GROWTH RESPONSES OF DOUGLAS-FIR AND WESTERN HEMLOCK AROUND VINE MAPLE PRIORITY GAPS IN SOUTHWESTERN BRITISH COLUMBIA

by

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ABSTRACT

Vine maple is a shade-tolerant, multi-stemmed, deciduous tree of the understory of conifer forests in the Pacific Northwest. Vine maple is distinct in its ability to establish 'priority' gaps -- gaps that establish at the time of stand initiation and persist through several stages of forest development. Priority gaps represent distinct microenvironments within the forest ecosystem and provide a diversity of resources to flora and fauna.

On 20 paired plots, I examined the gap size, morphology of conifers, site chronologies and site productivity in 75 year old, Douglas-fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) stands. For both species, trees on the edge of gaps had significantly larger crowns (182% for Douglas-fir and 132% for western hemlock) and boles (46% and 69%) than trees in the closed canopy. I found no differences in the patterns of radial growth between the sites for Douglas-fir or western hemlock sapling growth (~ 1 - 13 years breast-height age). For Douglas-fir on the edge of gaps, significantly higher annual basal area increments did occur in the years after 1945 due to the higher radial growth rates compared to Douglas-fir in the closed canopy. Western hemlock on the edge of gaps had consistently higher BAIs than hemlock in the closed canopy for 1945-1995, but the initial difference between the sites may have been due to the differing sizes of seedlings and saplings that occupied each site immediately after logging. Site index was significantly higher for Douglas-fir adjacent to the gap (42.6 m) than for Douglas-fir in the closed canopy (40.2 m), indicating vine maple may play an important role in the long-term productivity of these stands.

Median priority gap size was 79.9 m^2 in Douglas-fir stands and 197.1 m^2 in western hemlock stands. On Douglas-fir priority gap sites, potential growing space was 61% greater than that of closed canopy trees, but current BA productivity and site BA did not significantly differ from the adjacent canopy sites. The current BA productivity for western hemlock around the gap was only 62% that of western hemlock in the adjacent canopy, as western hemlock around the gap occupy 150% the potential growing space of western hemlock in the closed canopy.

Priority gaps offer an excellent opportunity for B.C. silviculturalists to meet biological and structural diversity goals by incorporating distinct microhabitats into management prescriptions. Integrating priority gaps into the stand mosaic was not associated with significant losses to timber production in the Douglas-fir stand, but was associated with losses in timber production in the western hemlock stand.

DEDICATION

To the Love of my life - *my wife, Kim Wardman*
Can I ever return the immeasurable love and support
you have always given me?
Your confidence in my ability and gentle reminders
to stay focussed have been both
the rock that has anchored me and the wings that have helped me soar.
You are my inspiration.
I respect and admire you more than any words could say.
Thank-you,... just for being you.

QUOTATIONS

"As we approach the 21st century, the question of how to integrate the conservation of biological diversity with social and economic goals is one of the most important human challenges of our time." (Pederson 1996)
Larry Pederson -- B.C. Chief Forester

"Over the long haul of life on this planet, it is the ecologists, and not the bookkeepers of business, who are the ultimate accountants." (Hammond 1991)
Stewart L. Udall -- U.S. Congressman

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My Family: As you all have always been so supportive of me, I cannot deny you this chance to be famous. My mom, (Marlene) and Maurice, thank-you for your love, talks, sharing, and kindness over the years. To my father, Clark, who instilled in me a good work ethic and a love and appreciation for life, thank-you. And the two best brothers a guy could have, Cory and Todd, thanks for all the years of memories and good times. Also, thank-you Julia for your never-ending support and the ability to always understand what being a student is like; and Grandma (& Grandpa) Olson, for your kindness and caring since the day I met you.

TABLE OF CONTENTS

List of Tables

List of Figures

Chapter 1

INTRODUCTION

The Biodiversity Guidebook of the British Columbia Forest Practices Code (B.C. Ministry of Forests and B.C. Environment 1995a) requires foresters to incorporate clear commitments in management prescriptions to conserve biological diversity (biodiversity) while meeting the needs of an economically viable forest industry. Biodiversity can be defined as:

> The diversity of plants, animals, and other living organisms in all their forms and levels of organization, and includes the diversity of genes, species and ecosystems, as well as the evolutionary and functional processes that link them. (B.C. Ministry of Forests and B.C. Environment 1995a)

Protecting habitat diversity is often the best strategy for protecting biodiversity (B.C. Ministry of Forests and B.C. Environment 1995a; Lertzman et al. 1997). Commitments to maintaining biodiversity require that foresters manage for stand structural attributes, understory vegetation diversity and any hardwood populations that naturally occur in stands (B.C. Ministry of Forests and B.C. Environment 1995a; Tappeiner et al. 1997). As "timber management, ... when carried out without respect to whole functioning forests, presents the largest threat to the protection of biological diversity at the stand level" (Hammond 1991), forester managers need to explore ways to retain the current levels of timber production, without incurring costs to the biodiversity of forest ecosystems (Puttonen and Murphy 1996).

Hardwoods are often viewed largely as competitors to merchantable conifer species and many research efforts have focussed on ways to suppress them, particularly during early stages of stand development (Kufeld 1983; Wenger 1984; Anonymous 1988; Haeussler et al. 1990, Biring et al. 1996). However, the interest in managing for biodiversity on regenerating sites has attracted the attention of researchers to the potential benefits of maintaining hardwoods in conifer forests (Lefevre and Klemmedson 1980; Vitousek and Denslow 1986; Boettcher and Kalisz 1990; Biondi et al. 1992; Peuttmann et al. 1992; Enns et al. 1993; Ogden 1996). My research focusses on the dynamic relationship between a hardwood species, vine maple (Acer circinatum), and conifers situated on the periphery of gaps within which vine maple is growing. I am motivated by the potential for this relationship to meet both biodiversity and productivity objectives in Douglas-fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) stands in southwestern British Columbia.

