

**UNDERSTORY LIGHT AND VEGETATION
IN TWO FLOODPLAIN FORESTS
IN COASTAL BRITISH COLUMBIA**

by

Ian J.W. Giesbrecht
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APPROVAL

Name: Ian J.W. Giesbrecht
Degree: Master of Resource Management
Project No.: 508
Title of Thesis: Understory light and vegetation in two floodplain forests in coastal British Columbia

Examining Committee:

Chair: Matthew Tutsch

Kenneth P. Lertzman
Senior Supervisor
Professor of Resource and Environmental Management
Simon Fraser University

Andy MacKinnon
Research Ecologist, Coast
BC Ministry of Natural Resource Operations

Sari C. Saunders
Research Ecologist, Coast
BC Ministry of Natural Resource Operations

Alton Harestad
Professor Emeritus, Department of Biological Sciences
Simon Fraser University

Date Defended/Approved:

ABSTRACT

Understanding the interactions of environmental and vegetation characteristics is necessary for effective ecosystem management. I examined how environmental heterogeneity affects understory vegetation within older floodplain stands in coastal temperate rainforests. In two one-hectare sites, I estimated vegetation and environment characteristics on a systematic grid and generated maps of understory light transmission. Both sites have $\geq 92\%$ area in canopy gap or expanded gap and abundant (18% full sun), spatially variable understory light. Within sites, understory composition varies over short distances in correlation with light transmission. Shrub cover increases with light and may play a role in maintaining the amount and spatial pattern of canopy openness. At one site, point diversity decreases as light increases, suggesting that shady microsites can provide refugia from intense competition. Management practices encouraging canopy openness and spatial heterogeneity in second growth stands may accelerate development of similar processes and patterns; this prediction should be evaluated experimentally.

Keywords: riparian forest; canopy gaps; light transmission; environmental heterogeneity; understory vegetation; species diversity.

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INTRODUCTION

Understanding how communities are organized by environmental gradients and disturbance processes is a fundamental aim of many ecologists (Whittaker 1975, Grime 1979, Huston 1994, Ritchie 2010). Environmental heterogeneity plays a role in the spatial and temporal patterns of composition, structure, and function in ecosystems ranging from coral reefs and tropical forests to northern wetlands and pastures (Connell 1978, Pollock et al. 1998, Grime 2001). Environmental heterogeneity is one of the factors that creates and maintains species diversity (MacArthur and MacArthur 1961, Whittaker 1975, Grime 1979, Denslow 1985, Huston 1994, Ritchie 2010). Disturbance plays an important role in the creation and maintenance of environmental heterogeneity (Pickett and White 1985), and may interact with productivity to determine levels of species diversity (Huston 1979). In forest ecosystems with long intervals between high severity, stand replacing disturbances, small-scale disturbances to the forest canopy increase the availability and heterogeneity of resources (Runkle 1984, Denslow 1985, Canham et al. 1990), with consequences for the productivity, composition, and diversity of understory vegetation (Denslow 1985, Mladenoff 1990, McCarthy 2000, Chávez and Macdonald 2010).

Gap phase processes are the creation of gaps in forest canopy by patchy tree mortality, the subsequent filling of gaps by establishment, release, and growth of young trees, and lateral growth of canopy trees (Watt 1947, Bray 1956). Gap phase processes produce spatial heterogeneity of structure, light, and other plant resources, within forest stands (Denslow 1985, Canham et al. 1990, Lertzman et al. 1996, Frazer et al. 2000a, McCarthy 2000, Franklin and Van Pelt 2004, Griffiths et al. 2010). In many cases, distinct differences are observed between gaps and closed canopy areas, in terms of canopy openness or light transmission (Levey 1988, studies reviewed by Coates and Burton 1997) and understory vegetation (Levey 1988, Mladenoff 1990, Goldblum 1997).

Despite the sometimes stark differences between gaps and closed canopy areas, the patterns and processes of light transmission are often more complex than can be

adequately described by a gap versus closed-canopy dichotomy (Lieberman et al. 1989). Particularly in higher latitude forests, the angle of solar insolation causes a spatial offset of understory light patterns from the vertical projection of canopy gaps (Canham et al. 1990). Attenuation in subcanopy and understory vegetation layers also modifies spatial patterns of light transmission (Messier et al. 1998, Montgomery and Chazdon 2001). Thus, in addition to the ubiquitous effects of slope and aspect, the spatial effects of an opening in the forest canopy on light patterns in the understory can be displaced or diffused from the actual gap by the effects of tall canopies, latitude, and intervening canopy layers. As a result, canopy gap and closed canopy areas in high latitude forests may have similar mean light levels due to variation within both gaps and closed canopy areas (Bartemucci et al. 2002).

Even where gap and closed canopy sites are distinct, dichotomizing the broad distribution of openness can obscure a great deal of potentially ecologically meaningful variation in light within both gaps and closed canopy (Lieberman et al. 1989). Characterizing the continuous distribution of light increases our ability to make sense of the spatial patterns of light and how light drives understory vegetation characteristics (Lieberman et al. 1989, Nicotra et al. 1999, Frelich et al. 2003, Chávez and Macdonald 2010). For example, continuous sampling allows us to better describe the interactions of diversity and productivity: the shape and predictability of this relationship is currently debated by ecologists (e.g., special Forum in Ecology 91(9), 2010). If we take light as an indicator of (potential) productivity, diversity could have a positive, negative, or hump shaped relationship (Grace 1999, Mittelbach et al. 2001, Gillman and Wright 2006, Whittaker 2010) with light transmission.

Key problems for riparian coastal temperate rainforest research

Gap-phase processes and environmental heterogeneity may influence the ecology and management of an important and understudied ecosystem type: riparian forests in the coastal temperate rainforest (CTR). These are among the most productive forests in North America, with floodplain stands attaining among the highest canopy volumes on earth (Van Pelt et al. 2006). As a result, these stands contain immense amounts of sequestered

carbon. These forests also support high understory vegetation biomass, tend to have higher plant species diversity than upland forests (Gregory et al. 1991, Pabst and Spies 1998, Smith 2005), and host productive occurrences of numerous culturally important plant species (Turner 1998). Riparian forests in the CTR also provide valuable habitat for a diversity of wildlife species, and interact with river systems in ways that create and maintain salmon habitat and linkages between terrestrial and marine ecosystems (Gregory et al. 1991, Peterson et al. 1997, Naiman et al. 2000, Naiman et al. 2010).

Despite the ecological and social significance of these forests, we lack sufficient understanding of their patterns and dynamics. Existing research on riparian forests in the coastal temperate rainforests of North America (Schoonmaker et al. 1997) represents a small sample of bioregional, latitudinal, climatic, and floristic variation. This has implications for the application of ecological knowledge to management. Research is only beginning to unveil the multiscale mechanisms that create and maintain plant diversity in riparian forests of the CTR (e.g., Pabst and Spies 1998, Pollock et al. 1998, Smith 2005, Sarr and Hibbs 2007a). Detailed studies that examine drivers of understory structure and composition (e.g., Fonda 1974, Minore and Weatherly 1994, Pabst and Spies 1999, Wimberly and Spies 2001, Sarr and Hibbs 2007b) and stand dynamics (e.g., Greenwald and Brubaker 2001, Balian and Naiman 2005, Van Pelt et al. 2006, Villarin et al. 2009, Naiman et al. 2010) are more numerous. However, little research on these topics has emerged from British Columbia's extensive portion of the CTR (Peterson et al. 1997, Roburn 2003, Smith 2005), and a number of questions remain unanswered across the bioregion – particularly in relation to within-stand patterns and processes in older floodplain forests.

The roles of gap processes and patterns of light transmission are poorly understood in older floodplain stands of the coastal temperate rainforest. A quantitative description of canopy gap frequency and origin has not been published for riparian forests of the CTR, despite the usefulness of such information for ecological research and forest management elsewhere (e.g., Runkle 1982, Lertzman and Krebs 1991, Lertzman et al. 1996, McCarthy 2000, Bartemucci et al. 2002, Ott and Juday 2002). Gaps typically originate from either tree mortality or edaphic conditions (Lertzman et al. 1996). Gaps can be maintained as persistent openings when understory plants limit conifer recruitment

(Henderson 1978, Harmon and Franklin 1989, Tappeiner et al. 1991, Minore and Weatherly 1994, Lertzman and McGhee 1996, McGhee 1996). Finally, little information is available to describe the amount and spatial patterns of light transmission in older floodplain stands of the CTR. Light transmission estimates were reported for riparian forests in coastal Oregon (Sarr and Hibbs 2007a), but within stand spatial patterns have yet to be examined.

We know that the determinants of riparian understory composition vary with the spatial scale of analysis (Sarr and Hibbs 2007b). For instance, climate appears to be a major determinant of composition across broad regional gradients when locations of substantially different climate are considered (Green and Klinka 1994, Sarr and Hibbs 2007b). However, within areas of similar climate, topographic position (e.g., valley floor, terrace, or hillslope) emerges as a major determinant of edaphic conditions and fluvial disturbances and thus of vegetation composition (Green and Klinka 1994, Pabst and Spies 1998, Sarr and Hibbs 2007b). Differences in light transmission may play a role in driving the compositional patterns observed across topographic gradients (Pabst and Spies 1998). Among sites across Oregon, the abundance of the *Rubus spectabilis* Pursh appears to have a major direct influence on riparian composition and indirectly reflects the climate and topographic position of a site (Pabst and Spies 1998, Sarr and Hibbs 2007b). However, questions remain unanswered about the patterns and drivers of understory composition within floodplain stands of similar climate, topographic position, and fluvial disturbance regime.

We lack sufficient understanding of the drivers of understory plant diversity within and among floodplain stands of the CTR. However, existing research in the CTR suggests that productivity, competition, disturbance, and spatial heterogeneity influence plant diversity in riparian areas. For example, across multiple watersheds in western Oregon, alpha diversity (sensu Whittaker 1977) of woody plants in streamside sites showed a strong negative relationship with both gross primary productivity and the cover of *R. spectabilis* (collinear explanatory variables) (Sarr and Hibbs 2007a). In Alaska, Pollock et al. (1998) sampled 20-m x 50-m (1000-m²) sites with widely different flood regimes and found that alpha diversity had a hump shaped relationship with both mean flood frequency (modeled from microsite elevation) and productivity, and was positively

related to spatial heterogeneity of flood frequency (measured from 55 nested subplots). Point diversity (*sensu* Whittaker 1977) showed a weaker but significant relationship with productivity.

There is also some evidence that stands with greater light heterogeneity have greater understory alpha diversity. Across a broad climatic gradient, Sarr and Hibbs (2007a) found that hectare-scale woody species richness – from a sample including streamside, midslope, and hillslope topographic positions – is directly negatively related to abundance of *R. spectabilis* (and indirectly climate) and topographic heterogeneity, and positively associated with exposed rock and light heterogeneity within stands. However, these authors measured only woody species diversity. Furthermore, composition varies substantially among the three topographic positions of the study sites (Sarr and Hibbs 2007b), indicating that the one-hectare samples may represent more than one plant community. Thus, it is unclear if diversity would also be associated with light heterogeneity among stands of a single riparian community type with relatively homogeneous topographic position and fluvial disturbance regime.

An improved description and understanding of the patterns and processes of vegetation variation within older floodplain forests would be valuable for ecosystem based management in the CTR. Valley bottom forests of the CTR have been preferentially harvested compared to upland forests (Pearson 2010) due to their productivity, timber quality, and accessibility. As a result, the proportion of valley bottom forests in a mature or older developmental stage may be well below the range of natural variability under a natural disturbance regime (Pearson 2010). Furthermore, a number of floodplain plant communities are considered threatened or endangered in coastal British Columbia (Green 2005). Under such circumstances, management regimes that aim to maintain ecological integrity may need to undertake active management to achieve socially desired ecological conditions across a region or landscape (Grumbine 1984, Lertzman et al. 1997, Landres et al. 1999, Price et al. 2009). Where older riparian forests are underrepresented, forest managers may seek to maintain or restore a degree of old-growth character – including diverse and productive understories – in second growth stands (e.g., ongoing restoration of riparian forests at Lyell Island and Kennedy Flats in coastal BC: A. Pearson, personal communication). However, effective management will

require a more complete descriptive and functional understanding of natural examples of this forest type.

Given the knowledge gaps identified above, I aim to extend the body of riparian rainforest research in British Columbia, testing and building on knowledge accumulated from other regions. In particular, I seek to examine fine-scale patterns and drivers of understory light, vascular plant species composition, vegetation structure, and species diversity within two older floodplain stands. I focus on overstory structure as a potential driver of within-stand patterns and processes. I describe patterns observed in two model natural systems, compare those patterns to predictions derived from previous theoretical and empirical research, and subsequently suggest additional support for, or modification to, a conceptual model of selected ecological patterns and driving processes. Specifically, in two structurally contrasting conifer dominated stands on edaphically similar floodplains I will:

- Describe canopy gap structure and fine-scale patterns of light transmission.
- Examine the role of environmental heterogeneity in shaping fine-scale patterns of understory vegetation structure and composition.
- Examine the role of spatial environmental heterogeneity in preventing dominance (enabling co-existence) in highly productive forest stands.
- Examine whether point diversity is negatively associated with productivity, taking light transmission and total understory vascular cover as indicators of understory productivity/biomass within stands.

METHODS

Site descriptions

I conducted my research as a component of the Coastal Old Growth Dynamics Project of the BC Forest Service (www.for.gov.bc.ca/rco/research/eco/oldgrowthforests/oldgrowthdynamics/index.htm). The project is a continuation and expansion of a long term old-growth forest monitoring study initiated by Dr. Paul Alaback and Fred Nuzdorfer in 1992 and 1993. In 2007 and 2008, a research team led by Andy MacKinnon and Dr. Sari Saunders of the BC Forest Service re-measured and expanded a number of these plots. Upon resampling, the original 50-m x 50-m plots were expanded to 100-m x 100-m (one-hectare) in size. All trees and coarse woody debris were measured and mapped in each one-hectare area, and understory vegetation and environmental attributes were described in 25 subplots. The broad goals of the project are to better understand the patterns and dynamics of coastal old-growth structure and composition and to facilitate other research with applications to ecosystem based management.

I studied two sites which occur within the submontane variant of the very wet maritime subzone of the Coastal Western Hemlock zone (CWHvm1) of the British Columbia coast (Meidinger and Pojar 1991). Carmanah is located in Carmanah Walbran Provincial Park on the west coast of Vancouver Island and the Kitlope site is located in the Kitlope Heritage Conservancy Area, at the end of Gardener Canal on BC's North Coast (Figure 1 and Table 1). Mean annual precipitation for the CWHvm1 in the (former) Vancouver Forest Region is 2682 (1555-4387) mm, summer (May-Sept.) precipitation is 611 (364-1162) mm, mean temperature of the warmest month is 16.3 (13.8-18.8) °C, and growing degree days average 1633 (1313-2011) (Green and Klinka 1994) (Table 1). At the Old Growth Dynamics website (as above), these sites are described in more detail.

In the following, I describe the study sites using data collected for the Old Growth Dynamics Project. Both the Kitlope and Carmanah stands are High Bench floodplain sites with edaphic conditions and the corresponding *Picea sitchensis* – *Rubus spectabilis* Plant Association for Site Series CWHvm1/09 (Green and Klinka 1994, A. MacKinnon personal communication 2008). This ecosystem type is among the most productive in British Columbia (Peterson et al. 1997). In general, Green and Klinka (1994) describe High Bench sites as “the highest and most infrequently flooded (>5 year return interval) portion of a floodplain” (p. 72). Although the local flood regime has not been determined for either study site, field observations suggest that Kitlope has recently (<1 year) experienced a low energy depositional flood event and both sites have experienced one or more flood events in recent decades (alluvial deposition at tree bases and/or alluvial deposition over organic horizons).

Field data show that the soil is a fine textured alluvium with varying degrees of humus development at each site. At Carmanah, median thickness of LFH (organic horizons: BC Ministry of Forests and BC Ministry of Environment Lands and Parks 1998 – hereafter BC MoF and MELP 1998) is 3.5 cm over a 1.3 cm Ah horizon (humus enriched mineral horizon: BC MoF and MELP 1998). Leptomodors (Green et al. 1993) are the dominant humus form (75% frequency). At Kitlope, recently buried forest floors predominate and a recognizable humus form has yet to (re)develop; typically (median) 0.5 cm of fresh litter covers a 1.0 cm unmodified layer of recent fine fluvial sediment. Below the recent fluvial deposits, a very thin buried litter layer (≤ 0.4 cm) is often found (63% of subplots) on top of median 4.1 cm of moderately humified organic matter. The forest floor is underlain by ≥ 70 cm of fine textured mineral soil at both sites (S. Saunders, personal communication).

In each stand, the largest overstory trees are *Picea sitchensis* (Bong.) Carr., with multiple trees well over 150 cm diameter at breast height (max 283 and 293 cm). Otherwise, the two stands differ substantially in overstory composition and structure, likely reflecting greater age of the Carmanah stand. Stand age has been estimated as 350 years for Carmanah and >90 years for Kitlope (www.for.gov.bc.ca/rco/research/eco/oldgrowthforests/oldgrowthdynamics/index.htm). Carmanah has a negative exponential diameter distribution – as is expected for an old-

growth forest (Giesbrecht 2010). In the small to intermediate diameter classes (i.e., <150 cm DBH), shade tolerant *Tsuga heterophylla* (Raf.) Sarg. is the most abundant species, *Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes is common, and *Picea sitchensis* is virtually absent. Most of the understory *T. heterophylla* are found growing on logs (A. MacKinnon, personal communication). At Kitlope, *P. sitchensis* is more or less equally represented across a broad range of size classes, other conifers are rare, and densities of small trees (<50 cm DBH) are much lower than at Carmanah. At both sites, shade intolerant (Klinka et al. 1989) deciduous species are relatively common in the smaller size classes (<50 cm DBH) – *Malus fusca* (Raf.) Schneid. at Kitlope and *Alnus rubra* Bong. at Carmanah. The occurrence of these tree species suggests that relatively high light levels have been present in at least portions of each stand for many years. Recent conifer regeneration is limited at both sites. At Kitlope, no conifers were observed in the low shrub layer (<2 m) of subplots, and seedlings (all *P. sitchensis*) were reported in only 5 (21%) subplots. At Carmanah, no seedlings and only one conifer <2 m were observed in subplots.

Despite differences in age, both stands show a degree of “old-growthness.” Kitlope lacks large snags, abundant large logs, and abundant *T. heterophylla* development – characteristics expected in the old-growth stage (Wells et al. 1998, Van Pelt et al. 2006, Franklin et al. 2002) – yet these features are present at Carmanah. However, both sites have numerous very large trees, open and structurally diverse canopies, and very productive understory vegetation. These attributes of old-growthness are most relevant to the questions of my study. Floodplain forests develop a degree of old-growth character much earlier than upland forests (Van Pelt et al. 2006). In the Queets Valley, Washington, tree diameter in floodplain forests attained standard deviation characteristic (SD-DBH) of upland old-growth by “early in the second century” (Van Pelt et al. 2006, p. 292). Both Kitlope and Carmanah have SD-DBH (55 and 41 cm respectively) consistent with stands considered old-growth by Van Pelt et al. (2006) in the Queets Valley. For the above reasons, I refer to both the Kitlope and Carmanah stands as *older floodplain forests*. A closer examination of stand history and characteristics would be needed to more precisely embed my study sites within existing conceptual models for

forest developmental stages and pathways (e.g., Franklin et al., 2002, Van Pelt et al. 2006).

Understory vegetation in each site is characterized by high total shrub layer cover (median >75%) dominated by *R. spectabilis* (median $\geq 55\%$). Point species richness of understory vascular plants varies from 5 to 19 species in a 4-m² area (subplot). Understory composition differs between the two stands. For example, *Oplopanax horridus* (Smith) Miq. is present only at Kitlope; *Polystichum munitum* (Kaulf.) K. B. Presl is present only at Carmanah. Both sites have composition within the expected variation of the *Picea sitchensis* – *Rubus spectabilis* plant association in the CWHvm1 (Green 2005). However, at both my study sites median *R. spectabilis* cover is higher and median *O. horridus* cover is lower than typical of the 49 sites described by Green (2005). This comparison illustrates that these sites represent only two data points for a plant association that varies substantially across the region (Green 2005).

Sampling

In 2007 and 2008, a research team led by Andy MacKinnon and Sari Saunders – both of the BC Ministry of Forests and Range – sampled two 100-m x 100-m (one-hectare) macro-plots. These were re-measurements and expansions of 50-m x 50-m plots installed and sampled 15 years earlier by Dr. Paul Alaback and associates. The field team mapped and measured all trees, snags, and coarse woody debris (CWD) in each macro-plot. To study within stand patterns, we sampled understory vegetation and microsite characteristics in 25 2-m x 2-m sub-plots and took hemispheric canopy photographs at 50 points, with all sampling distributed systematically through the macro-plot (Figure 2). In each subplot, we took a canopy photograph, estimated percentage cover of all shrubs, herbs and bryophytes, and described microsite characteristics including humus form, substrate cover, and microtopography. For each plant species, we estimated the percent foliar cover based on a vertical projection of the drip-line to the ground. Subplots had a minimum separation of 20 m and canopy photos had a minimum separation of 14.14 m. Canopy photo locations were offset as necessary to avoid undue impact of very close tree boles, though offsets rarely needed to be applied. If a tree bole was within 60-100 cm of

plot centre, the photo location was offset in the direction of the larger side of the plot. The offset was 60 cm for trees <80 cm DBH and 100 cm for trees \geq 80 cm DBH. Unless noted otherwise, field procedures for vegetation and micro environment characteristics follow Land Management Handbook 25 (BC MoF and MELP 1998). A more detailed description of the field procedures for vegetation, substrate, and canopy photography is available in Giesbrecht (2010) and at the Old Growth Dynamics website.

