LIGHT TRANSMISSION AND UNDERSTORY VEGETATION IN TWO OLD-GROWTH RIPARIAN STANDS: A STUDY IN SPATIAL PATTERN

by

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Title of Project

Light transmission and understory vegetation in two old-growth riparian stands: a study in spatial pattern

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Abstract

Characterizing the structure of old-growth forests is crucial to understanding their ecological dynamics. I examined canopy openness, understory gap-light, and understory vegetation in two old-growth floodplain stands in southwestern British Columbia. The younger stand was in the "horizontal diversification" stage, and the older stand was in the "pioneer cohort loss" stage and contained a large vine maple gap. I determined spatial patterning of canopy openness and understory gap-light using hemispheric photography at closely spaced (2m) photosites on perpendicular transects, and explored how gap-light transmission, space, and distance from water features affected understory vegetation composition. The frequency distribution of light and openness values in the older stand had a mode at low values in conifer-dominated areas undergoing pioneer cohort loss, and a long tail of variable and higher values in the vine maple gap. The younger stand exhibited a trimodal distribution. Spatial autocorrelation of light and canopy openness values between photosites was clearly significant on all transects, with positive spatial autocorrelation significant to at least 12.5 metres in all cases. Depending on the goals of future studies in similar forests, either a sampling step of 30m or a systematic cluster sampling design is recommended.

Patterns of understory gap-light on the transects varied over the small scale of 100m, a scale considerably smaller than the typical scale of forest management in British Columbia. Comparatively high and spatially and temporally variable values of gap-light transmission in the vine maple gap, combined with a distinct understory community in the vine maple gap, reaffirm the ecologically distinct role of vine maple in coastal temperate rainforests of the Pacific Northwest. Multivariate analysis showed that gap-light transmission did not have a large influence on understory composition at the measurement scale of this study. In the younger stand, distance to small streams explained some of the variation in understory communities. Restoration efforts aiming to re-establish old-growth conditions in floodplain forests of the Pacific Northwest need to account for variable overstory spatial pattern over small scales (100m), the distinct role of hardwood patches such as vine maple gaps, and the influence of small streams on understory plant communities.

Quotation

The clearest way to the Universe is through a forest wilderness.

-John Muir (1838 - 1914) US naturalist, writer

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1. Introduction

Old-growth temperate rainforests are characterized by high structural, compositional, and functional diversity (Franklin and Spies 1991, Lertzman et al. 1997). Because many of the compositional and functional characteristics of these forests are a result of structural elements (Franklin and Spies 1991, Spies 1998), characterizing forest structure is key to understanding old-growth ecosystem dynamics. Structural elements of old-growth temperate rainforests include large, very old live trees for species and site conditions, large snags, large logs of varying decay classes, a wide range of tree size and ages, multiple canopy layers, canopy gaps, and patchy understory communities (Franklin and Spies 1991, Wells et al. 1998). Understory heterogeneity is in part a result of varied overstory conditions, especially those arising from the mortality and dynamics of canopy trees, with canopy gaps and well-developed understories at one extreme, and heavily shaded sites ("antigaps") and nearly bare forest floors at the other (Franklin and Spies 1991).

Coastal British Columbia contains ancient coastal temperate rainforests representing some of the most productive ecosystems on the planet (Pojar and MacKinnon 1994). Public and political interest in the conservation of these old growth rainforests has grown, locally and internationally, as a result of an increased understanding of both their scarcity and their ecological uniqueness (Wells et al. 1998).

Traditional forest management has introduced processes at spatial (and temporal) scales that are foreign to forest ecosystems, shifting the spatial (and temporal) structure of ecosystems outside their range of natural variability (Hansen et al. 1991, Lertzman et al. 1996, Lertzman et al. 1997, Landres et al. 1999, Dorner 2002).

Industrial logging practices tend to homogenize forest stands and landscapes, creating "anthropogenic landscapes with a regular pattern and a uniform grain" (Lertzman et al. 1997, Lertzman and Fall 1998). At the stand level, second-growth stands that are intensively managed for wood production are very different from natural forests in composition, function, and structure (Franklin 1998). For example, intensively managed plantations are less structurally complex than natural forests and are often lacking in large trees, snags, and fallen logs that provide critical habitat for many specialist organisms (Hansen et al. 1991). Common forest management practices such as planting and thinning promote uniformity in tree species, size, and spacing, further reducing the heterogeneity of managed stands (Hansen et al. 1991).

1.1 Forest understories and spatial pattern

Forest understories, composed of herbs, shrubs, seedlings, and saplings, are of high intrinsic and functional value (Miller et al. 2002). In coastal temperate rainforests, understory plants help to maintain ecosystem diversity and wildlife habitat, provide forage and cover for animals, cycle nutrients, and contribute to long-term ecosystem productivity (Yarie 1980, Alaback and Herman 1988). In addition, the forest understory serves as a nursery for future canopy trees, affecting the future composition of the stand. Light is often the most limiting factor for understory species growth at light levels of less than 20% of full sun (Chazdon 1988), and the understory light environment plays a key role in determining patterns of tree regeneration (Canham and Burbank 1994). Forest canopy structure is one of the major sources of heterogeneity in understory light environments (Canham et al. 1990, Frazer et al. 2000), which in turn drive understory dynamics. Subcanopy trees, saplings, ferns, shrubs and herbs can also have a large influence on resource availability and thus seedling regeneration (Montgomery and Chazdon 2001).

Canopy structure, understory light environment, and understory species composition change as forests age. Immediately following a stand-replacing disturbance, understory light levels are typically high, and herbs and shrubs dominate the site (Alaback and Herman 1988). When canopy closure occurs, light levels are greatly reduced, resulting in the suppression of understory tree, shrub, and herb growth (Alaback and Herman 1988, Franklin et al. 2002). Once the thinning of canopy overstory dominants allows more light to reach the understory, the understory community begins to re-establish (Franklin et al. 2002). In old forests, large, relatively unevenly spaced canopy gaps resulting from the mortality of one or more dominant trees generate spatial variability in environmental variables such as moisture, coarse woody debris, nutrients, light, and temperature (Bradshaw and Spies 1992, Frazer et al. 2000, Franklin et al. 2002, Lertzman et al. 1996). Spatial variability in understory light conditions contributes to spatial heterogeneity in understory vegetation (Chazdon 1988), and thus to diversity of habitat, structure, and function of old growth forests.

Forest ecologists and managers also need to understand spatial pattern in forests in order to optimize sampling strategies and to analyze spatially-structured data. One of the fundamental assumptions of classical inferential statistics is that observations are independent of one another. In many ecological studies, this assumption is violated, because different samples are closely enough spaced to lie within the zone of spatial influence of an underlying ecological phenomenon (Legendre and Fortin 1989). A variable is considered to be autocorrelated "when it is possible to predict the values of this variable at some point of space [or time], from the known values at other sampling points, whose spatial [or temporal] positions are also known" (Legendre and Fortin 1989). Quantitative measures of autocorrelation can be used to adjust sampling patterns and can also be incorporated in other spatial analyses to improve results.

A few forest ecology studies have considered autocorrelation in understory light or vegetation (Becker and Smith 1990, Walter and Himmler 1996, Trichon et al. 1998, Montgomery and Chazdon 2001, Miller et al. 2002). They reported either no spatial autocorrelation, or positive spatial autocorrelation over distances ranging from 2.5 m to 21 m, depending on forest age and type. Because spatial autocorrelation in understory light is affected by the architecture and arrangement of dominant canopy species and the age and developmental stage of forests, results from these past studies cannot be generalized to future studies in different forest types. One of the objectives of this study is to quantify autocorrelation in understory light conditions in two floodplain stands in different stages of old-growth within the Coastal Western Hemlock biogeoclimatic zone of British Columbia.

1.2 Influence of understory light

An understanding of the relationship between forest canopies and understory vegetation is necessary for predicting changes in understory communities due to succession or forest management activities (McKenzie et al. 2000). Past research has reported varying relationships between canopy openness or light transmission and understory vegetation. In some studies of unmanaged forests, canopy cover clearly affected understory diversity, productivity, or composition (Stewart 1986, Riegel et al. 1995, McKenzie et al. 2000). In other cases, canopy cover had little influence on understory species composition (Ehrenfeld 1980, Alaback 1982, Collins and Pickett 1987, 1988). In managed forests, research has shown a link between canopy cover and understory communities. Several authors have shown that the increased resource availability (including light) following partial cutting result in a growth response of seedlings and saplings or an increase in conifer regeneration, sometimes to the exclusion of herb and shrub communities (Alaback and Herman 1988, Deal and Farr 1994, Canham 1998, Deal 2001, Drever and Lertzman 2001).

1.3 Floodplain Forests: a mosaic of riparian and upland influence

Riparian forests are floristically and structurally the most diverse vegetation type in the Pacific temperate rainforests (Naiman et al. 2000), and as a result their management has become a focal point for discussions of biodiversity and forest management in the region (Pabst and Spies 1999). Riparian forests are ecologically distinct because they are at the interface between aquatic and terrestrial ecosystems (Naiman et al. 2000, Helfield and Naiman 2001). Recent research has focused on aquatic-forest interactions, highlighting the reciprocal nature of the exchange of nutrients and organisms between water and land (Bilby et al. 1996, Willson et al. 1998, Helfield and Naiman 2001). Studies of the nutrient contribution of spawning salmon to riparian forests, a relationship mediated by predators such as bald eagles, bears, and wolves, show that salmon provide limiting nutrients such as phosphorus and nitrogen to riparian forests (Bilby et al. 1996, Willson et al. 1998, Helfield and Naiman 2001). Helfield and Naiman (2001) demonstrated that nitrogen derived from spawning salmon significantly increased growth rates of Sitka spruce near spawning streams.

1.4 Vine maple

Vine maple (*Acer circinatum*) is a common understory species in the coastal temperate rainforests of southwestern British Columbia. Although it most commonly occurs in the understory and subcanopy under conifers, vine maple may be present at any stage of forest succession (O'Dea et al. 1995), and it occasionally persists in canopy openings in older coniferous forests, most likely as an alternative state to the surrounding coniferous forests (Lertzman and McGhee 1996, McGhee 1996). Although the ecological role of vine maple has not been extensively studied, existing research demonstrates that vine maple improves site fertility (Tashe and Schmidt 2001) and contributes to heterogeneity in conifer forests through the creation and maintenance of canopy gaps (McGhee 1996). Vine maple gaps can also lead to a large enough increase in growth rates of conifers adjacent to the gap (probably due to increase light availability) to make up for the "loss" of area to vine maple (Wardman and Schmidt 1998).

1.5 Research objectives

In this study I examine understory light and understory species composition in two old-growth floodplain stands near Vancouver, BC. The younger site is in the horizontal diversification stage of forest succession: gap creation and expansion is creating multiple structural units and high horizontal variability in the stand (Franklin et al. 2002). Sitka spruce dominants form a significant component of the canopy. The older site is in the pioneer cohort loss stage (Franklin et al. 2002): Sitka spruce is disappearing from the stand, which is becoming dominated by amabilis fir and western hemlock. This study site also contains a large vine maple and salmonberry-dominated gap.

My study objectives are

(1) to quantify the spatial structure and heterogeneity of canopy openness and understory light in the study stands. A key element of this objective is to determine the scale and pattern of autocorrelation of canopy openness and understory light, as a methodological guideline for future sampling;

(2) to examine how the presence of vine maple, both in a large gap and as an understory tree, affects the understory light environment;

(3) to explore the relationships between understory plant community pattern and composition, understory light environments, and other environmental variables;

(4) to link my results to applications of ecosystem-based management, particularly variable retention logging and habitat restoration in old-growth riparian stands in coastal British Columbia.

2. Methods

2.1 Study area and study sites

I collected light and vegetation data in two forest stands in the Lower Seymour Conservation Reserve (LSCR) (Figure 1). The 5,668 hectare LSCR encompasses the lower part of the Seymour Valley, located north of Vancouver in the Pacific Ranges of the Coast Mountains of British Columbia. The valley is drained by the Seymour River, which extends through the lower valley from the Seymour Falls Dam to Burrard Inlet about 20 km further south (Lian and Hickin 1993). The Seymour River basin is deep and narrow, ranging in elevation from near sea level to over 1400 m on mountain peaks (Lian and Hickin 1993).

2.1.1 Geomorphology

The Seymour Valley is a U-shaped valley that has undergone repeated glaciations (Kahrer 1989, Lian and Hickin 1993). The ice last retreated about 11.5 thousand years ago, and vegetation returned to the valley within a few hundred years (Lian and Hickin 1993, 1996). The glaciers left behind glacial sediments that were soon overlain by paraglacial fans and aprons deposited by the Seymour River's tributaries between about 11.4 and nine thousand years ago (Lian and Hickin 1993, 1996). This valley fill forms a bench at about 200 m above sea level between Seymour Lake and Rice Lake (Lian and Hickin 1993). Near Seymour Lake, the Seymour River flows near the surface of the valley fill, but the river has incised by about 100 m at the southern end of the study area near Rice Lake, creating several levels of terraces (Lian and Hickin 1993). Today, the

Seymour River continues to erode the glacial and paraglacial valley-bottom deposits (Lian and Hickin 1996).

2.1.2 Development history

The Seymour Valley has a long history of human use. Although there are no documented Aboriginal archaeological sites in the LSCR, there is no doubt that First Nations people used the land in this area (Anonymous 2001). From about 1860 until the early 20th century, selective logging, placer mining, and gold and mineral prospecting were the main human activities in the Seymour Valley (Kahrer 1989). However, the Seymour River was soon recognized as a valuable water source for the population of the rapidly growing Vancouver area. By 1936 the Seymour River was dammed to create the Seymour Lake reservoir, logging in the watershed had ceased, and the Seymour catchment area was closed to the public (Kahrer 1989). Until 1963, management in the watershed involved interventions intended to protect water quality, such as fire suppression and prevention, removal of dead and dying trees resulting from insect damage, and wildlife extermination (Kahrer 1989). The Seymour Falls Dam was rebuilt at Seymour Lake in 1961, increasing the storage capacity of the lake (Kahrer 1989), and further altering natural flooding regimes downstream.

In 1963, a comprehensive management plan was introduced with the goal of "multiple use sustained yield management", where mature and "overmature" forests were to be replaced with even-aged stands of young trees, partly to reduce fire hazard (Kahrer 1989). In 1979 a salmonid hatchery was opened just south of the Seymour Falls dam, in order to sustain declining fish stocks. In 1987 the area south of the Seymour Falls dam was opened to the general public as the Seymour Demonstration Forest, and in 1999, the area was re-named the Lower Seymour Conservation Reserve to reflect changing public values and multiple use interests in the area. A recent management plan for the LSCR based on public consultation lists sustainability, the balancing of multiple values, public input, ecosystem-based planning, stewardship, and adaptive management among its guiding principles (Anonymous 2002).

2.1.3 Ecosystems

The LSCR falls within the Coastal Western Hemlock biogeoclimatic zone (CWH), which is characterized by high rainfall (ranging from 1000 to 4400 mm annual mean precipitation across the biogeoclimatic zone) and a cool, mesothermal climate (mean annual temperature ranging from 5.2 to 10.5 degrees Celsius) (Pojar et al. 1991). Arsenault and Bradfield (1995) reported mean annual precipitation of 3841 mm near Seymour Falls (based on data from 1982). CWH zonal ecosystems are characterized by the predominance of western hemlock (*Tsuga heterophylla*), a sparse herb layer, and the prevalence of a few moss species, particularly *Hylocomium splendens* and *Rhytidiadelphus loreus* (Pojar et al. 1991). CWH forest soils grade from Hummo-Ferric Podzols to Ferro-Humic Podzols as precipitation increases (Pojar et al. 1991). Sitka spruce is a widespread species in the CWH, but in the southern part of the zone its ecological range is restricted to "specialized habitats such as floodplains and exposed beaches" (Pojar et al. 1991, p.96).

2.1.4 Study sites

I chose two old-growth mixed-species floodplain stands for the study. Although the stands are of different ages, both of them exhibit old-growth structural characteristics (Franklin and Spies 1991, Wells et al. 1998) including many large living and dead trees, multi-layered canopies, large snags, coarse woody debris of varying decay classes, and canopy and understory patchiness. Both stands are dominated by gap replacement disturbance regimes, classified (at least in part) as ancient forests, and adjacent to areas that were logged in the past century (Greater Vancouver Regional District 2001b, 2001c, n.d.). Pilot work in both stands was conducted by successive graduate forest ecology classes in Resource and Environmental Management at Simon Fraser University (Broberg et al. 1999, Denholme et al. 2001).

