
  Rubenstein School of Environment and Natural Resources
  343 Aiken Center,
  Burlington, VT 05405.

[3] Cary Institute of Ecosystem Studies,
  P.O. Box AB,
  Millbrook, New York 12545

*Corresponding Author
    Dana R. Warren, Ph.D.
    Department of Fisheries and Wildlife,
    Oregon State University
     109 Nash Hall, Corvallis, Oregon
    97330
    dana.warren@oregonstate.edu
    541-737-5319

Abstract

Light availability strongly influences stream primary production, water temperatures and resource availability at the base of stream food webs. In headwater streams, light is regulated primarily by the riparian forest, but few studies have evaluated the influence of riparian forest stand age and associated structural differences on light availability. In this study, we evaluate canopy cover and streambed light exposure in four second-order streams with paired reaches of primary old-growth versus second-growth mature riparian forests. Stand age class is used as a proxy here for canopy complexity. We estimated stream canopy cover using a spherical densiometer. Local streambed light exposure was quantified and compared within and between reaches using fluorescein dye photodegradation. Reaches with complex old-growth riparian forests had frequent canopy gaps which lead to greater stream light availability compared to adjacent reaches with simpler second-growth riparian forests. We quantified light exposure at relatively high resolution (every 5m) and also found greater variability in stream light along the reaches with old-growth riparian forests in three of the four streams. Canopy gaps were particularly important in creating variable light within and between reaches. This work demonstrates the importance of the age, developmental stage, and structure of riparian forests in controlling stream light. The highly variable nature of light on the stream benthos also highlights the value of multiple measurements of light or canopy structure when quantifying stream light.

Key words: Riparian forest, stream light, PAR, Solar radiation, canopy gap, sunfleck

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Introduction

55   Forested headwater streams are important landscape features with tightly coupled

56   aquatic-terrestrial linkages (Fisher and Likens 1973; Wallace et al. 1997). In addition to

57   well-established influences of riparian forests on allochthonous carbon inputs, and stream

58   structural characteristics (e.g. large wood) (Wallace et al. 1997; Sabater et al. 2000; Bott et

59   al. 2006; Warren et al. 2007), riparian forests strongly influence autotrophic production

60   and temperature in streams by regulating light availability (Johnson 2004; Bott et al. 2006;

61   Julian et al. 2008; Kreutzweiser et al. 2009). Light availability is a fundamental organizing

62   feature in both aquatic and terrestrial ecosystems, and the factors controlling light can

63   have both direct and indirect influences on a range of ecosystem processes. In headwater

64   streams specifically, light is a key factor limiting primary production (Boston and Hill 1991;

65   Hill et al. 1995; Von Schiller et al. 2007; Julian et al. 2011).

66   Most studies quantifying the influence of riparian forests on stream light and

67   temperature dynamics have focused on the presence or absence of forests within the

68   riparian area with limited consideration for the age, developmental condition, disturbance

69   history, or structural complexity of the riparian forest when present (Noel et al. 1986; Bilby

70   and Bisson 1992; Hill et al. 1995; Stone and Wallace 1998; Sabater et al. 2000). There is

71   increasing recognition, however, that variation among forest developmental stages, with

72   associated differences in stand structure characteristics, in the riparian zone can strongly

73   affect stream light and associated ecosystem processes (Valett et al. 2002; Nislow and Lowe

74   2006; Stovall et al. 2009; Brooks et al. 2012). In this study we use the well-documented

75   history of a USFS experimental forest in the Cascade Mountains of western Oregon to

76 identify four replicate streams where we could establish a case study of paired stream

77 reaches in close proximity to one another but with riparian forest dominated by either

78 structurally complex old growth forest or more structurally simple mature riparian cover.

79 By comparing light between the paired reaches in each stream, we evaluated whether

80 differences in riparian forest stand structure translate to associated differences in stream

81 light availability.

82   As has been widely demonstrated in both natural and planned experiments,

83 removing riparian vegetation and the shade that it provides leads to increased primary

84 productivity and numerous changes to stream ecosystem processes, such as net ecosystem

85 metabolism and food web dynamics (Noel et al. 1986; Bilby and Bisson 1992; Stone and

86 Wallace 1998; Roberts et al. 2007). More subtle changes in stream light availability have

87 also been shown to alter the availably of periphyton at the base of stream food webs

88 (Kiffney et al. 2004; Wootton 2012; Matheson et al. 2012;). Many of the studies evaluating

89 or manipulating cover and light in streams assume a relatively uniform light environment

90 when shading is present (e.g. Hill and Dimick 2002; Johnson et al. 2009; Matheson et al.

91 2012). This may indeed hold for streams with riparian forests in the early stages of stand

92 development (Nislow and Lowe 2006) or in cases where stream width is the driver of

93 changing light (Finlay et al. 2011; Julian et al. 2011), however, it is unlikely that light

94 availability is uniform in systems with old-growth riparian forests where frequent canopy

95 gaps can create "hotspots" of light on the stream benthos (Keeton et al. 2007; Stovall et al.

96 2009). In this study we explicitly evaluate the issue of spatial variability in light along a

97 stream reach. We hypothesize that stream reaches with old-growth riparian forests will

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98   have both higher mean light levels and greater variability in light than stream reaches with

99   more uniform second-growth riparian forests.