In each subplot, I recorded canopy cover class (closed canopy, expanded gap, canopy gap) and gap origin (developmental, edaphic, unknown origin) following the methods of Lertzman and Krebs (1991) and Lertzman et al. (1996). An opening in the forest canopy was defined as a canopy gap if it exceeded $\frac{1}{2}$ a tree crown width in diameter. Expanded gap refers to the region from a canopy gap boundary (crown margins) to a line connecting the boles of trees that define the canopy gap. Closed canopy refers to the area beyond the boundary of an expanded gap. Developmental origin gaps have evidence of a gapmaker: a tree that died to create the gap. Edaphic origin gaps are openings associated with edaphic conditions (e.g., stream channel); gap makers may be present but cannot, on their own, explain the opening. Unknown origin gaps are openings not obviously associated with tree mortality or edaphic conditions. Trees \geq 10 m tall, with DBH \geq 22 cm, were considered canopy trees. Because closed canopy microsites were rare, for most analyses I lumped closed canopy and expanded gap and assigned both to “non-gap” for comparison to “gap.” I estimated the percentage of the subplot covered by each of 11 different growth substrate types (with numerous subtypes for coarse woody debris in different size classes and decay stages).

I used a mini soil pit to describe the organic horizons and mineral soil texture of each subplot. For each organic horizon (L, F, and H), as well as Ah or Ae layers if present, I recorded the thickness and any modifier codes necessary to identify humus form. Humus form was identified in the field following BC MoF and MELP (1998), which follows the system of Green et al. (1993). Soil mini pits were installed near subplot centre, but adjusted as necessary to be representative of the subplot (e.g., if there was a small clump of dead wood at subplot centre, we offset from the dead wood). I assessed ‘representativeness’ of humus form classification from this mini-pit by pulling back LFH at a few other locations within the subplot (e.g., to confirm the mycelia predominate over

soil fauna). If necessary, the soil pit was re-sampled and average measurements were recorded. The mineral soil underlying the organic horizons was hand textured. A detailed map of all water bodies was drawn to scale in the field, visually locating water body boundaries in reference to the sub-plot locations and each 20 m grid interval.

Hemispheric canopy photographs were taken above the shrub layer at each photo point, using a Cannon 5D digital SLR camera and the Sigma 8-mm fisheye lens. Photo height varied between sites to ensure a clear view of the overstory was achieved despite changes in mean shrub height between sites (180 ± 5 cm at Carmanah; 195 ± 5 cm at Kitlope). Such minor variations in canopy photograph height have little impact on estimates of canopy structure and light transmission (see literature review by Roburn 2003), yet allowed us to greatly reduce the impact of shrub layer vegetation on photographs intended to estimate overstory structure and light transmission. Shrubs extending above the lens height were pulled away from the field of view. The camera height occasionally needed to be adjusted upwards by 5 to 10 cm to keep ubiquitous shrubs from obscuring canopy openings close to the horizon. We used a custom-built lens plate to register a small LED at the North edge of each image.

Exposure settings were generally adjusted as lighting conditions varied to achieve images with consistently high contrast between foliage and sky. Auto exposure bracketing was generally used to record three images at different exposures – in which case, I selected the highest contrast image that still maintained any small gaps near the horizons (Frazer et al. 2000). I selected images that were underexposed, generally by $1/3$ to $1 \frac{2}{3}$ f-stop, except in a few cases where autoexposure bracketing was not used.

Data preparation and processing

Calculated environmental variables

I calculated three types of environmental variables after collecting the raw field data in each subplot: distance to water, proportion of soil volume in three textural classes, and canopy structure and light transmission from hemispheric canopy photos. For each subplot, the distance to the nearest waterbody was manually estimated from the map of

waterbodies (described above). I also used the SPAW Model with Soil Water Characteristics program (and accompanying spreadsheet) to estimate soil water properties – including saturated hydraulic conductivity (Ks: cm/hr) and Plant Available Water (PAW: cm³ water/cm³ soil) – from field data on soil textural class and coarse fragment content. The SPAW model uses the empirical equations of Saxton and Rawls (2006). I converted textural class data to point estimates of percentage clay and sand content according to the values used in the SPAW model (Saxton and Rawls 2006) (e.g., Silty Clay Loam has 34% clay and 10% sand). The SPAW model is available online (<http://hydrolab.arsusda.gov/SPAW/SPAWDownload.html>) Accessed February 17, 2009). See also Appendix 1.

Hemispheric canopy photograph analysis

I used Gap Light Analyzer Version 2.0 (GLA 2.0) (Frazer et al. 1999, Frazer et al. 2000b) to estimate light transmission and leaf area index from each canopy photograph. Total photosynthetically active radiation (PAR: 400-700 nm) is the sum of direct (beam) and diffuse PAR. Direct radiation emanates from the solar disk and is neither absorbed nor scattered by the atmosphere. Diffuse radiation is scattered toward a point on the ground from all regions of the sky (Frazer et al. 1999).

GLA models light transmission through forest canopies as a function of canopy cover and the light incident above the forest canopy. I used site specific configurations for elevation, latitude, longitude, and growing season, and subplot specific configurations for slope, aspect, and topographic features visible in each photo to generate accurate estimates of light above and below the forest canopy (Frazer et al. 2000b). For regions with seasonally variable climate, such as coastal British Columbia, GLA produces very accurate estimates of light transmission when provided with monthly values for the following three parameters (Frazer et al. 2000a). I developed and used monthly parameters for cloudiness index, spectral fraction, and beam fraction based on solar radiation data collected at the most representative coastal meteorological station (Port Hardy) using equations provided with GLA (Frazer et al. 1999). GLA also requires growing season start and end dates to calculate PAR received over the same period. I

estimated the growing season start and end dates based on a combination of expert opinion (Dr. K. Lertzman, Andy MacKinnon) and local climate normals for growing degree days (degree days above 5°C) and the frost free period.

I calibrated GLA for the Sigma 8-mm F3.5 fisheye lens. This lens uses an equisolid angle projection to display points from the hemisphere onto the circular image plane. However, a projected fisheye image may deviate significantly from design due to angular distortion, making calibration necessary (Herbert 1987, Frazer et al. 1999). I used 24 calibration data points provided by Sigma Corporation to define a custom projection transformation in GLA (Frazer et al. 1999). Given the radial distance and zenith angle of each calibration point, GLA applies a linear interpolation to estimate the radial distance of objects between calibrated points (Frazer et al. 1999). Although most researchers use an n^{th} order polynomial for interpolation, the linear spline (of the form $y=ax+b$) used by GLA has the advantage of preserving the integrity of observed calibration points while achieving accurate prediction between points (G. Frazer, personal communication April 11, 2008)

I took a number of additional steps to ensure accurate results from canopy photo analysis. I derived custom configuration settings for each site before processing the canopy photographs (see Frazer et al. 1999). This included corrections for lens distortion, a locally appropriate growing season, locally appropriate cloud cover parameters, and other data such as elevation, slope, and aspect. GLA requires a manual image thresholding procedure that designates each pixel as sky or non-sky. I used a two thresholding rules for each photograph. First, even the lightest vegetation tones were designated as non-sky following Roburn (2003). Second, I used regional thresholding (Frazer et al. 1999) to avoid loss of smaller gaps near the horizon, or conversely, loss of light foliage adjacent to open sky.

Outliers in the light data can result from sampling and measurement error, or real differences in light levels. To check for errors from GLA processing, I plotted a histogram and boxplot of the percentage total transmission observing likely outliers and extreme values. I then re-processed any outliers or extreme values. The re-processed GLA estimates were always slightly different from the original estimates, as would be

expected, but the differences were not large. I also visually inspected the saved workspace image from the first processing (i.e., a copy of the image after thresholding was done) and confirmed that no obvious mistakes had been made during the initial thresholding. Thus, I concluded that these are valid data points and retained the original GLA estimates.

Precision of light estimates – how much variation is the result of surveyor error?

To provide at least a rough indication of precision with GLA light transmission estimates (i.e., the thresholding procedure), I examined the degree of difference between initial processing and re-processing that was done to check for outliers (see above) in GLA estimates from 9 photographs. Photos were not randomly selected, yet should provide an approximate measure of precision. I found that differences in percentage full sun estimates between runs were 0.31% full sun on average. Differences were never more than 3% full sun; 6 of 9 differed by less than 2% full sun and more than half (5 of 9) were within 1% full sun. Were all photos reprocessed, the resulting precision would be lower than suggested here by a sample of only 9 photos. Extrapolating to the whole population of photos, I think that most of my GLA estimates would be $\pm 2\%$ full sun if reprocessed and few would differ by more than 3%.

Indices of species diversity and dominance

I calculated species richness (S), evenness (E), and dominance (Ls) for each subplot. Species richness is the number of species. Evenness – how evenly cover is distributed among species – is calculated as:

$$E = H / \ln(S)$$

(Pielou 1969)

where H is Shannon diversity index

$$H = -\sum(p_i \ln(p_i)),$$

where p_i is the proportion of cover in the i th species ($p_i = n_i/N$)

(Gurevitch et al. 2002)

Dominance (Simpson's dominance index) expresses the probability that two randomly chosen individuals belong to the same species, calculated as:

$$L_s = D - 1$$

(Gurevitch et al. 2002)

where D is Simpson's diversity index

$$D = 1 / \sum(p_i^2)$$

I used PC-ORD 5 (McCune and Mefford 2006) to calculate S, E, H, and D.

Removal of problem plots

At Carmanah, five subplots that occurred on an elevated bench formation or in flood channel were removed from the dataset before analysis; the elevated bench subplots (3) are judged to be from a different Site Series (more upland), and the channel subplots (2) are unrepresentative of overstory influences on light and vegetation due to the confounding influence of the fluvial channel. For vegetation analyses, I omitted one additional subplot (5,45) because the herbaceous layer and forest floor had been almost entirely buried by recent flood sediment deposits, producing an outlier in multiple analyses. Furthermore, a recent wind disturbance at Carmanah (presumably the winter before sampling) substantially affected three subplots via the direct influence of overstory removal and/or slash accumulation. These subplots were subjected to a sensitivity analysis and removed from subsequent analysis – an effort to control for the temporal lag of understory vegetation response to canopy disturbance (e.g., Nicotra et al. 1999). At Kitlope, one subplot landed in a small waterbody and was not re-sampled at an offset location. As a result of these subplot omissions, the sample size for subplot based analysis is $n=16$ at Carmanah and $n=24$ at Kitlope. For analysis based on all photo points, the sample size is $n=39$ at Carmanah and $n=49$ at Kitlope.

Analysis

Light transmission

For each site, I used ESRI's ArcGIS 9.1 software to display estimated light transmission values on a map of the macroplot. In order to visualize assumed light gradients between sample points, I generated a raster of light values using a tension spline interpolation method. This interpolation method creates a smooth, minimum curvature surface that passes exactly through the data points. To visually represent the interpolated light gradients, I assigned progressively darker shading to progressively lower light transmission categories and drew contours for each 1% full sun isoline. I used box-plots and a two-sample Mann-Whitney *U* test to compare light distributions of canopy gap and non-gap microsites. The test was implemented in the PASW Statistics 18 software package.

Univariate correlation analysis

I used linear correlation analysis to examine relationships among measures of light transmission, vegetation structure, and diversity – accounting for spatial autocorrelation. A number of the vegetation and environment variables in the dataset show positive spatial autocorrelation at 20 m, the minimum distance between subplots (Appendix 2). Spatially autocorrelated data violate the assumption of independence that characterizes most statistical procedures. In correlation analysis, two variables with positive spatial autocorrelation tend to have an inflated Type I error rate (Legendre and Legendre 1998, Dale and Fortin 2002). Due to the potential for positive spatial autocorrelation within stands (e.g., Roburn 2003, Nicotra et al. 1999), I applied Dutilleul's correction for *t*-tests of correlation significance (Dutilleul 1993) in the software PASSaGE v2 (Rosenberg 2009). The Dutilleul procedure uses Moran's *I* estimates of spatial autocorrelation (Appendix 2 and Appendix 3) to compute an effective sample size (n_e) (and degrees of freedom) – the sample size after correcting for spatial autocorrelation (Dutilleul 1993, Fortin and Dale 2005). The corrected sample size (degrees of freedom) is then used in a *t*-test of correlation significance (Dutilleul 1993,

Fortin and Dale 2005). The correction may result in a gain or loss of statistical significance. Positive spatial autocorrelation reduces the effective sample size (n_e), whereas negative spatial autocorrelation can lead to an increased effective sample size (Dale and Fortin 2002). Although an increased effective sample size is a valid result of the Dutilleul correction (MJ Fortin, personal communication, 2009), I took a conservative approach by not declaring statistical significance in cases where applying the Dutilleul correction results in a gain of ‘statistical significance.’ The Dutilleul procedure is robust to departures from a first-order autocorrelation structure and is appropriate for use with a variety of spatial structures (Legendre et al. 2002, Marie-Josie Fortin personal communication, 2009).

Community ordination and environmental gradients

For each site, I used non-metric multidimensional scaling (NMS) (Mather 1976, Kruskal 1964) to reduce and describe variation in species composition on multivariate axes (McCune and Grace 2002 for practical guidance). I conducted the NMS with the Sørensen (Bray-Curtis) distance measure, using the autopilot mode in PC-ORD 5 (McCune and Mefford 2006) with the “slow and thorough” setting. To determine the optimal number of dimensions (axes), the autopilot mode at this setting iteratively computes the stress associated with the best one through six dimensional solutions (250 runs with real data) and selects the highest dimensionality that reduces the final stress by ≥ 5 and has $p \leq 0.05$, based on 250 runs of a Monte Carlo randomization procedure.

To aid interpretation, I rotated the resulting ordination graphs to maximize the correlation of axis 1 with percentage full sun (McCune and Grace 2002). My approach of maximizing the loading of light on axis 1 means that axes 2 and 3 describe compositional variation that is independent of light. At Carmanah, a second variable – LnClay – was a relatively strong correlate ($r^2=0.36$) of one unrotated axis. To aid with interpretation, I used rotation to load LnClay on axis 2, after loading percentage full sun on axis 1, to display and report the maximum correlation that exists in the three-dimensional joint plot.

After applying the rotations, I used a combination of correlations and ordination diagrams to describe the compositional axes in terms of species abundances and to

examine relationships between compositional axes and environmental variables. I used joint plots to relate environment variables to the ordination axes. I assessed the quality of the NMS solution, before and after rotation, based on the proportion of variance in the original data represented by each axis and the three axes cumulatively. This proportion was computed using the Sørensen (Bray-Curtis) distance measure – the same distance measure used in the ordination (McCune and Grace 2002).

Prior to conducting the NMS ordination I deleted rare species: species with less than five occurrences (5/24=21% minimum frequency at Kitlope; 5/16=31% at Carmanah). Based on this rule, I deleted 14 species at Kitlope and 15 at Carmanah, leaving 19 and 15 species respectively. I liberally deleted rare species (e.g., more than McCune and Grace's general rule of 5%) for three reasons. First, to avoid needing to interpret species present in very few sample units. Second, eliminating rare species tends to reduce the noise in the data and enhance detection of structure among remaining species (McCune and Grace 2002). Third, because (at least at Kitlope) deleting this number of rare species reduced the number and severity of outlier subplots compared to deleting fewer rare species (e.g., if I deleted species with less than three occurrences at Kitlope).

I applied a relativization to species abundances instead of using raw abundance data because my interest is more in compositional (relative abundance of species) than structural changes (McCune and Grace 2002). I used a relativization by species maximum¹, which balances the emphasis on dominant species and species with lower abundances, effectively equalizing “the heights of peaks along environmental gradients” (McCune and Grace 2002). After relativizing the data, I applied an arcsine square root transformation to all species to reduce the positive skew that characterizes community data (McCune and Grace 2002, p. 73). These data adjustments improved the diagnostic statistics (skewness, Kurtosis, coefficients of variation). I checked for multivariate outliers more than 2.0 standard deviations from the mean of Euclidean distances. One

¹ Relativization by species maximum adjusts the raw values into a proportion of the maximum cover observed for a given species: $b_{ij}=x_{ij}/x_{maxj}$ where i are subplots, j are species, x_{ij} is the observed cover of j and i , and x_{maxj} is the maximum observed cover of species j .

subplot exceeded this criterion at Kitlope, but marginally so ($SD=2.06$)². This subplot was left in the analysis because it is a weak outlier (i.e., 2-2.3 SD; McCune and Grace 2002), and there was no biological reason to remove it. Similarly, a single subplot exceeded the outlier criterion ($SD=2.67$) at Carmanah, but was left in the analysis because it is not a strong outlier (i.e., <3 SD; McCune and Grace 2002), and there is no clear biological reason to remove it³.

Prior to creating joint plots and correlating ordination axes with environment variables, I applied transformations to improve the normality, skew, and kurtosis of select variables. Other environment variables, such as MTHet – representing microtopographic heterogeneity within subplots – were omitted from the analysis due to a large number of zeros in the dataset producing distributions significantly different from normal (Kolmogorov-Smirnov test). Before interpreting the linear correlation coefficients (of species with axes), I examined the overlay plots for strong non-linearities or influence of outliers. A few species show a nonlinear relationship with axis 1.

² After rotating the ordination results, it is clear that the subplot (Kitlope (25, 45)) is not an outlier on axis 1 or 3 – the two axes that represent the most variation. And, although this represents the maximum value on axis 2, it does not appear to be an outlier (is not far from the cloud of points). Also, I tried removing (25, 45) and rerunning the NMS; the results were similar in terms of the species associated with axis 1, the relative importance of light (compared to other environmental variables), and the roughly similar strength of correlation between light and axis 1. Therefore, I found no good reason to delete it from the analysis.

³ Axis 3 is clearly dedicated to explaining the subplot (5, 25) outlier at Carmanah. However, it is not an outlier on axis 1 or 2.

Composition of gap and non-gap areas

I used a Multi Response Permutation Procedure (MRPP) (Mielke 1984, Mielke and Berry 2001) to test for compositional differences between gap and non-gap areas. MRPP is a non-parametric procedure that requires no distributional assumptions (McCune and Grace 2002)⁴. I calculated and rank transformed a Sørensens⁵ distance matrix and used the group weighting method

$$C_i = n_i / \sum n_i,$$

where n_i is the number of subplots in group i and C_i is the weight applied to each subplot in group i (McCune and Grace 2002). I used Indicator Species Analysis (Dufrêne and Legendre 1997) to describe compositional differences between gaps and non-gaps. Indicator Values range from zero (no indication) to 100 (perfect indication). I used Monte Carlo tests with 4999 permutations to determine if Indicator Values differed between gaps and non-gaps. I used PC-ORD 5 (McCune and Mefford 2006) to execute the MRPP and the Indicator Species Analysis.

⁴ Although MRPP does not require distributional assumptions, the procedure does assume independence of sample units (McCune and Grace 2002). I think gap and non-gap subplots were reasonably independent. I did not directly assess this in the field, but I think most gaps did not have multiple subplots and no individual trees covered multiple subplots. Furthermore, all subplots were separated by at least 20 m. Thus, I think the assumption of independence is not seriously violated.

⁵ Although MRPPs based on Euclidean distances and Sørensens distances often show similar results, Sørensens distances are less sensitive to outliers and are increasingly the distance measure of choice for MRPPs (McCune and Grace 2002).

RESULTS

Gap structure and light transmission in older floodplain stands

Canopy gap structure and origins

Closed canopy microsites are rare at both Kitlope (8%, of $n=50$) and Carmanah (2%, of $n=42$)⁶; at least 92% of each site is in expanded gap or canopy gap (Figure 3). The majority of microsites are under expanded gap (54% at Kitlope, 62% at Carmanah), although canopy gap is also common (38% at Kitlope, 36% at Carmanah). At Carmanah, 27% of canopy gap and 12% of expanded gap microsites are located in an area of recent windthrow (presumably the winter before sampling, when extensive wind disturbance occurred across the BC south coast). Recent windthrow was not observed at Kitlope.

Overall, most gap areas at Carmanah are developmental in origin (83%) – clearly associated with a dead tree – while the remainder (17%) have edaphic origins (Figure 3, Table 2). Surprisingly, few gap microsites at Kitlope are clearly associated with tree mortality (2%) or edaphic factors (9% of gaps).

Understory light transmission

Mean percentage PAR is similar between the study areas but frequency distributions of percentage PAR (hereafter percentage “full sun”) are different (Figure 4). Kitlope and Carmanah each have median 18% full sun⁶ (Table 3). At Kitlope, mean light transmission is $18.8 \pm 4.8\%$ full sun, ranging from 10.0 to 33.9%. At Carmanah, mean

⁶ For the descriptive summary of %CC, EG, CG, I omitted the eight raised bench microsites but kept the channel and recent windthrow in the dataset. I retained the channel microsites for this descriptive summary because the gaps over the channels are likely important sources of light transmission to the understory, including and extending horizontally beyond the channel itself (i.e., could be a source of light to adjacent microsites with understory plants). By contrast, for light descriptives, I omitted the channel microsites because I want to describe light environment only for microsites known to be available to plants (i.e., currently have plants).

light transmission is $17.9 \pm 5.7\%$, and varies from 9.0 to 28.3%. Carmanah has more microsites with $<12.5\%$ full sun and a weak bi-modal distribution, which taken together result in greater variation among microsites (Figure 4 and Figure 5). Light transmission at Kitlope is unimodal and more strongly concentrated around the mean.