HD site

The first study site is located next to the Seymour River at an elevation of 140 m. At this location, the river has a gradient of about 5% and a braided channel bed dominated by boulders, cobbles, and some gravels (Denholme et al. 2001). The stand likely lies in a transitional area between the CWHdm (dry maritime) subzone and CWHvm1 variant (Greater Vancouver Regional District 2001a). The main tree species in the stand are western hemlock, Sitka spruce, and western redcedar. The age of the stand is estimated at approximately 214 years, based on the age of the oldest tree cored in a sample of eight Sitka spruces in the stand (Denholme et al. 2001). I have named this stand the HD site, short for "Horizontal Diversification" (Franklin et al. 2002). The stand does not fit unambiguously into the Franklin et al. (2002) classifications. The stand is relatively young, and its canopy composition is dominated by Sitka spruce with western hemlock and western redcedar as codominants, which would place it in the Vertical Diversification stage. However, the stand also contains gaps created by the mortality of several large trees, and also contains several very large and old Sitka spruce, indicating that despite its relatively young age, the stand is in the beginning of

Horizontal Diversification. The exceptionally rich soils and frequent small-scale disturbances associated with riparian areas may have allowed rapid structural development of this stand (Denholme et al. 2001). I used a GPS to geo-reference the stand to N 49°22′, W 122°59′. I located a 100 by 100 m study plot in the HD stand at 50 m from the edge of the Seymour River. The location of the study plot was constrained by evidence of previous logging in adjacent stands, which may have influenced the light environment at the edge of the study plot.

PCL study site

The second study site is located on a bench created by the last glaciation at about 180 m above sea level, just south of the Seymour Falls Dam near a side-channel of the Seymour River (Lian and Hickin 1993, 1996). It lies in the CWHvm1 (submontane very wet maritime) variant (Greater Vancouver Regional District 2001a), roughly six kilometres north of the PCL study site. The site is flat overall, with variable microtopography, and is composed of about 1 m of sand and silt deposited over earlier glacial and paraglacial deposits (Broberg et al. 1999).

The study plot contains two distinct plant communities: a large vine-maple gap (O'Dea et al. 1995, Lertzman and McGhee 1996, McGhee 1996, Ogden and Schmidt 1997, Wardman and Schmidt 1998, Tashe and Schmidt 2001) ringed by large conifers (including Sitka spruce) with a salmonberry-dominated understory (probably Sitka Spruce-Salmonberry floodplain (09) site series association), and a closed-canopy forest dominated by western hemlock and amabilis fir (probably Western hemlock-Amabilis fir-Deer fern (06) site series association) (Green and Klinka 1994, Broberg et al. 1999). The latter component is thought to be a stand in transition from dominance by

Sitka-spruce, a pioneer species which typically establishes post-flooding, to dominance by western-hemlock, a shade-tolerant, late seral species (Broberg et al. 1999) I have thus named this site the PCL site, short for "Pioneer Cohort Loss", based on structural development stages described by Franklin et al. (2002). Stand age is estimated to be at least 302 years, which is the age of the oldest sampled Sitka spruce tree in the stand (Broberg et al. 1999).

I situated a 100 m by 100 m study plot within the stand which:

(1) includes both site series associations, and

(2) is far enough away from the main stem of the Seymour river (over 50 m) to eliminate its direct gap influence on the understory light environment.

I used a GPS to geo-reference the study site to N 49°25′, W 122°58′.

2.1.5 Study plot design

I established two perpendicular 100 m transects within each of the two study plots. In each stand, one of the transects ran roughly parallel to the Seymour river, and the other ran perpendicular to it, in order to capture any directional gradients due to the river. In the HD stand, the transects crossed in the middle, while in the PCL stand they crossed near 72 m along the transect running parallel to the Seymour river. This allowed me to sample the vine maple gap, the transition between the vine maple gap and the adjacent conifer forest, and the conifer forest. These transects are hereafter referred to as Transects HD1, HD2, PCL1, and PCL2. Transects numbered 1 are parallel to the nearest channel of the main Seymour River, while Transects numbered 2 are perpendicular to the river.

2.2 Data collection

2.2.1 Hemispheric photography

The aim of my hemispheric photo sampling strategy was to capture the gap-light environment at the top of the shrub layer. This led me to use different methods from those used by researchers aiming to quantify canopy structure. I placed photosites at two metre intervals on each transect. If a live or dead stem prevented photography at a given photosite, or the presence of a stream precluded sampling vegetation there, I offset that site perpendicular to the transect at the smallest distance possible, and recorded the x and y coordinates at the new location. Such offsets were typically less than 2.5 m. I took one or more photos at each photosite using a Nikon F 35-mm camera and Nikkor 8 mm f/8 180 degree fisheye lens, with an LA1 (UV) filter. I took photos with Fuji NPH 400 (colour) film using various exposures, but found that photos taken with aperture f/8 and shutter speed 1/500 were suitable for processing in most cases (see Frazer et al. 2000).

The camera was mounted on a Manfrotto tripod at 170 (plus or minus 15 cm) above the ground in most cases (see below). In order to capture the light environment at the shrub layer and below, I pushed out of the camera's view any understory shrubs obstructing the sightline between the camera and the canopy (Frazer et al. 2000). I considered tall vine maple to be part of the overstory, but did remove vine maple leaves *close* to the camera from the camera's line of view in order to prevent their disproportionate influence on canopy openness and light estimates; a single vine maple leaf very close to the camera lens could fill the photograph frame and result in inaccurately low estimates of percent cover/ canopy openness.

In some cases, the shrub layer was so dense and so tall that simply pushing shrubs out of the field of view of the camera was impossible. In these cases, I mounted the tripod on a ladder and took the photos just above the shrub layer, at about 2.7 m above the ground. I used this ladder method at approximately one tenth of all the photosites (N=19), all of which were found in the vine maple gap of the PCL study site. There may have been some error introduced by taking a portion of the photos at a greater height above the forest floor. However, the difference in height was relatively small, and the error introduced was much less than the error in understory light estimates that would have existed had I taken photographs under the shrub layer. Previous research suggests that small changes in height above ground of photos do not necessarily affect light estimates: for example, Whitmore et al. (1993) found no change in data derived from hemispheric photos with photo height varying by up to 50 cm in tropical forests. In addition, studies of vertical stratification of light show little measurable change in light in the lowest several metres of the canopy, except below the shrub layer (G. Frazer, pers. comm.). Parker et al. (2001) documented almost no change in fractional transmittance from ground level to about 13 m height in an old-growth Douglas-fir forest (Wind River, Oregon) using a hemispheric quantum sensor. Weiss (2000) took hemispheric photographs in the same study area, and estimated only about a 1.0 % (of maximum measurements) change in diffuse and direct radiation factors over every 1 m change in height for measurements taken at 1.5 to 10 m above the ground.

In all cases, the camera was leveled and oriented so that the long axis of the camera pointed north-south. I used a registration plate, which consisted of fibre optics leading from LEDs mounted on a plastic plate that fit around the lens, to mark magnetic north and south on the photographs. I took photos under overcast sky conditions in June-August of 2001, and again once vine maple leaves had fallen in overcast or sunny conditions in November-December of 2001.

I used a Minolta camera and lens for some of the June-August 2001 photos (N=33) in areas with no overstory vine maple; I substituted these in my analysis with photos taken using the Nikkor lens in November and December of 2001 in order to ensure that all photos were taken with the same camera and lens, increasing methodological consistency.

I used hemispheric photography to estimate gap-light levels in the understories of two old-growth stands. Gap-light is an estimate of the amount of incident photosynthetically active radiation (PAR) transmitted through canopy gaps over the course of the growing season (Canham 1988). This estimate excludes two important components of understory light: the diffuse and beam radiation transmitted through leaves and between needles, and beam radiation that is reflected downward by foliage (Canham et al. 1994). These unmeasured components of understory light may be important to the growth and survival of understory plants, and may influence ecosystem function (Chazdon and Pearcy 1991). Throughout this study I refer to measures of understory light transmittance as "understory light" or "percent PAR transmitted". These terms refer to estimates of gap-light based on hemispheric photography, and do not include transmitted light or beam enrichment.

2.2.2 Understory vegetation

At each photosite, I visually estimated percent cover by species in the herb and shrub layers in circular plots of 0.5 m^2 (June-August 2001). I lumped all grass species together, as these formed only a minor part of the herb layer. I also grouped *Vaccinium alaskaense* and *Vaccinium ovalifolium* together, due to their ecological similarity and the difficulty in distinguishing between the two species in the field. When analyzing the vegetation data, I used a moving window to average percent cover estimates over each set of three adjacent plots.

2.2.3 Water features

I mapped the occurrence of streams and standing water in each stand in November of 2001, using parallel transects spaced at 10 m intervals along one transect in each stand, and by directly measuring distance to water features for each photosite if that distance was less than 10 m. For streams, I measured bankful widths. I recorded standing water by noting not only puddles and pools of water, but also areas where soils appeared waterlogged, and in which there was no evidence of vegetation growth apart from skunk cabbage (*Lysichitum americanum*), an indicator of wet and seasonally flooded sites (Klinka 1989). Although only a rough estimate, mapping standing water enabled me to identify areas where the groundwater table was at the surface most of the year. Most of these areas had been completely dry at mid-summer.

I constructed maps of standing water, streams, and photosites in each of the study sites using Arcview (version 3.2a). I then used Arcview to calculate the shortest distance to standing water and the shortest distance to a stream for every photosite.

2.3 Data pre-processing

I digitized the colour photo negatives from all photosites at 1012 dpi, using SprintScan 35 Direct (version 2.7.2) and a Polaroid SprintScan 35ES scanner. I used Gap Light Analyzer (GLA) (Frazer et al. 1999), a program designed specifically for analyzing hemispheric photos, to estimate percent canopy openness (% CO) and percent of photosynthetically active radiation incident on the canopy transmitted to the understory (% PAR). The software uses a single threshold to classify each pixel in a photograph as sky or non-sky. It then tracks the sun path through those pixels, given latitude, growing season, and information about solar intensity, site topography, and various other user-defined parameters. The program uses the seasonal solar path and diffuse sky-brightness model, combined with the spatial distribution of canopy gaps, to estimate a number of parameters describing canopy structure and light transmittance. I used solar radiation data from the nearest measuring station (University of British Columbia) to estimate an average cloudiness index for my site. Because the study site is located in a microclimate that receives more rain than U.B.C., outputs from GLA may overestimate absolute values of above-canopy light, but it will not influence relative measures such as %PAR or comparisons among photosites.

The most time-consuming, sensitive, and subjective step in analyzing photos using GLA is thresholding, where the user decides for each photo at what pixel intensity (0-255) to separate sky and canopy. I employed a thresholding rule whereby even the lightest vegetation tones were assigned a pixel value of non-sky. This eliminated many of the smaller gaps near the horizon in the photos, but was the threshold rule that designers of software found to be most accurate when calibrating the software using data obtained from light sensors (G. Frazer, pers. comm.). I analysed only the Blue colour plane of all photos, which enhanced contrast in all cases.

2.4 Data analysis

I used several different types of spatial analyses to meet my research objectives. First, I used correlograms to describe the scale and pattern of autocorrelation of canopy openness and understory light. Second, to assess the impact of vine maple on understory light environments, I used partial Mantel tests comparing light values before and after vine maple leaf fall, and light values inside and outside the vine maple gap. Third, to explore the relationships between understory plant communities, understory light environments, and other environmental variables, I used ordination methods and variance partitioning. All of these methods are outlined below.

2.4.1 Spatial pattern of canopy openness and light transmission (Objective 1)

Spatial autocorrelation

I used Moran's I and Geary's c spatial correlation coefficients and correlograms to determine the extent, pattern, and statistical significance of autocorrelation of both canopy openness and light variables. A variable is autocorrelated "when it is possible to predict the values of this variable at some point of space [or time], from the known values at other sampling points, whose spatial [or temporal] positions are also known" (Legendre and Fortin 1989). Correlograms are graphs of autocorrelation coefficient estimates versus distance classes.

Moran's I is calculated as:

$$I = n\frac{\sum_{ij} w_{ij}(y_i - \bar{y})(y_j - \bar{y})}{W\sum_{i=1}^{n}(y_i - \bar{y})^2}$$

Where

y_i and y_j represent the variable values at the i^{th} and j^{th} location, respectively;

n = the number of points;

w_{ij} = the spatial relationship between i and j. w_{ij} can be determined using a variety of weighting systems; I used a binary weighting system so that only those points included in the distance class influenced the calculation of I for that distance class;

$\sum_{ij}$ = the double of sum over all i and all j;

$i \neq j$; and

W = the sum of all the values in the weight matrix, or $\sum_{ij} w_{ij}$.

(Fortin et al. 1989, Rosenberg 2002)

Moran's I behaves like Pearson product-moment correlation coefficient, and because it compares all values to the mean, it is sensitive to skewness and extreme values (Fortin et al. 1989, Legendre and Fortin 1989, Rosenberg 2002). Values of Moran's I range from −1 to +1, where a positive value indicates positive spatial autocorrelation (meaning the variable has similar values) and a negative value indicates negative spatial autocorrelation (meaning the variable has dissimilar values).

Geary's *c* is a squared-difference coefficient calculated as:

$$c = (n-1)\frac{\sum_{ij} w_{ij}(y_i - y_j)^2}{2W\sum_{i=1}^{n}(y_i - \bar{y})^2}$$

Values of Geary's *c* range from 0 to infinity, with a value of 1 indicating no autocorrelation. Values between 0 and 1 indicate positive autocorrelation, while values greater than 1 (usually up to about 2) indicate negative autocorrelation. Geary's *c* coefficient is a distance-type function (Fortin et al. 1989, Legendre and Fortin 1989, Fortin 1999a), and is less sensitive to non-normal distributions than is Moran's *I* (M.-J. Fortin, pers. comm.).

I used Passage Version 1.0 (Rosenberg 2002) to construct correlograms with both Geary's *c* and Moran's *I* values for % CO and % PAR for each transect, and calculate significance of each point on the correlogram at the alpha = 0.05 level. Passage also calculates global significance levels for the correlogram using a Bonferroni procedure which corrects for the lack of independence of the distance classes. I chose equal interval distance classes rather than distance classes containing equal numbers of samples because it is easier to interpret the shape of the correlograms and the zone of influence/patch size that can be inferred from the correlograms (M.-J. Fortin, pers. comm.).

Spatial autocorrelation analysis assumes stationarity in the data (Fortin et al. 1989), meaning that the statistical properties of the data (mean, variance, isotropy) remain constant throughout the study plot. I assessed normality and skewness of canopy openness and light transmission data for each transect, and normalized the data using transformations where appropriate. Data for transect HD2 were normally distributed, and I used a natural logarithmic transform on transects PCL1 and PCL2. I was unable to normalize data from transect HD1, but the departure from normality was probably not severe enough to affect correlogram results (C. Schwarz, pers. comm.; Kolmogorov-Smirnov statistical tests yielded *p* values of 0.012 for % CO, and 0.058 for % PAR on transect HD1.)

2.4.2 Effects of vine maple: partial Mantel tests (Objective 2)

In order to examine the effect of vine maple on the understory light environment, I performed two types of comparisons: (1) I compared % PAR values before and after vine maple leaves fell in the autumn at the same photosites in both study sites, and (2) I compared % PAR values in the vine maple gap and in the adjacent conifer forest of the PCL study site. I chose to examine % PAR and not percent canopy openness in these analyses because % PAR is a more direct measure of the understory light environment.

Partial Mantel tests are one way of examining the relationship among spatially autocorrelated data while controlling for spatial pattern (Fortin 1999a). The partial Mantel test is a multivariate equivalent of a partial correlation coefficient based on three distance matrices. These matrices represent relationships among points, which may be based on qualitative or quantitative data (Legendre and Fortin 1989). The matrices may be distance matrices reflecting Euclidean distances between sample points, matrices of distances between values of a given variable for all possible combinations of sample points, or even binary matrices used to test a hypothesis regarding the relationships among points (e.g. A_{ij} = 1 if values are in the same forest type and 0 if they are not) (Rosenberg 2002).

Given two distance matrices (A and B), the partial Mantel test establishes the degree of relationship between the two matrices while the effects of a third matrix (C) are kept constant (Fortin and Gurevitch 1993, Fortin 1999a, Rosenburg 2002). First, matrices of residuals (A' of the linear regression between A and C, and B' of the linear regression between B and C) are computed, then the Mantel statistic is computed using the two residuals matrices (A' and B') (Fortin and Gurevitch 1993). The Mantel statistic is calculated as:

$Z = \sum A_{ij}B_{ij}$, for

Where $\sum$ is the double sum of all i over all j, where $i \neq j$ and A and B are square matrices (Fortin and Gurevitch 1993, Rosenberg 2002).

One of the disadvantages of the Mantel statistic, Z, is that it is unbounded, and therefore does not allow for comparison between studies (Fortin and Gurevitch 1993). However, the Z statistic can be normalized and converted to a normalized Mantel statistic (r), which, like any product-moment coefficient, varies between –1 and 1 (Fortin et al. 1989, Fortin and Gurevitch 1993, Rosenberg 2002). I have report r values in my results.