100   Secondary forests recovering either from 19th century land-use in the eastern U.S.,

101   or 20th century logging in the Pacific Northwest, are the predominant riparian cover along

102   much of the stream network in these regions (Pan et al. 2011). Now in various stages of

103   structural development (Franklin et al. 2002), these mostly young to mature riparian

104   forests tend to have less heterogenous canopy structure both vertically and horizontally

105   (Van Pelt and Franklin 2000; Keeton et al. 2007). In the Pacific Northwest in particular,

106   second-growth forests dominate much of the landscape with many of these regrowing

107   forest comprised primarily of a single cohort of early-successional deciduous or coniferous

108   trees. This is in contrast to the pre-European settlement condition in which landscapes

109   were dominated by primary forests with complex, often old-growth structures, including

110   variable tree density, frequent forest gaps, multiple canopy layers, and higher densities of

111   large living and dead trees (Franklin et al. 2002; Keeton 2006; D'Amato et al. 2009; Curzon

112   and Keeton 2010). These changes in age-class distribution and stand structure are likely to

113   have profound consequences for light dynamics along low order streams, since canopy

114   architecture strongly influences light attenuation. Light attenuation is often spatially and

115   temporally transient in tall, complex canopies due to solar position, for example creating

116   low-angle sunflecks originating from spatially offset canopy gaps (Chen and Black 1992;

117   Chen and Cihlar 1995; Van Pelt and Franklin 2000). Yet the vast majority of research on

118   stream ecosystem function in forested streams has been conducted in young and early-

119   mature second growth forests; systems where in-stream light is low and the influence of

120   heterotrophic processes is large relative to autotrophy. Our understanding of forest-

121 stream interactions and the influence of forests on stream ecosystems may be incomplete if

122 the interactions between streams and the associated riparian forest do indeed differ in

123 these younger simpler forests and older more complex forests.

124

Methods

Study site

127   This study was conducted in four headwater streams, each having a paired up and

128 downstream sample location, in the HJ Andrews Experimental Forest (hereafter "HJAEF")

129 located in the Cascade Mountains of western Oregon. There were eight study reaches in

130 total. Riparian forests investigated in our study were dominated by Douglas fir

131 (*Pseudotsuga menziesii,* Franco) in two different age classes, early mature (dominant trees

132 40 – 60 years) and old-growth (dominant trees ∼ 500 years). The juxtaposition of recently

133 logged stands with adjacent stands of old-growth forest in the same watershed creates a

134 unique opportunity to compare the influence of stand age and structure on light dynamics

135 in upstream vs. downstream reaches of individual streams. Comparing riparian forest

136 stand structure along a single stream eliminates the stream-to-stream variability that often

137 complicates comparisons across streams.

138   The HJAEF encompasses the Lookout Creek basin on the eastern side of the Cascade

139 Mountains in central Oregon (44.2 latitude and 122.2 longitude). This region has a

140 maritime climate with wet, mild winters and dry, cool summers. The elevation of the four

141 study streams ranges from about 500 m (Stream 3) to about 1100 m (Stream 4). The old-

142 growth forests in this area are dominated by Douglas-fir, western hemlock (*Tsuga*

143 *heterophylla* (Raf.) Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don). Dominant

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144 canopy trees in the old-growth forests are about 500 years old. The second-growth forests

145 are dominated by Douglas fir but red alder (*Alnus rubra,* Bong.) also regenerates naturally

146 in some areas creating a localized deciduous overstory. Understory trees were limited in

147 the second-growth riparian forests adjacent to Streams 1-3. Stream 4 also had an

148 understory of vine maple (*Acer circinatum*).

149   We selected four second-order fish-bearing headwater streams in the HJAEF that

150 were representative of low-order streams in the study area (bankfull widths between 3.0

151 and 7.3 m, gradients between 3% and 10% and basins that were unmodified apart from

152 forest management over the past 20 to 60 years). Each stream had adjacent reaches with

153 riparian zones that contained primary old-growth or mature second-growth forests and

154 which were generally reflective of different canopy structures – homogeneous closed

155 canopy (mature second-growth) versus frequent canopy gaps (primary old-growth). We

156 deliberately focused on second-order fish-bearing headwater streams for two reasons.

157 First, the presence of fish sets a biologically relevant size limit, which also has implications

158 for riparian buffer delineation and management (Gregory 1997). And, because small

159 streams create little to no break in the canopy directly over channels, they represent

160 systems where riparian forest influences on light availability if present are strongest

161 (Finlay et al. 2011). Because influences of riparian forest structure have not been well

162 explored, we are focusing first on the systems where hypothesized differences in stream

163 light associated with the different stand ages are likely to manifest most clearly.

164   We first surveyed two south-facing streams in mid-July 2012. McRae tributary

165 (Stream 1), had an 80m long upstream section that was clearcut 59 years prior to our study

166 and a contiguous 80m long downstream section of old-growth forest (circ. 500 yrs). Study

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167 reaches were about 300 m apart with no tributaries entering between the reaches. The

168 second-growth stand was not actively replanted in this site and was instead allowed to

169 regenerate naturally following harvest. Regeneration of Douglas fir at this site was strong,

170 with recruitment well established within a few years post-harvest (Table 1).

171   The second stream is a headwater section of McRae Creek (Stream 2). This site had

172 a 100m long upstream reach of old-growth riparian forest and a 100m long downstream

173 reach in which the riparian forest had been cut in 1958 (Table 1). The managed forest at

174 this site was replanted after harvest (Table 1). The study reach with old-growth riparian

175 forest was about 200 m upstream of the reach with the second-growth riparian forest.

176   We surveyed our other two study streams in mid-September 2012. Gipsy Camp

177 Creek (Stream 3) is a small tributary draining a northwest-facing watershed that runs

178 directly into the Lookout Creek mainstem. The upstream section of this stream was

179 harvested in 1952. The site was replanted with Douglas fir and had strong growth of

180 Douglas fir seedlings (Table 1). The downstream section of this stream has not been

181 harvested. We established 70m study reaches in sections with the two age classes of

182 riparian forest. Study reaches were about 400m apart. The managed forest at this site

183 underwent a pre-commercial thin of saplings in 1965 and a commercial thinning in 2000

184 (Mark Schultz, Director HJ Andrews Experimental Forest).