1.1 Gaps in Coastal Forests

Forest management practices, such as clearcutting, often homogenize a forest stand (Urban et al. 1987; Kohm and Franklin 1997) by reducing the structural and biological heterogeneity that results from gap dynamics (Brokaw 1985; Spies and Franklin 1989; Oliver and Larson 1990; Lertzman and Krebs 1991; Lertzman 1992). In the west coast temperate rainforests, the return interval for severe fires is relatively long (Stewart 1986; Spies et al. 1990), often more than 300 years, and some ecosystems are rarely affected by fire (Agee 1993). Gap dynamics and the multi-aged stands that develop from patchy disturbances play a key role in the maintenance and development of forest structure and composition in these ecosystems (Connell 1989; Spies and Franklin 1989; Spies et al. 1990; Lertzman and Krebs 1991; Lertzman 1992; Lertzman et al. 1996; Lertzman et al. 1997). For instance, in mature and old-growth stands in Clayoquot Sound, on the west coast of Vancouver Island, approximately 56% of the forest area is directly influenced by some type of expanded gap (Lertzman et al. 1996). In a sub-alpine old-growth forest in the Mountain Hemlock Zone of southwestern B.C., Lertzman and Krebs (1991) found that 52% of the forest area is under expanded canopy gap. Spies et al. (1990) also noted similar levels of gap disturbance in the mature Douglas-fir forests of the Cascade Mountains, where 41.7% of the forest area is under expanded canopy gap.

'Gaps' in this thesis are broadly defined as not only gaps in the canopy formed by the mortality of trees, as Runkle (1985) suggests, but as any opening in the canopy occurring from tree mortality, edaphic characteristics, competitive advantage or other dynamic process.

1.1.1 Developmental Gaps

Developmental gaps are openings in the forest canopy associated with the mortality of one to many trees (Brokaw 1985; Runkle 1985; Spies et al. 1990; Lertzman and Krebs 1991). They are created by events such as windthrow, fire, disease, logging, or some other localized disturbance. It is generally assumed gaps will fill by a combination of lateral expansion of adjacent conifers towards the gap center (Frelich and Martin 1988; Spies and Franklin 1989), the release of understory saplings (Runkle 1982; Veblen 1986;

Brokaw and Scheiner 1989; Schaetzl et al. 1989; Lertzman 1992) and/or the establishment of seedlings within the gap (Connell 1989; Spies et al. 1990). Canopy gaps that function in this way are common in many forest ecosystems and have received considerable attention by researchers (Mladenoff 1987; Alaback and Herman 1988; Canham 1988; Lorimer 1989; Brokaw and Scheiner 1989; Canham et. al 1990; Spies et. al. 1990; Lertzman and Krebs 1991; Lertzman 1992; Kamaluddin and Grace 1993; Orwig and Abrams 1995; Lertzman et al. 1996). Preferential species replacement in developmental gaps is an important catalyst for successional change and has a strong influence on the trajectory of the species composition of the canopy (Brokaw and Scheiner 1989; Martinez-Ramos et al. 1989; Whitmore 1989; Lertzman 1992).

1.1.2 Edaphic Gaps

Gaps in the canopy which exist due to identifiable edaphic or topographic conditions are called edaphic gaps (Lertzman et al. 1996). The gap in the canopy exists largely because the underlying substrate is not conducive to the establishment of dominant tree species. In Clayoquot Sound, Lertzman et al. (1996) found that an average of 16% of the forest area was under edaphic canopy gaps. The majority of these gaps were associated with stream courses.

1.1.3 Persistent Gaps

Some forests contain gaps that are associated with no obvious gap-maker, have little or no regeneration within the gap and demonstrate little difference in edaphic characteristics compared to the adjacent forest (Ehrenfeld et al. 1995; Ogden 1996). These gaps appear to have persisted for long periods of time and, therefore, are referred to as persistent gaps. The ability of some of these gaps to persist may be due to the abundant shrub layer in the gap which appears to perpetuate the opening in the canopy (McGhee 1996) or intense, localized fires which consume the litter layer (Ehrenfeld et al. 1995).

Examples of persistent forest openings have been observed in the deciduous forests of the southern Appalachians (Barden 1989), in the New Jersey Pinelands (Ehrenfeld et al. 1995), and in the Douglas-fir--western hemlock stands of the Pacific Northwest (Spies et al. 1990; McGhee 1996; Ogden 1996).

1.1.3.1 Vine Maple Priority Gaps

Until recently, it was assumed that canopy gaps in mature and old-growth forests with vine maple growing in them were developmental gaps that had been invaded by vine maple (McGhee 1996). However, vine maple gaps can readily be found in the Douglas-fir and western hemlock forests of the Pacific Northwest where there is no obvious gap-maker (Spies et al. 1990; McGhee 1996), and which appear not to be edaphic in origin (Ogden 1996). McGhee (1996) argues that many vine maple gaps do not result from vine maple invading pre-existing gaps, but represent a persistent alternative 'state to surrounding conifers due to vine maple's ability to establish dense mats of foliage in early seral stages, which resist the invasion of conifers through several stages of stand development. McGhee (1996) has called this type of persistent gap, which establishes at stand initiation, a *priority* gap.

In a coastal hemlock forest on the north shore of Vancouver, McGhee (1996) found that only 6.3 % of forest ground area is associated with a developmental expanded gap, whereas 19.7 % is a result of vine maple priority gap establishment. McGhee (1996) emphasizes the role priority gaps play in adding structural heterogeneity in earlier seral stages where the role of developmental gaps is minimal.

1.2 Vine Maple

1.2.1 Vine Maple Ecology

Vine maple is a shade-tolerant, multi-stemmed, deciduous tree (Fig. 1.1) which is commonly found in the understory of conifer forests, from California to southwestern British Columbia (Haeussler et al. 1990; Pojar and MacKinnon 1994). Vine maple occurs most commonly in the understory of Douglas-fir stands (Anderson 1969; Haeussler et al. 1990) and less frequently in association with western hemlock (Haeussler et al. 1990).