Because the distances in each matrix are not independent of each other, the Mantel statistic cannot be assessed using standard significance tests (Fortin and Gurevitch 1993, Rosenberg 2002). Significance is instead assessed using a permutation test or an asymptotic t-approximation test (Fortin and Gurevitch 1993, Legendre 2000, Rosenberg 2002). I used a permutation method which establishes a reference distribution of Z statistics based on random reshuffling of the elements of the residual matrix. If the null hypothesis of no relationship between the first two distance matrices is true, then the observed partial Mantel statistic is expected to have a value located near the mode of the reference distribution (Fortin and Gurevitch 1993). The minimum number of permutations recommended is 1000; the higher the number of permutations, the more accurate the significance test (Fortin and Gurevitch 1993). I used 2000 permutations. Although permutation of a raw data matrix is preferable to permutation of the residual matrix (Legendre 2000), the latter method is the most commonly used method, and the problems it can create appear only in extreme conditions (M. Rosenberg, pers. comm.).

I used partial Mantel tests to compare light values in the vine maple gap versus the adjacent conifer forest in the PCL study site. I used Passage 1.0 (Rosenberg 2002) to calculate the following distance matrices:

(1) Understory light matrix: % PAR distance matrix for all PCL stand sample points;

(2) Gap matrix: a binary distance matrix, calculated from a linear matrix where points were classified as either 1: within the vine maple gap or 2: not within the gap. I based the boundary of the vine maple on my field observations; and

(3) Geography matrix: a geographic distance matrix based on the Euclidean distance between points.

I then calculated values of Mantel, partial Mantel, and normalized partial Mantel statistics using Passage 1.0, and assessed significance levels using the permutation method with 2000 permutations in Passage 1.0. This allowed me to test the relationship between light levels and the vine maple gap while removing the effects of spatial autocorrelation.

In order to compare vine maple % PAR values before and after vine maple leaves fell in the autumn at the same photosites, I used a partial Mantel test with the following matrices for each of the study sites:

(1) Understory light matrix: distance matrix calculated from % PAR values for both before and after vine maple fall, listed in sequence;

(2) Leaf fall matrix: distance matrix calculated from a binary matrix separating sample points into before (0) and after (1) vine maple leaf fall; and

(3) Geography matrix: Euclidean distance matrix calculated from the geographic coordinates for all points in the first two matrices. This is essentially the list of Euclidean distances listed twice.

I then repeated the test with the last two matrices reversed, in order to test for spurious effects due to spatial autocorrelation. I assessed significance using 2000 permutations in Passage 1.0.

2.4.3 Vegetation data (Objective 3)

Variance partitioning

I used variance partitioning (Borcard et al. 1992) to explain the sources of variation in the composition of the understory species data. Canonical ordination can be used in two separate analyses to explain the total importance for the species data of (1) the effects of environmental variables and (2) the effects of spatial structure (Borcard et al. 1992). However, it is possible for environmental variables and species to share a common spatial structure, which can be caused either by the effects of spatially structured environmental variables on species data, or by the effects of another, unmeasured variable that causes common spatial structure to appear in both the species and the environmental variable data (Borcard et al. 1992). Variance partitioning techniques can be used to determine what portion of the species data can be explained by such spatially structured environmental variation. I used variance partitioning to separate the total overall variation in the species data into four components: non spatial environmental variation, spatially structured environmental variation, purely spatial variation, and unexplained variation and stochastic fluctuations (Borcard et al. 1992). I used % PAR and distance to nearest water feature as explanatory environmental variables, and simple x y coordinates as spatial variables. The analysis is performed using partial canonical ordination (partial RDA or CCA), a direct ordination method that removes the effects of covariables (ter Braak 1994). I began the analysis using DCA (Detrended Correspondence Analysis) in order to determine the appropriate choice of direct ordination methods. The DCA analysis showed long gradients in the data (>3 standard deviation units), which lend themselves better to unimodal methods than to linear methods. I used CCA and partial CCA in my subsequent analyses for a few reasons: because of these long gradients in the data, because CCA provided a better fit to the species data than did RDA, and because CCA is robust to both skewed species distributions and high noise levels (McGonigal et al. 2000). I used CANOCO 4.0 (ter Braak and Smilauer 1998a) for my ordination analyses, and performed variance partitioning using the methods described in Borcard et al. (1992). I excluded significance tests from my results because I was unable to perform accurate Monte Carlo significance tests given my sampling design; CANOCO 4.0 cannot restrict permutations to account for a crossing transect design.

Forward Selection

I used forward selection in CCA to explore the influence of each of the measured environmental and spatial variables on the species data. Forward selection can be used for ranking variables in the order of their relative importance for explaining variation in the species data. In CANOCO, variables can be automatically selected on the basis of maximum extra fit to the unimodal model. "Marginal effects" values show the variance in the species data that each variable explains on its own. "Conditional effects" values shows the order of inclusion of the variables in the CCA model in order to produce the best fit to the data, and the variance each variable explains once it is added to the model (ter Braak and Smilauer 1998b).

3. Results

3.1 Understory light

Canopy openness (% CO) and light transmission (% PAR) varied considerably both within and between study sites, reflecting heterogeneity in canopy structure within and between study sites. These data are presented along each transect (Figure 2, Table 1), and grouped by study site (Figure 3, Table 2). The light environment in the HD stand was similar on both transects, although mean and median values of light transmission and canopy openness were slightly higher for transect HD2 than transect HD1 (Table 1). The PCL site showed two very different patterns between transects (Figure 2). Transect PCL1, which passes through a large vine maple gap, shows high maximum values of % CO and % PAR, low minimum values, high variability, and high mean and median values (Table 1). Values for transect PCL2, through fir-hemlock forest, were uniformly low (Table 1).

Frequency distributions of % CO and % PAR values differ between study sites (Figure 3). Values of % CO and % PAR from the HD site clearly form a trimodal distribution, with strong peaks between 1–1.5 % canopy openness and 1-2% PAR and between 4-5 % canopy openness and 4-5 % PAR, and a smaller peak between 6.5% and 7% CO and 11-12% PAR. In contrast, in the PCL site, both % CO and % PAR have a distribution with a mode at low values and a long tail. The values from the vine maple gap make up the tail of this distribution, with values spread over the full range of % CO and % PAR values (% CO= 0.2-19.4; % PAR= 0.3-31.1). The mode of the distribution is composed mainly of values from the hemlock-amabilis fir conifer forest, with uniformly low values of % CO and % PAR (% CO=0.1-6.2; % PAR=0.1-8.5). For % CO, the mode is at 0-1%. For % PAR, the mode is at 0-2%.

3.1.1 Percent Canopy Openness versus percent Photosynthetically Active Radiation

The correlation between % CO and % PAR is high for both study sites (Figure 4), with R^2 values of 0.82 for the HD study site ($p= 0.00$) and 0.92 ($p= 0.00$) for the PCL study site. Residuals around the regression line reflect differences in canopy gap size, shape, and orientation between photosites. In general, photosites with smaller values of % CO show smaller deviations from the regression line.

3.1.2 Spatial autocorrelation of understory light

Correlograms for each transect for both % Canopy Openness and % PAR show several different patterns (Figure 5). Data for transects PCL1 and PCL2 were normalized using a natural logarithmic transformation. Because the correlograms were built using equal-interval distance classes, the last distance class was based upon a small number of pairs of localities, making it more difficult to interpret (Legendre and Fortin 1989). I therefore did not include it in the correlograms. All correlograms except the Geary's *c* correlograms for the vine maple gap (Figure 5i) are globally significant ($p \leq 0.05$). Transect HD1 (parallel to the river) shows a pattern typical of ecological variables, with positive autocorrelation at small distance classes grading to negative autocorrelation at larger ones. Significant positive autocorrelation occurs up to a minimum of 14.3 m and a maximum of 42.9 m in distance depending on the autocorrelation coefficient used and the variable measured. Negative autocorrelation is significant for points separated by more than 42.9 m. The pattern displayed on this transect is typical either of a gradient or a single sharp step in a variable; the two patterns cannot be distinguished using correlograms (Legendre and Fortin 1989). For Transect HD2 (running perpendicular to the river), autocorrelation is positive to at least 12.5 m, and the shape of the correlograms probably reflects a repeated pattern of peaks and troughs or a few narrow waves rather than a simple gradient (Legendre and Fortin 1989). This pattern is significant only for the Moran's *I* coefficient, and not for the Geary's *c* coefficient. Moran's *I* tends to capture known patterns in ecological data more cleanly than does Geary's *c*, with more easily-interpretable results (Urban 2001). I based the interpretation of pattern on transect HD2 in the Discussion section on the Moran's *I* statistic.

Correlograms for transect PCL1 showed a pattern similar to transect HD1, with significant positive spatial autocorrelation to at least 14.3 m and significant negative spatial autocorrelation at distances from more than 42.9 m to at least 71.4 m, for both percent canopy openness and percent PAR transmitted. However, for this transect, the stationarity assumption is violated: as the transect passes from the vine maple gap into conifer-dominated forest, values of the mean and standard deviation for % CO and % PAR transmitted change substantially (Figures 2c and 3cd and Table 2). I therefore used several different analyses to characterize the spatial pattern within this transect.

First, I constructed correlograms for transect PCL1 using untransformed % CO and % total PAR values for only those points lying within the vine maple gap (Figure 5i,j). The resulting correlograms are globally significant for Moran's *I* only for % CO, and for both Moran's *I* and Geary's *c* for % PAR values. The pattern suggests a wide wave form or single fat bump (Legendre and Fortin 1989). However, this pattern is difficult to interpret because so few of the autocorrelation coefficients are significant. Next, I constructed correlograms using % CO and % PAR values within the vine maple gap after vine maple leaves had fallen in the autumn (Figure 5k,l). This produced similarly-shaped correlograms, with a stronger pattern: autocorrelation coefficients are significant for all distance classes, for both correlation coefficients, and for both variables. Third, in order to eliminate the non-stationarity in the data set, I fitted a linear trendline to the data and performed correlogram analysis on the residuals (Urban 2001). This analysis produced correlograms that are globally significant only for Geary's *c* for % CO and Moran's *I* for % PAR, with too few distance classes showing significant autocorrelation coefficients to identify any kind of pattern (results not shown). Last, I used wavelet analysis (Mexican hat and Haar wavelets) to briefly examine data for all transects, and found a scale of 4-7 m to be the most important scale of pattern (and therefore probably the dominant gap size) on transect PCL1. Because of the short length of these transects, limited sampling resolution, and insensitivity of fisheye photography, I have chosen not to include wavelet analysis here; however, it does indicate that a different scale of pattern may exist than what the correlogram analysis alone detected. All of the above analyses suggest that there may be two scales of pattern on transect PCL1, one in the form of a gradient between forest types, and one unique to the vine maple gap. Non-stationarity in the dataset and the short transect length involved obscured my ability to resolve these patterns.

Transect PCL2 shows a pattern typical of a wave form or single large peak in the data for both % CO and % PAR (Legendre and Fortin 1989), with significant positive autocorrelation in both the smallest and the largest distance classes (0 to 14.3 m and 71.4 to 85.7 m) and significant negative spatial autocorrelation for distance classes in between (28.6 to 57.1 m).

Because I chose equidistant distance classes, the correlograms were built on fairly long spatial lags (12.5 or 14.3 m wide). Large spatial lags are better for detecting larger scale patterns and process, while smaller spatial lags are better for detecting more local micro-site variability (M.-J. Fortin, pers.comm.). For comparison, I also built correlograms based on distance classes containing an equal number of samples (not shown). This second set of correlograms showed the same patterns as the correlograms presented here, but in some cases autocorrelation coefficients were slightly larger. My results are consistent with Fortin (1999b), who found that correlograms built on larger spatial intervals showed weaker spatial autocorrelation because they included more environmental variability in each distance class (resulting from the influence of processes occurring at multiple spatial scales as well as noise), but preserved the shape of the spatial correlogram provided the spatial signal was strong.

In all cases, canopy openness and percent transmitted PAR measurements are clearly spatially autocorrelated at a scale considerably larger than the distance between sampling points. Subsequent analyses must therefore assume spatial dependence between points.

3.1.3 Influence of vine maple

Vine maple gap

The vine maple gap in the PCL site had significantly different canopy openness and light levels than the adjacent conifer forest when spatial autocorrelation was accounted for (Figure 6c, Tables 2 and 3). Both mean values and standard deviations were very different in the two types of plant communities. Mean values were 10.8 % PAR transmitted in the gap before vine maple leaf fall, and 21.5 % PAR transmitted after leaf fall (N=25), versus 3.0 % PAR transmitted before vine maple leaf fall, and 4.0% PAR after in adjacent coniferous forest (N=77) Standard deviations were 10.0 before vine maple leaf-fall and 14.1 after leaf-fall in the vine maple gap, versus 2.2 before leaf fall and 3.6 after leaf-fall in conifer forest. Mantel tests showed a significant relationship between % PAR values and gap versus non-gap both before and after vine maple leaf fall (Table 3A and 3B). This relationship was equally strong when geographic distances were partialled out (partial Mantel test, correlation= 0.37 before leaf fall and 0.58 after, p= 0.0005 based on 2000 Monte Carlo permutations). The lack of a significant correlation between % PAR and geographic distance when gap versus non-gap was partialled out indicates that the relationship was not a spurious correlation attributable to spatial autocorrelation in the data set.

Vine maple leaf fall changed values and distributions of canopy openness and light transmission values in the vine maple gap (Figure 6c, Tables 2 and 3), considerably increasing both mean values and their standard deviations. Partial Mantel tests revealed a significant difference between light transmittance before and after vine maple leaves fell in the vine maple gap that was not attributable to spatial autocorrelation (Table 3C). (correlation r= 0.12, p= 0.003 based on Monte Carlo permutation test with 2000 permutations).

Non-gap vine maple in the Horizontal Diversification Stand

Vine maple leaf fall in the understory of the HD stand had a similar albeit smaller influence on canopy openness and light transmission than it did in the old growth stand, (Figure 6ab, Tables 2 and 3). For photosites where vine maple was present, vine maple leaf fall slightly increased the mean and spread of % CO and % PAR: mean % CO increased from 3.0±1.4 to 3.5±1.8, and mean % PAR increased from 4.5±2.2 to 5.0±2.4. However, partial Mantel tests did not reveal a statistically significant difference between the two groups of observations when the effect of space were removed from the data ($r = -0.002$. $p = 0.87$ based on 2000 Monte Carlo permutations). The relationship between % PAR and geographic coordinates was highly significant for % PAR in the HD stand (Mantel $r = 0.16$, $p = 0.0005$ based on 2000 Monte Carlo permutations).

3.2 Vegetation data

Mean percent cover values for recorded species are presented in Figure 7. The vegetation communities were considerably different in the two stands, as well as within and outside of the vine maple gap in the old growth stand. In the HD stand, the most common species in the herb layer (by percent cover), collectively representing 35.8% cover were *Lysichiton americanum* (skunk cabbage, 21.9%), followed by *Athyrium filix-femina* (lady fern, 4.0%), *Tiarella trifoliata* (three-leaved foamflower, 3.0%), *Blechnum spicant* (deer fern, 2.6%), *Tolmiea menziesii* (piggy-back plant/youth-on-age, 1.5%), *Dryoperis expansa* (shield fern, 1.5 %), and *Polystichum munitum* (sword fern, 1.3%). The most common shrub layer species, representing collectively 16.7% cover, were *Rubus spectabilis* (salmonberry, 13.6%), *Vaccinium alaskaense* and *V. ovalifolium* (blueberry, 1.9%), and *Sambucus racemosa ssp. Pubens* (red elderberry, 1.2%). Vegetation composition was quite different between gap and non-gap in the PCL study site. In the vine maple gap, the most common species in the herb layer were *Dryoperis expansa* (6.6 %), *Athyrium filix-femina* (6.4%), and *Tiarella trifoliata* (3.1%) and the most common species in the shrub layer were *Rubus spectabilis* (22.3%), *Ribes* *bracteosum* (stink currant, 9.6%), *Sambucus racemosa ssp. Pubens* (5.6%), and *Acer circinatum* (Vine maple, 1.7%). The shrub layer was thick in the vine maple gap, accounting for an average percent cover of 49.5%, versus 20.9% in the herb layer. In the adjacent coniferous forest portion of the PCL stand, the reverse was true, with 32.1% average percent cover in the herb layer and only 9.9% in the shrub layer. The most common herb layer species in the conifer-dominated portion of the stand were *Athyrium filix-femina* (11.9%), *Dryopteris expansa* (8.3%), *Blechnum spicant* (6.7%), *Rubus pedatus* (five-leaved bramble, 2.3%), and *Tiarella trifoliata* (2.1%) and the most common shrub layer species were *Rubus spectabilis* (2.2%), *Vaccinium alaskaense,* and *Vaccinium ovalifolium* (3.0%).