Within each site, light transmission estimates at adjacent sample points (14 m separation) range from very similar ($\pm 0.5\%$ full sun) to very different ($\pm 19\%$ full sun) (Figure 6 and Figure 7). These data show that light transmission can both vary substantially over short distances (e.g., a change of 19% full sun over 14 m) and more gradually over longer distances (e.g., $<1\%$ full sun over 20 m), depending on location or direction within the stand. These spatial gradients are also visually represented with the contour-shading in Figure 6 and Figure 7, based on interpolated light values between photo locations. It is likely that additional variation exists between sampled locations, beyond what is represented by the interpolated light maps. If so, data collected at a greater density would reveal even finer scale variation and might reduce the appearance of gradual change over longer distances.

The data displayed in Figure 6 and Figure 7 show that variation of understory light transmission over short distances results in complex spatial patterns within each one-hectare site. The sampling design I used did not provide reliable quantitative descriptions of spatial patterns (via correlogram analysis; see Appendix 3). However, visual inspection of light estimates and interpolations (Figure 6 and Figure 7) suggest that distinct elements of patch structure would emerge from a higher density and/or larger extent of sampling. Evidently, a one-hectare plot is not large enough to describe the full range of variation and potentially repeating patterns within the older floodplains forest at Carmanah. At Kitlope, the sampling extent may be sufficient, but the resolution too coarse to quantitatively describe the very fine-scale patterns suggested by visual inspection of the light maps (see Appendix 3).

At both sites, canopy gap microsites tend to occur in the brighter half of the distribution, expanded gaps are dominant in the middle of the distribution but are found across most light levels, and closed canopy microsites are rare (Figure 4). At each site, the brightest $\sim 10\%$ of microsites are primarily in canopy gap and the darkest $\sim 10\%$ are

primarily in closed canopy or expanded gap. Consequently, median light transmission is higher in canopy gap microsites (21% full sun) than non-gap microsites (16% full sun; expanded gap and closed canopy) at both sites (Figure 5). At Kitlope, there is a pronounced separation of gap and non-gap light distributions (Figure 5), and the distributions are significantly different (Mann-Whitney $U=75$, $P<0.001$, two-sided test). At Carmanah, light levels vary substantially among canopy gap and among non-gap microsites; despite this heterogeneity, the light distributions are significantly different (Mann-Whitney $U=92$, $P=0.015$, two-sided test).

The greater overlap of gap and non-gap light regimes at Carmanah is likely due to the more widely differing size of gap and non-gap areas within the site. This is apparent when examining the light map and frequency distribution from Carmanah. First, the brighter tail of the distribution originates in a large central gap-complex created by the combination of a recent disturbance adjacent to a dry fluvial channel; the large majority of light transmission values $>20\%$ full sun are found within this area. Within this central zone, a number of trees remain standing, creating small non-gap patches within a larger gap complex (Figure 7). Second, in the surrounding forest, bright patches appear to be smaller and dark patches appear to be larger than in the bright central zone, likely reflecting the presence of smaller gaps and larger non-gap areas (assuming the patch size of light availability is a good indication of gap size: Nicotra et al. 1999).

Species composition in relation to environmental heterogeneity

At both sites, fine-scale variation of the understory plant community is organized along recognizable compositional gradients. The autopilot NMS procedures recommended three compositional axes for each site. At Kitlope, the three axis solution represents 79% of variance in the original data (Table 4), has a final stress of 14.05, final instability <0.00001 , and is significantly stronger than expected by chance ($P=0.004$). At Carmanah, the three axis solution represents 90% of variance in the original data, has a final stress of 8.32, final instability <0.00001 , and is significantly stronger than expected by chance ($P=0.004$).

Composition in relation to the environmental continuum at Kitlope

The strongest compositional axis at Kitlope is best explained by light transmission. Axis 1 at Kitlope has a strong positive linear relationship with light ($r^2=0.52$), while no other continuous environmental variable explains more than ~15% of variation in axis 1 as a linear relationship⁷ (Table 5 and Figure 8). However, an overlay on the ordination graph shows that canopy gaps also correspond with higher axis 1 scores (Figure 8 and Table 6), suggesting that light related compositional differences may also be associated with canopy gap versus non-gap overstory structure.

Axis 1 at Kitlope (Table 5 and Figure 8) represents 41% of the variance in the original data and describes a compositional gradient with *Ribes bracteosum* and *Circaea alpina* increasing along this gradient more or less linearly toward their maximum abundances. *Oplopanax horridus*, *Dryopteris expansa*, and *Osmorhiza berteroi* decrease toward their minimum abundances along this gradient. Examination of the overlay-scatter plot graphs⁷ revealed that five additional species increase along axis 1, but their responses are nonlinear and/or obscured by outliers (*Sambucus racemosa* ssp. *pubens*, *Polystichum braunii*, *Stellaria crispa*, *R. spectabilis*, and *Stellaria crispa*), hence rather low r and r^2 for linear correlation in Table 5. For example, maximum abundance of *R. spectabilis* clearly increases along axis 1, yet the overall response is quite variable at the upper end of the axis. Additionally, *S. racemosa* shows a threshold increase at roughly the midpoint of axis one; the species is generally absent below that level and reaches maximum abundance above that level. Similarly, examination of the overlay-scatter plot graphs revealed that *Galium triflorum* and *Osmorhiza berteroi* exhibit nonlinear decreases with axis 1, and *Tiarella trifoliata* exhibits a decrease that is obscured by the influence of an outlier. Finally, *O. horridus* shows signs of a threshold along axis 1 (in addition to the

⁷ In some circumstances, it can be misleading to interpret a linear correlation coefficient of species abundance over a compositional or environmental gradient, particularly in the absence of a scatterplot (McCune and Grace 2002). A number of features common to community datasets can make a linear correlation coefficient misleading either by under-representing a relationship that exists (non-linear response, solid response curve) or over-representing one that does or does not exist (zero truncation and outliers). I have attempted to avoid such interpretation errors by examining overlays and scatter plots for each species and environmental variable on the ordination axes. After examining each, I recorded cautionary notes and have presented and discussed results accordingly.

fairly strong linear correlation) with most occurrences and higher abundances in the lower two thirds of the axis.

Axis 2 represents 17% of the variance in the original data and primarily describes increasing relative abundance of *Streptopus lanceolatus* var. *curvipes*, as well as *O. horridus* and *Athyrium filix-femina* (Table 5 and Figure 8). This axis is unrelated to measured environmental variables. Axis 3 represents 21% of the variance in the original data and primarily describes increasing *R. spectabilis*. To a lesser degree, it describes decreasing *S. racemosa* and *Streptopus amplexifolius*, and increasing *Osmorhiza purpurea*. This axis is unrelated to measured environmental variables and may reflect competitive effects of *R. spectabilis* on composition independent of habitat characteristics.

Composition in relation to the environmental continuum at Carmanah

The strongest compositional axis at Carmanah is best explained by light transmission. As with Kitlope, after rotations, Carmanah axis 1 is positively correlated with light ($r^2 = 0.33$). Axis 1 at Carmanah represents 34% of variance in the original data and describes a compositional gradient characterized by increasing cover of *R. spectabilis* and *R. bracteosum*, and decreasing cover of *Blechnum spicant* (Table 7 and Figure 9). A few species show relationships with axis 1 that are not well captured by the linear correlation coefficients, either due to nonlinearities or outliers. For example, *Galium triflorum* and *Mitella ovalis* are only – but not always – present in the darker half of the axis 1 distribution (a non-linear solid response curve that is not represented by the linear correlation coefficient and coefficient of determination).

Axis 2 represents 27% of variance in the original data and describes a compositional gradient characterized by increasing cover of *B. spicant* and *Dryopteris expansa* and decreasing cover of *Prosartes smithii* and *Claytonia sibirica*. The composition of this axis is most strongly correlated with substrate properties, particularly higher clay content ($r^2 = 0.45$) and thinner humus horizons ($r^2 = 0.31$), independent of light ($r^2 < 0.01$). See also Appendix 1.

Axis 3 represents 28% of variance in the original data. Visual inspection of ordination scatterplot suggests that Axis 3 is largely dedicated to explaining a single outlier subplot. Supporting this conclusion, r^2 of Axis 3 falls from 0.28 to 0.15 when the outlier plot is removed. Not surprisingly, Axis 3 is not correlated with the environmental variables we measured (all $r^2 < 0.1$).

Composition-environment correlations differ between Kitlope and Carmanah

At Kitlope, light explains a greater proportion of compositional variation than it does at Carmanah (Table 5 and Table 7). Two aspects of the analysis support this interpretation. First: at Kitlope, light explains a greater proportion of the variation in the light axis compared to Carmanah. Second: at Kitlope, the light axis represents a greater percentage of variance in the original data. I ruled out the possibility that the differences between Kitlope and Carmanah are simply due to sample size differences by re-running the NMS with a sample size of $n=16$ for Kitlope. I took three random subsamples of 16 from the total sample of 24 at Kitlope. In the $n=16$ and $n=24$ analyses, light showed very similar correlations with the compositional gradients ($r^2=0.54 \pm 0.06$ versus 0.52 and $r=0.73 \pm 0.05$ versus 0.72, respectively). The $n=16$ and $n=24$ ordinations represented very similar proportions of the original compositional variation on axis 1 (after rotating to light) (41 ± 1 % versus 41% respectively).

Role of substrate heterogeneity in understory organization

Axis 2 at Carmanah is correlated with substrate properties independent of light levels. The axis represents – most notably – increasing cover of *B. spicant* and *D. expansa* and decreasing cover of *P. smithii* and *C. sibirica*, and the axis is correlated with increasing clay content and decreasing humus horizon thickness. A number of alternative mechanisms could produce the observed pattern. Perhaps the most likely possibility is that compositional change along this gradient reflects differing soil moisture adaptations. Although all four species mentioned are indicative of the same moisture regime – fresh to very moist – defined at the landscape scale (Klinka et al. 1989), this does not preclude the possibility that the species are differentiated along a moisture gradient within a site.

In a chronosequence study of comparable floodplain forests in the Hoh River valley, Fonda (1974) found that soil moisture increased through stand development and attributed this to increased clay and organic matter content. Fonda concluded that reduced summer time moisture stress was the primary mechanism for compositional change that included decreasing *C. sibirica* and increasing *B. spicant* and *D. expansa* (Fonda 1974). Following on this, it seems reasonable to hypothesize that spatially varying clay content within the Carmanah stand could produce similar organization of species along a gradient of soil moisture, possibly even a gradient of summer moisture stress if Carmanah, like the Hoh, sometimes experiences the dry summers of the “seasonal rainforest” (Alaback and Pojar 1997). Soil moisture gradients may be particularly influential on ferns, which require a film of water for sexual reproduction (A. MacKinnon, personal communication). During a dry period, a microsite with higher clay content (lower hydraulic conductivity; Saxton et al. 1986) would presumably drain more slowly, perhaps allowing more time for shallow rooted plants to uptake water (See also Appendix 1). Conversely, microsites with lower clay content with presumably drain more quickly following floods and rains and are more likely to experience moisture stress in summer. Consistent with this explanation for the pattern observed at Carmanah, Klinka et al. (1989) describe *C. sibirica* as tolerant of fluctuating groundwater tables, which have reduced summer moisture levels.

There are two ways to explain the lack of correlation between measured soil variables and composition at Kitlope. Either there is no relationship, or there is a subtle relationship (small effect size) that could not be detected because of low power (sample size and measurement precision) to detect relationships over a relatively narrow range of soil conditions. It appears that if strong relationships exist among the measured soil properties and understory composition, they are expressed at larger scales, or at least over larger ranges of variability in soil properties. Although I found no correlation between soil variables and composition at Kitlope, I did not directly measure potentially important soil properties such as soil moisture or nutrients; thus, I cannot reject the hypothesis that soil properties (more generally) structure understory composition at Kitlope.

Composition of canopy gap and non-gap microsites

The Multi Response Permutation Procedure (MRPP) confirmed that gap and non-gap microsites at Kitlope have significantly different composition ($P=0.004$), but the difference (effect size) is not large ($A=0.10$). Indicator Species Analysis (Dufrêne and Legendre 1997) showed that *S. racemosa* has higher than expected indicator values for canopy gap ($P=0.045$), while *O. horridus* and *D. expansa* are indicative of non-gap microsites ($P=0.018$ and 0.045 respectively; Table 6). Other species were marginally significant indicators ($0.05 \leq P < 0.1$) of gap (*R. spectabilis* and *S. crispa*) or non-gap microsites (*T. trifoliata* and *T. caroliniensis*), or were clearly unrelated to gap status ($P > 0.1$).

At Kitlope, most of the compositional change between canopy gap and non-gap microsites is also associated with light. Both non-gap indicator species (*O. horridus* and *D. expansa*) are associated with the shadier portion of axis 1, and the gap indicator species (*S. racemosa*) is associated with brighter portions of axis 1 (Table 6 and Figure 8). However, none of the other light associated species at Kitlope (e.g., *R. bracteosum*) were significant indicators of gap or non-gap.

The MRPP for Carmanah also shows that canopy gap and non-gap areas have significantly different composition ($P=0.002$), and again the difference (effect size) is not large ($A=0.15$). *B. spicant* and *D. expansa* have higher than expected indicator values for canopy gap microsites ($P=0.0012$ and 0.0002 respectively) based on Indicator Species Analysis (Dufrêne and Legendre 1997) (Table 6). One other species (*Vaccinium parvifolium*) was a marginally significant indicator ($0.05 \leq P < 0.1$) of gap microsites and all others were unrelated to gap status ($P > 1.0$).

At Carmanah, light transmission and gap status show surprisingly different associations with understory compositional patterns. None of the species positively associated with the light axis are significantly associated with gap microsites, nor are any shade correlated species associated with non-gap microsites. In fact, one of the species associated with the shadier portion of the light axis – *B. spicant* – is a gap indicator species. More generally, it is clear from the ordination joint plot that the brighter portion

of the light compositional axis is associated with non-gap microsites and vice versa (Figure 9).

These counterintuitive results at Carmanah appear to arise because my subplot sample ($n=16$) over represents dark gap microsites (e.g., small gaps or southerly locations within gaps) and over represents bright non-gap microsites (e.g., adjacent to large gaps or at the northerly edge of gaps), compared to the full sample of microsites with photographs ($n=32$, omitting recent windthrow) (See Appendix 4). This could explain why shade tolerant species (Klinka et al. 1989) typical of relatively darker upland forests (*B. spicant*, *D. expansa*, and *V. parvifolium*) are associated with canopy gap microsites in this subsample. Within the subsample, these species are associated with shady gap microsites: either small canopy gaps or southerly locations within canopy gaps. At Kitlope, by contrast, the subsample appears to give a non-biased estimate of the light environment in gap and non-gap microsites (See Appendix 4).

Cover of understory layers and a dominant shrub in relation to light

The summed cover of species in herb, shrub, and herb plus shrub layers show differing degrees of correlation with light transmission through the canopy. As expected, shrub cover is positively correlated with light transmission at both sites ($r=0.48$, $P_{Dut}=0.02$ Kitlope; $r=0.63$, $P_{Dut}=0.008$ Carmanah) (Table 8) after stratifying to exclude very recent openings (windthrow presumably from the winter before sampling) consistent with a hypothesis of light limited shrub biomass. Herb cover is not significantly correlated with light levels above the shrub canopy or shrub cover in either site. Herb cover is weakly negatively correlated with above-shrub light at Kitlope, though not significantly ($r=-0.33$, $P_{Dut}=0.11$). Total vascular cover is significantly positively correlated with above-shrub light at Carmanah ($r=0.59$, $P_{Dut}=0.03$), but not at Kitlope – likely because Kitlope herbs have a weak negative correlation with light that weakens the positive correlation of shrubs with light when the two are combined.

R. spectabilis cover shows a strong and significant positive correlation with light transmission at Carmanah ($r=0.79$, $P_{Dut}=0.001$) but, surprisingly, not at Kitlope ($r=0.24$, $P_{Dut}=0.25$) (Table 8). At Kitlope, *R. spectabilis* shows only weak non-significant positive

correlation with light. However, *R. spectabilis* cover is correlated with light after controlling, using partial correlation (Legendre and Legendre 1998) for the cover of other shrubs ($r=0.52$, $P=0.011$; not corrected for spatial autocorrelation). This suggests that *R. spectabilis* response to light is mediated by competition with other shrubs, or some other environmental factor – an interaction not observed by Klinka et al. (1996), nor apparent in the Carmanah stand. A larger dataset would be required to appropriately model *R. spectabilis* cover in relation to multiple biotic and abiotic factors and resolve this uncertainty.

Although shrub cover is positively correlated with light at both sites, the correlation is weaker at Kitlope. This probably reflects the fact that one shrub species – *O. horridus* – is in fact more abundant in shady areas (see ordination results), thereby weakening the positive correlation of summed shrub cover with light. If *O. horridus* is removed from the dataset, the summed cover of all other shrubs has a stronger positive correlation with light ($r=0.75$, $P<0.001$) than the correlation of all shrubs (including *O. horridus*) with light ($r=0.48$).

Point scale diversity in relation to productivity

Species diversity is known to vary with productivity, although the relationship may be positive or negative and may depend on the scale of analysis (e.g., Mittelbach et al. 2001, Gillman and Wright 2006, Whittaker 2010); here I assume that within such nutrient rich sites, increasing light availability represents increasing (potential) productivity. At Kitlope and Carmanah, although point species diversity varied substantially among subplots, neither species richness nor evenness increased along the light gradient at either site (Table 9). My findings clearly do not support the hypothesis that greater light availability supports greater understory point diversity, across this range of light levels and within stands of this forest type. By contrast, my results provide some support for the idea that point diversity decreases with light, as a measure of productivity. At Carmanah, but not Kitlope, dominance (L_s) has a strong positive correlation with light ($r=0.72$, $P_{Dut}=0.004$), and species evenness ($r=-0.64$, $P_{Dut}=0.01$) has a negative correlation with light. Species richness at Carmanah has a weak negative correlation with

light ($r=-0.47$, $P_{Dut}=0.08$). In my study, light transmission appears to exert a stronger influence on species evenness than richness. However, a larger sample would be needed to confidently reject the hypothesis that competition reduces species richness at higher light within older floodplain forests of the coastal temperate rainforest.

Neither species richness nor evenness is correlated with vascular cover – as a proxy for biomass – at either site (Table 9). This suggests that competitive exclusion does not show a strong linear increase with total vascular species biomass. If a biomass-diversity relationship exists at this fine-scale, a more accurate measure of biomass – including both matter and litter – may be needed to show the relationship (Grace 1999). A larger and more variable sample may also be needed to describe such a relationship. Alternatively, the vegetation could still be recovering from disturbance such that competitive exclusion has not yet occurred in those subplots where vascular cover is especially high. A more complex model that incorporates disturbance and non-linear patterns, for example, may be needed to describe and explain biomass-diversity relationships within these forests (e.g., Pollock et al. 1998).

DISCUSSION

The older floodplain stands I studied were both very open, but also quite variable in understory growing conditions. Both Kitlope and Carmanah have a high proportion of area in canopy gap and expanded gap, and abundant and spatially variable understory light. Composition of the understory plant community varies substantially within each site. Light transmission is correlated with microsite composition at both sites. Substrate properties explain additional compositional differences among microsites at Carmanah, but not at Kitlope. Shrub cover is positively correlated with light transmission at both sites. Herb cover, however, has a more complex relationship with light or shrub cover than could be revealed through simple linear correlations. I found no evidence that microsite diversity increased with light: in fact, I found evidence of the opposite in one of the sites.

Gap structure and light transmission in older floodplain stands

Canopy structure in these floodplain forests is characterized by a very high proportion of canopy gap and expanded gap, compared to many forests. At both study areas, closed canopy microsites are rare (<10%); expanded gap is the most common cover type and canopy gap microsites are also common. These floodplain forests have very high frequency of gap and low frequency of closed canopy, compared to the watershed-averages for Coastal Western Hemlock *vm1* variant in Tofino Creek (Lertzman et al. 1996) on the west side of Vancouver Island. However, the Mountain Hemlock zone of the Tofino Creek study area had very low (1%) area in closed canopy (Lertzman et al. 1996), similar to the Kitlope and Carmanah floodplain sites of my study. In Mountain Hemlock stands near Vancouver, Lertzman and Krebs (1991) reported 18% canopy gap, 52% expanded gap and 29% closed canopy – more than three times as much closed canopy as I have reported for the Kitlope and Carmanah floodplains. For my study areas, the amount of area in canopy gap and expanded gap, combined, is also high

compared to upland coastal temperate rainforests in south-east Alaska (18 to 44%: Ott and Juday 2002), and compared to boreal (50%), sub-boreal (57%), sub-alpine (73%), and northern temperate (32%) forests in northern British Columbia (Bartemucci et al. 2002).

The canopy disturbance history differs remarkably between sites, possibly reflecting differing developmental processes and pathways. Most gap microsites at Carmanah arise from the mortality of one to a few trees, and snags and logs are abundant within the study site (unpublished data from Old Growth Dynamics Project), as is expected for a forest driven by gap-phase processes. At Kitlope, by contrast, most gaps do not clearly have an associated gap-maker, and snags (especially of the overstory size class) and logs are found in relatively low abundance across the one-hectare site. These gaps could represent microsites that have never filled in with mature trees or microsites where all evidence of tree mortality has been removed by flooding. While removal-by-flooding might explain the lack of gap-makers in a few gaps, it seems unlikely that it explains the overall shortage of snags, logs, and stumps, across the one-hectare site. More likely, many of the Kitlope gaps are legacy openings that have never filled with conifers, despite the stand having aged sufficiently to develop many >100-cm DBH conifers. Consistent with the idea that openings at Kitlope have persisted through stand development, many of the *P. sitchensis* have clearly open-grown architecture (personal observation).