Vine maple can be found during all stages of stand development (Anderson 1967; Russel 1973; Haeussler et al. 1990; O'Dea et al. 1995). Its ability to reproduce vigorously by basal sprouting enables vine maple to quickly regenerate after a disturbance, making it an abundant species during early seral stages (Anderson 1969; Russel 1973; Tappeiner and Zasada 1993; O'Dea et al. 1995). Russel (1973) found that vine maple abundance is high prior to canopy closure, but declines during the stem exclusion phase of stand development. Vine maple's ability to reproduce by layering allows it to exploit gaps which occur in the canopy during stem re-initiation (Anderson 1967; O'Dea et al. 1995). Vine maple often becomes a dominant understory shrub in mature and old growth stands that it occupies (Anderson 1969; Russel 1973; Spies et al. 1990; O'Dea et al. 1995).

Figure 1.1. A vine maple clone. This clone has likely maintained the opening in the above canopy since stand origin, creating a vine maple priority gap. The convex shape of clonal stems is a common growth form and aids in the propagation of vine maple by layering and basal sprouting (Anderson 1967; O'Dea et al. 1995). The presence of the cedar stump within the gap indicates these sites are not edaphic in origin and were previously occupied by conifers (McGhee 1996). Note the large size of the Douglas-fir boles on the edge of the gap.

1.2.2 Influence of Vine Maple Priority Gaps

1.2.2.1 Alteration of Climatological Variables within Gaps

Gaps in the canopy often result in the establishment of distinct microenvironments in the forest and provide "a vital part of the support system for forest diversity" (Hammond 1991). The lack of an overstory results in an increase in temperature (Cooks and Lyons 1983; Vitousek and Denslow 1986; Schaetzl et al. 1989; Boettcher and Kalisz 1990) and light (Canham 1988; Poulson and Platt 1989; Orwig and Abrams 1995) within most developmental gaps. However, Canham et al. (1990) found that developmental gaps in temperate rainforests that were formed by the mortality of a single tree offer little increase in insolation to the forest floor due to the high ratio of canopy height to gap diameter and lower sun angles at higher latitudes.

Priority gaps differ in form and function from developmental gaps, resulting in a different allocation of resources. Ogden (1996) found that spring and summer air temperatures are significantly lower under vine maple canopy gaps than in the adjacent closed canopy, likely due the cooling effect associated with vine maple's high rates of transpiration. McGhee (1996) reports light levels in priority gaps, measured 1.3 m above the forest floor, are not significantly different than under the closed canopy, though this is largely attributable to the shading effects of vine maple foliage (McGhee 1996).

Vine maple's high rates of transpiration can rapidly deplete soil moisture in the surface layers during the growing season (Haeussler et al. 1990). Ogden (1996) found that larger vine maple clones are associated with significantly lower soil moisture values in the rooting zone (30 cm).

1.2.2.2 Gaps and Biological Diversity

Gaps provide an important ecological function by increasing resource diversity to flora and fauna (Schaetzl et al. 1989; Hammond 1991; Lertzman 1992). Vine maple provides food and cover for wildlife populations (Tappeiner and Zasada 1993). Vine maple is an important browse species for black-tailed deer and elk populations (Haeussler et al. 1990; Tappeiner and Zasada 1993). Lertzman et al. (*unpubl.*) note that the total number and diversity of bird species can be significantly higher within the vine maple gap environment than under the closed canopy, and attribute this to the greater diversity of resources associated with the vine maple gap.

1.2.2.3 Vine Maple Nutrient Cycling

Deciduous trees often increase the concentrations of nutrients in the soil on sites that they occupy (Krajina et al. 1982; Mladenoff 1987; Fried et al. 1990; Ogden 1996). In the mixed Ponderosa pine (Pinus ponderosa) -- Gambel oak (Quercus gambelii) stands in Arizona (Lefevre and Klemmedson 1980), levels of nitrogen increased and the carbon:nitrogen ratio dropped as the density of Gambel oak in the understory increased. In the Douglas-fir -- bigleaf maple (Acer macrophyllum) forests of coastal Oregon, Fried et al. (1990) determined that annual inputs and cycling of all macro-nutrients were significantly higher under bigleaf maple than under Douglas-fir, and suggest that hardwoods play an important role in the maintenance of long-term site productivity.

Vine maple provides a rich supply of bases to the forest floor (Russel 1973; Krajina et al. 1982; Ogden 1996). Ogden (1996) noted that the organic (LFH) layer under vine maple clones contains a higher concentration of calcium, magnesium and potassium than beneath the closed canopy. Ogden also found that the concentration of nitrogen at 20 cm depth in the soil profile increased as the number of vine maple clonal stems increased. Ogden indicates that improvements to the soil nutrient status under vine maple has important implications on long-term site fertility in west coast ecosystems. The cycling of nutrients within and around vine maple clones is currently being studied further by Tashe (*unpubl.*).

1.2.2.4 Suppression of Conifer Regeneration

Vine maple is regarded as a strong competitor to merchantable conifer species during the first ten years of stand development, particularly in Washington and Oregon (Haeussler et al. 1990). Vine maple's dense foliage inhibits light from penetrating to the forest floor (Haeussler et al. 1990; McGhee 1996), shading regenerating seedlings.

Inhibitory extracts found in the litter of vine maple indicates that vine maple may have allelopathic effects on conifer seedlings (Haeussler et al. 1990). The result of the vine maple's allelopathy and dense foliage is that seedlings can rarely establish directly beneath vine maple clones (Fig. 1.1). Seedlings that do establish in a priority gap almost exclusively colonize the edge of the gap (McGhee 1996).

1.2.2.5 Growing Space and Competition

The presence of large stumps in existing vine maple priority gaps indicates that these gaps occur somewhat randomly across the landscape (McGhee 1996). Ogden

(1996) supports this conclusion, noticing no significant differences between inherent soil or substrate characteristics under priority gaps when compared to closed canopy plots. This suggests that priority gaps occupy sites that could otherwise be utilized by conifers in the absence of vine maple, reducing the number of conifer stems in a stand.

Vine maple gaps create a much larger space among conifer stems than in the absence of vine maple (McGhee 1996). An increase in growing space results in decreased competition between conifers (Biondi et al. 1992; Tang et al. 1994). In pure conifer stands, crown competition for light is the driving force behind growth responses (Mitchell 1975; West et al. 1989) and increased light interception leads to greater foliage and greater basal area (BA) growth (Aplet et al. 1989; Oliver and Larson 1990; Law et al. 1992).