Several species were present in one stand but not the other. Species found only in the HD stand were *Boykinia elata* (coast boykinia, an indicator of flooding and nitrogen-rich soils, Klinka 1989), *Cardamine oligosperma* (few-seeded bitter-cress), *Circaea alpina* (enchanter's nightshade), *Galium triflorum* (sweet-scented bedstraw), *Stellaria crispa* (crisp sandwort, an indicator of very moist and wet soils, Klinka 1989), and *Gaultheria shallon* (salal, an indicator of nitrogen-poor soils, Klinka 1989). Species found in the PCL stand but not the HD stand are *Rubus pedatus* (five-leaved bramble, an indicator of fresh and very moist soils, Klinka 1989), *Tiarella trifoliata var. unifoliata* (one-leaved foamflower,some taxonomists consider this to be a separate species from three-leaved foamflower; Pojar and MacKinnon 1994), and *Abies amabilis* (Amabilis fir) seedlings. The fact that *Rubus pedatus* and amabilis fir seedlings were found only in the PCL site likely reflects the wetter biogeoclimatic subzone and higher elevation of this site, which result in greater rain and snow influence. Both species are typical of wetter, cooler, higher elevation forests (K. Lertzman, pers. comm.).

3.2.1 Detrended Correspondance Analysis

DCA is a form of indirect gradient analysis which provides a picture of the overall variation in the data and the relative similarity between sample points, but does not directly link this variation to environmental data. Results of this analysis are presented in Figure 8. Each point represents the species composition of a sample site. DCA axes are measured in standard deviation units. The DCA for both study sites combined showed long gradients (up to about 4 SD units on the first axis and 3SD units on the second), indicating that almost no species are shared between samples at opposite ends of the axes. A score of 4 SD indicates that samples have no species in common, as a Gaussian response curve with a tolerance of 1 rises and falls over an interval of about this length (ter Braak 1995). DCA showed a clear separation between vegetation communities in the vine maple gap, the adjacent conifer forest, and the HD study site.

3.2.2 Variance partitioning

Variance partitioning of species composition data using spatial and environmental variables showed different patterns for the two stands (Figure 9). In the HD stand, spatially structured environmental variation accounted for the largest explained portion of the variation in the species data (13.6%), indicating that either spatially structured environmental variables had an important impact on the species data, or that an extraneous process caused common spatial structuring in both the species and the environment data (Borcard 1992). Next in importance was purely (non-spatial) environmental variation (11.2%), followed by purely spatial variation (3.7%). A large proportion of the variation, 71.5%, remained unexplained. In the PCL stand, the order of importance of different types of variation was different, with the largest portion of species variation explained by purely (non-spatial) environmental variation (14.2%), followed by purely spatial variation (10.8%) and spatially structured environmental variation (10.3%). 64.7% of the variation in species composition in the PCL stand remained unexplained.

3.2.3 Forward selection

Automatic forward selection in CANOCO allowed me to evaluate the relative influence of each of the measured environmental variables on species composition in each stand (Table 4). The contrast between marginal effects and conditional effects of the variables reflects overlap in the influence of environmental variables. In the HD stand, distance to streams explained 16.1% of the species composition variance, and was the first variable included in the model. Once the effect of distance to streams was included in the model, none of the remaining variables explained more than an additional 5% of the species variance, although distance to standing water, percent total PAR transmitted, and spatial position all explained portions of the variation. Although vine maple above the shrub layer also explained a portion of the variation in species composition based on conditional effects, this number is so small that it is probably due to chance alone: even significance tests unconstrained for sample design did not find a significant relationship (results not shown).

In the PCL stand, the planimetric x coordinate (which refers to distance in a direction parallel to the Seymour river) was the best predictor of vegetation species composition, accounting on its own for 12.8% of variation. The predictive power of the x coordinate probably reflects the fact that transect PCL1 runs parallel to the x direction, and passes from the vine maple gap into the hemlock-fir forest. In fact, vine maple above the shrub layer explained 8.3% of the species variation on its own, but once the x, y, and distance to standing water variables were included in the analysis, it explained only 4.0% more of the variation. Percent total PAR transmitted explained 7.2% of the variation on its own, but once included in a model in which variables are selected sequentially on the basis of maximum extra fit, % PAR was the least important variable, and explained only an additional 1.6% of the species variation. This suggests that the influence of % PAR overlapped with the influence of other environmental variables. The y coordinate (which refers to distance in a direction perpendicular to the Seymour river), distance to standing water, and distance to streams also explained portions of the variation.

4. Discussion

My two study sites had very different distributions of canopy openness and understory light: the PCL site had a mode at low values and a long tail made up of vine maple gap values, while the HD stand formed a trimodal distribution. Spatial autocorrelation was clearly significant on all transects, with positive spatial autocorrelation to at least 12.5 metres in all cases. The vine maple gap had different canopy openness and understory light values than the adjacent forest, and these values changed significantly when vine maple leaves fell in the autumn. Non-gap vine maple in the forest understory did not significantly affect canopy openness or understory light. The vine maple gap also had a different understory plant community than the adjacent forest. Variance partitioning revealed that spatially structured sources of variation were important in both stands, although a large portion of the variation remained unexplained. Forward selection revealed the influence of spatial gradients and streams on understory communities.

Because the PCL study stand contains two different types of plant associations, I have chosen to consider it both as a single site reflecting the internal heterogeneity common in riparian stands, and as a site composed of two distinct entities worthy of separate consideration. The classic definition of a stand, "a group of trees relatively homogenous in structure and composition" (Franklin et al. 2002), suggests that this site is composed of two different stands. However, riparian stands are often composed of a mosaic of different site types. Plant communities in riparian zones are dynamic and heterogenous, reflecting a dynamic landscape (Naiman et al. 2000). Despite idealized models of stand development, actual stands are often composed of two or more structural units resulting from multiple disturbances (Spies 1997, Franklin et al. 2002). The PCL study site can be considered to be a plant association complex, where different "plant associations are interspersed at scales smaller than the scale of interest" (Ott and Juday 2002). The gap in this study was exceptionally large; however, it is not, either in composition or in size, outside the range of what other authors have reported in similar ecosystems (Fonda 1974, Minore and Weatherly 1994, Pabst and Spies 1999). I have therefore chosen to consider the entire PCL site as a single plant association complex, while at the same time comparing the differences between the two types of plant communities in this study site.

4.1 Values of canopy openness and PAR transmittance

4.1.1 Coniferous forests

I found values for canopy openness and PAR that are generally comparable to, or lower than, what other authors have documented for similar old growth forests (Table 5). In this study, values of canopy openness were 3.4±1.8% in the HD stand (range 0.2-6.9) and 3.0±3.5% in the PCL stand (range 0.1-19.4), and values of % PAR transmittance were 4.9±2.8% (range 0.2-12.4) in the HD stand and 4.6±6.3% (range 0.1-31.1) in the PCL stand. To my knowledge, the only published study reporting values of canopy openness or PAR-transmittance in Sitka-spruce dominated old growth forests is that of Hanley and Brady (1997). They reported mean values of canopy openness ranging from 9.6 to 22.5 (with standard deviations ranging from 1.0 to 1.3) for old-growth western hemlock–Sitka spruce forests in Alaska, based on spherical densiometer measures. Although these standard deviations are smaller than but comparable to those I found, the values for canopy openness in the Alaska study are much higher. The most likely explanation for the difference is the difference in methods. Several authors have compared different methods of estimating canopy openness and light transmission, including spherical densiometers, canopy photography, and solar radiation sensors (Comeau et al. 1998, Gendron et al. 1998, Machado and Reich 1999, Frazer et al. 2000). In most cases different instruments provide reasonable estimates of percent light transmittance as compared with solar radiation sensors. However, there is not necessarily a close relationship between estimates produced by two different optical methods, and this difference in techniques may explain the difference between my estimates and those of Hanley and Brady (1997). Another possible explanation for the difference between Hanley and Brady's (1997) canopy openness estimates and my estimates for similar forests is their location in southeastern Alaska. Species and region-specific canopy architecture can have a significant effect on light transmission.

Several studies have considered canopy openness and light transmittance in western hemlock and/or Douglas-fir old-growth forests, and generally reported values higher than mine (Table 5). My canopy openness values are lower than those reported by Frazer et al. (2000) for both western hemlock old growth forests and Douglas-fir old-growth forests, by Weiss (2000) for Douglas-fir – western hemlock forests, and by Hanley and Brady (1997) in western hemlock-Sitka spruce forests. My mean % PAR values are comparable to those documented by Parker (1997), Parker et al. (2001), and Canham et al. (1990) in Douglas-fir-western-hemlock old-growth forests, although Parker (1997) and Parker et al. (2001) found larger standard deviations between stands than I found within stands. Mean values documented by Stewart (1986) for percent diffuse and direct beam radiation are an order of magnitude greater than those detected in this study and by several other authors. Differences between this study and other researchers' findings may reflect either differences in the canopy structures of the forests or differences in methodologies used to collect data.

Field and photo analysis methodologies can influence canopy openness and light transmittance estimates. Several of my methods may have resulted in lower-than-average mean estimates for canopy openness and light transmission. These include locating photosites next to boles and under saplings, and thresholding technique.

I specifically designed my sampling protocol to estimate the amount of understory light available to the shrub layer. I only re-positioned photosites off the transect line if it was physically impossible to take a photo and sample a vegetation plot at that location. This meant that I occasionally placed photosites next to large stems and under saplings. The subcanopy, including subcanopy trees, saplings, shrubs, ferns, and herbs, has a major influence on light availability (Montgomery and Chazdon 2001). Although I eliminated the effects of shrubs, ferns, and herbs on light estimates, I did not eliminate the effect of saplings, subcanopy trees, and tree stems. This makes my data a realistic estimate of gap-light transmission at the shrub layer at my photosites, and of gap-light transmission in the study stands. Other studies that sought mainly to quantify overstory canopy structure and light transmission using hemispheric photography may have chosen to locate photosites in areas unobstructed by boles and saplings, resulting in higher estimates.

One of the most subjective steps in hemispheric photo analysis is adjusting digitized images to determine sky and non-sky ("thresholding"). The thresholding rule that I used in this study (see Methods) was consistent between photos, and followed the same rule that designers of the GLA software recommend based on a calibration of the software PAR estimates with direct radiation sensor measures of light transmission (G. Frazer, pers. comm.). This rule produced threshold values that were higher than the values I would intuitively have chosen, and thus resulted in estimates of canopy openness and PAR that were lower than I expected. Other users of GLA or similar software who did not have the benefit of the advice I received may well have chosen threshold values that were too low.

The effectiveness of hemispheric photography for estimating understory light conditions has been widely debated. Several users have suggested that calculations of light transmission based on canopy photos either overestimate (Chazdon and Field 1987, Whitmore et al. 1993) or underestimate light transmission (Roxburgh and Kelly 1995). Some authors have suggested that under low light conditions, hemispheric photos become less effective for predicting light transmittance; estimates of this point include 15% canopy openness (Whitmore et al. 1993), 3% measured photosynthetic photon flux density (%PPFD) (Roxburgh and Kelly 1995), 10% canopy openness (Walter and Himmler 1996), and 6% PPFD (Machado and Reich 1999). In contrast, Rich et al. (1993) suggest that canopy photographs effectively predict PPFD at values as low as 1% full sunlight. Overestimation of PAR transmittance at low light levels can be due to the "halo effect", whereby hemispheric lenses can create haloes of light around small canopy gaps (Whitmore et al. 1993). Conversely, underestimation can be more pronounced at lower canopy openness values because hemispheric photos do not account for light transmitted through leaves and closed canopy (Roxburgh and Kelly 1995).

Despite the inherent limitations of hemispherical photography and the methodological issues addressed above, I believe that the difference between my % CO and % PAR estimates and those of other authors reflects the forests themselves. Apart from the vine maple gap, both of my study plots were quite dark, and despite the developmental stage of both sites, neither had the open and "gappy" feel of many old-growth forests. I believe that this reflects the species composition and structure of the stands. Tree species-specific canopy architecture affects light transmission: leaf shape, size, orientation, and clumping, branching structure and crown depth can have significant influences on light transmission (Canham and Burbank 1994, Frazer et al. 2000). In general, shade-tolerant species are the most efficient at collecting solar radiation, and therefore also tend to block the most light, casting the deepest shade (Canham and Burbank 1994). Both of my study sites contain a high proportion the shade-tolerant species amabilis fir and western hemlock. It is therefore not surprising that I found lower openness values than in comparable studies in Sitka-spruce or Douglas-fir dominated old-growth forests. In addition, site-specific factors such as site orientation, soil chemistry and moisture, and disturbance history can have a significant influence on forest structural development, and therefore on canopy openness measures (Frazer et al. 2000). It is likely that the low openness values I found reflect the particular topography, soil conditions, and disturbance histories of these two fertile floodplain sites. With regard to topography, my study sites were surrounded by steep mountains that blocked out a portion of the true horizon from every photo. Such topographic shading may have resulted in lower estimates of canopy openness and percent PAR than in comparable forests on flatter terrain.

Models of stand development suggest that the older forests in a chronosequence should have greater mean openness and greater variability in openness than younger forests (provided the younger forests have reached canopy closure) (Oliver 1980, Spies 1997, Frazer et al. 2000, Franklin et al. 2002). Frazer et al. (2000) found that old-growth stands had larger and relatively less evenly spaced canopy openings than younger stands, that they showed substantial spatial variation in gap characteristics, and that the most important changes in canopy structure emerged in the later stages of stand development (150-200 years). However, not all results have been consistent with these expectations, and more complex variation with stand age has emerged. Spies et al. (1990) found that although the old-growth Douglas-fir – western-hemlock stand they sampled had a larger median gap size than the mature stand, the mature stand had a greater overall area in canopy gaps. Lertzman et al. (1996) also found that some mature CWHvm stands had more area in gaps than did old-growth stands. This deviation from the expected model of stand development may also reflect the fact that neither of the latter two studies was explicitly designed to represent chronosequences of similar matched sites.

My results do not conform to the expectation of greater openness in the older stands. The older stand is slightly less open on average than the younger site, although it exhibits greater variability in canopy openness and light transmittance than the younger study site. If the salmonberry-vine maple gap is excluded from the comparison, mean, median, and standard deviations of CO and PAR are clearly lower in the older site. There are two primary explanations for this difference from the results predicted by canopy development models. First, although the PCL conifer stand is older than the HD stand, it is in fact dominated by amabilis fir and western hemlock that are younger than many of the trees in the HD stand (Broberg et al. 1999). The older stand appears to be in a transition phase of pioneer cohort loss (Franklin et al. 2002), where old Sitka-spruce are being replaced by shade-tolerant western hemlock and amabilis fir (Broberg et al. 1999). On alluvial terraces not subject to flooding, large Sitka spruce dominants eventually die and are replaced by western hemlock and other shade-tolerant species as a "climax" community (Fonda 1974, Hanley and Hoel 1996, Peterson et al. 1997). In my older study stand, the dominant western hemlock and amabilis fir trees range in age from about 55 years to 175 years (Broberg et al. 1999). A stand dominated by trees of this age might normally be classed as mature, and forms a canopy structure more similar to what might be expected in a mature stand than in an old-growth stand. This explains the relative uniformity and low light levels in the coniferous portion of the older stand. Over time, the stand will likely conform to the expectation of greater canopy openness. However, this result has important management implications: despite old-growth definitions that emphasize the presence of large, old trees, canopy gaps, and understory heterogeneity, not all old-growth forests are dominated by large, old trees, high canopy openness, or high heterogeneity in canopy structure.

The second explanation for a lack of fit between my results and the expectation of greater openness and variability in the older stand is the likelihood that the two stands are not part of the same chronosequence. Differences in site factors, such as biogeoclimatic subzone, soil drainage, and elevation, suggest that the two sites are on different developmental trajectories. Frazer et al. (2000) found that site factors could be important drivers of canopy development. Lertzman et al. (1996) suggested a similar hypothesis to explain why they found more area in gaps in mature stands than in old-growth stands.

4.1.2 Vine maple-dominated gaps

McGhee (1996) reported much higher levels of canopy openness for vine maple gaps than do I. The highest value I found for canopy openness (19.4 for foliage on) is below the mean of her samples, and she reported standard deviations about three times as high as mine. There are several possible explanations for these differences, none of which are mutually exclusive. First, McGhee's study was conducted in vine maple gaps that were likely much younger (60-80 years old) than the one in which I conducted my study; results which may indicate that openness decreases in vine maple gaps as they age. Second, the difference may be attributable to the different nature of the gaps studied. The gap I sampled contained scattered conifers and standing snags that may have resulted in lower mean openness values than would be found under vine maple alone, and combined with the very thick shrub layer and large coarse woody debris in the gap seem to suggest that the gap is at least in part a developmental gap resulting from windthrow, flooding, or a combination of these events. McGhee argued that the gaps she studied were "priority gaps" formed by the initial establishment of vine maple and subsequent exclusion of conifers in these areas. Unlike my study, her study excluded vine maple sites with a clear association with a stream or other edaphic features. Third, it is possible that the difference is attributable to differences in methodologies, including different software for the analysis of hemispheric photos, and different thresholding techniques. The fact that McGhee found similarly high mean values of percent canopy openness (35±8.4) in mature conifer forest adjacent to her study gaps, which is much higher than the values I found in coniferous forest in either study site, supports this explanation.