Potential mechanisms for initial creation of such persistent legacy openings include frequent flooding and soil saturation, and/or intense competition with shrubs and herbs, early in stand development. In their conceptual models of stand development, Van Pelt and Franklin (2006) suggest that conifer invasion of early seral floodplain stands may be delayed by competition (from grasses and trees) or flooding, and Franklin et al. (2002) account for the possibility that low initial conifer tree densities may increase canopy openness later in development.

Maintenance of the very high proportion of area in gaps is likely the result of slow rates of understory tree establishment in floodplain forests (Harmon and Franklin 1989, Pabst and Spies 1999), in combination with recent windthrow at Carmanah and

developmental legacies at Kitlope. Similarly, Lertzman and Krebs (1991) hypothesized that slow rates of gap filling were responsible for the high proportion of area in canopy gap and expanded gap in Mountain Hemlock forests. Gap filling occurs slowly in mountain hemlock forests due to slow growth rates, short growing seasons, and low productivity sites. By contrast, the mechanism for slow gap filling in highly productive floodplain stands more likely reflects the effects of understory competition on recruitment of canopy trees (see Harmon and Franklin 1989), although other mechanisms such as flooding could also play a role and require further assessment. Persistent shrub-maintained gaps have been observed in a variety of forests. In Douglas-fir forests of the Pacific Northwest, Spies and Franklin (1989) hypothesized that competition with understory shrubs and herbs may explain why gaps in old-growth fill slowly (e.g., >50 years before saplings develop). In sub-boreal forests, Bartemucci et al. (2002) assigned a substantial proportion of the forest area to gaps of shrub-origin (19%) or a combination of shrub and mortality origins (34%).

Despite differences in gap origin, mean light transmission at both sites is high compared to many forests, yet markedly lower than others. Kitlope and Carmanah each have median 18% transmission of the above canopy PAR (i.e., percentage full sun) through to the forest understory. Median percentage full sun at Kitlope and Carmanah is higher than reported for most riparian forests in Oregon sampled by Sarr and Hibbs (2007a) – four watersheds with forests that ranged from *Picea sitchensis* stands in humid climates to *Quercus garryana* Dougl. stands in notably drier climates (Sarr and Hibbs 2007b). Roburn (2003) reported mean 5% full sun transmission in each of two *Picea sitchensis* floodplain forests in the Seymour Valley of southwest British Columbia – substantially less than I have reported for Kitlope or Carmanah. Median site openness at Kitlope and Carmanah (~11%) is higher than the median openness estimates for upland old-growth in the CWHvm on (western) Vancouver Island, and similar to the median openness on eastern Vancouver Island (CWHxm forests) (Frazer et al. 2000a). Mean percentage full sun transmission (18-19%) in my study is greater than reported for a range of temperate and tropical forests (Canham et al. 1990, Nicotra et al. 1999, Lhotka and Loewenstein 2006), which have mean values between 0.5 and 7.0% total transmission. Mean percentage full sun is remarkably similar to the sub-boreal (18.0%),

sub-alpine (19.0%), and northern temperate (16.0%) stands of old-growth in northern British Columbia (Bartemucci et al. 2002). By contrast, mean light transmission at Carmanah and Kitlope is markedly lower than reported for a number of boreal forests (Bartemucci et al. 2006) from Quebec (Bartemucci et al. 2006) and northern BC (26.7%; Bartemucci et al. 2002). For example, Bartemucci et al. (2006) found that percentage full sun ranged from 6.2 to 61.9% and averaged 27% in old-growth southern boreal forests of Quebec.

Light levels in these forests vary substantially over short distances, creating fine-scale heterogeneity of light environments. Contour maps of light at the top of the shrub layer provide a clear visual representation of the degree to which the abiotic environment of microsites separated by less than 15 m can differ (by almost 20% full sun) as a result of variable shading from trees. Such light variations have implications for ecosystem processes and animal habitat, in addition to the vegetation attributes examined in this study. In one of the few other studies to map understory light at this scale, Capers and Chazdon (2004) showed fine-scale light heterogeneity in the understory of a tropical forest. In Colorado, Hardy et al. (2004) generated understory light maps that show greater fine-scale variation under a discontinuous *Pinus contorta* canopy than a uniform canopy. Stand models have also been used to predict and map spatial pattern of understory light (e.g., Canham et al. 1999). Based on modeled light values at various heights, Mariscal et al. (2004) showed that fine-scale horizontal heterogeneity of light transmission in a tall old-growth forest was maximized at intermediate heights in the stand, but remained variable near ground level. Canham et al. (1999) used the simulation model SORTIE to generate a contour map of understory light index, which showed that adjacent gap and non-gap microsites create strong gradients of light transmission over short distances.

In my research sites, the spatial pattern of light transmission is clearly related to stand structural processes, yet has a complex relationship with canopy gap versus non-gap status immediately overhead. Canopy gap and non-gap microsites have surprisingly distinct light environments at Kitlope, likely because gap and tree-patch sizes are relatively consistent across that site. At Carmanah, the light regimes of canopy gap versus non-gap microsites overlap substantially, and the modes of the site-scale light regime do not correspond to a simple gap versus non-gap dichotomy. Rather, it appears that widely

differing gap and tree-patch sizes within the site produce the greater overlap of gap and non-gap light regimes observed at this site. We know that the relationship between forest canopy structure and understory light can be complex (Canham et al. 1990, Messier et al. 1998, Canham et al. 1999, Montgomery and Chazdon 2001). My results, like many others (Montgomery and Chazdon 2001, Van Pelt and Franklin 1999, Van Pelt and Franklin 2000, Bartemucci et al. 2002), support Lieberman et al. (1989) in their argument that measuring light along a continuum provides a substantially richer description of the understory light environment than is afforded by a simple gap versus non-gap description, particularly when gap sizes vary. Extending this further, spatially explicit sampling along the light continuum, when combined with a tree stem map and information about disturbance history, allows for mapping and visualization of the “moving window of light availability” (Nicotra et al. 1999, p. 1924) and exploration of potential implications for understory plant communities. For example, the potential for a “moving window of light availability” is readily visualized on the map of light and trees at Carmanah, where a recent disturbance has produced a zone of increased light availability surrounded by darker microsites.

Understory vegetation in relation to environmental heterogeneity

The spatial pattern of understory vegetation composition is partially related to light transmission patterns. At each site, one of the compositional gradients is best explained by overstory light transmission. Between two and six species increase, and five species decrease, with the light axis at each site. *R. bracteosum* increases with the light axis at both sites, and *G. triflorum* decreases at both. At Kitlope, *R. spectabilis* and *S. racemosa* show non-linear increase with light. *O. horridus* is present only at Kitlope, where it abruptly increases in shadier than average microsites.

Competition is likely an important mechanism for producing species associations with portions of the light gradient. Species negatively associated with axis 1 may be confined to shady locations due to intense competition in the brighter locations, particularly by the shrubs that are positively correlated with light. *O. horridus* is a good example: the species increases abruptly in shadier than average microsites and is never

abundant above about 21% light transmission. This occurs despite the fact this species can be observed thriving in much brighter environments elsewhere (Burton 1998), suggesting that the species realizes only a portion of its fundamental light niche at Kitlope. Presumably then, *O. horridus* persists in this stand by tolerating – and/or outcompeting other species in – shady microsites created by trees. Klinka et al. (1989) considered *O. horridus* to be more consistently shade tolerant than *R. bracteosum*, *R. spectabilis*, *S. racemosa* (the other shrubs common at Kitlope). My findings are consistent with the prediction of Roorbach (1999) that *R. spectabilis* and other light responsive plants (*Acer circinatum* in that case) will outcompete *O. horridus* in high light environments.

Species positively associated with the light-axes may have evolved strategies to exploit and dominate higher light microsites. *R. spectabilis* is a good example: widely known as a strong competitor (Klinka et al. 1996, Kennedy and Quinn 2001, Hauessler et al. 1990, Tappeiner et al. 1991), the species is often compositionally dominant at higher light levels with the Kitlope and Carmanah sites. This species benefits from architecture and growth rates that enable it to rapidly colonize openings and overtop other plants (Tappeiner et al. 1991, Tappeiner et al. 2001), although other physiological mechanisms could also be important. However, despite this adaptation for dominance, *R. spectabilis* dominance does not appear to be a foregone conclusion in all bright microsites, all of the time. In at least a few subplots at Kitlope, *R. spectabilis* is less abundant than expected for a linear relationship with light, and *S. racemosa* and *R. bracteosum* are more abundant than expected. These other shrubs have presumably overtopped *R. spectabilis*: a pattern I observed and noted at numerous unsampled locations within the stand (Figure 10).

Despite overlapping light environments, gap and non-gap microsites at Kitlope have different understory vegetation composition, although the magnitude of the difference is not large. Differences in light environment appear to explain most of the compositional differences between gap and non-gap microsites, however differences in below ground resource competition and other direct tree-influences such as litterfall, could also be important (e.g., Lindh et al. 2003). In boreal mixedwood stands of Alberta, Chávez and Macdonald (2010) used a similar method and also found that understory composition differed between gaps and non-gaps within stands. Evidently, compositional

differences between gap and non-gap areas can be observed in higher latitude forests, such as Kitlope and boreal forests in Alberta, despite the spatial displacement of some gap-effects at higher latitudes (e.g., Bartemucci et al. 2002).

My results corroborate the assertion of Pabst and Spies (1998): that light is an important driver of composition within riparian stands. In their study, conifer cover was correlated with vegetation composition along a streamside-to-hillslope topographic gradient and was interpreted as a proxy for light. Much like the study by Pabst and Spies (1998), Sarr and Hibbs (2007b) examined drivers of composition (only woody species in this case) across streamside-to-hillslope topographic gradients in Oregon and found that, after accounting for the effects of climate variation across their study, a complex topographic gradient was most important for explaining compositional variation. Fluvial scouring and conifer cover were the two main factors that corresponded with this gradient. Although the authors did not estimate light transmission, they found that 22% of species were associated with gaps, and a smaller number (3%) with non-gaps, across this complex topographic gradient. My results build on this conceptual model by confirming that when the floodplain is examined independent of hillslope sites, light transmission is a driver of understory composition patterns within older stands. My results are an interesting contrast to those of Roburn (2003) who also examined within stand variation of light and vegetation in *P. sitchensis* floodplain forests of BC (2003), but found that light transmission explained only a small fraction (2 to 8%) of the variation in understory vegetation. Our contrasting results could arise due to differences in sampling methods or differences in site specific ecology (e.g., Roburn's sites are darker, more edaphically heterogeneous, and likely older than Kitlope).

It appears that light heterogeneity enables a diversity of species to reach abundance within a highly productive forest (i.e., alpha scale evenness), consistent with the idea that heterogeneity promotes co-existence (Grime 1979, Denslow 1985, Svenning 2000). This assertion is also supported for the coastal temperate rainforest by the findings of Sarr and Hibbs (2007a) in Oregon. These authors showed that in topographically complex riparian stands (streamside, midslope, hillslope), woody species richness was higher with more heterogeneous light environments. Spatial heterogeneity could help explain why floodplains in British Columbia have greater species diversity than most

upland site types (Smith 2005). However, my finding that most of the compositional variation remains unexplained by light or other environmental attributes suggests that, as Wright (2002) hypothesized for tropical forests, spatial heterogeneity alone can not account for maintenance of high alpha diversity in older floodplain forests. Other mechanisms, or other types of abiotic heterogeneity, must also be important.

In my study, light heterogeneity influences understory composition, whether the spatial pattern of stand structure arise from gap-phase processes or it persists as a legacy from early stand developmental processes. Composition varied with light transmission for both a stand where light heterogeneity is clearly induced by tree mortality (Carmanah), and a stand where heterogeneity may be a result of stand development patterns largely independent of tree mortality (Kitlope). This suggests that the mosaic of gaps and non-gap patches in the forest canopy influence understory composition even if they do not arise from tree mortality.

The degree to which light organizes understory composition varies between the two sites and may be related to local characteristics. At Kitlope, light explains a greater proportion of compositional variation than it does at Carmanah. Two alternative explanations are noteworthy. First, differences in the pool of available species might explain differences in the degree to which light organizes understory composition. Specifically, *O. horridus* is present only at Kitlope where it primarily occupies the shady two thirds of the light gradient and is the species most strongly associated with the light axis. The light-composition correlation at Carmanah may be weaker because, in contrast to Kitlope, Carmanah lacks a single species that shows an especially strong association with light.

Second, the strength of light effects on composition may depend on the temporal stability of the light environment. Despite the fact that Kitlope is a younger stand, various lines of evidence suggest that Carmanah has had a more dynamic light environment in recent years: most gaps are developmental as opposed to persistent legacy openings; some portion of the currently observed canopy openness is the result of recent windthrow; and vertical and horizontal growth of *T. heterophylla* crowns (a species that is far more abundant in the understory and midcanopy of Carmanah than Kitlope) in the

understory and subcanopy likely creates temporal heterogeneity in the light environment. Taking these lines of evidence together, and assuming that the understory plants were largely unaffected by the recent flood at Kitlope (i.e., that plants either were not affected much by the recent Kitlope floods or they recovered rapidly in the same locations), I infer that the understory community at Kitlope has had more time to organize and develop in relation to the currently observed light gradient. If this is an accurate representation of the recent history of light regimes, it would be consistent with the idea that niche differentiation, in relation to spatial heterogeneity, becomes a more important influence on alpha diversity (via compositional organization along gradients) as the community moves toward equilibrium (i.e., time since disturbance: Connell 1978).

Role of substrate heterogeneity in understory organization

Spatial heterogeneity of edaphic conditions and below-ground competition may also play a role in fine-scale community organization and stand level species co-existence (Svenning 2000, Lindh et al. 2003) in these highly productive forests. My results suggest that at Carmanah, substrate attributes – and by inference, below-ground resources – spatially organize a portion of the understory plant community. Although light heterogeneity explained substantially more compositional variation at each site, I undoubtedly used a more accurate measure of light than of below-ground resources. It would be instructive to research more intensively the relative importance of edaphic heterogeneity for organizing fine-scale variation in highly productive floodplain forests in the coastal temperate rainforest. For example, microtopographic variation within a stand may reflect fine-scale heterogeneity of flooding disturbance (Pollock et al. 1998).

Other drivers of fine-scale compositional patterns

Despite the observed environmental correlates of understory composition, much of the variation in understory composition remains unexplained. This appears to be typical of studies that examine environment-composition relationships within forest stand understories (Frelich et al. 2003, Roburn 2003, Chávez and Macdonald 2010). Roburn (2003) also found that much of the compositional variation within older floodplain stands

was unexplained by environmental variables. I can only speculate on the other processes, deterministic or stochastic, that might explain the remaining community variation. Deterministic patterns may be driven by competition (or other biotic interaction), herbivory, some unmeasured environmental variable, or a combination of factors (e.g., light and soil resources), and may show complex responses (e.g., interactions and non-linearities) not well described by my study. Disturbance may have both deterministic (e.g., flood frequencies that vary with elevation – Pollock et al. 1998) and stochastic (chance tree-fall locations) components. If the community is still re-organizing following disturbance, equilibrium process of niche differentiation – to produce organization along environmental gradients – would not be strong (e.g., Connell 1978). Chance likely plays a role in dispersal patterns and population demographics for individual species, in turn adding a stochastic component to community organization.

Other specific drivers of fine-scale understory compositional patterns in riparian forests might include soil moisture and nutrients (e.g., Fonda 1974), elevation and flooding frequency (Menges and Waller 1983, Pollock et al. 1998), ground water upwelling (Mouw et al. 2009), salmon derived nutrients (Bilby et al. 2003), and time lagged responses to overstory change (e.g., Nicotra et al. 1999, Barbier et al. 2008). Overstory composition, particularly conifer versus hardwood cover, is correlated with understory composition across riparian stands (Hibbs and Bower 2001) and could play a role within stands (e.g., Pabst and Spies 1998, Barbier et al. 2008, Chávez and Macdonald 2010). Lindh et al. (2003) showed the influence of below-ground competition with trees on understory biomass, and the same could be true for understory composition. Although my gap/non-gap variable might give a crude measure of below-ground competition, it likely does not reflect the full influence of below-ground competition. Interestingly, Lindh et al. (2003) hypothesized that a lack of perfect overlap of above-ground and below-ground gaps might explain the spatial displacement of understory vegetation patterns from canopy gaps.

Shade refugia for diversity in very open forests

At Carmanah, there is greater dominance by a smaller number of species (i.e., lower evenness) in the brightest, presumably most productive, microsites. This suggests support for the idea that point diversity is reduced as productivity increases and competition becomes intense (e.g., Grime 1973, Whittaker 2010). I suggest that, under conditions similar to the Carmanah site (similar productivity, light availability, species pool, etc.), increased light reduces point diversity within this community type by promoting dominance of *R. spectabilis*. As a corollary, shady microsites could provide refuge from intense *R. spectabilis* competition, where a greater diversity of species can reach relative abundance. These “shade refugia” would also contribute to greater community scale diversity by allowing poorer light competitors to reach relative abundance somewhere in the stand; a hypothesis also supported by my ordination findings. This idea builds on the hypothesis of Kennedy and Quinn (2001) that CWD contribute to greater species richness by providing refugia from intense competition in *R. spectabilis* dominated understories of the coastal temperate forest.

The occurrence of a shade refugia pattern of point diversity may not be ubiquitous among older floodplain forests. In my study, point diversity is unrelated to light transmission at Kitlope, an interesting contrast to the apparent shade refugium pattern of point diversity observed at Carmanah. At Kitlope, evenness is not as high in the shade or as consistently low in the bright locations. Two of the potential hypothesis for explaining this difference between Kitlope and Carmanah are particularly noteworthy, although this is by no means an exhaustive exploration. First, there is a different species pool at the two sites. For example, *S. racemosa* is present only at Kitlope where it occasionally overtops – but does not exclude – *R. spectabilis* in bright microsites. Second, the light environment may have been more temporally stable in recent history at Kitlope. Perhaps time is what is required for a taller species like *S. racemosa* to establish and overtop *R. spectabilis*, thereby increasing diversity in high light microsites. Larger datasets, collected from a larger number of sites, would be needed to test these hypotheses and would enable use of structural equation modeling or other methods suited to examination

of complex relationships of multiple variables (light, multiple shrub species, time, and species diversity).

Persistent shrub-maintained gaps in older floodplain forests

The high biomass of understory plants such as *R. spectabilis* may also play a role in shaping the patterns and dynamics of stand structure. At Kitlope and Carmanah, shrubs are widespread and abundant, but regenerating conifers (in seedling and low shrub layers) are not – despite light transmission levels more than sufficient for growth of the conifers present in the stand (Wright et al. 1998, Coates and Burton 1999, Drever and Lertzman 2001). It has long been hypothesized that *R. spectabilis*, among other shrub species, invades forest openings, inhibits conifer regeneration (Tappeiner et al. 1991, Minore and Weatherly 1994, Pabst and Spies 1999, Kennedy and Quinn 2001, Tappeiner et al. 2001), and may be able to maintain persistent canopy openings (Henderson 1978, Tappeiner et al. 1991, Minore and Weatherly 1994). Tappeiner and colleagues (1991 and 2001) demonstrated the likely mechanism by which clonal shrubs maintain a persistent cover. *R. spectabilis* annually extends rhizomes and continually produces new aerial stems, thereby filling any gaps created by stem mortality. By these processes, *R. spectabilis* maintains a dense cover that frequently excludes tree and shrub species otherwise capable of overtopping it (e.g., *T. heterophylla*, *S. racemosa*) (Tappeiner et al. 1991, Tappeiner et al. 2001). Similarly, Lertzman and McGhee (1996; McGhee 1996) found support for the hypothesis that *A. circinatum* can maintain a persistent gap through stand development by excluding conifers.

My data and observations are consistent with the persistent shrub cover model, which – in combination with canopy disturbance – could explain why Kitlope and Carmanah have very high proportions of canopy gap and expanded gap compared to other forests. Other processes such as flooding could also play a role and require further assessment. Although experimental evidence to date supports the competition hypothesis over other mechanisms that might inhibit conifer regeneration in similar forests (Harmon and Franklin 1989), these results may not hold under different flood regimes. For example, if Kitlope experiences more frequent flooding than typical of a high bench

floodplain (>5 year return interval; Green and Klinka 1994), flooding might also slow the establishment of flood intolerant species such as *T. heterophylla* in the stand (see Van Pelt et al. 2006). Additional research is needed to characterize the flood regimes of these sites and examine the role of flooding in shaping overstory and understory vegetation dynamics.

My results (light versus shrub and *R. spectabilis* correlations) can be used to further specify a spatial component to the persistent shrub-gap hypothesis. We know from research elsewhere that conifer regeneration density decreases with *R. spectabilis* cover (Pabst and Spies 1999). If greater shrub cover reduces the rate of conifer establishment in these stands, it follows that persistent shrub-maintained openings should have spatial patterns (e.g., size and shape) that are partially controlled by spatial patterns of light transmission. By invading and dominating new openings, clonal shrubs make persistent the spatial pattern of openness created by canopy tree mortality. Although typical gap phase processes may promote a “moving window of light availability” (Nicotra et al. 1999) (which may be occurring at Carmanah), my results suggest that intense understory competition may provide a counterforce that maintains a “persistent window of light availability.” However, existing evidence of conifer recruitment on logs (e.g., Harmon and Franklin 1989, Pabst and Spies 1999) suggests that introduction of CWD into such gaps will facilitate recruitment of canopy trees and thus gap filling.