185   The fourth and final reach pair was established in Upper Lookout Creek (Stream 4).

186 This reach pair had an upstream section with a second-growth riparian forest and a

187 downstream section with an old-growth riparian forest. In contrast to the other three

188 streams, it took ten years after harvest before acceptable stocking and canopy cover were

189 reached for Douglas fir and even then the stem density at this site was reported as being

190 low relative to the second-growth forests along the other managed forest stream reaches

191 (Mark Schultz, HJ Andrews Experimental Forest, personal communication). This relatively

192 poor establishment of Douglas fir resulted in different composition and structure of the

193 riparian forest relative to the other second-growth sites. The second-growth reach at

194 Upper Lookout Creek had fewer conifers next to the stream but there was an understory

195 cover of vine maple (*Acer circinatum*), which shaded the stream. Although second-growth

196 forest stand structure differed here, we selected this site as a representative of this

197 alternative recovery trajectory. Study reaches were about 50m apart at this site.

198

199 *Field Measurements*

200 We used two methods to estimate stream light availability across the eight study

201 reaches. First, we used a spherical densiometer to quantify forest cover over the stream

202 every five meters. Spherical densiometers use a convex reflective lens with a pre-defined

203 grid on which one estimates canopy coverage. Densiometer measurements are not a direct

204 measure of stream light; they are an estimate of canopy cover that is often used as a proxy

205 for light availability. A number of studies have noted that densiometer measurements are

206 prone to observer bias and sometimes less accurate than other measures of canopy (Vales

207 and Bunnell 1988; Tinya et al. 2009). Yet densiometers do correlate with potential PAR in

208 many cases (Comeau et al. 1998) and it remains the most commonly applied method to

209 estimate or account for potential light availability in stream ecosystem studies (e.g. Nislow

210 and Lowe 2006; Kreutzweiser et al. 2009; Moslemi et al. 2012; Riley and Dodds 2012). We

211 were interested in quantifying the relationship between densiometer-based canopy cover

212 estimates and specific quantified light measurements collected at a high frequency along

213 each stream reach to assess potential error in this method as a proxy for benthic light

214 exposure in stream studies. We avoided observer bias in our densiometer measurements

215 by ensuring that the same individual conducted all of the estimates.

216   Point locations for densiometer readings were established systematically every five

217 meters along the thalweg of each stream reach. At these points, a single densiometer

218 operator estimated the percent overhead cover from each of four directions – upstream,

219 downstream, left bank, and right bank (Kelley and Krueger 2005). It should be noted that

220 the frequency of densiometer measurements here is high compared to other studies. We

221 chose this close spacing in order to match densiometer values with specific in-stream light

222 data collected at the same 5 m intervals. This high frequency in survey locations leads to

223 overlap in the canopy included in adjacent survey locations, and can therefore result in

224 counting a given gap (or tree crown) multiple times. Therefore although our analysis

225 comparing densiometer measurement to the dye photodegradation values used all data

226 points, we used only the densiometer values collected every 15 m to estimate the overall

227 mean percent cover along each study reach (see below).

228   The method that we used to estimate light reaching the bottom of the stream (the

229 stream benthos) is a new technique which quantifies light exposure based on the

230 photodegradation of a fluorescent dye (Bechtold et al. 2012). We deployed an array of

231 three replicate dye vials every five meters at each of the same locations where densiometer

232 measurements were conducted. Prior to deployment dye concentrations were measured in

233 each vial on a Turner Designs Aquaflor fluorometer (Turner Designs, Sunnyvale, CA). The

234 vials were then attached to a wire flag that was secured to the stream benthos with rocks.

235 Neither the flag nor the rocks securing the vial array shaded the vials. We used fluorescein

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236 dye in this study which photodegrades rapidly (within a day in full sunlight; see Bechtold et

237 al. 2012 for details) and we therefore implemented short deployments (two to three days).

238 After deployment, we collected vials from the stream and placed them directly into a

239 darkened cooler. All samples were allowed to sit in the dark in the lab for 24 hours so that

240 they would return to the temperature at which concentrations were initially measured (the

241 temperature of the sample can affect fluorometic reading – see Bechtold et al. 2012). The

242 concentration of fluorescein in each vial was then measured on the same Aquaflor

243 fluorometer. In addition to the open vials deployed in the field for light exposure, we also

244 included a foil covered "field-dark" sample every 20 m. These field "blanks" were used to

245 correct for non-light related changes in concentration (e.g. poor seals on the caps leading to

246 dilution of the sample). We compared photodegradation responses only between reaches

247 in the same stream. We did not compare photodegradation values across streams because

248 deployment times (one to three days) and dates of deployment (mid-summer versus late-

249 summer) differed between streams.

250

251 *Data analysis*

252 　　We compared the direct measure of light availability (dye decay) and indirect

253 measure of light potential (canopy cover) between the old-growth and second-growth

254 riparian forest reaches separately in each of the four streams using a single-factor ANOVA.

255 To avoid the inclusion of overlapping canopy images from adjacent densiometer sampling

256 locations, we used the canopy cover data from sites every 15 m (rather than every 5 m) in

257 the comparison of canopy cover between the two age classes along each reach. The

258 distribution of the data from each reach were tested for normality (values every 15m for

259 densiometer and values every 5 m for dye photodegradation). In most cases data were

260 normally distributed, except for the densiometer data in the second growth section of

261 Stream 1, dye photodegradation data the old-growth section of Stream 1, the second-

262 growth of Stream 3, and the old-growth section of Stream 4. In order to make consistent

263 comparisons within and among sites all data were natural log-transformed for analysis.

264 For the figures, however, we used the actual values to allow for easier interpretation and

265 comparison to other studies. We used linear regression analysis to compare values from

266 the mean densiometer readings with the mean dye photodegradation at each site location

267 (every 5 m) in each reach. The linear regression was run on the natural log transformed

268 data. To more clearly illustrate the spatial dynamics and correlation between dye

269 photodegradation and cover, we plotted photodegradation values against the inverse of

270 our cover values (i.e. open space) from each location. Finally, in order to evaluate the

271 hypothesis that light in the old growth forest streams would be more variable than in the

272 second-growth forest streams, we compared the standard deviations of the densiometer

273 values (measurements every 15m in each reach) and natural-log transformed dye

274 photodegradation values (measurements every 5 m in each reach) from the four old-

275 growth reaches (n = 4) versus the four second-growth reaches (n = 4) using an ANOVA.