Following the creation of a developmental gap, an increase in annual ring width of more than 2.5 times for a period of at least four years is often seen in trees adjacent to the gap (Henry and Swan 1974; Spies and Franklin 1989). Growth releases of this magnitude are common ways of dating canopy gap formation (Schaetzl et al. 1989) and result from the surrounding vegetation's response to the reduction in resource utilization and the increased input of other resources. Growth responses associated with priority gaps have not been documented, but in one study, the mean breast-height diameter (DBH) of conifer stems (greater than 16 cm in diameter) adjacent to priority gaps (54.9 cm) was found to be larger than the mean DBH of closed canopy stems (42.6 cm) by 29% (McGhee 1996).

1.3 Objectives and Hypotheses

The recent discovery of priority gaps offers an excellent opportunity to quantify the impact that vine maple priority gaps have on the development and growth of conifers on the periphery of priority gaps compared to conifers in the adjacent forest matrix. In the previous literature review I outlined numerous relationships present within and around the priority gap environment. My research goal is to determine the influence of vine maple priority gaps on the morphology, basal growth, and the productivity of Douglas-fir and western hemlock within a temperate rainforest. To meet this goal, I have established five research objectives:

1. To determine if vine maple priority gaps influence the bole size, crown width and depth, or crown volume of trees on the gap periphery.
2. To determine if gap size influences the crown or bole size, basal growth, growing space, site BA or current BA productivity of Douglas-fir or western hemlock on the edges of priority gaps.
3. To determine if priority gaps influence the basal growth rates of trees on the gap periphery compared to those in the forest matrix.
4. To determine the influence of priority gaps on current BA productivity and site BA.
5. In the Douglas-fir stand, to determine if priority gaps sites are associated with a higher site index than closed canopy sites, and to determine the influence of the abundance of vine maple on site index.

A priori, I established two hypotheses about the expected responses of conifers to the priority gap. First, I hypothesized that in both stands vine maple priority gaps would be associated with greater spacing between conifer boles, resulting in:

- deeper and wider crowns
- larger basal size
- larger crown volumes
- faster rates of radial and basal growth

for conifers adjacent to gaps as compared to closed canopy conifers. I expected, *a priori*, that increases in basal growth rates for conifers next to gaps would largely compensate for the increase in growing space associated with the gap site. Second, I hypothesized that the rich supply of bases vine maple adds to the forest floor (Krajina et al. 1982; Ogden 1996) would be associated with an increase in site index around priority gap sites in the Douglas-fir stand. I also expected, *a priori*, that a greater abundance of vine maple would be associated with a higher site index.

1.4 Thesis Overview

In Chapter 1, I have introduced a distinct type of persistent gap in the canopy -- the vine maple priority gap -- and outlined some potential impacts priority gaps may have on a variety of characteristics of conifers and ecosystems. I established several hypotheses by which to examine these responses. In Chapter 2, I introduce my study sites and the methods employed in data collection and data analysis. Chapter 3 presents the major findings of the research. In Chapter 4, I discuss my results and relate them to the findings of other studies. In Chapter 5, I summarize my major findings, address the application of my research to forest management, and suggest ideas for future research.

Chapter 2

METHODOLOGY

2.1 Study Area

The study area consists of two adjacent stands, one dominated by Douglas-fir and the other by western hemlock. The stands are located on the upslope from the 2.5-3.0 km markers along the main road in the Seymour Demonstration Forest, North Vancouver, British Columbia (Fig. 2.1). The study stands are on the south-east, moderate slopes (Table 2.1) of the glacially-carved Seymour Valley (Lian and Hickin 1992). These submontane sites, which range in elevation from 227 m to 290m, are transitional between the Moist Maritime and Dry Maritime subzones of the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991). The mean annual precipitation averaged for the two subzones is approximately 2088 mm (Meidinger and Pojar 1991), of which less than 15% falls as snow (Watts 1983). The majority of precipitation occurs during the mild winter months (Oct. - Mar.) and a hot, dry period often occurs in late summer (Pojar and Klinka 1983). The dominant soils in the area have developed from glacial till parent materials and are moderately well to well-drained Orthic Ferro-Humic Podzols and Duric Ferro-Humic Podzols (Luttmerding 1980). The soil moisture regime grades from sub-xeric to sub-hygric.

Both study stands are 70-75 year old second-growth stands that have naturally regenerated after clearcut logging in the early 1920's. The vegetation in both stands is a