If competition with understory plants limits recruitment of canopy conifers at these sites, how did so many *Tsuga* and *Abies* reach the small-to-intermediate size classes at Carmanah? (See diameter distributions in Giesbrecht (2010): unpublished data from Old Growth Dynamics Project.) Likely explanations are logs and time, although shade could also play a role. Carmanah, being an older stand, has abundant logs in all stages of decay, suggesting that logs have been abundant for many years. Most of the mid and understory *Tsuga* were observed to be growing on logs (A. MacKinnon, personal communication). Alternatively, these trees may have established in deep shade microsites where shrubs were reduced in abundance. Regardless of what type of microsite enhanced establishment rates, the greater age of the Carmanah stand means that more time has passed for understory trees to establish and overtop shrubs. Relative to Carmanah, Kitlope is younger and has very few logs, particularly in older decay stages (see unpublished data

from Old Growth Dynamics Project). Perhaps an historical lack of logs at Kitlope explains why *Tsuga* and *Abies* are not more abundant in the stand; the site lacks this mechanism for trees to escape intense understory competition.

Regional controls on shrub abundance

Kitlope and Carmanah differ from other older floodplain forests of the coastal temperate rainforest in a number of interesting ways. These sites have much higher shrub cover than observed in many riparian (A. Pearson, personal communication) and upland forests of Haida Gwaii due to the hyperabundance of introduced deer on those islands (Stockton et al. 2005). The understories of Kitlope and Carmanah also appear to have far greater shrub cover than observed in otherwise similar forests of the Olympic Peninsula. For example, Fonda (1974) reported <6% cover for all shrub species except *A. circinatum* (32%), and Schreiner et al. (1996) reported <15% shrub cover outside ungulate exclosures in the South Fork Hoh valley. Two mechanisms might explain these differences. First, our study sites probably lack the dense populations of elk observed in Olympic National Park. These herbivores preferentially forage in floodplain forests and thus dramatically reduce shrubs (*S. racemosa* and *R. spectabilis* in particular) and other vegetation attributes (Woodward et al. 1994, Schreiner et al. 1996). Second, it is possible that our sites have more open forest canopies, producing a greater mean abundance of light demanding shrubs. Based on these alternative mechanisms, I predict that differences in shrub abundance across the region correspond to differences in light transmission and ungulate herbivory. A dataset of multiple stands from multiple watersheds would be needed to address this question.

Conceptual model

Considering my results and the existing literature, I propose the following conceptual model for influences of canopy structure, light transmission, and understory shrubs on stand development and understory vegetation characteristics in older floodplain spruce stands of the coastal temperate rainforest. This model may be specific to stands where ungulates have not denuded the shrub layer.

Small scale disturbances create canopy openings and sometimes result in stands with high gap to non-gap ratios. Gaps may also arise or persist due to edaphic conditions or developmental legacies. Regardless of gap origin, in stands and developmental stages with abundant canopy openings, a high proportion of photosynthetically active radiation is transmitted to the understory relative to many other forest types. Gaps are important sources of light and gap microsites tend to be brighter than non-gap (expanded gaps and closed canopy) microsites. However, due to structural complexity within the stand, the light environments of gap and non-gap microsites overlap, particularly when the sizes of gap and non-gap patches vary substantially within a stand. In such open stands/stages, understory vascular plants reach very high cover values. Dense cover of shrubs inhibits conifer re-initiation, thereby maintaining gaps and the high levels of openness that characterize these stands. This produces temporally persistent patterns of canopy openness. Where and when conifers do overtop shrubs – as may be facilitated by logs on the ground (e.g., Harmon and Franklin 1989) – they induce light heterogeneity in temporal and spatial dimensions. This environmental heterogeneity shapes understory vegetation. The understory exhibits fine-scale variation of species composition that is partially organized along gradients of light transmission and substrate characteristics, although much of the variation is unrelated to these factors. Finally, in some but not all of these very open and productive forests, trees also create shade refugia where a greater number of species can reach relative abundance in a stand where *R. spectabilis* is otherwise dominant.

Additional research is needed to test these predictions over a wider range of floodplain sites and to elucidate what drives differences of pattern and process among stands (e.g., developmental stage and pathway, flood regime, time since disturbance). Furthermore, future research could more fully examine fine-scale ecology within floodplain forests by using larger samples collected at finer resolution and greater extent, allowing integrated analyses of multiple explanatory factors.

Implications for management

If the processes and patterns observed in the older floodplain stands at Kitlope and Carmanah are considered desirable, how can they be achieved in second growth stands? This question is relevant for ecosystem based management where older riparian forests are under-represented and forest managers aim to accelerate the recovery of old-growth characteristics in second growth stands. In the following, I recommend strategies that might achieve understory light and vegetation patterns and processes similar to the sites I have studied. Likely candidate areas for these activities include early seral sites (harvested in recent decades but not yet dominated by trees), young alder dominated stands, and dense conifer dominated stands. The management strategies involve using disturbance (thinning and spacing), as well as planting and vegetation control treatments. This is not intended to be a comprehensive set of management recommendations for this forest type as it does not consider all potential trade-offs, nor synergies, with the multiple other objectives that might guide stand management decisions (e.g., objectives for economic values, carbon sequestration, or specific wildlife habitat attributes).

If the management goal for a stand is to achieve vegetation patterns and processes similar to those that appear to operate at Kitlope and/or Carmanah:

- Manage for abundant and heterogeneous light:
 - By creating gaps and non-gaps of varying sizes and spatial arrangements (during removal or planting of conifers).
- Manage for some persistent shrub-gaps:
 - By leaving patches unplanted with conifers (in understory of young deciduous dominated stands for example)
 - Preferably areas with little CWD and with clonal shrubs already present
 - By creating gaps in dense second growth stands
 - Preferably areas with little CWD and with clonal shrubs already present
- Manage for some areas of deeper shade as shade refugia
 - By planting or underplanting conifers in clusters

- By leaving coniferous trees, generally in clusters

Recognizing that managing for persistent shrub-gaps represents a compromise for tree recruitment, particularly *P. sitchensis*:

- Manage for some *Picea* recruitment gaps (gaps with suitable seedbeds, sufficient light, and reduced competition from shrubs, herbs, and mosses)
 - By creating or leaving gaps with CWD
 - By removing/reducing competing vegetation (e.g., shrubs)

Considering the differences of both pattern and process between Kitlope and Carmanah and the likelihood that even greater variability is present across a larger number of natural stands:

- Apply these recommended treatments to different degrees in different stands to ensure heterogeneity is maintained across landscape to regional scales

My recommendations should be considered alongside existing research in similar forests that points to the management implications of various riparian forest attributes and stand level processes including overstory composition (e.g., *Tsuga* versus hardwoods) (Pabst and Spies 1998, Hibbs and Bower 2001, Roburn 2003), CWD (Harmon and Franklin 1989, Kennedy and Quinn 2001), herbivory (Woodward et al. 1994, Schreiner et al. 1996), trophic cascades (Beschta and Ripple 2008), wildlife habitat (e.g., Saunders et al. 2006), insect effects on *Picea* regeneration (Heppner and Turner 2006), and fluvial disturbance (Pabst and Spies 1998, Pollock et al. 1998, Sarr and Hibbs 2007a and 2007b). For example, where ungulates are hyperabundant, predation, hunting, or exclosures may be needed to attain abundant shrub cover on the forest floor (Woodward et al. 1994, Schreiner et al. 1996, Stockton et al. 2005). Finally, stand level management strategies should also be informed by knowledge of, and objectives for, valley wide processes of geomorphic disturbance, landform creation, and the resulting shifting-mosaic of vegetation patch types (Latterell et al. 2006, Van Pelt et al. 2006).

Ecosystem managers and restoration practitioners often seek reference or benchmark ecosystems for comparison to managed and degraded systems. Data from the Kitlope and Carmanah sites begin to address this information-need for older floodplain

forests of the coastal temperate rainforest. However, there are important limitations on the use of my results as an ecological benchmark. At the regional scale, two sites represent only a portion of the observed range of natural variability in overstory openness/light-transmission (i.e., Green 2005, and this study compared to Roburn 2003) and understory vegetation (e.g., Fonda 1974, Hanley and Hoel 1996, Green 2005) for unmanaged examples of this ecosystem type.

It is unclear how frequently older floodplain forests exhibit the high levels of canopy openness, vigorous understory vegetation, and other patterns and processes that characterize Kitlope and Carmanah, or what controls the variation of these factors among sites. For example, differences in canopy openness and heterogeneity among older floodplain forests might reflect differing phases of old-growth development (e.g., Franklin et al. 2002), alternative developmental pathways (e.g., Van Pelt et al. 2006), or chance disturbance events, but this question remains unanswered. Similarly, understory vegetation can vary substantially among riparian forests for various reasons including climate, chance, regional species pool and landscape connectivity, flood regime, and developmental stage and pathway (e.g., Fonda 1974, Van Pelt et al. 2006, Sarr and Hibbs 2007b), although specific factors are not well understood for older floodplain understories. To guide effective ecosystem based management, new research needs to describe and understand the range of natural variability of within-stand patterns (e.g., amount and heterogeneity of understory light) and processes (e.g., occurrence of persistent shrub-maintained gaps and shade refugia) among older floodplain stands of the coastal temperate rainforest.

There are also remaining knowledge gaps for floodplain forest management regarding the temporal patterns and processes of canopy openness and understory vegetation change through stand development. Although chronosequence research has been undertaken for both understory (Fonda 1974) and overstory (e.g., Van Pelt et al. 2006) vegetation, it remains unclear how overstory-understory interactions change through stand development or across developmental pathways. For example, it is unclear how frequently young riparian forests experience the dark and depauperate understories that characterize upland sequences (Alaback 1982, Hanley and Hoel 1996).

CONCLUSION

My examination of the Kitlope and Carmanah sites suggests a number of conclusions regarding the patterns and processes of overstory structure, light transmission, and understory vegetation in older floodplain forests of the coastal temperate rainforest, including:

- Coniferous floodplain stands can attain very high proportions of area in canopy gap and expanded gap, resulting in abundant understory light and vegetation biomass.
- Gap and non-gap (expanded gap and closed canopy) patch types have distinct light regimes yet light varies along a continuum creating overlapping boundaries between gap and non-gap patch types.
- Understory vegetation composition varies at fine scales and is partially associated with light transmission and substrate properties, although other factors must also be important.
- Depending on local factors, point diversity may decrease as light increases horizontally within a stand, in which case shady microsites provide refugia from intense competition.
- Shrub biomass is positively correlated with the spatial pattern of light transmission and may play a role in maintaining persistent spatial patterns of canopy openness by inhibiting conifer recruitment.
- Stand management practices that encourage canopy openness and spatial light heterogeneity in second growth stands may accelerate development of similar processes and patterns; however, managers will need to evaluate the effectiveness of these strategies.

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TABLES AND FIGURES

Tables

Table 1. Geographic and growing season characteristics for Kitlope and Carmanah.

	Kitlope	Carmanah
Location		
Latitude (N)	53°12'10.0"	48°40'07.6"
Longitude (W)	127°49'35.9"	124°41'10.8"
Elevation (m)	8	138
Growing season start and end		
DD5-100: date of budburst for most plants	May 9	April 5
bFFP: beginning of the frost free period	May 18	April 11
eFFP: end of the frost free period	Oct 3	Nov 2
Inferred start of growing season	May 9	April 5
Inferred end of growing season	Sept 12	Oct 12

Table 2. Descriptive statistics for canopy cover type and canopy gap origin. All but the 8 bench locations at Carmanah were included the analysis.

		Kitlope		Carmanah	
		(n=50)		(n=42)	
		Count	%	Count	%
Cover type	Closed Canopy (CC)	4	8	1	2
	Expanded Gap (EG)	27	54	26	62
	Canopy Gap (CG)	19	38	15	36
Gap origin	Developmental Gap (dvG)	1	2	34	83
	Edaphic Gap (edG)	4	9	7	17
	Unknown	41	89	0	0

Table 3. Descriptive statistics for environment variables at each site. Organic and mineral horizon descriptors (LFH, Ah) follow the Canadian System of Soil Classification (Soil Classification Working Group 1998).

Variable	Kitlope					Carmanah				
	<i>n</i>	Median	Mean	SD	CV (%)	<i>n</i>	Median	Mean	SD	CV (%)
Substrate and Forest Floor										
Forest Floor (% cover)	24	3	6	14	223	16	85	81	21	26
CWD (% cover)	24	0	5	9	193	16	15	18	21	115
Humus thickness (cm)	24	0.0	0.0	0.0	490	16	2.5	2.6	1.7	66
LFH thickness (cm)	24	0.5	0.6	0.5	89	16	3.5	4.0	2.3	58
Ah thickness (cm)	24	4.1	4.9	2.7	55	16	1.3	1.5	1.2	80
Decaying Wood (% vol.)	24	0	1	3	237	16	0	6	12	193
Soil Texture and Water Properties										
% Clay	24	20	21	11	53	16	10	11	8	72
% Silt	24	56	53	20	37	16	25	32	28	88
% Sand	24	20	26	23	89	16	65	58	31	54
% Coarse Fragments	24	0	0	0	na	16	3	26	34	133
Plant Available Water (cm ³ water/cm ³ soil)	24	17	17	5	29	16	8	10	8	77
Hydraulic conductivity (cm/hr)	24	12	21	22	106	16	33	38	26	68
Overstory Structure and Light Transmission										
<i>All available microsites in ecosystem of interest¹, including recent windthrow</i>										
% Site openness	49	11.6	11.5	2.6	22.9	39	11.0	11.1	3.3	30.1
LAI 4 – Leaf Area Index 4	49	2.5	2.5	0.2	9.6	39	2.5	2.5	0.4	15.4
LAI 5 – Leaf Area Index 5	49	2.5	2.5	0.2	8.9	39	2.7	2.7	0.3	11.5
Direct PAR (mol/m ² /d)	49	0.6	0.7	0.3	46.1	39	0.6	0.6	0.3	40.6
Diffuse PAR (mol/m ² /d)	49	3.8	3.8	1.0	26.1	39	3.5	3.4	1.1	32.1
Total PAR (mol/m ² /d)	49	4.3	4.5	1.1	25.4	39	4.1	4.1	1.3	31.9
% Direct PAR	49	14.8	17.2	8.0	46.2	39	17.6	17.6	7.1	40.5
% Diffuse PAR	49	18.7	19.1	5.0	26.1	39	18.0	17.9	5.8	32.1
% PAR (aka. % full sun)	49	17.7	18.8	4.8	25.3	39	17.9	17.9	5.7	31.9
<i>All available microsites in ecosystem of interest¹, less recent windthrow</i>										
% Full sun	49	17.7	18.8	4.8	25.3	32	16.2	16.6	5.0	30.4
<i>Vegetation subplots in ecosystem of interest¹, less recent windthrow</i>										
% Full sun	24	18.9	18.9	4.5	24	16	19.1	17.9	5.2	29

¹Ecosystem of interest does not include the raised terrace bench or the fluvial channel.

Table 4. The slow-and-thorough autopilot procedure in PC-ORD was used to generate and assess NMS solutions, using 250 runs with real data and 250 runs with randomized data. Stress levels below 15 are satisfactory (McCune and Grace 2002).

	Kitlope (<i>n</i>=24)	Carmanah (<i>n</i>=16)
# Dimensions recommended	3	3
Monte Carlo <i>P</i> value after 250 runs	0.0040	0.0040
Final Stress	14.051	8.32
Final instability	<0.00001	<0.00001
Number of iterations	125	51
Cumulative R^2 (proportion represented)	0.79	0.90

Table 5. Summary statistics for ordination results at Kitlope ($n=24$). The cumulative proportion of variation represented by the three axes (R^2) is 0.79 before and after rotation. I used bold font to identify correlations with $r^2 \geq 0.3$. Species names follow Meidinger et al. (2009).

		Axis 1		Axis 2		Axis 3	
% represented after rotation		0.41		0.17		0.21	
		<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
Species Name	Species Code						
<i>Oplopanax horridus</i> (Smith) Miq.	OPLOHOR	-0.659	0.434	0.542	0.294	-0.348	0.12
<i>Ribes bracteosum</i> Dougl. ex Hook.	RIBEBRA	0.642	0.412	0.154	0.024	-0.093	0.009
<i>Rubus spectabilis</i> Pursh	RUBUSPE	0.334	0.111	-0.318	0.101	0.632	0.399
<i>Sambucus racemosa</i> ssp. <i>pubens</i> (Michx.) House	SAMBRAC	0.374	0.140	0.085	0.007	-0.515	0.265
<i>Athyrium filix-femina</i> (L.) Roth	ATHYFIL	-0.340	0.116	0.481	0.231	-0.107	0.011
<i>Circaea alpina</i> L.	CIRCALP	0.462	0.214	-0.390	0.152	-0.352	0.124
<i>Dryopteris expansa</i> (K.B. Presl) Fraser-Jenkins & Jermy	DRYOEXP	-0.613	0.376	-0.153	0.024	-0.294	0.086
<i>Galium triflorum</i> Michx.	GALITRI	-0.432	0.186	-0.226	0.051	-0.437	0.191
Poaceae sp.	GRASS	0.136	0.018	0.368	0.135	-0.153	0.023
<i>Lysichiton americanus</i> Hult. & St. John	LYSIAME	-0.027	0.001	-0.192	0.037	-0.357	0.127
<i>Maianthemum dilatatum</i> (A. Wood) Nels. & J.F. Macbr.	MAIADIL	-0.334	0.111	0.391	0.153	-0.407	0.165
<i>Osmorhiza berteroi</i> DC.	OSMOBER	-0.560	0.314	0.319	0.102	0.062	0.004
<i>Osmorhiza purpurea</i> (Coult. & Rose) Suksd.	OSMOPUR	-0.252	0.064	0.111	0.012	0.511	0.262
<i>Polystichum braunii</i> (Spenner) Fée	POLYBRA	0.336	0.113	0.262	0.069	-0.153	0.024
<i>Stellaria crispa</i> Cham. & Schlecht.	STELCRI	0.321	0.103	-0.410	0.168	-0.390	0.152
<i>Streptopus amplexifolius</i> (L.) DC.	STREAMP	-0.157	0.025	-0.141	0.020	-0.501	0.251
<i>Streptopus lanceolatus</i> var. <i>curvipes</i> (Vail) Reveal	STRELAN1	-0.237	0.056	0.674	0.454	0.432	0.186
<i>Tiarella trifoliata</i> L.	TIARTRI	-0.430	0.185	0.241	0.058	-0.347	0.121
<i>Trautvetteria caroliniensis</i> (Walt.) Vail	TRAUCAR	-0.317	0.101	-0.115	0.013	0.053	0.003
Environment							
LF Thickness ¹ (LnLFwtPls1)		-0.259	0.067	-0.011	0.000	0.052	0.003
Ah+H Thickness ² (AhHwt)		-0.321	0.103	0.229	0.052	-0.026	0.001
% Sand ³ (LnSand)		-0.168	0.028	-0.113	0.013	-0.067	0.005
% Clay ³ (LnClay)		-0.301	0.091	-0.023	0.001	-0.101	0.010
% Silt (Silt)		0.311	0.097	0.131	0.017	0.113	0.013
Distance to Water (DistW)		0.327	0.107	-0.059	0.003	0.207	0.043
% Full Sun		0.722	0.522	0.020	0.000	-0.034	0.001

Note: To avoid use of collinear explanatory variables, I have not presented results for PAW or Ks. Both variables are statistically and functionally associated with soil texture. See Appendix 1.

¹ weighted by the % of the subplot covered by organic matter substrate type and transformed as natural log of (X+1).

² weighted by the % of the subplot covered by organic matter substrate type.

³ natural log transformed.

Table 6. Indicator Species Analysis was used to describe compositional differences between gap and non-gap. For each species, a Monte Carlo procedure with 4999 randomizations was used to test the hypothesis of no difference in Indicator Values (IV) between gaps and non-gaps. Results are shown only for species with significant or marginally significant results. Bold and underlined indicator values are significant at the 0.05 level.

Site	Species	Max Group	Observed IV	Randomized IVs		P
				Mean	SD	
Kitlope	<i>Oplopanax horridus</i>	Nongap	<u>60.2</u>	35.7	8.82	0.018
Kitlope	<i>Dryopteris expansa</i>	Nongap	<u>65.7</u>	55	5.34	0.045
Kitlope	<i>Tiarella trifoliata</i>	Nongap	59.7	44.4	8.77	0.065
Kitlope	<i>Trautvetteria caroliniensis</i>	Nongap	48.4	33.5	8.72	0.076
Kitlope	<i>Sambucus racemosa ssp. pubens</i>	Gap	<u>55.3</u>	37.7	8.77	0.045
Kitlope	<i>Stellaria crispa</i>	Gap	60.8	45.2	7.84	0.050
Kitlope	<i>Rubus spectabilis</i>	Gap	57.3	53.1	2.43	0.056
Carmanah	<i>Dryopteris expansa</i>	Gap	<u>95.2</u>	38.5	11.31	0.0002
Carmanah	<i>Blechnum spicant</i> (L.) Roth	Gap	<u>83.2</u>	49.0	8.98	0.001
Carmanah	<i>Vaccinium parvifolium</i> Sm.	Gap	48.3	28.7	10.67	0.072

Max Group is the canopy cover type with the maximum observed IV.

P represents the proportion of Indicator Values from randomized trials that equal or exceed the observed Indicator Value.

Table 7. Summary statistics for ordination results at Carmanah ($n=16$). The cumulative proportion of variation represented by the three axes (R^2) is 0.90 before and after rotation. I used bold font to identify correlations with $r^2 \geq 0.3$.