276

Results

278   Both methods, measuring potential (densiometer) or actual (dye photodegradation)

279 light exposure in the stream, indicated that headwater streams with old-growth riparian

280 forests are likely to receive more light than streams with early-mature riparian forests in

281 mid-and late-summer (Figure 1). The differences in stream light availability and percent

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282 forest cover between old-growth and second-growth reaches were significant in both of the

283 south-facing watersheds (Streams 1 and 2) in mid-summer at an alpha of 0.01 for the dye

284 results and 0.10 for the cover results (dye photodegradation analysis: $p < 0.001$, F= 35.67,

285 and $p < 0.001$, F = 19.09 for Stream 1 and Stream 2, respectively; densiometer analysis: p =

286 0.06, F= 4.41, and p = 0.03, F = 5.87 for Stream 1 and Stream 2, respectively; Table 2, Figure

287 1). Light availability results on the stream benthos, as measured by dye photodegradation,

288 in the north-facing watersheds were broadly consistent with results from the south-facing

289 watersheds, but the differences between old-growth and second growth riparian forest

290 reaches were significant only at Stream 3 (p = 0.013, F= 7.09, and p = 0.227, F = 1.51 for

291 Stream 3 and Stream 4, respectively; Table 2, Figure 1). Similarly, differences in canopy

292 cover over the old-growth reach was significantly lower in Stream 3 (p = 0.027, F= 7.32)

293 but not in Stream 4 (p = 0.262, F= 1.39; Table 2, Figure 1). In comparing the standard

294 deviation of forest cover between age classes statistically and visually (Figures 2-5),

295 streams with old-growth riparian forests had greater variability in cover (p = 0.006, F =

296 17.7). Average variability in streambed light exposure was also generally greater in

297 streams with old-growth riparian forests than in those with mature second-growth forests,

298 however, the difference was not significant (p = 0.275, F = 1.44).

299 　　　　There was a significant negative relationship between the mean photodegradation

300 loss and the cover estimate from densiometer readings in three of the four streams (p<

301 0.001, for Streams 1, 2, and 4; p = 0.34 for Stream 3; Figure 6), but the correlations were

302 poor as predictive relationships. Riparian forest cover directly over each sampling area

303 explained less than a third of the variability in dye decay in the three streams where we

304   found significant relationships between photodegradation and canopy cover (r^2 = 0.35,

305   0.29, 0.24 for Streams 1, 2, and 4, respectively; Figure 6).

306

Discussion

308   Overall, we found support for the hypothesis that headwater streams with complex

309   old-growth riparian forests receive more light in summer than streams with uniform

310   riparian forests that are in the early-mature stage of stand development. Canopy closure

311   along streams with old-growth riparian forests was also generally more spatially variable

312   than in streams with second-growth riparian forests. This corresponded with greater

313   variability in stream benthic light availability, although the canopy gaps did not necessarily

314   correlate directly overhead with the areas of greater light on the streambed due to the

315   effects of transient, spatially offset light (i.e. sunflecks) that can increase light to a large

316   degree some distance from a given gap. The irregular canopy gaps in old-growth forests

317   studied here created a mosaic of light on the stream benthos, with a mix of high and low

318   light availability patches. The young second-growth forest streams, in contrast, had

319   consistently lower light availability. Overall, light in the streams studies here has the

320   potential to be highly dynamic. Light varies spatially along a reach but it can also vary over

321   the day and over seasons as sun angle changes, and it can vary on decadal and centennial

322   time scales as riparian forests develop structural complexity (Van Pelt et al. 1992; Chen and

323   Black 1992). These results highlight the spatially complex nature of light in streams and

324   suggest that transient or offset light attenuation through complex forest canopies affects

325   both local and total light availability. The importance of sunflecks and light attenuation has

326   been well documented in terrestrial ecosystems (Sims and Pearcy 1993, Chen and Cihlar

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327 1995; Van Pelt and Franklin 2000; Pearcy and Way 2012;) and warrants similar

328 consideration in forested streams.

329   The method comparison here indicated that a mean densiometer value from

330 multiple points along a stream provide an accurate general picture of potential stream light

331 exposure at the reach scale and therefore potential light penetration to the stream benthos,

332 but this method may be inappropriate for quantifying light availability at specific locations

333 in the stream. Although there were significant correlations between the densiometer value

334 and the dye photodegradation across locations in three of the four streams, the relationship

335 strengths were surprisingly poor. In the sites where the correlation was significant, canopy

336 cover over a given point in the stream never explained more than 45% of the variability in

337 benthic light exposure (as measured by dye photodegradation). Despite poor correlation

338 on a point-by-point basis, when considered on a whole-reach basis, the two methods

339 yielded similar overall results in regard to stream light.   This suggests that for small

340 headwater streams, estimating canopy cover regularly along a reach may capture

341 influences of forest gaps even if the location of the light associated with a specific gap was

342 not necessarily directly related to the densiometer measurement location.

343   The poor correlation between these two methods highlights the need to consider

344 the whole of the riparian forest, not just a single point. Our results indicate that canopy

345 gaps can increase light in areas adjacent to the gap more than to the areas directly below

346 the gap, depending upon the angle of the sun (varying daily and seasonal time

347 scales)(Canham 1988; Van Pelt et al. 1992; Van Pelt and Franklin 2000). The process of

348 transient, spatially offset light (sunflecks) has been shown to be an important feature in

349 upland forests with implications for understory plant community dynamics (e.g. see Van

350 Pelt and Franklin 2000 or Pearcy and Way 2012). Similarly, in streams where riparian

351 canopy gaps create sunflecks, light intensity will vary along the streambed and throughout

352 the day and year. Spatially and temporally transient sunflecks may be an important, but to

353 date, unstudied consideration in forested headwater streams.