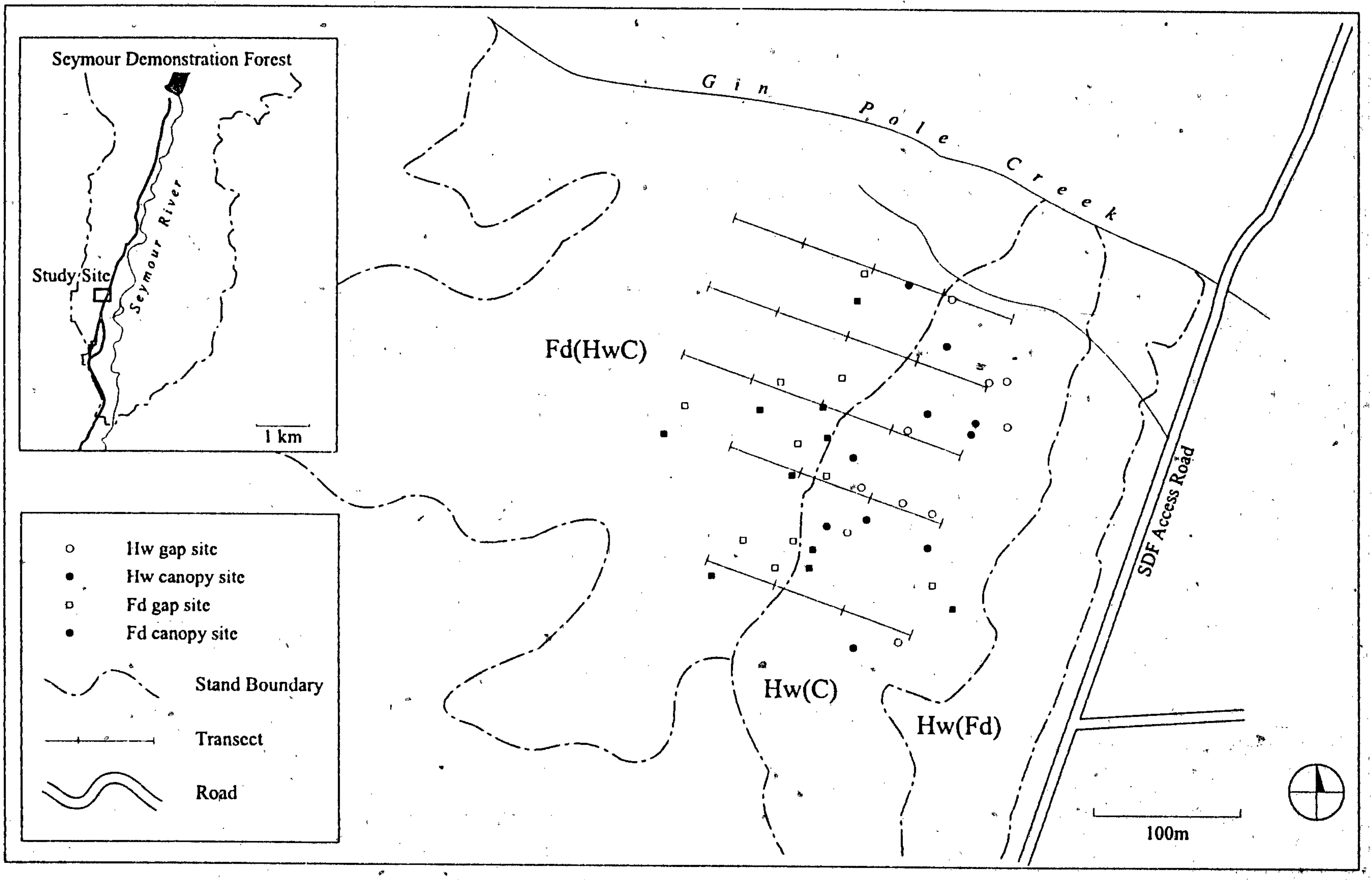


Figure 2.1. Location of the Douglas-fir (Fd) and western hemlock (Hw) stands in the Seymour Demonstration Forest (GVWD 1992). The Seymour Demonstration Forest is located on the North Shore of Vancouver, British Columbia. Priority gap sites were sighted from study transects and paired with an adjacent closed canopy plot. A cedar (C) component is present in both stands.

mosaic of relatively even-aged Douglas-fir, western hemlock and western redcedar (Thuja plicata) in the canopy, with the upslope stand containing a higher proportion of Douglas-fir, and the downslope stand a higher proportion of western hemlock. Red alder (Alnus rubra) occurs relatively infrequently throughout the stands and is generally restricted to riparian sites. The associated understory shrub and herb communities contain a good representation of vine maple, salal (Gaultheria shallon), and swordfern (Polystichum munitum), with skunk cabbage (Lysichiton americanum) occurring on some sub-hygric depressions.

Table 2.1. Site characteristics for gap and closed canopy sites. Means ± standard deviations for aggregated Douglas-fir and western hemlock sites are given. There are 10 paired gap and canopy sites for each species.

	Gap	Canopy
# of sites	20	20
Aspect	132° ± 13.3°	136° ± 13.3°
Elevation	254 m ± 15 m	255 m ± 16m
Slope	12° ± 6°	13° ± 6°
Minimum vine maple influence	41yrs ± 11 yrs	none

2.2 Sampling Design

A total of 232 increment cores were extracted from 116 trees (58 Douglas-fir and 58 western hemlock) located on 20 vine maple priority gap and 20 closed canopy sites

(Fig. 2.1). Ten paired sites were located in the Douglas-fir stand and 10 in the western hemlock stand. The morphology, chronologies and spacing of dominant Douglas-fir or western hemlock on each site were measured. The number of trees and sites sampled is comparable to Biondi et al. (1992), who, in determining the effect of Gambel oak (Quercus gambelii) density on the growth of Ponderosa pine (Pinus ponderosa) in central Arizona, found that 169 trees on 34 sites yielded appropriate statistical power. Ehrenfeld et al. (1995) sampled only 5 paired sites and was able to detect significant differences between the BA of trees within persistent gaps and those in the adjacent forest matrix.

I used existing transects (McGhee 1996), which ran upslope from east to west at 50 meter intervals within the study site, to locate vine maple priority gaps visible from transect lines (Fig. 2.1). A comprehensive sample of all appropriate sites in both stands was obtained.

Vine maple priority gap sites (Figs. 2.2a and 2.3) are gaps in the canopy that contained healthy vine maple which had a minimum temporal influence of 25 years, were associated with no obvious gap makers or apparent edaphic characteristics, and typically had at least three co-dominant conifers of the same species on the gap periphery. One Douglas-fir site and one western hemlock site had only two appropriate sample conifers adjacent to the gap but were chosen because they met the rest of the sample criteria. I did not mix species types when sampling (i.e. an individual paired gap and canopy site was sampled for Douglas-fir or western hemlock, but not both).

I paired each gap site with a canopy site (Spies et al. 1990; Ehrenfeld et al. 1995; Orwig and Abrams 1995; McGhee 1996). Canopy sites (Figs. 2.2b and 2.3) were located