% represented after rotation		Axis 1		Axis 2		Axis 3	
		0.344		0.271		0.282	
		<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
Species Name	Species Code						
<i>Ribes bracteosum</i>	RIBEBRA	0.669	0.448	0.061	0.004	0.216	0.047
<i>Rubus spectabilis</i>	RUBUSPE	0.730	0.533	0.109	0.012	0.009	0.000
<i>Vaccinium parvifolium</i> Sm.	VACCPAR	-0.514	0.264	0.393	0.154	0.149	0.022
<i>Athyrium filix-femina</i>	ATHYFIL	-0.246	0.060	0.349	0.122	0.462	0.213
<i>Blechnum spicant</i> (L.) Roth	BLECSPI	-0.656	0.431	0.736	0.542	0.194	0.038
<i>Boykinia occidentalis</i> T. & G.	BOYKELA	-0.273	0.074	-0.174	0.030	0.687	0.473
<i>Claytonia sibirica</i> L.	CLAYSIB	-0.043	0.002	-0.541	0.293	0.712	0.506
<i>Prosartes smithii</i> (Hook.) Utech, Shinwari & Kawano	DISPSMI	-0.364	0.133	-0.571	0.326	-0.121	0.015
<i>Dryopteris expansa</i>	DRYOEXP	-0.257	0.066	0.743	0.551	-0.164	0.027
<i>Galium triflorum</i>	GALITRF	-0.290	0.084	-0.203	0.041	0.743	0.552
<i>Maianthemum dilatatum</i>	MAIADIL	-0.506	0.256	0.354	0.126	0.213	0.045
<i>Mitella ovalis</i> Greene	MITEOVA	-0.282	0.080	-0.095	0.009	0.733	0.538
<i>Polystichum munitum</i> (Kaulf.) K.B. Presl	POLYMUN	-0.370	0.137	-0.385	0.149	-0.295	0.087
<i>Tiarella trifoliata</i>	TIARTRI	0.092	0.008	-0.194	0.038	0.549	0.302
<i>Trautvetteria caroliniensis</i>	TRAUCAR	0.192	0.037	-0.211	0.045	0.183	0.034
Environment							
Forest Floor Thickness (FF)		0.002	0.000	-0.507	0.257	0.138	0.019
LF Thickness ¹ (LnLFwtPls1)		0.292	0.085	-0.343	0.118	-0.280	0.078
H Thickness ² (Hwt)		-0.205	0.042	-0.559	0.312	0.143	0.020
Ah+H Thickness ² (AhHwt)		-0.034	0.001	-0.523	0.274	-0.013	0.000
% Sand (Sand)		0.341	0.116	-0.244	0.059	0.089	0.008
% Clay ³ (LnClay)		-0.242	0.059	0.673	0.453	-0.009	0.000
% Silt (Silt)		-0.345	0.119	0.111	0.012	-0.115	0.013
% Full Sun		0.571	0.326	-0.014	0.000	-0.001	0.000

Note: To avoid use of collinear explanatory variables, I have not presented results for PAW or Ks. Both variables are statistically and functionally associated with soil texture.

See Appendix 1.

¹ weighted by the % of the subplot covered by organic matter substrate type and transformed as natural log of (X+1).

² weighted by the % of the subplot covered by organic matter substrate type.

³ natural log transformed.

Table 8. Correlation analysis understory vegetation layers in relation to light, and total herb cover in relation to shrubs. After eliminating subplots in very recent openings, shrub cover is positively correlated with light transmission in both sites. Herb cover is not significantly correlated with light transmission at either site. Vascular cover is positively correlated with light at Carmanah but not Kitlope.

Variable 1	Variable 2	Kitlope					Carmanah					Carmanah				
		<i>n</i> =24					<i>n</i> =19 ¹					<i>n</i> =16 ¹				
		<i>r</i>	<i>P</i>	<i>P_{Dut}</i>	<i>n_e</i>	GL	<i>r</i>	<i>P</i>	<i>P_{Dut}</i>	<i>n_e</i>	GL	<i>r</i>	<i>P</i>	<i>P_{Dut}</i>	<i>n_e</i>	GL
Layer vs Light																
Shrub	% Full Sun	<u>0.48</u>	0.017	0.023	22		0.34	0.161	0.155	19		<u>0.63</u>	0.008	0.008	16	
Herb	% Full Sun	-0.33	0.110	0.112	24		-0.05	0.849	0.886	12		-0.01	0.957	0.959	15	
Vascular	% Full Sun	0.29	0.167	0.167	24		0.30	0.214	0.139	26		<u>0.59</u>	0.017	0.029	14	
sRUBUSPE	% Full Sun	0.24	0.260	0.248	25		0.45	0.052	0.052	19		<u>0.79</u>	0.000	0.001	13	
Layer vs Layer																
Herb	Shrub	-0.12	0.587	0.574	26		-0.24	0.314	0.336	18		-0.22	0.422	0.482	13	
Herb	sRUBUSPE	<u>-0.41</u>	0.044	0.040	25		-0.08	0.730	0.705	22		-0.01	0.964	0.965	15	

r: Pearson correlation coefficient. This estimate is not adjusted by the Dutilleul procedure.

Bold and underlined coefficients are significant at the 0.05 level according to Dutilleul corrected *P* values.

n_e: effective sample size, after Dutilleul correction.

P: the *P*-value from a conventional t-test, not corrected for spatial autocorrelation.

P_{Dut}: the *P*-value from a Dutilleul corrected t-test, which accounts for spatial autocorrelation of each variable.

GL: Gain or Loss of statistical significance (at the 0.05 level) after applying the Dutilleul correction.

"+" indicates a gain; "-" indicates a loss of statistical significance.

¹ correlations were examined with (*n*=19) and without (*n*=16) recent windthrow disturbance subplots.

Table 9. Correlation analysis of understory diversity with overstory light transmission and summed cover of the understory vascular plants (SumVasc). Species richness (S) is not significantly correlated with light or salmonberry. Evenness (E) is negatively correlated with light at Carmanah but not Kitlope. Dominance (Ls) is positively with light at Carmanah but not Kitlope.

Variable 1	Variable 2	Kitlope					Carmanah				
		<i>n</i> =24					<i>n</i> =16				
		<i>r</i>	<i>P</i>	<i>P_{Dut}</i>	<i>n_e</i>	GL	<i>r</i>	<i>P</i>	<i>P_{Dut}</i>	<i>n_e</i>	GL
Diversity vs Light											
S	% Full Sun	-0.22	0.292	0.336	20		-0.47	0.065	0.077	15	
E	% Full Sun	-0.09	0.668	0.640	28		<u>-0.64</u>	0.008	0.010	15	
Ls ¹	% Full Sun	0.13	0.537	0.511	27		<u>0.72</u>	0.002	0.004	14	
Diversity vs Cover											
S	SumVasc	0.14	0.515	0.436	33		-0.17	0.519	0.449	21	
E	SumVasc	0.36	0.080	0.076	25		-0.36	0.169	0.101	22	
Ls ¹	SumVasc	-0.40	0.056	0.049	25	+	0.31	0.242	0.144	24	

r: Pearson correlation coefficient. This estimate is not adjusted by the Dutilleul procedure.

Bold and underlined coefficients are significant at the 0.05 level according to Dutilleul corrected *P* values.

n_e: effective sample size, after Dutilleul correction.

P: the *P*-value from a conventional t-test, not corrected for spatial autocorrelation.

P_{Dut}: the *P*-value from a Dutilleul corrected t-test, which accounts for spatial autocorrelation of each variable.

GL: Gain or Loss of statistical significance (at the 0.05 level) after applying the Dutilleul correction.

"+" indicates a gain; "-" indicates a loss of statistical significance.

¹Ls was square root transformed for Kitlope analysis.

Figures

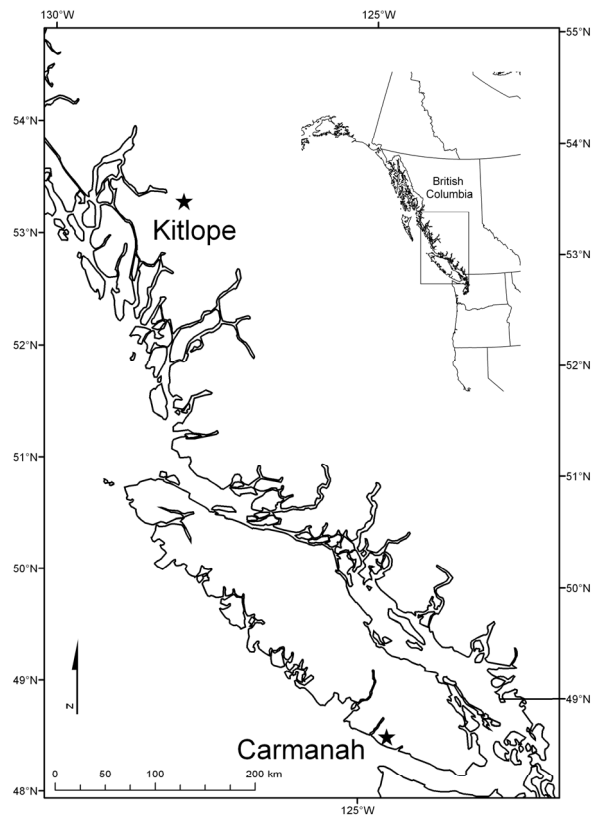


Figure 1. Map of Kitlope and Carmanah study locations in coastal British Columbia, Canada.

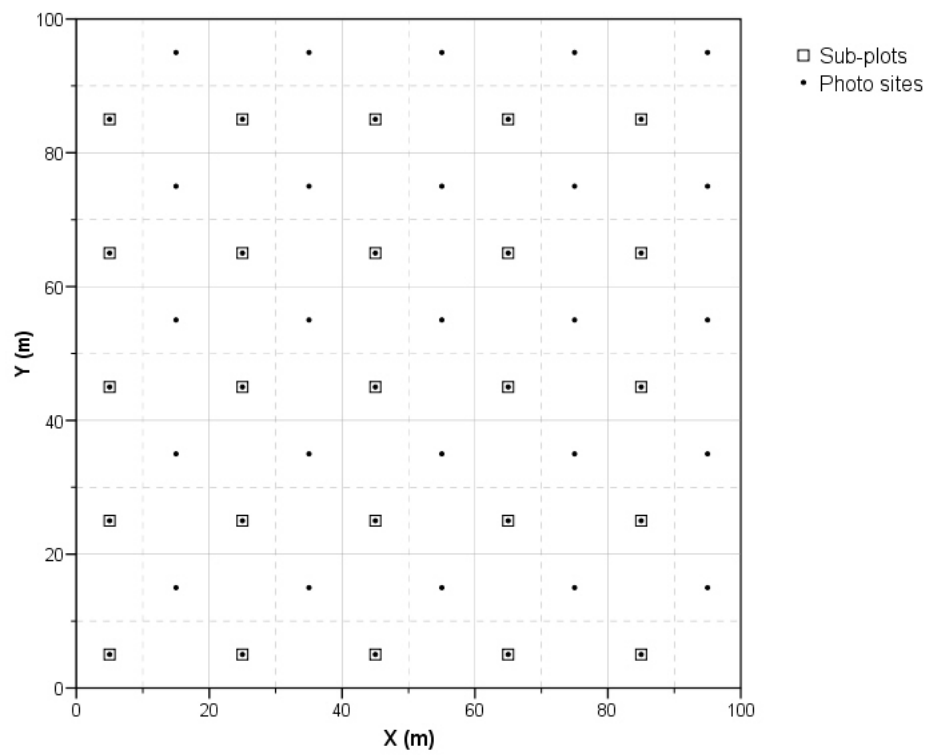


Figure 2. Plan view of sampling layout for subplots and photo sites in the one-hectare macroplots.

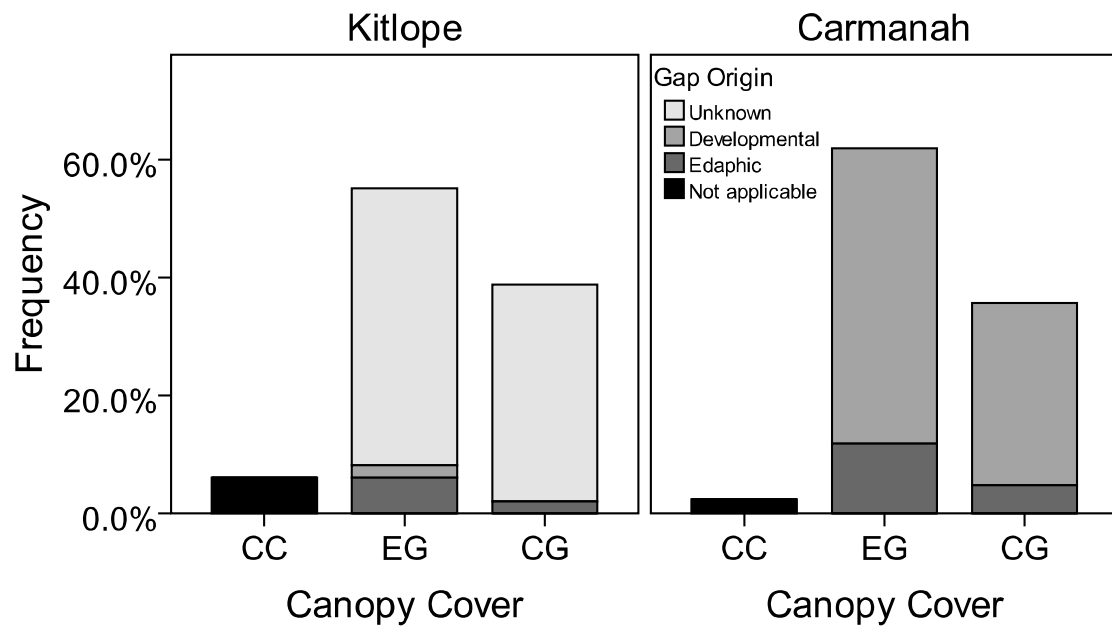


Figure 3. Frequency of three canopy cover types at each site. Closed canopy (CC) is rare and both sites have more expanded gap (EG) than canopy gap (CG). Developmental gaps are dominant at Carmanah, whereas most gaps at Kitlope had unknown origin. Figures are based on $n=42$ at Carmanah, after omitting raised bench microsites, and $n=50$ at Kitlope.

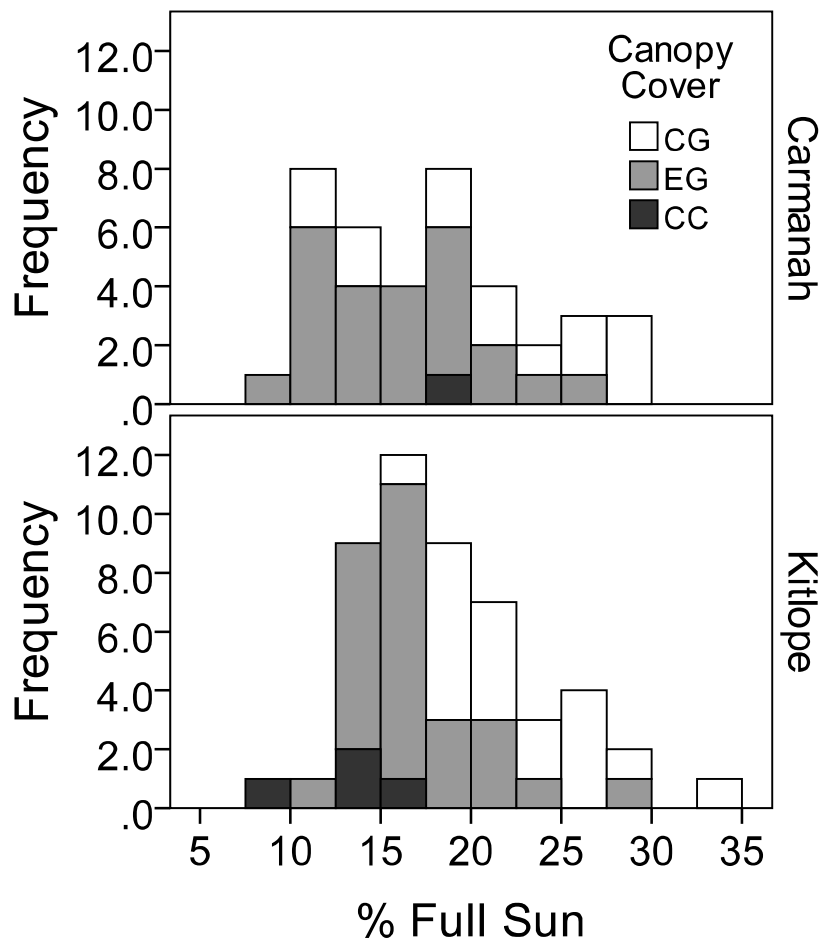


Figure 4. Frequency distribution of % full sun estimates. At both sites, canopy gaps (CG) tend to occur in the brighter half of the distribution, expanded gaps (EG) are dominant in the middle of the distribution but are found across most light levels, and closed canopy (CC) microsites are rare. Fluvial channel and raised bench microsites were omitted: $n=49$ at Kitlope, $n=39$ at Carmanah.

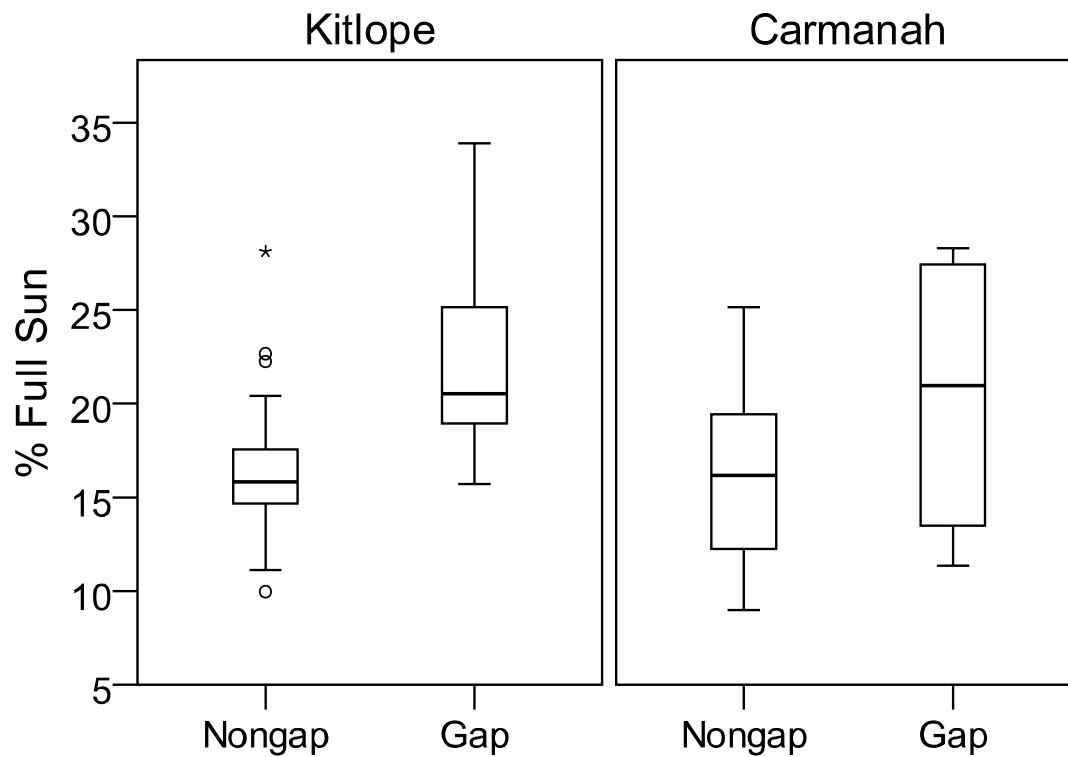


Figure 5. Box-plots of understory light in canopy gap and non-gap microsites. At both sites, median light transmission is higher in gap microsites than non-gap microsites and light distributions are significantly different between types (Kitlope $n=49$, Mann-Whitney $U=75$, $P<0.001$, two-sided test; Carmanah $n=39$, $U=92$, $P=0.015$). Fluvial channel and raised bench microsites omitted.