4.2 Patterns of canopy openness and PAR transmittance

4.2.1 Frequency distributions

The distributions of canopy openness and PAR are trimodal in the HD stand and J-shaped in the PCL stand. The three-peaked distribution in the HD stand may reflect two distinct gap sizes and a number of heavily-shaded sites. For both study sites, the lower peak of openness values reflects "anti-gaps" of low light and low understory cover (Franklin and Spies 1991). Although there are clear peaks in the distributions of openness that reflect the difference between gaps and non-gaps (Publicover and Vogt 1991), these results reaffirm the idea that forest canopies do not fit a simple gap versus non-gap dichotomy, since variation in understory light regimes is continuous in at least two spatial dimensions (Lieberman et al. 1989).

4.2.2 Spatial autocorrelation

Pattern

Correlograms revealed significant spatial autocorrelation of canopy openness and light transmission, but the pattern of autocorrelation varied considerably between transects. The diversity of patterns in such small study sites is surprising, and highlights the heterogeneity of canopy conditions in old-growth forests at a scale much smaller than the typical scale of forest management in British Columbia.

Gradients in canopy cover were not expressed primarily with increasing distance from a large stream or river, as reported for other old-growth riparian areas in the Pacific Northwest (Fonda 1974, Minore and Weatherly 1994, Pabst and Spies 1999, Nierenberg and Hibbs 2000). Instead, gradients were predominantly parallel to the Seymour River. The difference may be in part attributable to scale and location of samples; the studies cited above were based on transects beginning at the stream's edge and often crossing more than one landform (e.g. from terrace to hillslope). My transects began at least 50 m from the river edge to eliminate direct effects of the forest edge associated with the river channel. Further research is needed to consider whether gradients in old-growth forest canopy conditions parallel to rivers and streams on scales as small as one hectare are a common occurrence. One of the key concepts of river ecology is the river continuum concept (Vannote et al. 1980), whereby aquatic communities vary along a longitudinal gradient, shifting in function and composition depending on a given stream reach's location in the larger drainage network. Perhaps the gradients parallel to the river detected in this study reflect a longitudinal gradient in streamside vegetation on a smaller scale.

The spatial pattern of canopy openness reflects the spacing of canopy trees, sub-canopy trees, and saplings as well as branching patterns, leaf shape, orientation, and inclination, and tree species composition. The spacing of trees reflects in part the disturbance history of the stand, including small-scale gap creation; the presence of edaphic gaps; and patterns of tree establishment. Tree establishment was further influenced by factors such as microsite conditions, regeneration strategies, competition with understory plants and other tree seedlings, browsing, and clumping of cohorts of species. The pattern of % CO and % PAR visible on transect PCL1 reflects the difference between the two forest types in this study site, which is likely linked to persistent flooding in the vine maple gap. The gradient pattern on transect HD1 reflects dense regeneration on the latter half of that transect, as the transect moves away from edaphic gaps generated by streams. On the other two transects, the patterns detected by correlogram analysis are more complex and less easily explained, and may reflect the factors affecting tree establishment mentioned above.

Scale of autocorrelation and implications for future sampling design

Knowing the scale of positive autocorrelation allows for better sampling design. If the goal is to minimize the effects of spatial autocorrelation on statistical analyses , the scale of sampling should be larger than the patch size of the variable. The patch size of the variable is the distance at which the value of the spatial autocorrelation coefficient first crosses the expected value (0 for Moran's *I*, 1 for Geary's *c*) in the correlogram (Fortin 1999). My correlograms showed significant positive spatial autocorrelation up to at least 12.5 m for all transects, with the value of *I* or *c* crossing the expected value at about 30 m. A sampling step of 30 m for future studies would therefore be large enough to reduce the effect of positive spatial autocorrelation sufficiently to apply classical statistics in analysis of the data. However, if the goal of future studies is to capture spatial pattern effectively, a regular sampling step of 30 m would fail to detect the spatial structure in the data, as more localized variability is apparent. For example, on a transect such as HD2, where correlogram analysis detected a pattern of repeated peaks and troughs, spacing photosites at every 30 m would fail to detect existing spatial pattern because samples could consistently fall either at the peaks or between peaks (Fortin et al. 1989, Legendre and Fortin 1989). In order to adequately sample the various patterns found in these stands, while minimizing the amount of samples taken, a more effective sampling strategy would be to sample at two different scales in a systematic cluster design (Fortin et al. 1989, Legendre and Fortin 1989).

The few studies that have considered autocorrelation in forest understory light have reported quite variable scales of autocorrelation (Becker and Smith 1990, Walter and Himmler 1996, Trichon et al. 1998, Miller et al. 2002). In old-growth northern hardwood forests, Miller et al. (2002) found positive autocorrelation to distances of less than 2.5 m in stands with high sapling density, but positive autocorrelation at up to 21 m in stands with low sapling density. Scale of autocorrelation in different forest types ranged from no spatial autocorrelation at a scale of 10 m in Indonesian tropical rainforests (Trichon et al. 1998) to positive autocorrelation to about 10 m in a Scot pine stand (Walter and Himmler 1996) to weak positive autocorrelation only to distances of 2.5 m in moist tropical forests (Becker and Smith 1990). However, in an exceptionally dry year with very high leaf fall, Becker and Smith (1990) found positive autocorrelation up to 12.5-22.5 m in the same moist tropical forests. In my case, the absence of vine maple leaves did increase the significance of autocorrelation coefficients, but it did not change the extent or basic pattern of autocorrelation.

None of the autocorrelation studies cited above reported significant negative autocorrelation at scales larger than the limit of positive autocorrelation, although such a pattern is not unusual for ecological variables (Legendre and Fortin 1989). I found negative autocorrelation at larger scales in all cases, with negative autocorrelation at distances as large as 87.5 m (and perhaps larger). This may in part be an artifact of correlogram analysis; some authors suggest truncating the maximum distance class to at most half the minimum dimension of the data grid (Urban 2001). I used the more common approach of limiting distance class size so that a minimum of 30 pairs of points was included in each autocorrelation coefficient calculation (Urban 2001). Regardless, my results show that in my study stands, points separated by as much as 87.5 m are spatially autocorrelated, and data analysis must account for this relationship.

4.3 Understory vegetation and environmental variables

4.3.1 HD stand

Variance partitioning in the HD stand revealed that 87% of the explained species composition variation (24.8% of the overall variation) was attributable to either spatially structured environmental variation or purely environmental variation. Purely spatial variation accounted for a very small percentage (3.7%) of the overall variation, which suggests that no fundamental spatial process exists that was not accounted for in the analysis. However, it is possible that the spatial variables used (simple Euclidean x and y) did not capture the existing spatial pattern satisfactorily, in which case some of the spatial variation would appear as unexplained variation. The variation accounted for by environmental factors (24.8%) was roughly divided between purely environmental (11.2%) and spatially structured environmental variation (13.6%). The latter figure indicates that the species and environment data share some of their spatial structuring. This shared variation results partly from vegetation response to spatial structure in the measured environmental variables, and partly from the common response of species data and environmental variables to underlying spatial processes such as natural disturbances (Borcard et al. 1992).

Forward selection of spatial and environmental variables in the HD stand shows that distance to stream has the best explanatory power of all variables, and that this variable is spatially structured (because once distance to stream was included in the model, spatial coordinates, particularly the y coordinate, explained little additional variation). Understory light, distance to standing water, and presence of vine maple above the shrub layer were far less important variables.

4.3.2 PCL stand

In contrast to the HD stand, variance partitioning in the old growth stand reveals a strong influence (10.8%) of spatial factors not accounted for by environmental variables. Forward selection shows that the x variable (a purely spatial variable) explains the most variation in this stand. I believe that the primary factor influencing understory vegetation composition in this study site was the vine maple gap, and that the x variable best captured the presence of the gap. Purely spatial variation identified by variance partitioning may be a result of localized processes such as dispersal, competition for space (Borcard et al. 1992), and competition for below-ground resources (Riegel et al. 1995), or it may be attributable to spatial components of unmeasured environmental variables (Boehringer 2002). For example, environmental variables such as overstory species or forest floor type (moder, mor) might have better described the vine maple gap than did percent cover of tall vine maple directly above each sample plot, which accounted for 8.3% of the variation on its own. Nevertheless, substantial values of variance explained by spatially structured environmental variables indicate that understory species and measured environmental variables do share some spatial structuring. Understory light explained a relatively small portion of the variation (8.3%), which decreased substantially (to 1.6%) when all other variables were first included by forward selection, indicating that % PAR shares much of its influenced with other variables included in the analysis.

4.3.3 Overall implications

A large portion of the variation in species composition in each stand remains unexplained by variance partitioning, a result that is not unusual for studies of forest ecosystems (Asselin et al. 2001; see also Gagnon and Bradfield 1986, Borcard et al. 1992, Arsenault and Bradfield 1995, Boehringer 2002). Unexplained variation can be attributed either to unmeasured environmental variables, to spatial structures that require more complex functions to be described than those employed in the analysis (e.g. cubic trend surface regression; Borcard et al. 1992), to purely stochastic variation, or to limits of variance partitioning itself (Palmer 2003). In my study, several environmental variables that could affect understory vegetation production and composition were not measured. These include soil characteristics such as soil type, nutrient content, stoniness, temperature, texture, and flora and fauna; presence of coarse woody debris, which has been shown to affect tree regeneration (Harmon and Franklin 1989) and the distribution of understory vegetation (Gagnon and Bradfield 1986); overstory species composition and litter throughfall; microclimate; microtopography; and browsing by herbivores (Schreiner et al. 1996). I also did not assess competition from other forms of vegetation, both above-ground and below-ground, although these may have had an important influence on the patterns of understory vegetation (Harmon and Franklin 1989, Riegel et al. 1995). For example, in several vegetation plots near streams in the HD stand, snake liverwort (*Conocephalum conicum*) constituted a large portion of ground cover. I did not include liverworts or mosses in my analysis. Unexplained variation may also exist because processes that created the observed variability are no longer active, but their influence is still apparent in the distribution of vegetation. Last, ecological processes may have effects at a scale smaller than the scale of sampling.

An understanding of the relationship between forest canopies and understory vegetation is necessary for predicting the response of understory communities to stand succession or forest management activities (McKenzie et al. 2000). I found that light transmission explained only a small portion of the variation in understory vegetation. Other researchers have reported varying relationships between canopy openness and understory vegetation. In some cases, canopy cover clearly affected understory diversity, productivity, or composition (Stewart 1986, Riegel et al. 1995, McKenzie et al. 2000). In other cases, canopy cover had little influence on understory species composition (Ehrenfeld 1980, Alaback 1982, Collins and Pickett 1987, 1988). Particularly in older unmanaged forests, strong direct effects between canopy cover and understory vegetation may be masked by the effects of other environmental variables, interactions between vegetation layers, or legacies of past disturbances (Alaback 1982, McKenzie et al. 2000). In managed forests, research has shown a link between canopy cover and understory communities. Several authors have shown that the increased resource availability (including light) following from partial cutting results in a growth response of seedlings and saplings or an increase in conifer regeneration, sometimes to the exclusion of herb and shrub communities (Alaback and Herman 1988, Deal and Farr 1994, Canham 1998, Deal 2001, Drever and Lertzman 2001). In view of these findings, it is not surprising that understory light did not account for a large portion of the variation in vegetation in either of my study sites. Overstory openness and light availability may be better predictors of understory composition and biomass over broader ranges of light conditions.

Distance to streams was, however, a key determinant of understory composition in the HD study stand. This finding agrees with several studies from southeastern Alaska which have found soil drainage to be the main environmental factor determining understory species composition in old-growth forests (Ver Hoef et al. 1988, Alaback and Juday 1989, Hanley and Brady 1997).

4.4 Influence of vine maple

I have found that in a single gap dominated by vine maple and salmonberry, vine maple has a clear seasonal effect on understory light conditions. Only a few studies have considered the ecological role of vine maple in temperate rainforests of the Pacific Northwest (O'Dea et al. 1995, Lertzman and McGhee 1996, McGhee 1996, Ogden and Schmidt 1997, Wardman and Schmidt 1998, Tashe and Schmidt 2001, Boehringer 2002). Vine maple is known to form priority canopy gaps that contribute to heterogeneity and structural diversity throughout forest development (Lertzman and McGhee 1996, McGhee 1996, O'Dea et al. 1995). Vine maple also influences soil properties. For example, Ogden and Schmidt (1997) found that the vine maple gaps had higher pH levels and higher concentrations of calcium, magnesium, and potassium in the forest floor, thinner forest floors, and a weak trend toward higher pH values and total nitrogen concentrations in the surface mineral soil than did western hemlock conifer forests. Tashe and Schmidt (2001) found that vine maple increased site fertility in coastal Douglas-fir forests, and Boehringer (2002) found that moder forest floor, a result of vine maple overstory, had an important effect on variability in forest floor properties. I have shown a further effect of vine maple: it creates temporal heterogeneity in understory light conditions over the course of the growing season. Vine maple leaves emerge significantly later in the spring than the growing season begins for shrubs and herbs (at least a month, personal observation) in the study stands, and when they do emerge, leaves significantly alter light conditions in the understory. Because I sampled understory vegetation only once over the growing season, I could not determine to what extent the change in light conditions affects vegetation composition, structure, and biomass. This question merits further investigation.

My findings also indicate that vine maple has an impact on the magnitude and variability of understory light. In my study site, light transmission in the vine maple gap was both greater and more variable than in the adjacent conifer forests. My findings are not inconsistent with O'Dea et al.'s (1995) suggestion that vine maple cover can decrease light levels and therefore affect understory vegetation. However, they contradict McGhee's (1996) findings of little difference between canopy openness in vine maple gaps and adjacent forests when vine maple was fully leafed out.

The importance of hardwoods in riparian areas of the west coast of North America has often been understated by forest ecologists and managers (McGhee 1996, Nierenberg and Hibbs 2000). Hardwoods provide habitat diversity that sustains many different species, and aid in maintaining soil productivity (McGhee 1996). Forest understories in 40-year-old hardwood stands in southeastern Alaska have been shown to be highly productive and species-rich, more so than would be expected in coniferous forests of comparable age (Hanley and Hoel 1996). My research has shown that there is a different vegetation community in the vine maple gap than in adjacent conifer forest. Further research on understory light transmission and understory communities in vine maple gaps could clarify the ecological role of vine maple gaps in creating habitat diversity and biologically distinct communities within the matrix of coniferous forest.

4.5 Research and Management implications

Ecosystem-based management recognizes that (1) the dynamics of ecosystems function over multiple scales of time and space; (2) ecosystem function depends on ecosystem structure, diversity, and integrity; and (3) human knowledge is limited and uncertainty exists (Christensen et al. 1996). Managing temperate rainforest ecosystems to maintain or restore old-growth conditions requires knowledge of the structure, composition, and function of these forests. The data I have collected documents structural and compositional conditions in two very different stands in old-growth floodplain forests. Because my study does not involve replication, it cannot be generalized. Nevertheless, it does raise interesting management implications and questions for future research in similar forests.

4.5.1 Implications for future research

(1) Canopy openness and understory light values calculated from hemispheric photos are sensitive to the "thresholding" step in which sky and non-sky portions of photos are distinguished in digital image analysis. The effectiveness of hemispheric photography is greatly improved by the use of a consistent "thresholding rule". This issue should be addressed formally, and consistent decision rules should be adopted.

(2) Future studies in this forest type and at this scale cannot eliminate the effects of autocorrelation in canopy openness and understory light through the choice of fixed sampling interval. However, spacing photosites at every 30 m would eliminate the most important effects of positive spatial autocorrelation, allowing classical statistics to be used on the data. Conversely, if the goal of sampling is to capture spatial pattern effectively, a systematic cluster sampling design is recommended.

(3) Future research should include a comparable study in old-growth stands similar to those examined in this study, but in an intermediate successional stage. For example, a study could be conducted in stands in the later stages of horizontal diversification that are dominated by large canopy gaps, but still contain many living individuals of the pioneer cohort (in this case Sitka spruce). Such research would help us better understand the relationship between understory light and vegetation over successional time.

(4) Future research should consider structural patterns at the stand scale in the form of gradients parallel to large streams as well as perpendicular to them.

(5) Further research is needed to understand how changes in light environment over the course of the growing season affect understory plant communities in vine maple gaps.