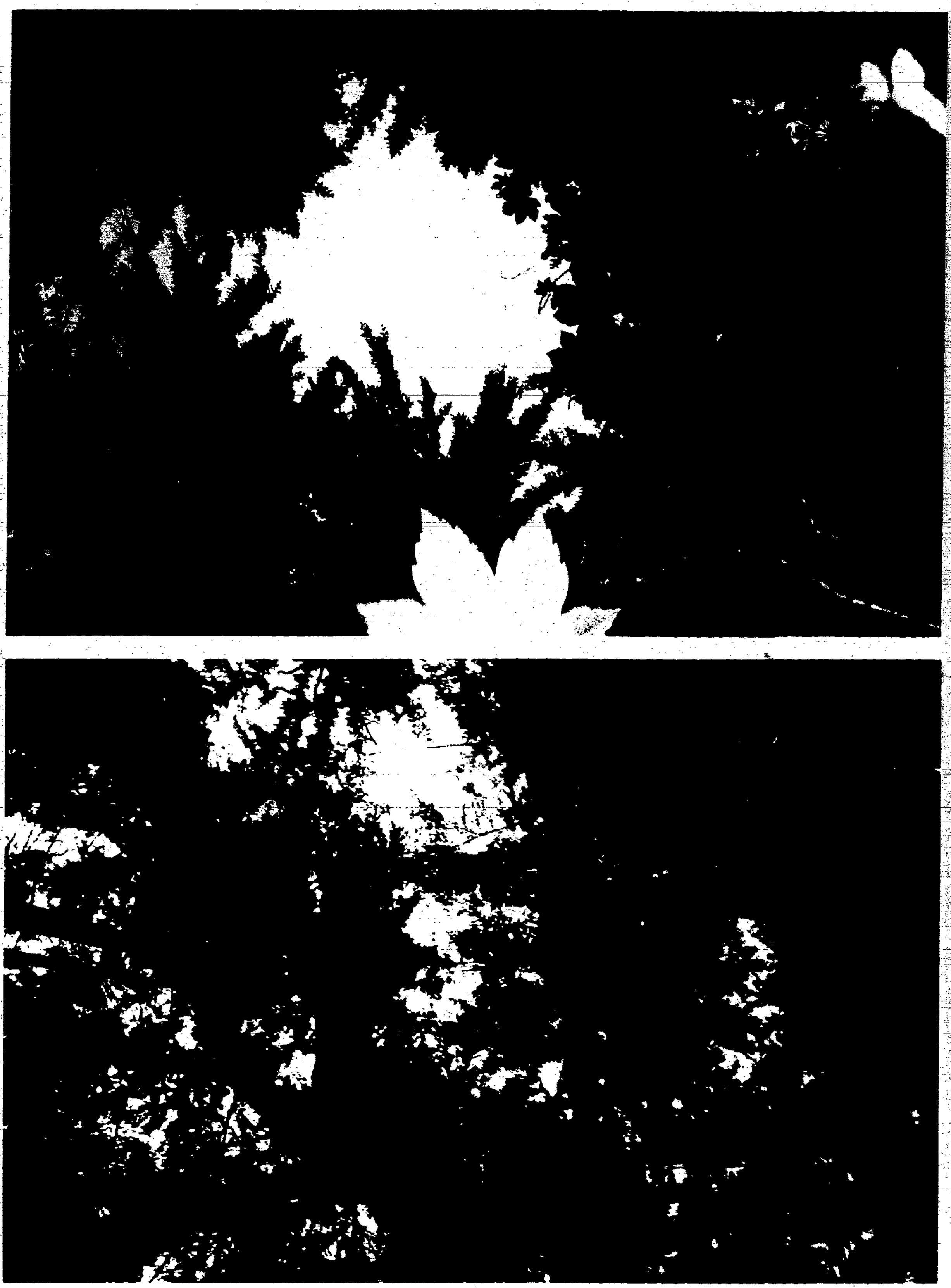


Figure 2.2. View of the canopy taken 1.3 m above the forest floor within a) a vine maple priority gap (top) and b) a closed canopy site (bottom). The canopy gap in the top photo has been occupied since stand origin by a vine maple clone.