354   Unlike the relatively uniform increases in light associated with increasing stream

355 size or manipulations using shade cloth, the differences in light between streams with

356 complex old-growth riparian forests and those with young even-aged riparian forests are

357 due to the presence of high light patches. This can translate to local and patchy increases in

358 primary production. DeNicola et al. (1992), for example, compared both hemispheric-

359 photos and PAR meter measurements at four locations along a single stream with 4

360 different canopy structures and found greater periphyton standing stocks in the sites with

361 less canopy cover (and therefore more light). Stovall et al. (2009) working across streams

362 with a range of riparian forest stand structures in the northeastern US also found greater

363 periphyton standing stocks in systems with more gaps in the canopy. Patch size and

364 frequency are clearly important in projecting how these local responses scale up to whole-

365 ecosystem processes, but to date the question of how these potential localized hotspots of

366 productivity translate to whole-stream ecosystem processes has not been widely

367 evaluated.

368   The riparian forest age classes in this study were representative of two different

369 stand development conditions with associated variation in stand structural complexity. We

370 compared light associated with the complex structure of an old growth riparian forest,

371 having variable canopy heights and multiple canopy gaps based on field observations, to

372 what we initially assumed would be fairly uniform closed-canopy riparian forest in the

16

373 second-growth sites. This was broadly true in regard to canopy gaps. The densiometer

374 assessments documented more and larger gaps in reaches with the old-growth riparian

375 forests compared to those with the second-growth riparian forests. However,

376 observational assessments of the second-growth riparian forests suggested greater

377 variability among these sites than initially anticipated and highlighted the importance of

378 considering thinning history, regeneration history, and degree of vertical layering when

379 using age class as a proxy for structure.

380   Light availability in the two north-facing streams broadly supported results from

381 the two south-facing streams, but the magnitude of the differences in light exposure were

382 not as large. We attribute this more moderate difference in benthic light exposure and

383 canopy cover to three primary factors. First, as noted above, forest regrowth was poor

384 along the previously logged section of Stream 4. While there was understory cover above

385 the stream, we observed less canopy cover from larger trees than in any of the other sites

386 with regenerating Douglas fir forests. There was more diffuse light reaching the stream in

387 this Upper Lookout Creek reach (Stream 4). At Stream 3, the managed site is part of an

388 active stand thinning experiment and was thinned within the past 10 years. In addition to

389 aspect and management history, the Streams 3 and 4 surveys were conducted later in the

390 summer when the sun angle was lower. These factors likely contributed to the more

391 moderate differences in benthic stream light availability as measured with the dye

392 photodegradation in streams 3 and 4.   This highlights the importance of considering not

393 only aspect but cloud cover and total daylight hours when using this new method.

394

395 *Conclusions*

396   The results from this study and related work in other regions demonstrate that

397 stand development conditions and the structural complexity of riparian forests are

398 important in controlling stream light (Nislow and Lowe 2006; Keeton et al. 2007; Stovall et

399 al. 2009). Riparian forests are changing across North America as ecosystems recover from

400 historic landuse, undergo species invasions, change in response to altered climate, and

401 experience new management pressures (Foster et al. 1998; Snyder et al. 2002).

402 Understanding how riparian forest structure – not just the presence or absence of a

403 riparian forest – relates to fundamental drivers of stream ecosystem processes such as light

404 and temperature will improve our understanding of how these landscape scale changes in

405 the forests will influence headwater streams.

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Figure Legends

564 Figure 1. Mean percent cover and mean loss in fluorescein in each of four reach pair with

565 old-growth (dark bars) and second-growth (light bars) riparian forests. Error bars

566 represent one standard deviation. Astrix symbols represent significant differences at p <

567 0.1 (*) and p < 0.05 (**).

568

569 Figure 2. Linear profile of fluorescein photodegradation and canopy cover estimate

570 densiometer measurements along the stream profile for old growth (a) and second growth

571 (b) reaches in Stream 1.

572

573 Figure 3. Linear profile of fluorescein photodegradation and canopy cover estimate

574 densiometer measurements along the stream profile for old growth (a) and second growth

575 (b) reaches in Stream 2.

576

577 Figure 4. Linear profile of fluorescein photodegradation and canopy cover estimate

578 densiometer measurements along the stream profile for old growth (a) and second growth

579 (b) reaches in Stream 3.

580

581 Figure 5. Linear profile of fluorescein photodegradation and canopy cover estimate

582 densiometer measurements along the stream profile for old growth (a) and second growth

583 (b) reaches in Stream 4.

584

585   Figure 6. Regressions of the natural log of percent cover estimates versus natural log of

586   fluorescein dye photodegradation (reflecting actual stream benthic light exposure).

587   Greater photodegradation indicates greater light exposure over the duration of

588   deployment. Lines indicate significant relationships between canopy cover and benthic

589   light exposure in Stream 1 (p <0.001, r^2 = 0.35), Stream 2, (p < 0.001, r^2 = 0.29) and Stream

590   4 (p < 0.001, r^2 = 0.24). The relationship was not significant in Stream 3 (p = 0.34, r^2 =

591   0.03)

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595 **Tables**

596 Table 1. Riparian forest and stream characteristics at each of the eight study reaches.

Stand type	Year of cut	Year of stand origin	Management notes	Estimated age of dominant canopy trees	Reach length (m)	mean (SE) bankfull width (m)	# LW per 100m
Stream 1							
old-growth	-	-	-	500	80	4.1 *(0.43)*	60
second-growth	1953	na	natural regeneration	59	80	3.6 *(0.12)*	53
Stream 2							
old growth	-	-	-	500	100	7.3 *(0.12)*	28
Second-growth	1958	1960	Planted; single thinning	52	100	6.6 *(0.14)*	14
Stream 3							
old growth	-	-	-	500	70	3.1 *(0.11)*	54
second growth	1952	1956	Planted; multiple thinnings	56	70	2.5 *(0.7)*	60
Stream 4							
old growth	-	-	-	500	90	4.6 *(0.51)*	39
second growth	1971	1981	poor regeneration; no thinning	31	90	3.0 *(0.08)*	13

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601 Table 2. Mean and standard deviation of the percent canopy cover and fluorescein

602 photodegradation for each reach.