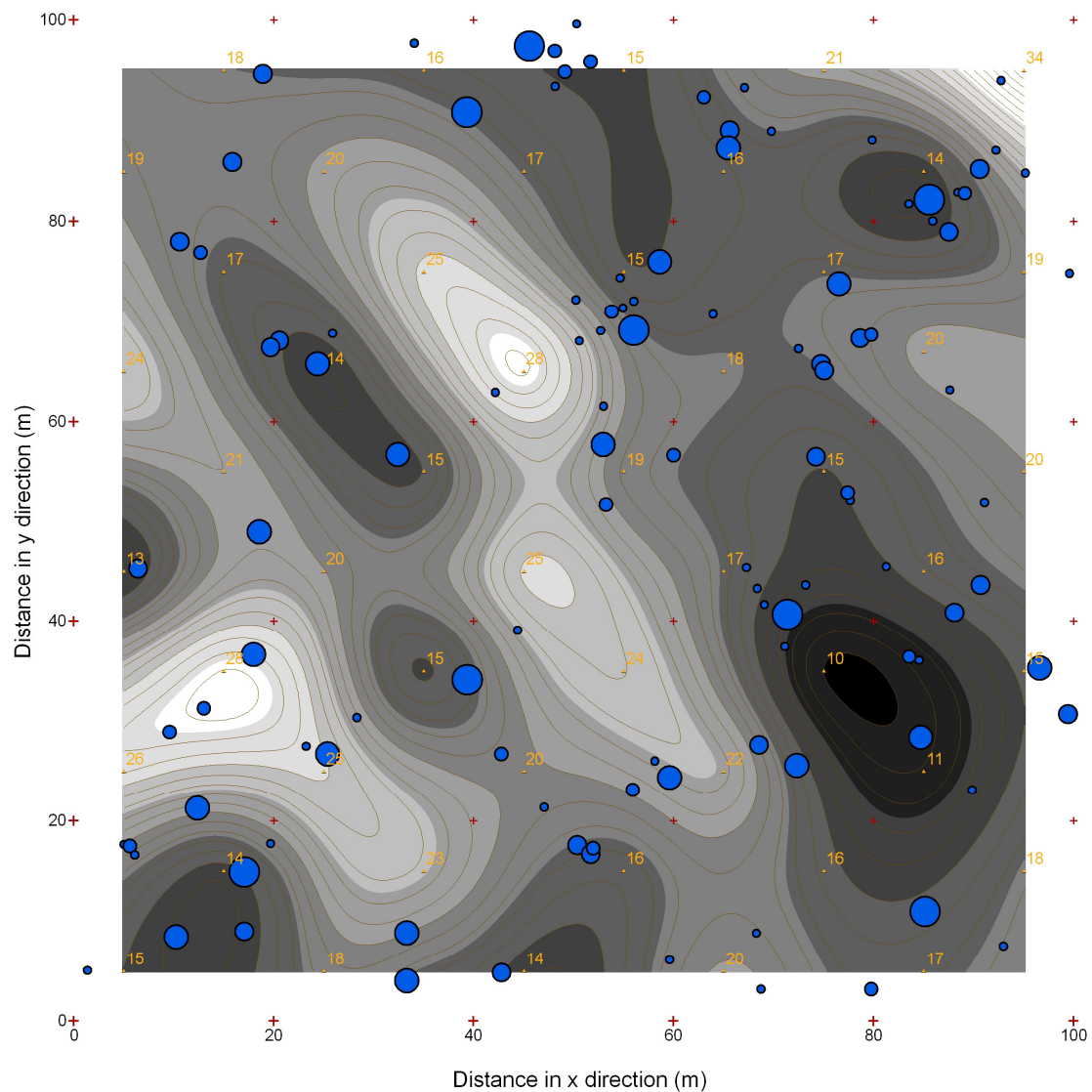
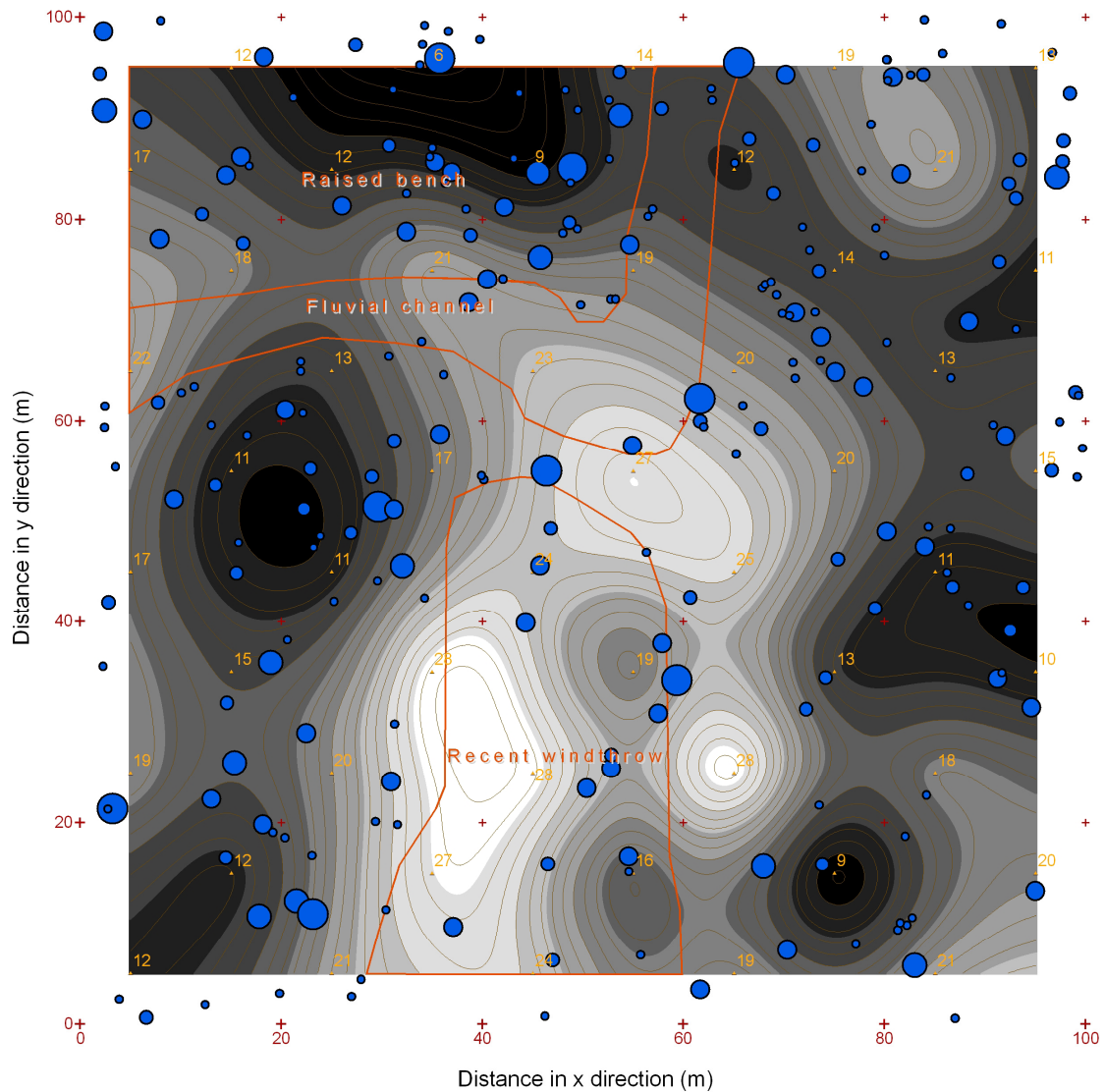


Figure 6. Map of estimated Kitlope understory light values in relation to overstory tree size and location. Light values between sample locations were estimated and mapped using a tension spline interpolation.



Legend

Tree DBH (cm)

- 5 - 25
- 26 - 50
- 51 - 100
- 101 - 150
- 151 - 300

% Full Sun

- 5.7 - 10
- 10.1 - 12.5
- 12.6 - 15
- 15.1 - 17.5
- 17.6 - 20
- 20.1 - 22.5
- 22.6 - 25
- 25.1 - 27.5
- 27.6 - 30

• Photo Location

— 1% Full Sun Contour

Figure 7. Map of estimated Carmanah understory light values in relation to overstory tree size and location. Light values between sample locations were estimated and mapped using a tension spline interpolation.

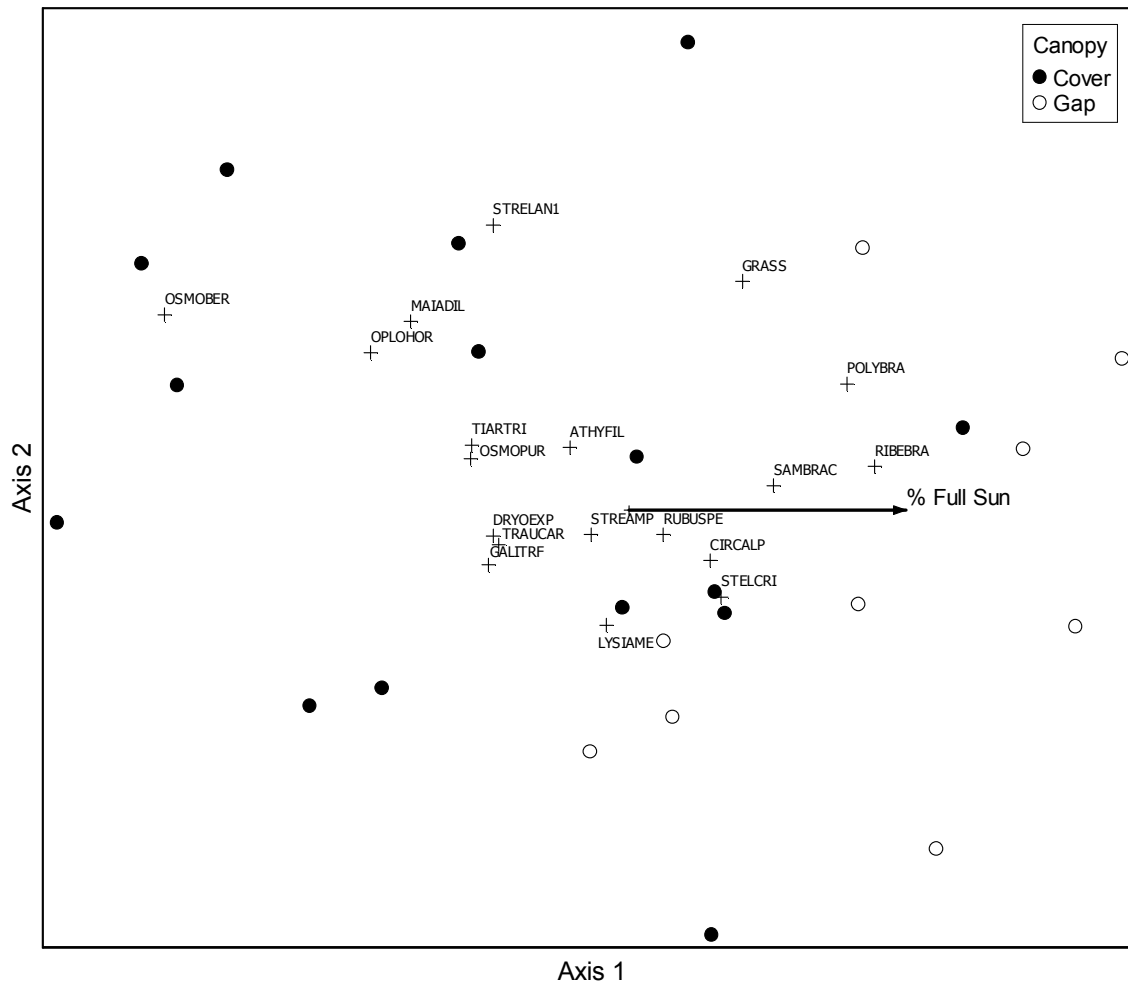


Figure 8. NMS ordination diagram and joint-plot for the two primary axes at Kitlope ($n=24$). The angle of the arrow represents the direction of correlation between ordination scores and light transmission. The length of the arrow represents correlation strength. Composition differs between gaps and non-gaps (cover).

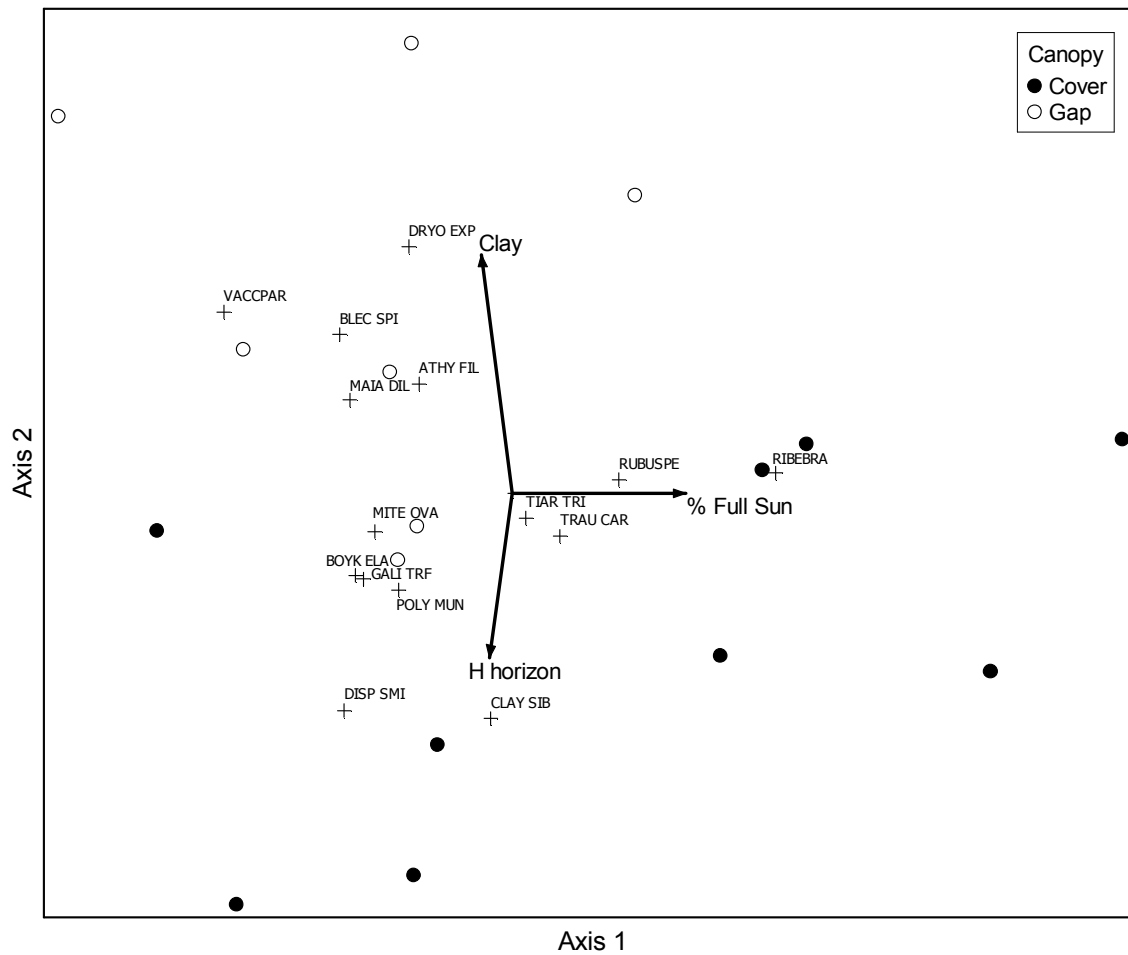


Figure 9. NMS ordination diagram and joint-plot for the two primary axes at Carmanah ($n=16$). Composition varies along two primary gradients, which are correlated with light transmission and clay content. Composition differs between gaps and non-gaps (cover).



Figure 10. Photo showing *Sambucus racemosa* overtopping *Rubus spectabilis* at Kitlope.

APPENDICES

Appendix 1. Soil water properties

I used the SPAW Model with Soil Water Characteristics program (and accompanying spreadsheet) to estimate soil water properties, including saturated hydraulic conductivity (Ks; cm/hr) and Plant Available Water (PAW; cm³ water/cm³ soil), from field data on soil textural class and coarse fragment content. The SPAW model uses the empirical equations of Saxton and Rawls (2006). However, to avoid use of correlated explanatory variables, I have not shown the results for PAW or Ks in the ordination diagrams or correlation tables. Both attributes have a strong statistical and functional association with soil texture (Saxton and Rawls 2006).

In summary, I found that saturated hydraulic conductivity is negatively correlated with Axis 2 at Carmanah ($r=-0.60$, $R^2=0.36$, for the natural logarithm of hydraulic conductivity) and unrelated to any other axis at either site ($R^2<0.1$). Plant available water is unrelated to any compositional Axis at either site ($R^2<0.16$ for any axis, with rotations as described). Thus, in terms of soil water properties, I interpret the Axis 2 clay correlation as reflecting decreasing hydraulic conductivity as opposed to Plant Available Water (though this is not the only ecological interpretation of clay influence on plants). Saturated hydraulic conductivity decreases rapidly with increasing clay content and increases, though less rapidly, with increasing sand content (Saxton et al. 1986). Balian and Naiman (2005) describe how hydraulic conductivity (and percentage water content) changes during stand development in Queets River floodplain forests. Ecologically, I interpret saturated hydraulic conductivity as an indicator of water infiltration and soil drainage; for a given available water content, a soil with higher saturated hydraulic conductivity would experience different rates and durations of wetting and drying during rains or floods and dry periods respectively, and may be differently affected by groundwater upwelling (which can influence riparian plants). With reference to my interpretation of Axis 2 at Carmanah: during a dry period, a microsite with lower saturated hydraulic conductivity (higher clay content) would presumably drain more slowly, perhaps allowing more time for shallow rooted plants to uptake water.

Appendix 2. Spatial analysis

Methods

I used Moran's *I* statistics to assess for spatial autocorrelation among neighbouring sample units and to quantify and describe spatial patterns of understory vegetation and light within stands. Moran's *I* values range from -1 to +1, corresponding to negative and positive spatial autocorrelation. Positive spatial autocorrelation indicates that nearby locations have similar values; negative autocorrelation indicates that nearby locations have substantially different values Rosenberg (2009).

I generated Moran's *I* correlograms in the software PASSaGE v2 (Rosenberg 2009). Moran's *I* coefficients for each distance class were tested for significance by comparing with all possible random permutations of the data (the random distribution assumption; Rosenberg 2009). Overall correlogram significance was assessed with a Bonferroni procedure because the distance classes of a correlogram are not independent (Rosenberg 2009, Fortin and Dale 2005). I applied the criteria in Table 10 before interpreting correlograms.

I used the maps and correlograms of Legendre and Legendre (1998) and Fortin and Dale (2005) (which are based on simulated data of well defined spatial patterns including gradients, steps, a single bump, waves, various repeating patch patterns, and randomness) as a reference when interpreting spatial patterns from the correlograms I produced. For patch-like structures, I interpreted patch size (diameter) as the distance at which the first maximum negative spatial autocorrelation (Moran's *I*) is found (criteria used by Legendre and Legendre 1998, p. 727).

Table 10. The following criteria were applied prior to interpreting correlograms.

Condition	Interpretation
If overall significant	Interpret full correlogram for spatial structure. E.g., "repeating patches."
If not overall significant, but significant Moran's <i>I</i> in the first distance class (first two for photo variables)	"Weak ill-defined structure," meaning that spatial structure exists but the overall pattern is not well defined.
Otherwise (non-significant overall <i>and</i> do not show significant SAC at ≤ 20 m).	"Random or inadequate sample."

Spatial analyses with Moran's *I* are sensitive to departures from normality, particularly skewness, and analysts typically attempt to normalize the data before generating correlograms (Legendre and Legendre 1998, Roburn 2003). Before conducting spatial autocorrelation analyses,

I assessed each variable for normality, skew and Kurtosis. For all variables with distributions significantly different from a normal distribution (Kolmogorov-Smirnov test), or strong skew, I applied a transformation prior to conducting the spatial autocorrelation analysis.

To conduct the correlogram analysis, I calculated a matrix of Euclidean distances between pairs of sample units and assigned pairs to distance classes. For subplot data, I used seven distance classes with user-defined boundaries. Most pairs of subplots have a discrete separation distance due to the systematic grid sampling design (20, 28.3, 40, 44, 72, 56.6, 60, 63.25 m; at greater distances these intervals become less discrete). I created the following distance classes, centered on these natural intervals: 19-21, 28-29, 39-41, 44-45, 56-61, 61-75, 75-83 m. PASSaGE plots Moran's I coefficients at the mid-point of each distance class. Because of this, I drew the class boundaries just above and just below the discrete intervals (imposed by the sampling design) to ensure that the Moran's I coefficients were plotted at a representative location on the X (distance) axis of the correlogram. For example: for the pairs separated by 20 m, the distance class 0-20 m would plot at 10 m, while the distance class 19-21 m plots (the same data) at 20 m exactly. Regarding the number of distance classes, Legendre and Legendre (1989) suggest Sturge's rule as an objective means of determining the number of distance classes to use. For my analysis, Sturge's rule recommends eight distance classes for $n=19$ (the smaller sample of the two stands), yet in my judgment this produces at least one distance class with too few pairs of points. I used seven distance classes because this seems to achieve the most even distribution of pairs between classes and ensures a reasonable minimum number of pairs in each class. The maximum distance considered was 83 m; too few pairs exist beyond that distance. At Carmanah, the 75-83 m distance class was also excluded from analysis due to a shortage of pairs. For all correlograms, I used a binary weight matrix.

For photo data, I used 10 distance classes with user-defined boundaries (Sturge's rule recommends 10 distance classes for $n=39$). Due to the greater sample size compared to subplots, the separation distances are less discrete beyond 50 m, yet distance classes are discrete over the first 50 m. I created the following distance classes, which again ensure accurate plotting of Moran's I values with respect to distance: 14-15, 19-21, 28-32, 39-43, 43-46, 46-56, 56-66, 66-76, 76-86, 86-96 m. The maximum distance is 96 m because too few pairs exist beyond that distance.

Results

A number of the vegetation and environment variables at Carmanah show positive spatial autocorrelation at 20 m, the minimum distance between subplots. At Carmanah, vascular understory species richness (S), evenness (E), dominance (Ls), herb cover, LF, sand, silt, and PAW, show positive spatial autocorrelation (Global Moran's I) at the 20 m sampling interval ($P < 0.05$) (Table 12). Each of the overstory (canopy openness, LAI-4 and LAI-5) and light (direct, diffuse, total, and percent total light transmission) variables at Carmanah show positive spatial autocorrelation at ~14 m, 20 m, or both ($P < 0.05$) (Table 11). At Kitlope, only AhHwt thickness and DistW are positively autocorrelated at 20 m ($P < 0.05$) (Table 12), while some vegetation attributes show negative spatial autocorrelation. None of the overstory or light variables at Kitlope show significant positive spatial autocorrelation at 20 m (Table 11). LAI-5 shows weak non-significant SAC at 20 m and LAI-4 shows significant but weak SAC ($I = 0.20$) at ~14 m ($P = 0.033$).