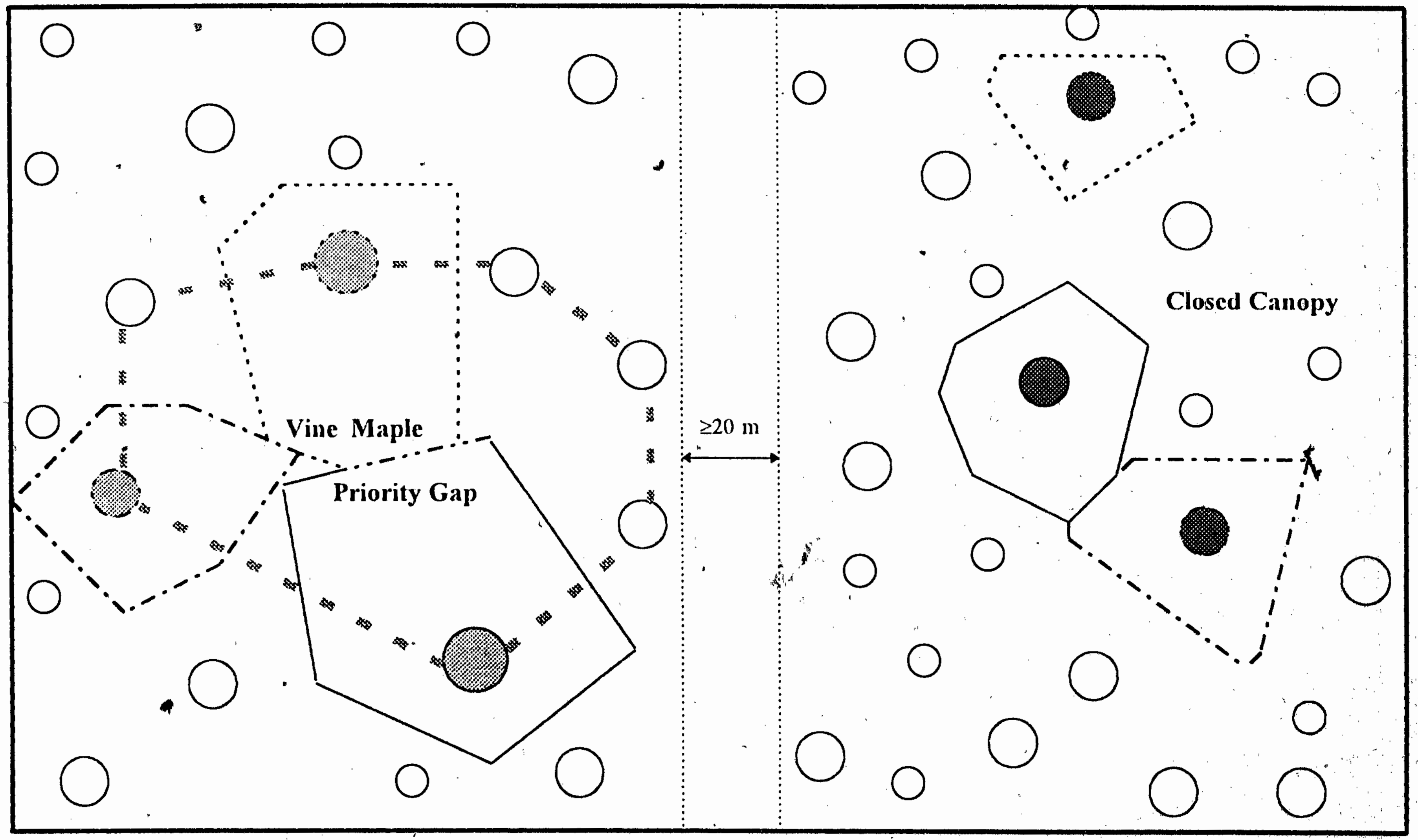


Figure 2.3. Plane view of a typical vine maple expanded priority gap (▨ ▨) and paired closed canopy site. Shaded boles (●) represent co-dominant conifers of a single species, Douglas-fir or western hemlock, depending on the stand. Polygons surrounding boles represent the potential growing space available to each subject tree. They are defined by inter-tree bisecting lines that are weighted by the relative basal area of the subject conifer to surrounding conifer boles (○). Map scale (excluding boles) is 1:200.

at least 20 m from the gap edge and contained no evidence of vine maple or other hardwoods.

2.3 Expanded Gap Size

I determined gap size by measuring the size of the *expanded* gap. The expanded gap is defined by the boles of the trees whose foliage defines the edge of the canopy opening (Veblen 1985; Spies et al. 1990; Lertzman and Krebs 1991; Lertzman 1992). I chose this method over measuring the size of the canopy gap (the vertical projection of the forest opening onto the ground; Veblen 1985, Lertzman and Krebs 1991, Lertzman et al. 1996), for three reasons: a) canopy gap size is dynamic while the expanded gap size remains constant, b) the size of the expanded gap is more indicative of the growing space available for conifers on the gap edge and c) for management purposes, a fixed value of gap size would be easier to implement in a silvicultural system. I measured eight radii, from the visual center of the gap, mapped the results to scale on graph paper, and used a planimeter to estimate the expanded gap area (McGhee 1996).

2.4 Conifer Morphology

Medium- to large-sized dominant and co-dominant conifers, formed the subset population from which I randomly selected three conifers (of the same species) on each site for analysis. Only trees which showed no signs of deformities, insect or pathogen infestation, substantial leaning, or other damage (Stokes and Smiley 1968; Biondi et al. 1992) were considered. All co-dominant and dominant trees that I sampled had DBHs greater than 30 cm. The DBH of conifers was taken at 1.3 m from the base of the upslope side of the tree (Jorsa 1988).

For trees in the closed canopy, I measured the radius (vertically projected) and the depth of the crown at two points on a line parallel to the topographic contours. On priority gap sites, the two crown radii and depth measurements were taken on an imaginary line which bisected the center of the gap. The angle to the base of the crown was taken at a right angle to the bole. The height to the crown base was then subtracted from tree height to obtain the crown depth. A *gap-side* crown is the half-crown portion of a tree adjacent to the gap that extends towards the gap center. A *canopy-side* crown is the half-crown of a tree adjacent to the gap that extends away from the gap and into the surrounding canopy. Mean canopy crown radius and depth were calculated by averaging crown dimensions for the north and south side of each closed canopy tree. Crown volume was calculated using the volumes for each of the half-cones generated by the data.

2.5 Reconstructing Site Chronologies

2.5.1 Coring Procedures

Two cores were removed from each study tree at 180° from each other, on a line parallel to the topographic contours (Stokes and Smiley 1968). This method of core collection yields more accurate data than taking several cores from random points on the bole (Jorsa 1988). Conifers were cored at breast-height to eliminate the time period between germination and when the tree reached breast-height, as this is often a period of highly variable and sporadic growth (Veblen 1986).

2.5.2 Analysis of Cores

Coring procedures, handling, and mounting followed the guidelines outlined by Stokes and Smiley (1968), Jorsa (1988), and Fritts and Swetnam (1989). I used a high resolution stereo-microscope to determine tree age and annual ring widths (to the nearest 0.002 mm). Radial increments were measured with a tree ring measuring device (Velmex 6000) equipped with a video camera and monitor. The Velmex 6000 was linked to a digital encoder and microcomputer running software capable of storing ring width measurements by year for each core. I then used the graphics feature of Microsoft's EXCEL 5.0 to visually cross-date cores against their partner core and against the site chronology (constructed using mean radial widths by year for each species) (Young et al. 1995). I used 1953-55 (3 relatively good consecutive growing years), 1969 (poor growing year), and 1991 and 1993 (relatively poor growing years) as signature years (Jenkins and Pallardy 1995). Given the easily discernable annual rings and the sensitivity of the response in the majority of cores, I consider the core data to be highly accurate. Cross-dating was double-checked to ensure accuracy.

2.5.3 Site Chronologies

Chronologies of radial growth were constructed from the raw ring width series. Annual ring widths were averaged for each site and these values were again averaged to construct the chronologies of mean radial growth for gap and canopy sites for both species. Chronologies of basal area increment (BAI) were constructed from the individual chronologies of radial growth and by measuring the radius of each core (Jenkins and

Pallardy 1995; Little et al. 1995). Where the pith was not present, I used a pith locator to determine the radius of the core (Jenkins and Pallardy 1995). To determine yearly increment, I determined the radius of the core at yearly intervals by subtracting the mean radius for year t from the mean radius of the following year (t+1). BAI, in cm^2, was derived using the following equation (adapted from Visser 1995):

$$BAI_t = \pi\ r^2_{(t+1)} - \pi\ r^2_{(t)}$$

where r is in cm. I assumed spherical growth for all trees. I then averaged annual BAIs for each site and these values were again averaged to construct the chronologies of mean BAI for gap and canopy sites for both species.