603

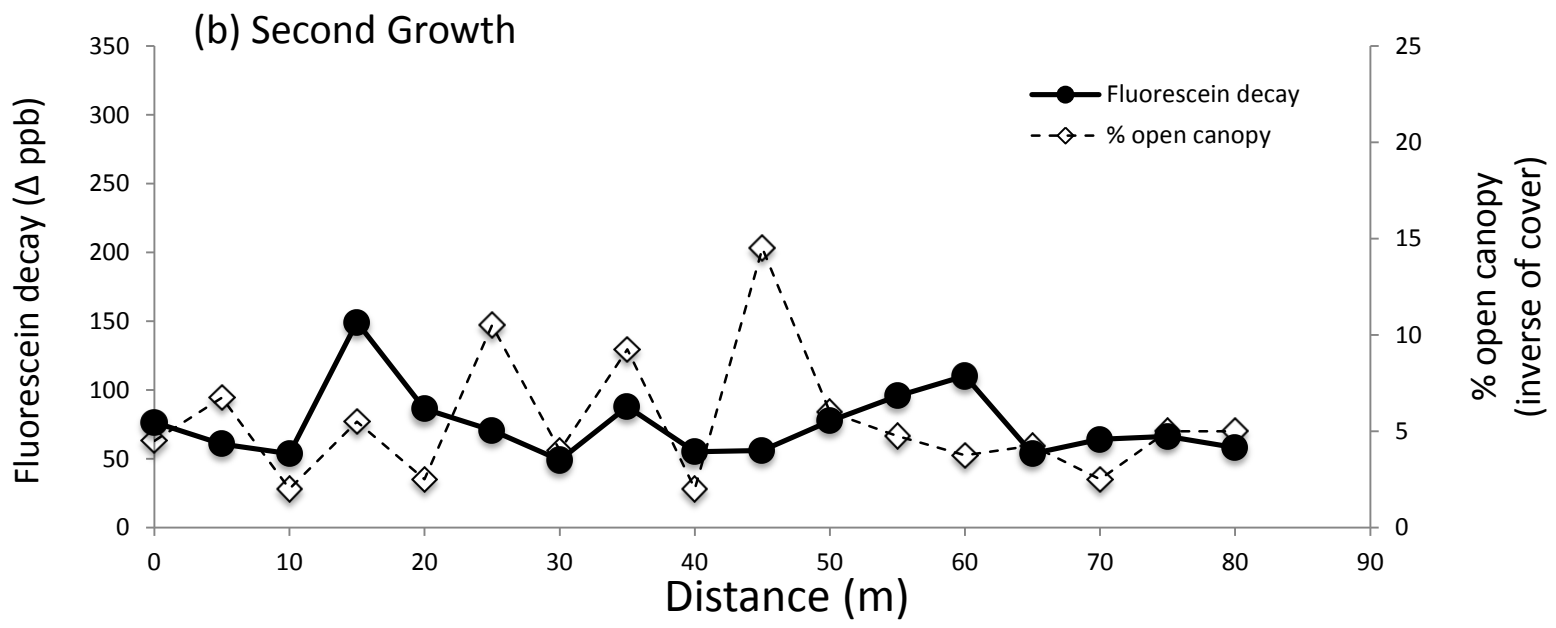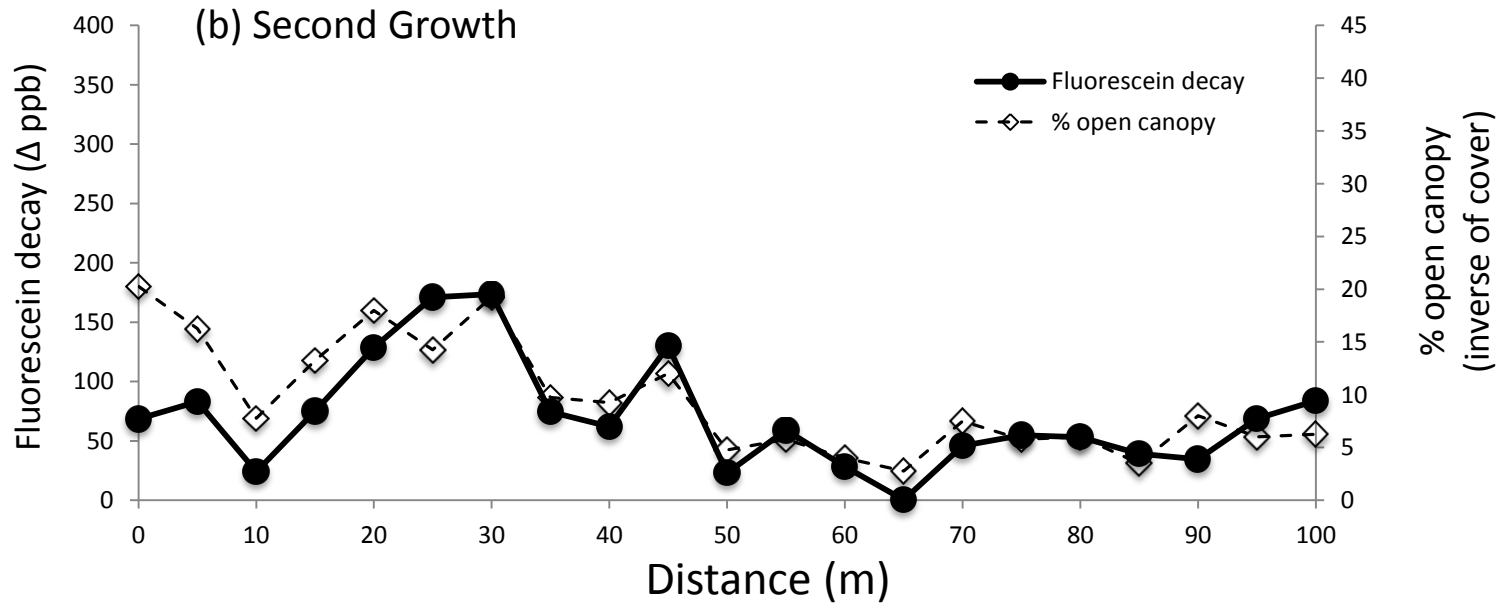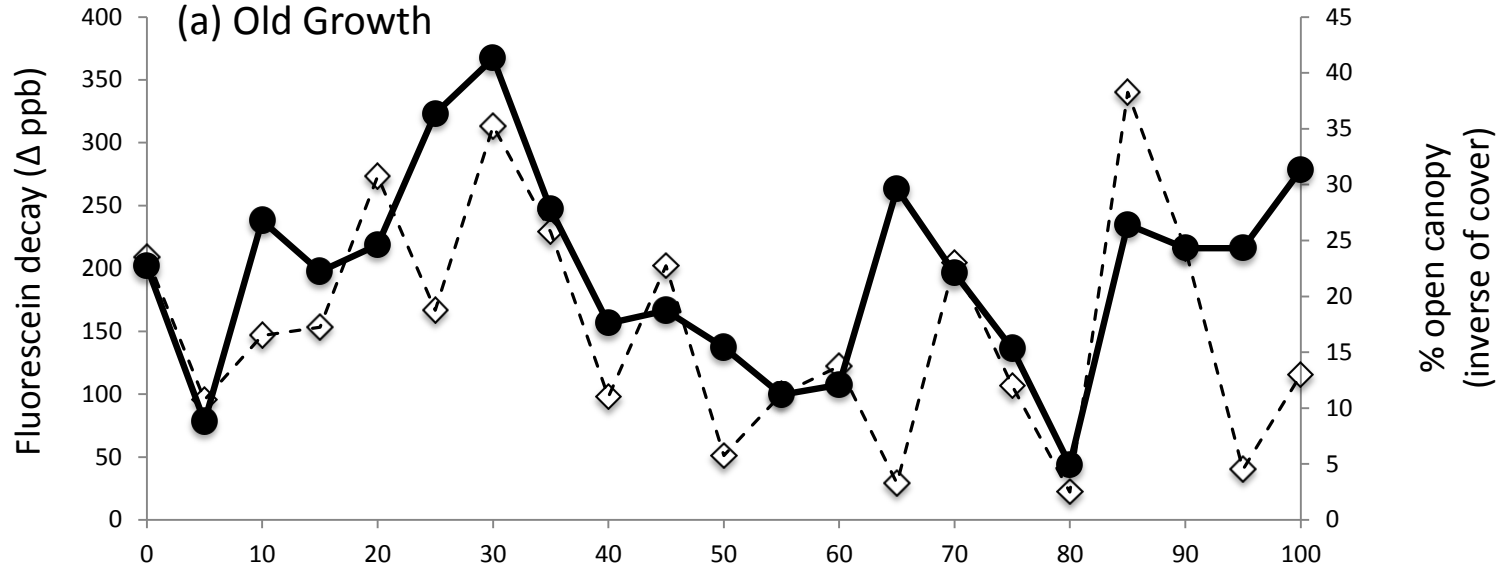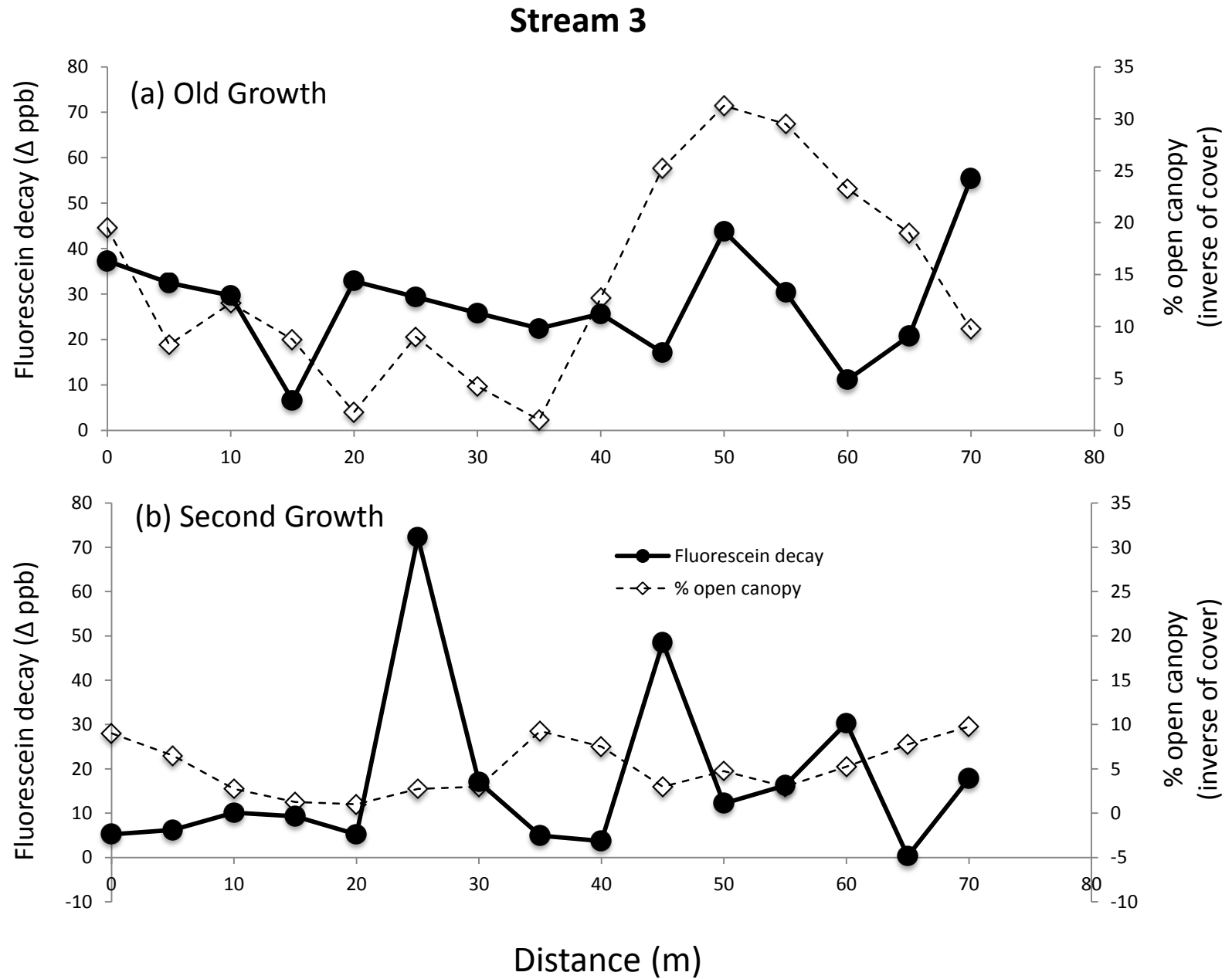| Stream	Riparian forest age class	Densiometer			Fluorescein dye		
		mean	n	standard deviation	mean Δ in concentration	n	standard deviation of Δ in concentration
Stream 1							
	old-growth	86.2	6	7.28	159.2	17	68.1
	second-growth	93.5	6	4.28	74.7	17	25.6
Stream 2							
	old-growth	77.9	7	8.17	196.4	21	79.9
	second-growth	87.7	7	6.59	70.5	21	46.2
Stream 3							
	old-growth	83.2	5	9.60	28.1	15	12.2
	second-growth	95.5	5	3.11	17.3	15	19.5
Stream 4							
	old-growth	89.1	7	8.06	54.7	19	36.8
	second-growth	92.9	7	3.10	38.6	19	17.8