The finding that positive spatial autocorrelation is present in some vegetation and environment variables indicates that the rate of Type I errors might be inflated for tests of significance in correlation and regression analysis with those variables (Legendre and Legendre 1998, Dale and Fortin 2002). This finding supports the use of Dutilleul's correction for t -tests of correlation significance, particularly for Carmanah. At Kitlope, although positive spatial autocorrelation is not prominent at 20 m, understory vegetation shows signs of spatial structure within the stand (see correlogram analysis below). Thus, for both Carmanah and Kitlope I have taken the conservative approach of using statistical techniques that aim to mitigate the effects of spatial autocorrelation on Type I error rates in correlation analysis.

Table 11. Moran's I spatial autocorrelation coefficients for overstory and light variables at the first two distance classes. Correlogram coefficients for each distance class were tested for significance by comparing with all possible random permutations of the data: * $P<0.05$, ** $P<0.01$, * $P<0.001$. Overall correlograms were tested with a Bonferroni procedure: bold font indicates $P<0.05$.**

Carmanah (<i>n</i> =39)										Kitlope (<i>n</i> =50)						
Variable	Min. Max.			Class	dist.	dist.	# Pairs	E(<i>I</i>)	<i>I</i>	SD(<i>I</i>)	Class		Overall		Class	Overall
											<i>P</i> -value	<i>P</i> -value	# Pairs	E(<i>I</i>)		
<i>Overstory</i>																
% Site Openness	1	14	15	60	-0.03	0.21	0.12	0.058	0.065	81	-0.02	0.07	0.10	0.405	1.000	
	2	19	21	57	-0.03	0.32**	0.13	0.006		80	-0.02	-0.06	0.11	0.674		
LAI 4 ring	1	14	15	60	-0.03	0.26*	0.12	0.022	0.066	81	-0.02	0.20*	0.11	0.033	0.334	
	2	19	21	57	-0.03	0.32**	0.13	0.007		80	-0.02	0.07	0.11	0.414		
LAI 5 ring	1	14	15	60	-0.03	0.28*	0.12	0.015	0.026	81	-0.02	0.15	0.10	0.110	0.504	
	2	19	21	57	-0.03	0.36**	0.13	0.003		80	-0.02	0.19	0.11	0.050		
<i>Light</i>																
Direct PAR (mol/m ² /d)	1	14	15	60	-0.03	0.43***	0.12	0.000	0.002	81	-0.02	0.16	0.10	0.089	0.706	
	2	19	21	57	-0.03	0.20	0.13	0.072		80	-0.02	0.03	0.11	0.644		
Diffuse PAR (mol/m ² /d)	1	14	15	60	-0.03	0.18	0.12	0.104	0.119	81	-0.02	0.06	0.11	0.449	1.000	
	2	19	21	57	-0.03	0.29*	0.13	0.012		80	-0.02	-0.09	0.11	0.518		
Total PAR (mol/m ² /d)	1	14	15	60	-0.03	0.26*	0.12	0.022	0.127	81	-0.02	0.05	0.11	0.494	1.000	
	2	19	21	57	-0.03	0.29*	0.13	0.013		80	-0.02	-0.10	0.11	0.455		
% PAR (aka. % Full Sun)	1	14	15	60	-0.03	0.26*	0.12	0.022	0.127	81	-0.02	0.05	0.11	0.490	1.000	
	2	19	21	57	-0.03	0.29*	0.13	0.013		80	-0.02	-0.10	0.11	0.454		

$E(I)$ is the expected value of I for a random distribution. $SD(I)$ is the standard deviation of I .

None of the light and overstory variables are significantly different from a normal distribution (Kolmogorov-Smirnov test, $P<0.05$) but most show moderate positive skew at Kitlope. For these variables I applied transformation and did a sensitivity analysis to determine if the transformed versus raw values would produce different interpretations from spatial autocorrelation analysis. The transformation in no case resulted in the gain or loss of significance for Moran's I values at any distance class or a gain or loss of overall correlogram significance, and the Moran's I values did not dramatically change. Thus, raw values were used in the final analysis, and the results are robust to the skew present.

LAI = Leaf Area Index.

Table 12. Moran's I spatial autocorrelation coefficients for subplot vegetation and environment variables, at the first distance class. Vegetation analyses based on summed cover values for respective layer or species. Correlogram coefficients for each distance class were tested for significance by comparing with all possible random permutations of the data: * $P<0.05$, ** $P<0.01$, *** $P<0.001$. Overall correlograms were tested with a Bonferroni procedure: bold font indicates $P<0.05$.

Carmanah (<i>n</i> =19)										Kitlope (<i>n</i> =24)							
Variable	Class	Min.		Max.	# Pairs	<i>E(I)</i>	<i>I</i>	SD(<i>I</i>)	Class		Overall	# Pairs	<i>E(I)</i>	<i>I</i>	SD(<i>I</i>)	Class <i>P</i> -value	Overall <i>P</i> -value
		Dist	Dist						<i>P</i> -value	<i>P</i> -value							
Shrub cover	1	19	21	27	-0.06	-0.07		0.18	0.949	1.000	36	-0.04	-0.38 *	0.16	0.032	0.214	
<i>R. spectabilis</i> cover	1	19	21	27	-0.06	0.00		0.18	0.767	0.900	36	-0.04	0.09	0.16	0.382	1.000	
Herb cover	1	19	21	27	-0.06	0.30 *		0.18	0.048	0.118	36	-0.04	-0.05	0.15	0.953	0.138	
Vascular cover	1	19	21	27	-0.06	-0.21		0.18	0.373	0.271	36	-0.04	-0.43 *	0.16	0.014	0.098	
S – richness	1	19	21	27	-0.06	0.31 *		0.17	0.036	0.218	36	-0.04	-0.08	0.16	0.813	0.886	
E – evenness	1	19	21	27	-0.06	0.38 *		0.17	0.014	0.082	36	-0.04	0.01	0.15	0.703	0.950	
Ls ¹ – dominance	1	19	21	27	-0.06	0.47 **		0.18	0.003	0.016	36	-0.04	0.00	0.15	0.767	1.000	
LF thickness ²	1	19	21	27	-0.06	0.35 *		0.17	0.021	0.127	36	-0.04	0.06	0.14	0.454	1.000	
H thickness ³	1	19	21	27	-0.06	-0.06		0.18	0.961	1.000	na	na	na	na	na	na	
AhH thickness ³	1	19	21	27	-0.06	-0.01		0.17	0.776	0.401	36	-0.04	0.42 **	0.15	0.003	0.018	
% Sand ⁴	1	19	21	27	-0.06	0.33 *		0.18	0.033	0.200	36	-0.04	0.02	0.16	0.680	0.355	
% Clay ⁵	1	19	21	27	-0.06	-0.16		0.17	0.556	0.223	36	-0.04	0.17	0.16	0.181	0.558	
% Silt	1	19	21	27	-0.06	0.38 *		0.18	0.014	0.082	36	-0.04	-0.10	0.15	0.719	0.019	
PAW	1	19	21	27	-0.06	0.42 **		0.18	0.008	0.047	36	-0.04	-0.10	0.15	0.714	0.019	
Ks ⁵	1	19	21	27	-0.06	-0.06		0.18	0.973	0.015	36	-0.04	0.24	0.16	0.065	0.041	
Distance to Water	1	19	21	na	na	na	na	na	na	na	36	-0.04	0.71 ***	0.16	0.000	0.000	

$E(I)$ is the expected value of I for a random distribution. SD(I) is the standard deviation of I .

¹ Ls was square root transformed for Kitlope analysis only.

² weighted by the % of the subplot covered by organic matter substrate type and transformed as natural log of (X+1).

³ weighted by the % of the subplot covered by organic matter substrate type.

⁴ natural log transformed for Kitlope analysis only.

⁵ natural log transformed.

Appendix 3. Quantitative analysis of spatial patterns

I undertook a quantitative analysis of spatial patterns for vegetation attributes, light transmission, and other environmental variables. However, my results were inconclusive due to insufficient sampling and are not reported here in detail. In the following, I provide a brief summary of the methods, key results, and conclusions to aid future researchers in developing appropriate sampling designs for these forests. I provided a detailed explanation of the basic analytical technique in Appendix 2.

Within-stand spatial structures, such as a gradient, patchiness, or a single large “bump,” can be detected and described using a combination of a correlogram and a map (Legendre and Legendre 1989, Fortin and Dale 2005). I used Moran’s *I* correlograms to quantify and describe spatial patterns of understory vegetation and light within floodplain stands, and supported each with a map. Fortin and Dale (2005) suggest a minimum of 20-30 sample locations for assessing spatial pattern with correlograms, suggesting that my sample would likely be adequately large for describing overstory and light attributes ($n=39$ and 50), but possibly inadequate for describing vegetation and edaphic variables ($n=19$ to 24). Thus, from the outset it is clear that my study lacks sufficient statistical power to reject the hypothesis of spatial patterning for variables measured in sub-plots. Nonetheless, I undertook the analysis to determine if particularly strong spatial patterns might be evident in the study sites.

With this sampling design, neither site provides clear empirical support for my expectation that measures of overstory structure (Leaf Area Index) and light transmission would exhibit fine-scale patch patterns within the stand. In fact, at Kitlope, correlogram and map interpretations suggest a random spatial distribution (Figure 12) of all overstory structure and light variables except LAI-4, which has ill-defined non-significant spatial structure. However, it remains possible that a patch structure would be expressed at finer scale (or larger extent) of sampling, as suggested by visual inspection of light estimates and interpolations on a map (Figure 6). At Carmanah, there is moderate support for the alternative hypothesis that overstory structure and light transmission exhibit a “single bump” spatial pattern corresponding to the recent canopy disturbance (Figure 11). The recent disturbance appears to have induced a spatial pattern that largely overrides any spatial patterns that might have been present prior to the disturbance. Although the area around the single bump shows variation in light levels (i.e., not a homogeneous region in the stand), it is not clear (because not enough area is sampled) if that variation has a spatial structure such as repeating small patches (e.g., as might be expected due to the influence

of canopy gaps) or is spatially unstructured (random) variation. A larger region of the stand, beyond the influence of this recent windthrow disturbance, would have to be sampled to resolve this question quantitatively.

Most of the variables sampled only in subplots (vegetation and substrate attributes) do not have significant overall correlograms, and many do not have significant spatial autocorrelation in the first distance class (Table 12). Together, these observations indicate that either an existing spatial pattern was not detected (see previous comments on low statistical power) or the variables are more or less randomly distributed within the stands. This is true, for example, for *R. spectabilis* cover and clay content in both stands. A few subplot sampled attributes do show signs of spatial patterns. For example, at Kitlope the correlogram for summed vascular cover is significant at the $\alpha=0.1$ level, and has significant autocorrelation in the first two distance classes (Table 12). This permits cautious interpretation of the correlogram, which suggests repeating patches of approximately 10-20 m diameter (Figure 13).

One key challenge with studies of spatial pattern is determining the necessary spatial extent, spacing, and layout of sample units to capture spatial patterns that exist in the field. My findings indicate that both a larger extent and shorter spacing between sample units may be needed to quantitatively describe spatial patterns of understory light and vegetation within floodplain *P. sitchensis* forests. By contrast, the contiguous plots method of Roburn (2003) was better suited to describing fine-scale spatial patterns in these forests.

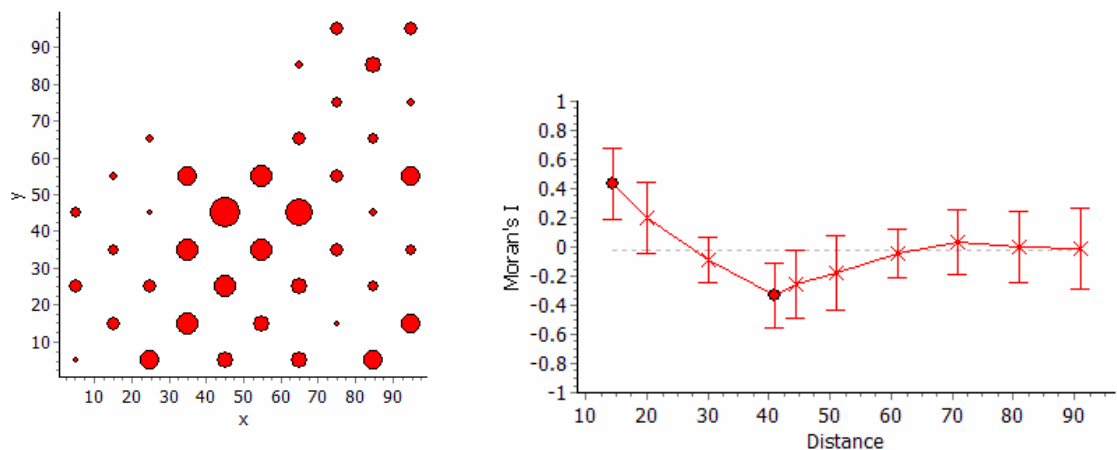


Figure 11. Map and correlogram of direct PAR at Carmanah ($n=39$). The correlogram is significant at the $\alpha=0.1$ level and suggests a single bump (~ 41 m diameter) or wave spatial pattern.

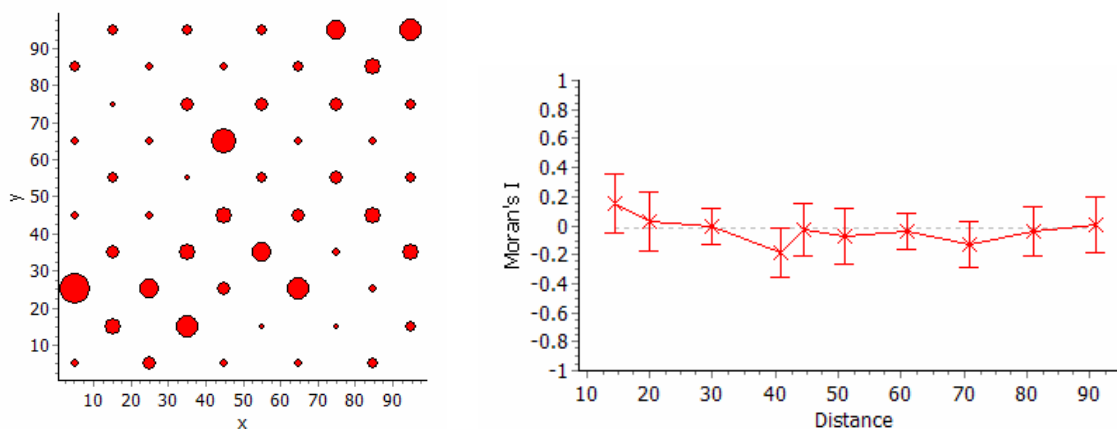


Figure 12. Map and correlogram of direct PAR at Kitlope ($n=50$). The correlogram is not significant (Bonferroni corrected $P=1.0$) and suggests a random spatial pattern or an inadequate sample.

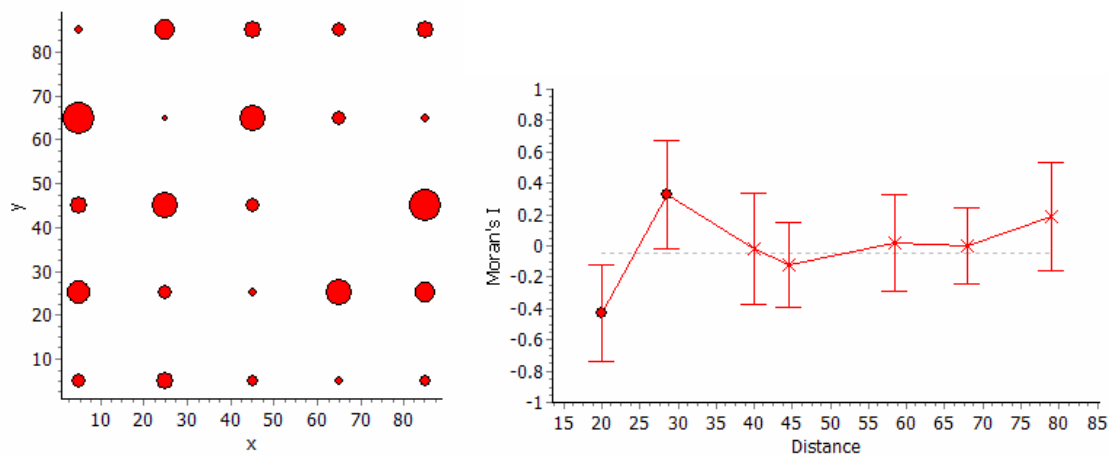


Figure 13. Map and correlogram of understory vascular plant cover at Kitlope ($n=24$). The correlogram is significant at the $\alpha=0.1$ level and suggests weak repeating patches of 10-20 m diameter.

Appendix 4. Light in subplots and full sample

I wanted to determine if the subplots provide a non-biased sample from the macroplot. In order to answer this question, I created box-plots that compare percentage full sun for gaps and non-gaps using two different samples: the full sample of available photo microsites (within the ecosystem of interest), and the subsample of photographs from vegetation subplots only (Figure 14).

At Kitlope, the vegetation subplots provide a non-biased representation of the full macroplot sample (Figure 14). First, median light of gaps and of non-gaps is very similar between the full sample ($n=49$) and the subplot sample ($n=24$). Second, the relationship between gaps and non-gaps is similar between the full sample ($n=49$) and the subplot sample ($n=24$).

At Carmanah, however, the vegetation subplots appear to under-represent bright gap microsites and over-represent bright non-gap microsites, compared to the full sample of microsites in the floodplain (not including recent disturbance, bench, or channel microsites). First, gap microsites are substantially darker (median) in the subplot sample, compared to the full sample. Second, non-gap median light level in the subplots is slightly higher than the median of non-gaps in full sample (full sample of $n=32$). As a result, in the subsample the rank order of brightness flips from gaps being brighter to non-gaps being brighter. The biased subsample at Carmanah could arise for a combination of two reasons. First, the subsample over-represents small gaps / under-represents large gaps (it is not just due to omission of recent disturbance subplots because I also omitted those from the “full sample” for comparison). Second, the subsample over-represents shady (southerly) locations within gaps / under-represents bright (northerly) locations within gaps.

The key implication is that this sampling bias could explain why the gap versus non-gap compositional differences at Carmanah are not as would be expected from a light-effect. That is, it might explain why in the ordination joint plot the non-gap subplots tend to fall on the brighter end of the light associated compositional gradient. The same could explain why one of the gap associated species is also a shade associated species. It appears that true composition driver within this sub-sample is indeed light: it just so happens – by sampling chance – that many of the brighter points are under expanded gap.

The occurrence of bias in the sub-sample at Carmanah suggests caution for interpreting compositional differences between gaps and non-gaps at this site. If my subplot sample of gap

and non-gap microsites is not representative of the light levels in those microsite types more broadly, then it is likely not representative of the vegetation in those microsite types (i.e., conclusions about gap versus non-gap associations might actually flip if I had a larger, non-biased, sample). This underscores the need for a larger sample, over a greater extent, to fully represent the fine-scale mosaic within the Carmanah floodplain.

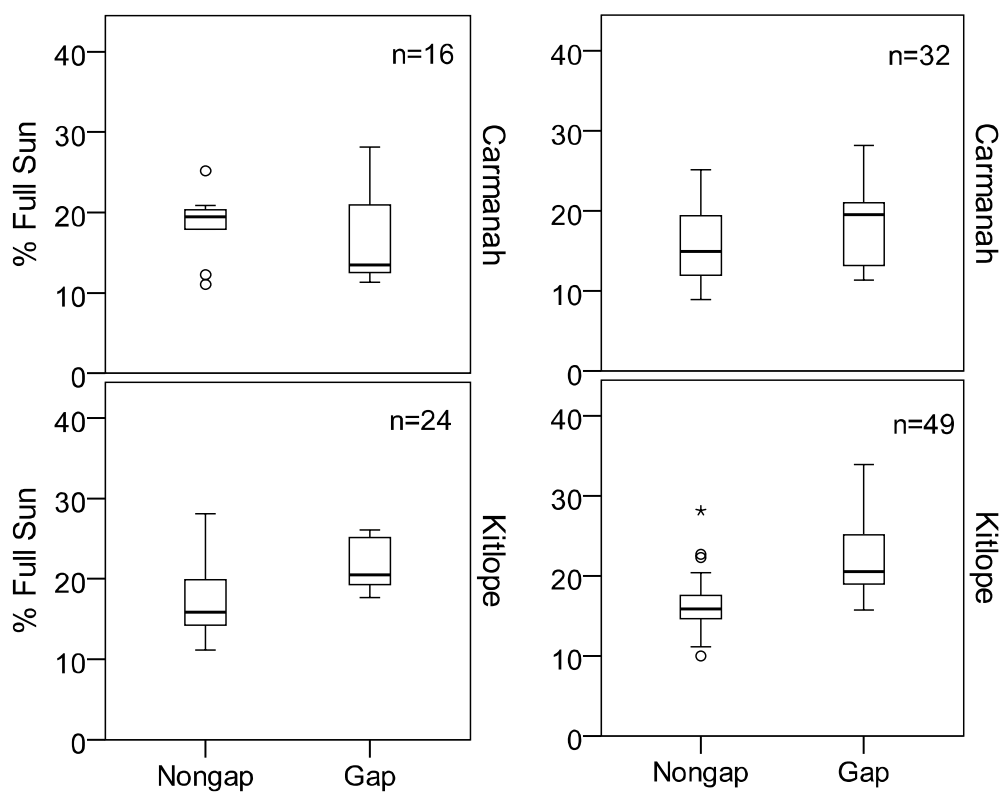


Figure 14. Light transmission differences between gap and non-gap microsites at Kitlope and Carmanah. The left panel shows data from the vegetation subplots only. The right panel shows data from all microsites within the ecosystem of interest, less recent windthrow microsites at Carmanah.