4.5.2 Implications for ecosystem-based management

(1) Understory light conditions can show complex and diverse patterns at a small scale (100 m).

(a) Management schemes that seek to replicate old growth conditions must consider scales of variability considerably smaller than the typical scale of forest management in British Columbia;

(b) Such management schemes should consider structural patterns in the form of gradients parallel to large streams as well as perpendicular to them.

(2) Partial cutting or thinning treatments that seek to replicate or restore old-growth structure in similar riparian forests:

(a) would fall within the range of natural variability if they maintained canopy openness values over a wide range, from very dark (near 0% openness) to light (near 20% openness), but with a mean at lower canopy openness levels (3%);

(b) should recognize that a variety of environmental factors affect understory plant diversity, and that establishing understory light conditions within this range of natural variability (RNV) does not guarantee that understory vegetation will also fall within the RNV of unmanaged old growth forests;

(c) should protect existing stream courses, because in riparian forests, soil drainage and the location of streams can be important determinants of understory composition and production, and are therefore important for maintaining full understory biodiversity.

(3) Contrary to the usual definitions of old growth, old growth coastal temperate rainforest floodplain stands that have moved into the pioneer cohort loss stage may have uniform and high canopy closure. Landscape level assessments of old growth need to account for this possibility.

(4) Vine maple alters the light environment over the course of the growing season, adding temporal heterogeneity to forest light environments, and vine-maple dominated gaps may have very different understory light conditions and understory plant communities than adjacent forests. Managers seeking to maintain the full range of habitat and understory vegetation species diversity found in old-growth forests should allow or encourage the establishment of vine-maple dominated gaps as well as the establishment of other hardwoods.

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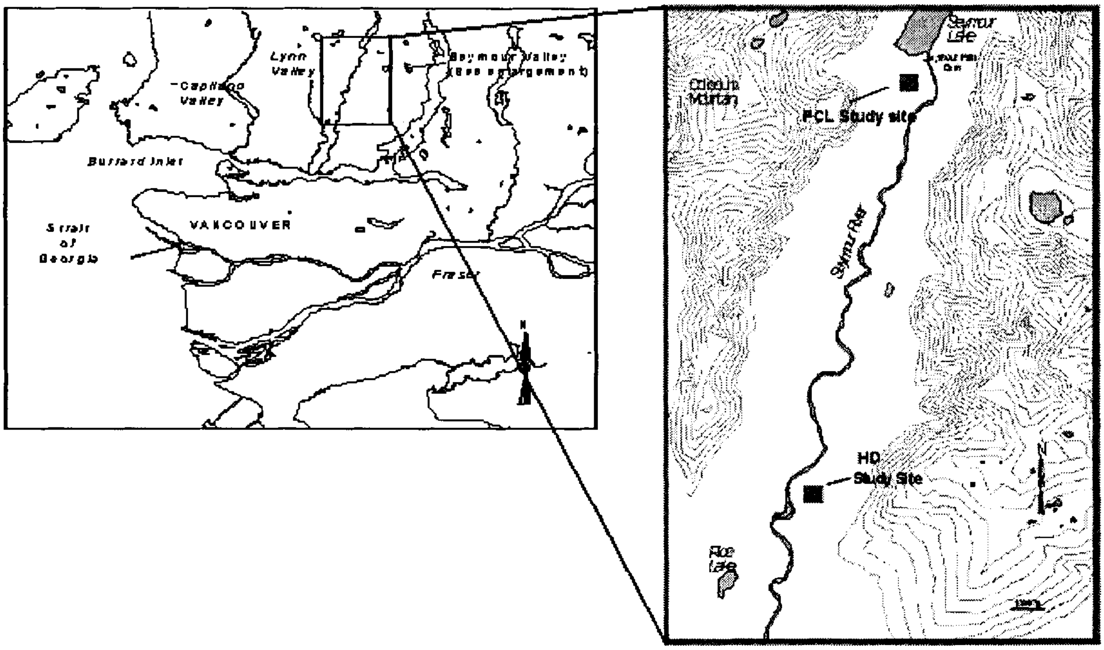
Figure 1: Study site location and sampling design

(a) Study site location. The steep walls of the Seymour valley limited direct sunlight in the early morning and late evening. Source: modified, with permission, from Denholme et al. 2001, Figure 1.1.



b) Generalized study site design. Each study site contained a one hectare study plot, within which I established two perpendicular crossing transects, at least 50 m in perpendicular distance from the river. Transects numbered 1 were parallel to the Seymour River, while transects numbered 2 were perpendicular to the river. In both study stands, if either a live or dead stem prevented photography or the presence of a stream precluded vegetation sampling, photosites were offset perpendicular from the transects at the smallest distance possible.

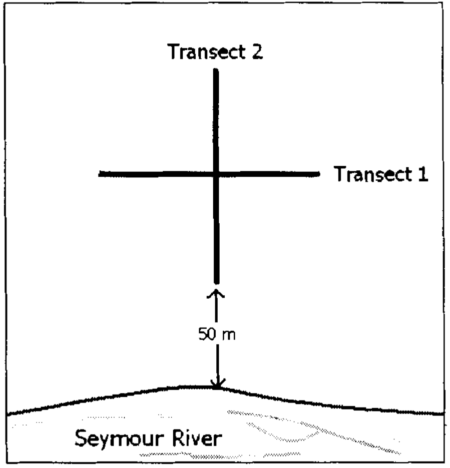


Figure 2: Percent canopy openness and percent total PAR transmitted by transect

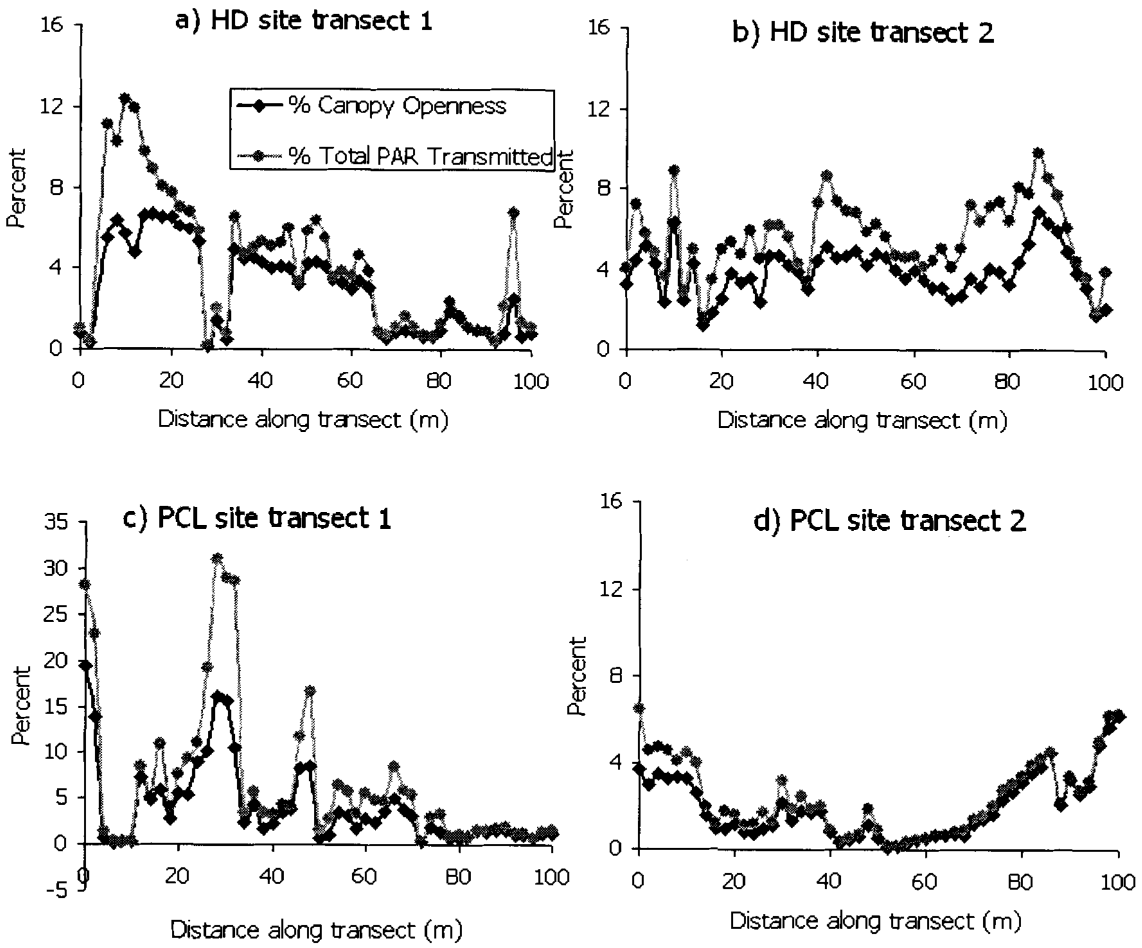
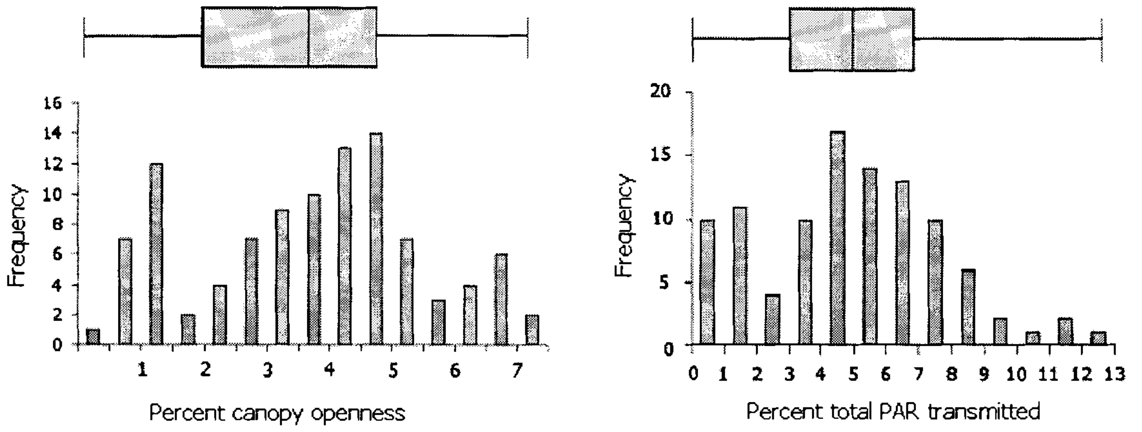
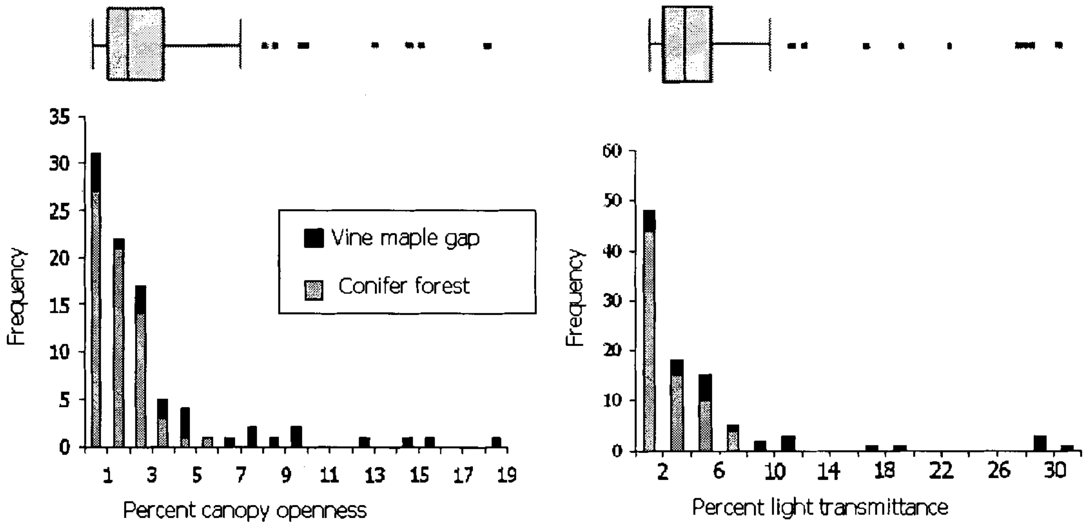


Figure 3: Percent canopy openness and percent total PAR transmitted: frequency distributions by site



a) HD site percent canopy openness

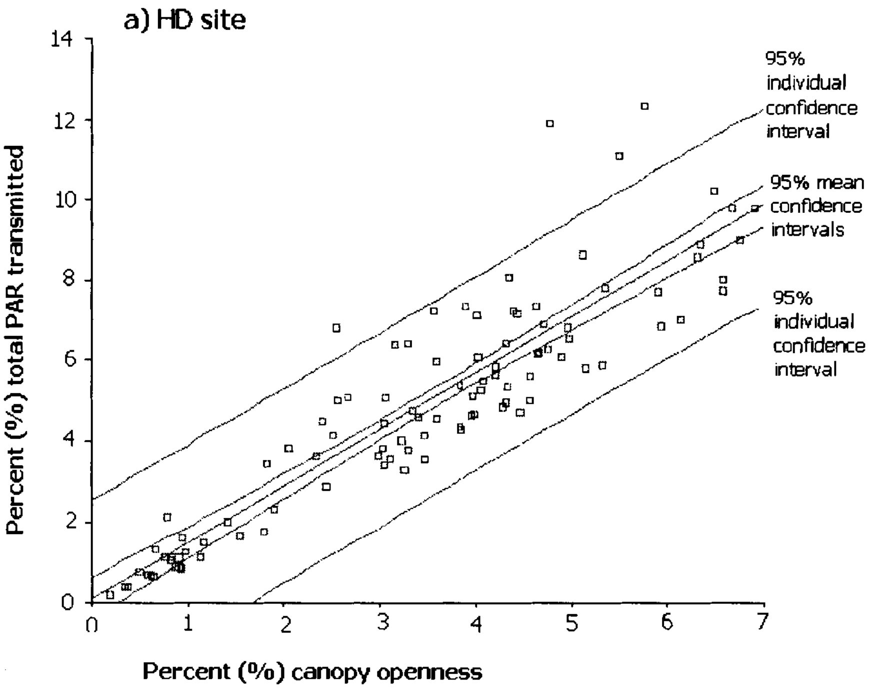
b) HD site Percent total PAR transmitted



c) PCL site percent canopy openness

d) PCL site percent total PAR transmitted

Figure 4: Percent canopy openness versus percent total PAR transmitted. $R^2=0.82$ for the HD site and 0.92 for the PCL site.