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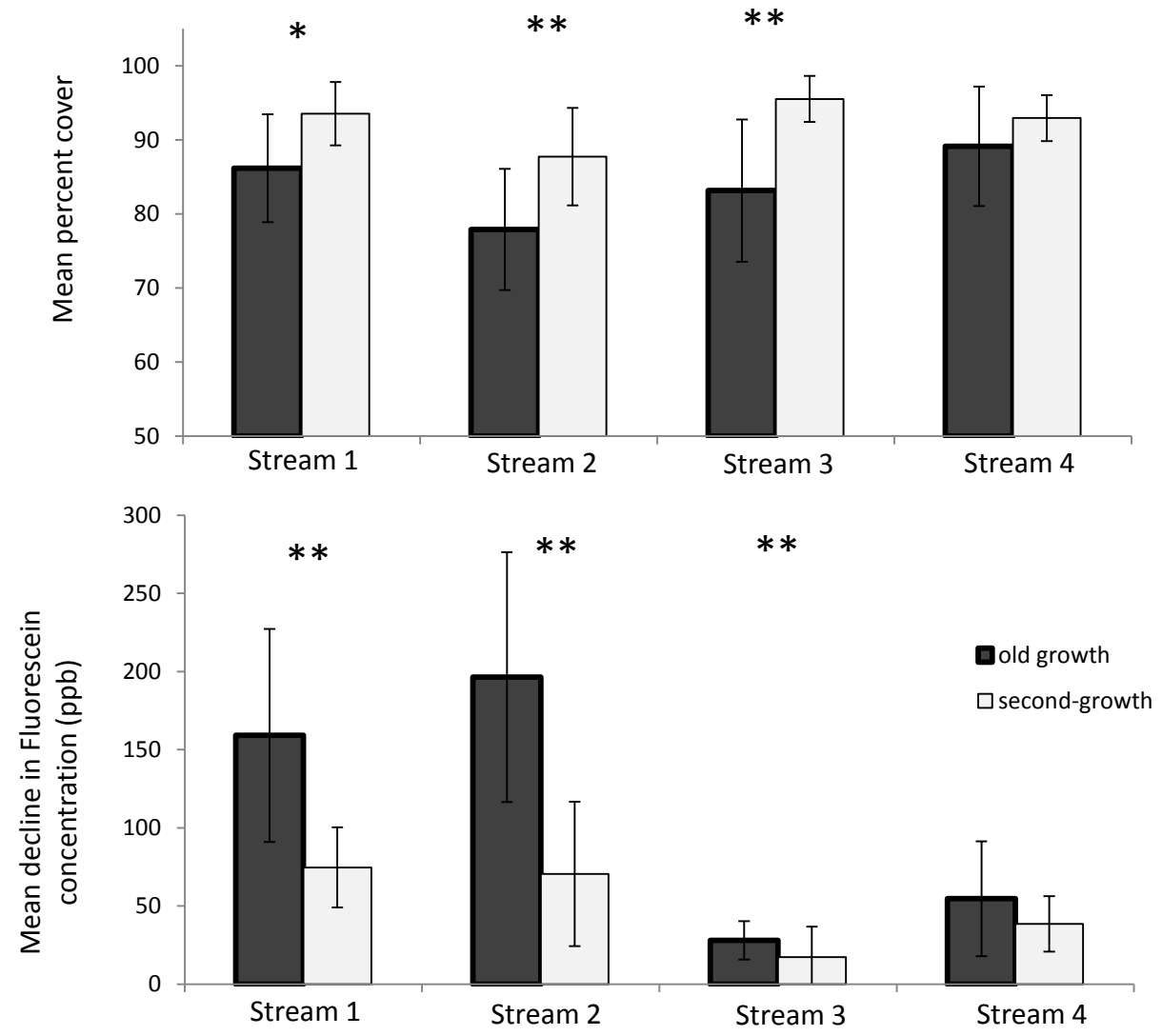
Figure 1

Figure 2

Stream 1

Figure 3

Stream 2

(a) Old Growth

(b) Second Growth

Figure 4

Stream 3

(a) Old Growth

(b) Second Growth

Distance (m)

Figure 5

Figure 6