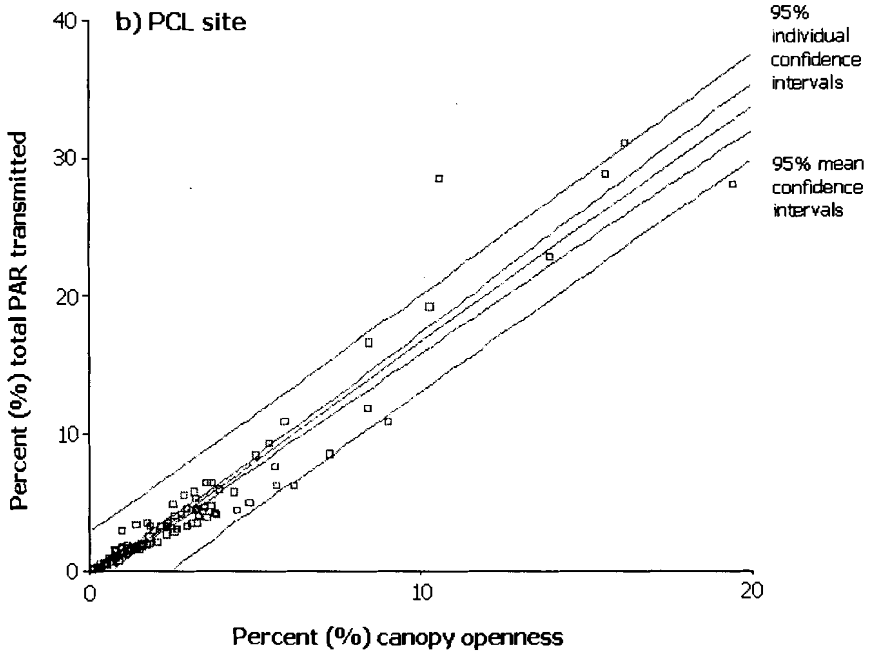
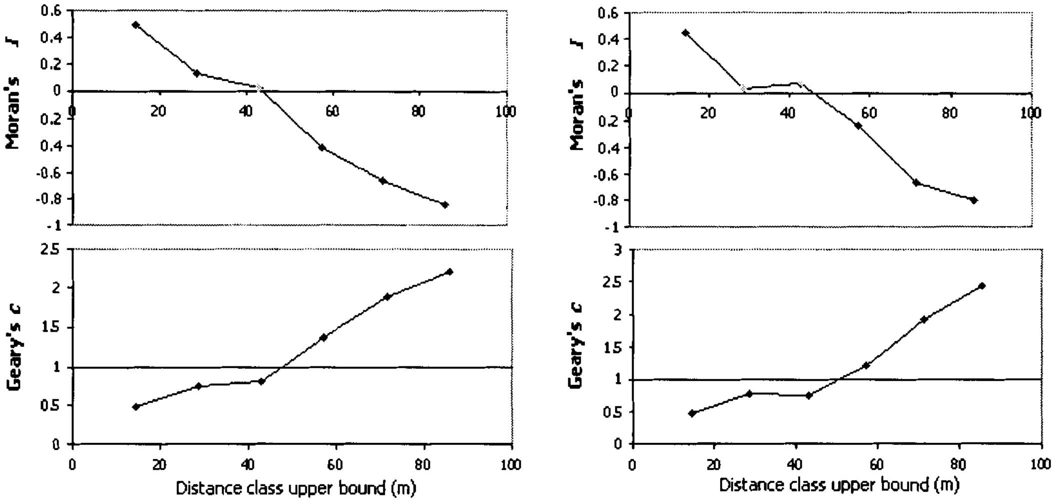
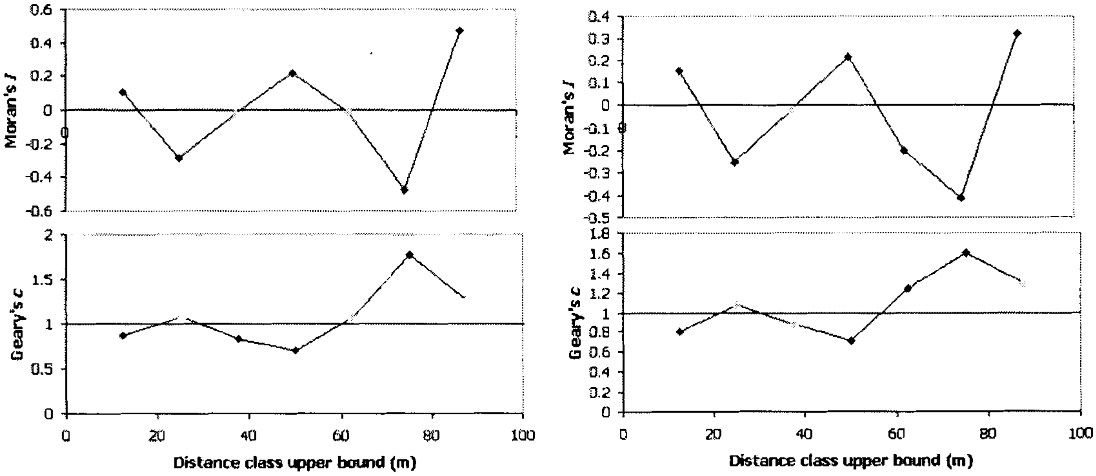


Figure 5: Correlograms. All correlograms are globally significant except for i) the Geary's *c* correlogram for PCL1 vine maple gap. Dark circles indicate significant autocorrelation coefficients (p≤0.05), while light circles indicate non-significant autocorrelation coefficients.



a) HD1 percent canopy openness

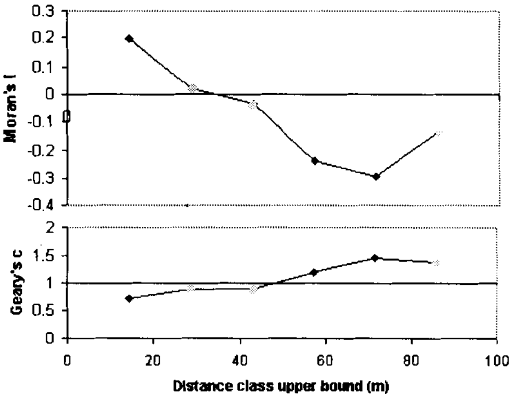
b) HD1 percent PAR transmitted



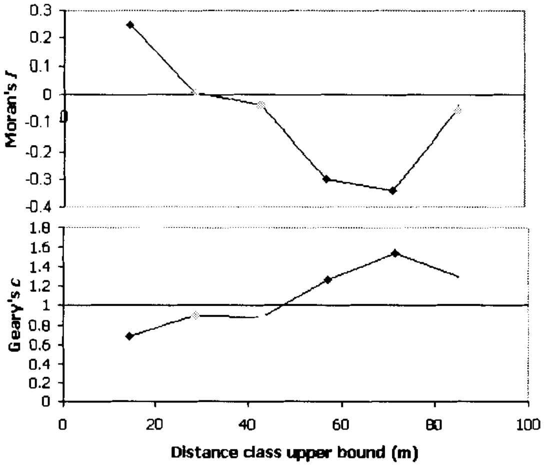
c) HD2 percent canopy openness

d) HD2 percent PAR transmitted

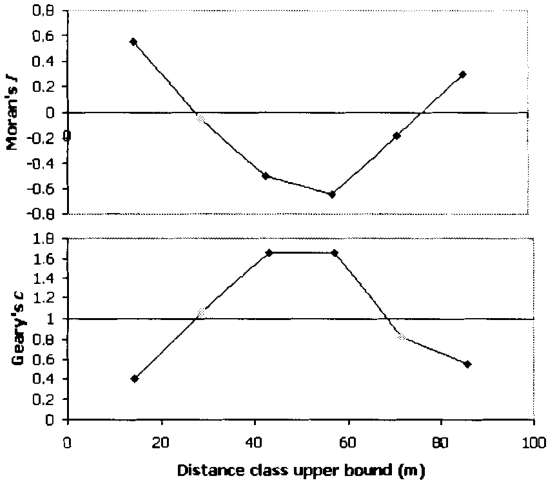
e) PCL1 ln percent canopy openness



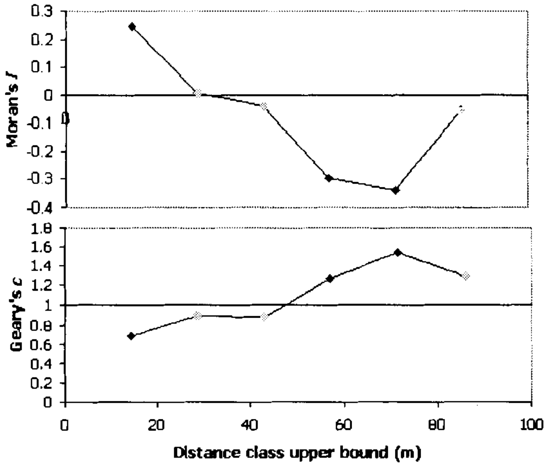
f) PCL1 ln percent PAR transmitted



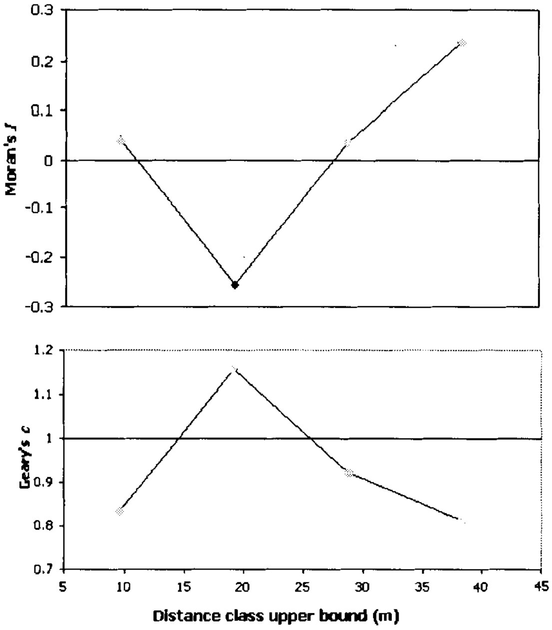
g) PCL2 ln percent canopy openness



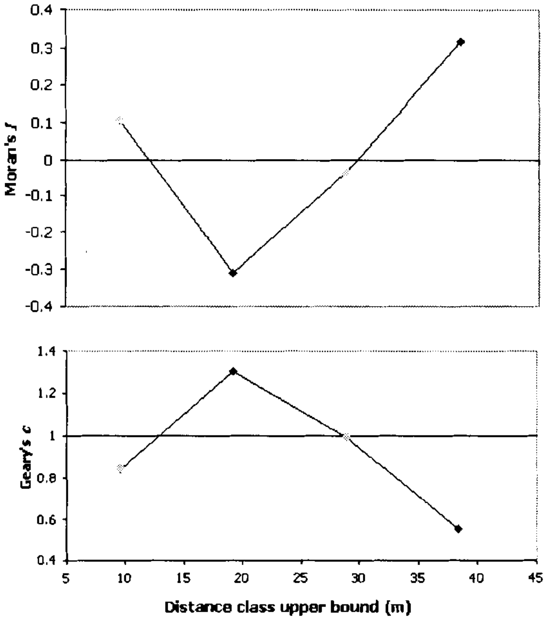
h) PCL2 ln percent PAR transmitted



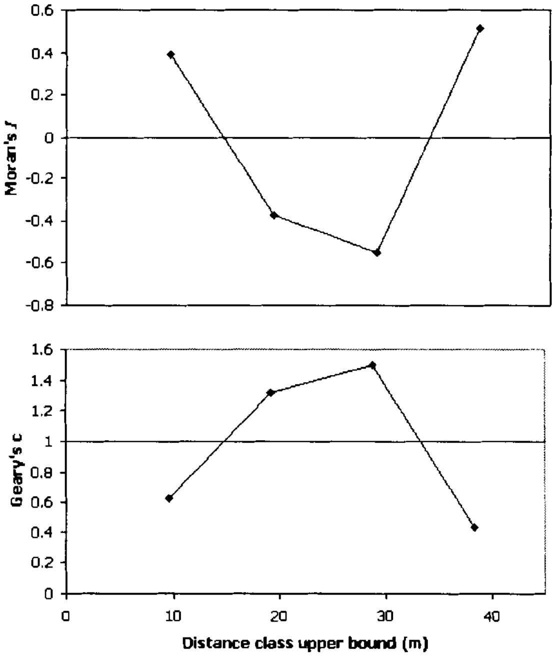
i) PCL1 vine maple gap percent canopy openness



j) PCL1 vine maple gap percent PAR transmitted



k) PCL1 vine maple gap percent canopy openness: without leaves



l) PCL1 vine maple gap percent PAR transmitted: without leaves

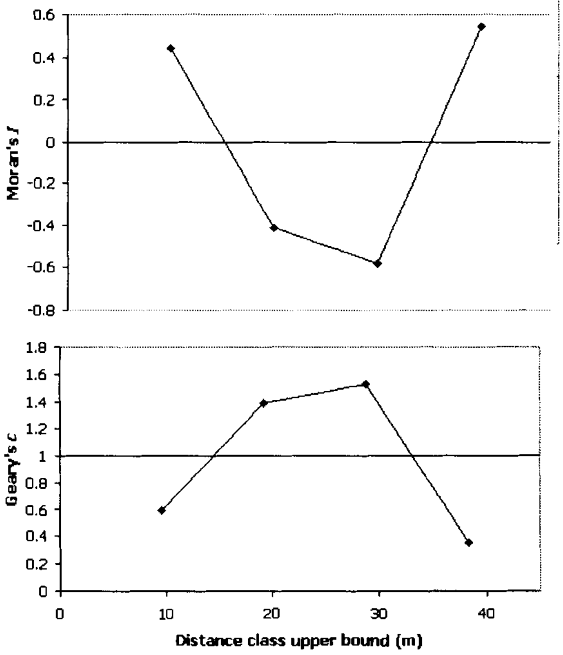
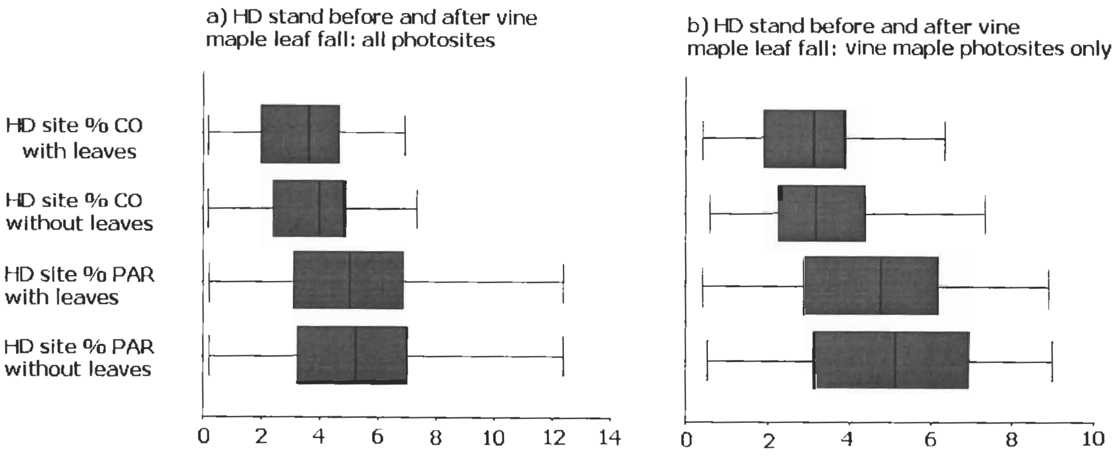


Figure 6: Effects of vine maple: boxplots


a) HD stand before and after vine maple leaf fall: all photosites

b) HD stand before and after vine maple leaf fall: vine maple photosites only

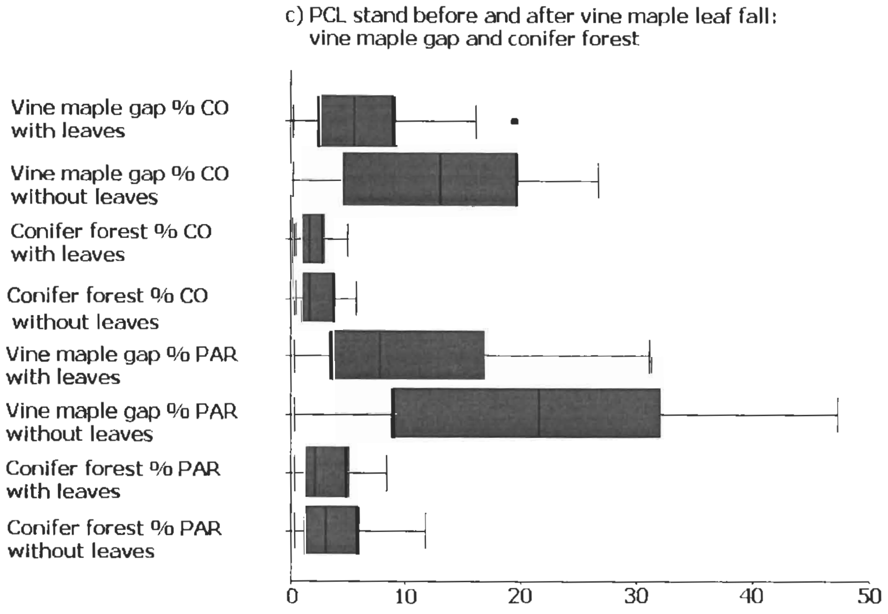
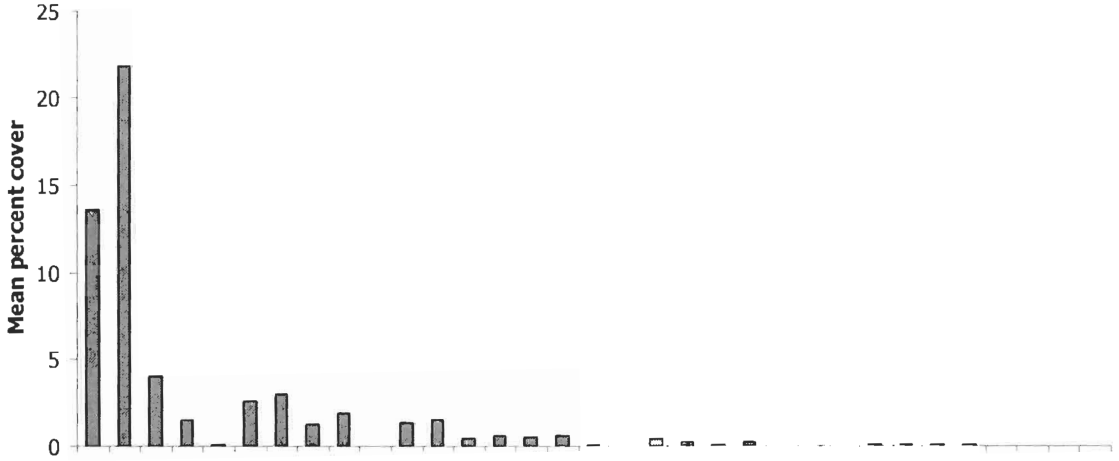

c) PCL stand before and after vine maple leaf fall: vine maple gap and conifer forest

Figure 7: Understory vegetation: mean percent cover by species in each study site.

a) HD site



b) PCL site

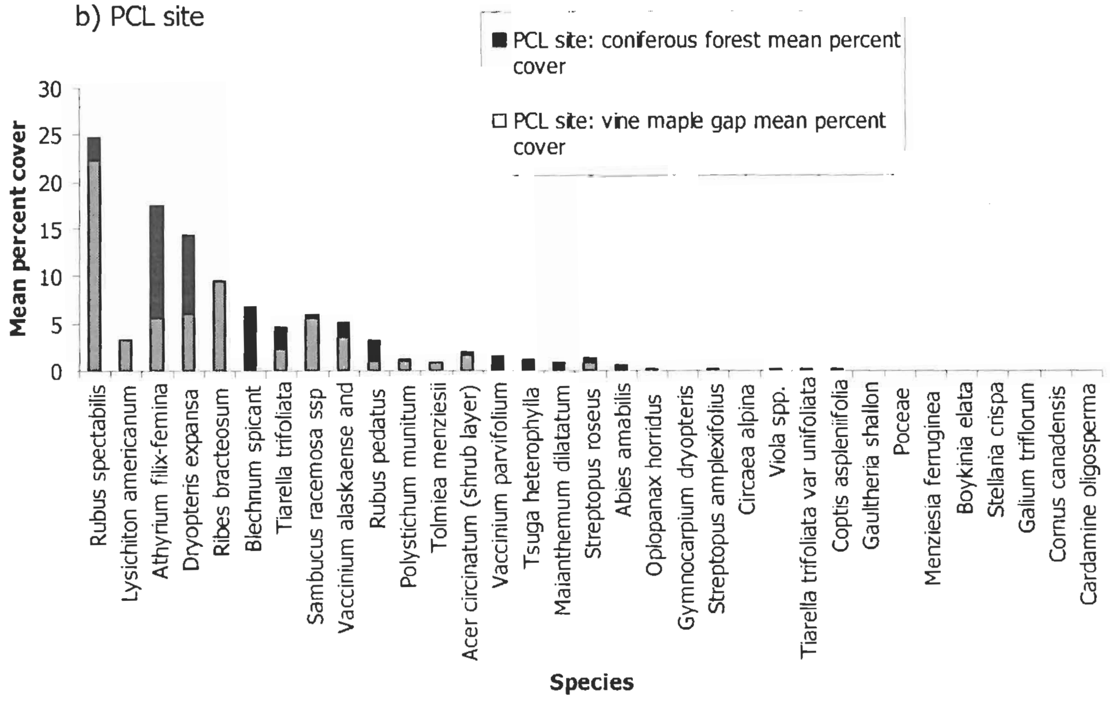


Figure 8: Detrended Correspondance Analysis (DCA). Each point on the graph represents the species composition of a sample site (sample score); species scores are not shown. DCA axes are measured in standard deviation units. The vine maple gap sample sites group separately from the values from the rest of the PCL site, which are also different from the values for HD site samples.

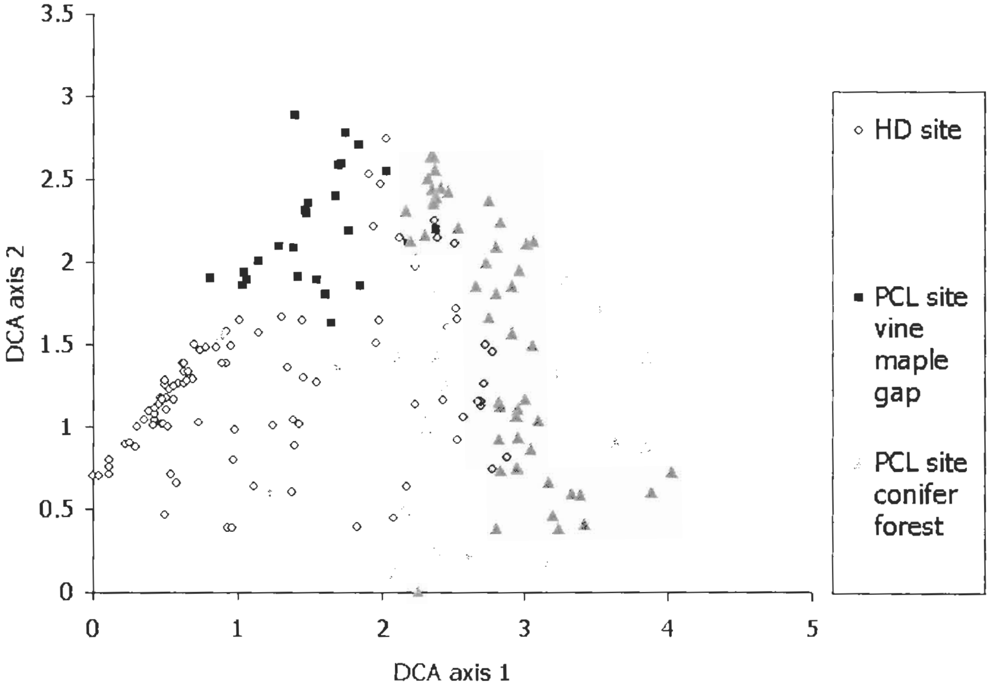


Figure 9: Variance partitioning. Analysis was based on canonical correspondance analysis of the species composition datasets for each stand.

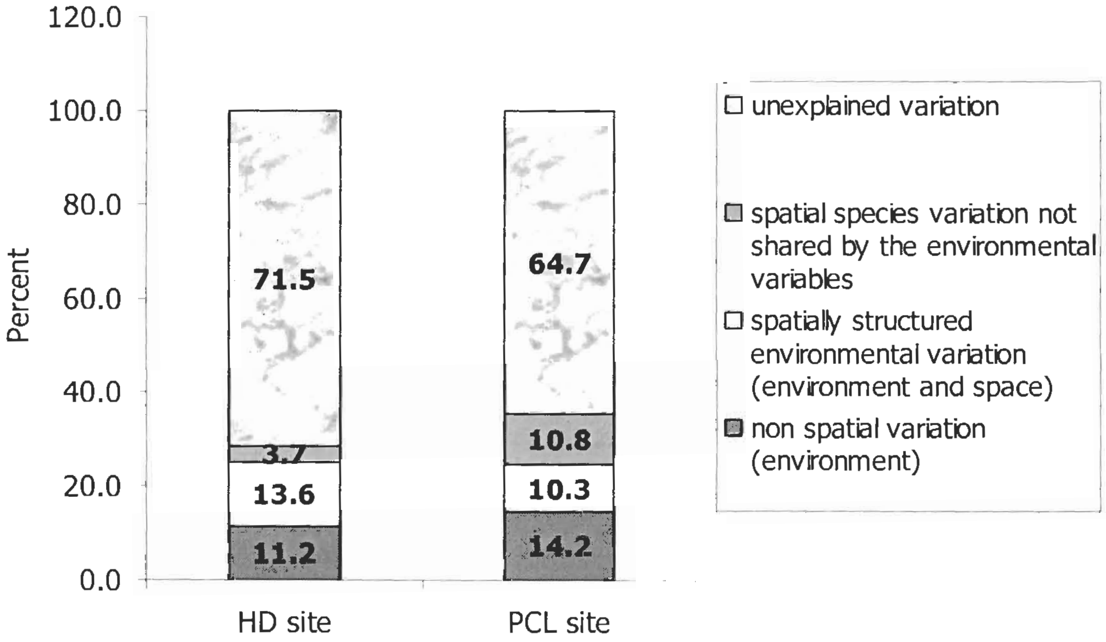


Table 1: Percent canopy openness and percent total PAR transmitted: statistics by transect

Transect		**HD1**	**HD2**	**PCL1**	**PCL2**
N		50	51	51	51
Percent canopy openness	mean	3	3.9	4.1	1.9
	median	3.1	3.9	2.5	1.5
	range	0.2-6.8	1.2-6.9	0.2-19.4	0.1-6.2
	standard deviation	2.2	1.2	4.5	1.5
	Kolmogorov-Smirnov normality test probability	*0.012	0.200	*0.0005	*0.004
Percent total PAR transmitted	mean	4.2	5.6	6.8	2.4
	median	3.7	5.6	4.1	1.9
	range	0.2-12.4	1.5-9.8	0.3-31.1	0.1-6.5
	standard deviation	3.4	1.8	8.1	1.7
	Kolmogorov-Smirnov normality test probability	0.058	0.200	*0.0005	*0.004

* indicates significant deviation from a normal distribution

Table 2: Percent canopy openness and percent total PAR transmitted: descriptive statistics by stand before and after vine maple leaf fall

	Mean	**Median**	**Standard Deviation**	**N**
HD site				
% CO with leaves all sites	3.4	3.6	1.8	100
% CO without leaves all sites	3.6	4.0	1.9	100
% PAR with leaves all sites	4.9	5.0	2.8	100
% PAR without leaves all sites	5.1	5.2	2.8	100
% CO with leaves vine maple sites	3.0	3.1	1.4	34
% CO without leaves vine maple sites	3.5	3.2	1.8	34
% PAR with leaves vine maple sites	4.5	4.8	2.2	34
% PAR without leaves vine maple sites	5.0	5.1	2.4	34
PCL site				
Vine maple gap % CO with leaves	6.5	5.4	5.3	25
Vine maple gap % CO without leaves	13.2	12.8	8.8	25
Conifer forest % CO with leaves	1.9	1.5	1.2	77
Conifer forest % CO without leaves	2.4	1.5	1.8	77
Vine maple gap % PAR with leaves	10.8	7.6	10.0	25
Vine maple gap % PAR without leaves	21.5	21.3	14.1	25
Conifer forest % PAR with leaves	3.0	2.0	2.2	77
Conifer forest % PAR without leaves	4.0	2.9	3.6	77

Table 3: Effects of vine maple: Mantel tests. The "Geography" matrices represent spatial distances. They were created with the spatial x-y coordinates.

Comparison	Mantel correlation (r)	Probability (p)
A. % PAR inside and outside vine maple gap before leaf fall		
Geography	0.2121	0.00100 *
Gap (0 or 1)	0.4184	0.00050 *
Geography/Gap	-0.0202	0.76100
Gap/Geography	0.3696	0.00050 *
B. % PAR inside and outside vine maple gap after leaf fall		
Geography	0.2988	0.00050 *
Gap (0 or 1)	0.6307	0.00050 *
Geography/Gap	-0.0676	0.23250
Gap/Geography	0.5846	0.00050 *
C. % PAR in vine maple gap before and after leaf fall		
Geography	-0.0304	0.75750
Before or after (0 or 1)	0.1249	0.00350 *
Geography/before or after	-0.0269	0.51050
Before or after/geography	0.1241	0.00300 *
D. % PAR at mature stand vine maple photosites before and after leaf fall		
Geography	0.1573	0.00050 *
Before or after (0 or 1)	-0.0050	0.53150
Geography/before or after	0.1572	0.00050 *
Before or after/geography	-0.0020	0.87350

* Mantel test is significant. Reported probabilities are two-tailed, based on 2000 Monte Carlo permutations.

Table 4: Forward selection. Marginal effects show individual environmental variables in order of the variance they explain singly. Conditional effects show the environmental variables in the order of their inclusion in the model, and the variance each variable explains once it is included. I used automatic forward selection with canonical correspondance analysis of the species composition datasets for each stand, with rare species downweighted.

Environmental variable	Canonical eigenvalue	Percent total variation explained
Marginal effects		
A. HD site		
Distance to streams	0.34	16.1
y (distance perpendicular to river mainstem)	0.23	10.9
Distance to standing water	0.15	7.1
Percent total PAR transmitted	0.14	6.6
x (distance parallel to river mainstem)	0.13	6.1
Vine maple above shrub layer	0.03	1.4
B. PCL site		
x (distance parallel to river mainstem)	0.48	12.8
Vine maple above shrub layer	0.31	8.3
Distance to standing water	0.31	8.3
Percent total PAR transmitted	0.31	8.3
y (distance perpendicular to river mainstem)	0.31	7.2
Distance to streams	0.27	7.2
Conditional effects		
C. HD site		
Distance to streams	0.34	16.1
Distance to standing water	0.10	4.7
Percent total PAR transmitted	0.07	3.3
x (distance parallel to river mainstem)	0.04	1.9
y (distance perpendicular to river mainstem)	0.03	1.4
Vine maple above shrub layer	0.02	0.9
D. PCL site		
x (distance parallel to river mainstem)	0.48	12.8
y (distance perpendicular to river mainstem)	0.31	8.3
Distance to standing water	0.20	5.4

Environmental variable	Canonical eigenvalue	Percent total variation explained
Vine maple above shrub layer	0.15	4.0
Distance to streams	0.12	3.2
Percent total PAR transmitted	0.06	1.6

Table 5: Comparison of canopy openness and light transmission measures values from other studies

Author	Year	Forest type (by dominant species)	stand age	method	% Canopy Openness	% total PAR transmitted
Hardwood forests						
This study	2003	vine maple - foliage on (PCL study site -- vine maple gap)	unknown (old)	hemispherical photos	6.5±5.3 *{0.2-19.4}*	10.8±10 *{0.3-31.1}*
McGhee	1996	vine maple - foliage on	60-80 years	hemispherical photos	(22.9-31.3)± (13.4-18.4)	N/A
Canham et al.	1990	hardwood- beech and sugar maple	old-growth	hemispherical photos	N/A	13 *{0.3-3.8}*
Coniferous forests						
This study	2003	western hemlock - Sitka spruce-western redcedar (HD study site)	> 200 years (old-growth)	hemispherical photos	3.4±1.8 *{0.2-6.9}*	4.9±2.8 *{0.2-12.4}*
This study	2003	western hemlock - amabilis fir - Sitka spruce (PCL study site -- coniferous portion)	> 300 years (old-growth)	hemispherical photos	1.9±1.2 *{0.1-6.2}*	3±2.2 *{0.1-8.5}*
This study	2003	western hemlock - amabilis fir - vine maple - Sitka spruce (PCL study site—entire site)	> 300 years (old-growth)	hemispherical photos	3±3.5 *{0.1-19.4}*	4.6±6.3 *{0.1-31.1}*
Hanley and Brady	1997	western hemlock - Sitka spruce	old-growth	spherical densiometer	(9.6-22.5)± (1.0-1.3)	N/A
Frazer et al.	1997	western hemlock	32-43 years (immature)	hemispherical photos	(2-5.4)±(0.6-1.7) *{1.3-7.9}*	N/A
Frazer et al.	1997	western hemlock	66-76 years (mature)	hemispherical photos	(2.6-6.3) ± (0.8-1.5) *{1.6-8.2}*	N/A
Frazer et al.	1997	western hemlock	176-435 years (old-growth)	hemispherical photos	(5.9-11.5) ± (1.9-3.6) *{3.5-16.0}*	N/A

Author	**Year**	**Forest type (by dominant species)**	**stand age**	**method**	**% Canopy Openness**	**% total PAR transmitted**
McGhee	1996	western hemlock - Douglas-fir - western redcedar	60-80 years old	hemispherical photos	35±8.4	N/A
Canham et al.	1990	Douglas-fir - western hemlock	old-growth	hemispherical photos	N/A	0.6* *{0.1-1.7}*
Parker	1997	Douglas fir - western hemlock	400-500 years (old-growth)	Li-Cor quantum sensor	N/A	5±15 *{0-60}*** ^
Parker et al.	2001	Douglas fir - western hemlock	400-500 years (old-growth)	Li-Cor quantum sensor	N/A	10±22.5**
Parker et al.	2001	Douglas fir - western hemlock	250 years (old- growth)	Li-Cor quantum sensor	N/A	(1-2)±(1-2)**
Weiss	2000	Douglas-fir - western hemlock	500 years (old-growth)	hemispherical photos	5-9**||	N/A
Frazer et al.	1997	Douglas-fir	32-43 years (immature)	hemispherical photos	(4.1-9.6) ± (1.7-4.3) *{1.3-18.1}*	N/A
Frazer et al.	1997	Douglas-fir	66-99 years (mature)	hemispherical photos	(7.8-10.9) ± (1.9-6.7) *{2.2-22.4}*	N/A
Frazer et al.	1997	Douglas-fir	245-330 years (old-growth)	hemispherical photos	(5.2-13.3) ± (1.9-3.7) *{2.8-16.1}*	N/A
Stewart	1986	Douglas fir	400-500 years (old-growth)	hemispherical photos	N/A	(42-53)

Percent Canopy Openness and Percent Photosynthetically Active Radiation are shown as mean±standard deviation *{range}*. If a range of means and/or standard deviations was reported it is enclosed in (parentheses).

* values are for closed canopy sites only

** values are estimated from figures

^ values at 2 m above the ground

|| range reflects uncorrected and corrected values