2.5.3.1 Basal Area Growth (1945-1994)

I constructed chronologies of radial growth and BAI for the years of 1945-1994 in order to compare the long-term growth histories on gap and canopy sites for each species. I chose 1945 as the starting point for the chronologies as the data set before this point contains a higher number of missing values due to missed piths, several large trees that could not be bored to the pith with available equipment, and younger trees which reached breast-height as late as 1938.

To determine if differences existed between site chronologies, I created a *difference* chronology. I subtracted the mean BAI chronosequence of the canopy from the BAI chronosequence of the gap for both species of conifers (Young et al. 1995). The distribution of values created by subtracting the two chronosequences was then compared to a theoretical normal distribution with the same standard deviation, but with a mean of 0. If the distribution created from the difference chronology and the theoretical distribution are significantly different, then the mean BAI chronologies for gap and canopy trees are significantly different (Wilkinson 1990). No standardization procedures were used since I was testing for differences between means (Biondi et al. 1992).

To determine if differences between gap and canopy BAIs occur only at specific stages of stand development, I calculated the mean BAI for each site for the five decadal periods between 1945-1994 (Jenkins and Pallardy 1995). The decadal segments were then compared between gap and canopy sites for both species.

2.5.3.2 Radial Growth Prior to 1945

For Douglas-fir, I determined sapling growth during the earliest stages of stand development using a subsample of 10 randomly selected trees taken from the population which had cores which penetrated the pith, and were greater than or equal to 63 years in breast-height age (to maximize time span). For western hemlock, due to the small number of hemlock which established around the time of stand regeneration, a sample size of only 5 each for gap and canopy sites was obtained. Only western hemlock with a breast-height age between 63-70 years were considered for this analysis. This maximizes the time span I am looking at and ensures that similar populations are compared. I reconstructed chronosequences of radial growth from 1932-1945 for gap and canopy sites for both species. The series were then tested in a similar fashion as the 1945-94 chronologies of BAI. Chronologies of BAI were not reconstructed for this time period as small differences in breast-height age would influence BAI values, which are largely dependant on a tree's radius (Visser 1995). As tree radius is very small when trees are young, differences in age could lead to exaggerated differences in BAI for this time period, resulting in misleading conclusions.

2.6 Site Productivity

2.6.1 Site Index

Site index is a standard measure, based on height growth, used to estimate the quality of a site (Carmean 1975). Because height growth occurs independently of stand density, it is a widely accepted measure of site quality (Carmean 1975; Larocque and Marshall 1993; Wang et al. 1994). However, overly dense stands may experience reduced height growth and stands with a very low density of stems may experience increased height growth (Carmean 1975). Site indices represent the height of dominant trees at age 50 and are calculated using age at breast-height and total tree height (Thrower and Nussbaum 1991).

Age at breast-height was determined by counting the number of rings from the pith to year 1994. For cores that did not contain the pith, I used a pith locator -- converging concentric circles drawn the same width apart as the inner rings of the core -- to estimate breast-height age. Cores were aligned for best fit on the pith locator and age was estimated by adding the number of concentric circles between the last recorded date on the core and the expected pith location on the pith locator (Jenkins and Pallardy 1995).

I determined tree height with the aid of a clinometer. The angle to the tree top was taken at right angles to the bole and trigonometric functions were used to calculate the height of the tree (Wenger 1984).

I calculated site indices using 'Freddie', a site index estimation program (Polsson 1993). Site index was only measured for Douglas-fir. Site indices were not measured for hemlock since suppression of currently dominant and co-dominant hemlock under the pre-logging canopy (see discussion) may make site index values for hemlock unreliable due to decreased height growth associated with intense canopy shading (Oliver and Larson 1990).

Mean site indices were derived for Douglas-fir on the edge of the gap and each Douglas-fir on closed canopy site by averaging individual tree site indices. Pairing of the sites eliminates problems associated with differences in slope position, aspect or elevation.

2.6.1.1 Vine Maple Influence

Since older stems originating from a single root ball often die and are replaced by younger stems (Russel 1973; McGhee 1996), the actual time vine maple has occupied a site cannot always be determined. The minimum temporal influence of vine maple is determined by measuring the age of the oldest living stem (O'Dea et al. 1995, McGhee 1996). In these stands, McGhee (1996) found that diameter (d) and age of a vine maple stem are highly correlated ($r^2 = 0.92$) when the following regression equation is used:

$$\text{stem age} = \frac{d}{0.24}$$

I used this relationship to relate stem diameter (taken 20 cm above the base) to stem age for the largest, live vine maple stem within each gap site (McGhee 1996). My study stands are just emerging from stem exclusion (McGhee 1996). All priority gap clones had a minimum temporal influence of >25 years; therefore, I would expect that most clones had become established during stand initiation, as O'Dea et al. (1995) report that the propagation of vine maple occurs infrequently in the dense stands that develop after canopy closure.

To determine if site index is associated with the percentage of vine maple cover directly around Douglas-fir, I estimated the percent area of ground, within 5 m of each bole, covered by the vertical projection of vine maple foliage onto the ground for each of 4 quadrants. I did not include western hemlock in this analysis since site index was not determined for western hemlock.

2.6.2 Potential Growing Space

The *area potentially available* index was first defined by Brown (1965) as a simple measure of growing space, where the area available to each tree was defined by the smallest polygon formed by bisector lines between the subject and surrounding trees. This index was later modified (Moore et al. 1973) to determine inter-tree bisectors based on the proportional size of the subject tree to adjacent trees, and was termed the *weighted area potentially available* (WAPA) index (Fig. 2.3). The WAPA index is a direct measure (in m^2) of the amount of forest ground area a subject conifer can potentially utilize given the proximity of adjacent trees. Moore et al. (1973) validated the WAPA index in a complex uneven-aged stand with 19 different hardwood species present. The WAPA index was also successfully used by Daniels et al. (1986), Tome and Burkhart (1989) and Biging and Dobbertin (1992).

The weighting function (Wij), based on comparative BA of competing conifers, is the distance from subject tree i to the weighted mid-point between subject tree i and competitor j. The weighting function is determined by the following equation (adapted from Moore et al. 1973; Daniels et al. 1986):

$$W_{ij} = \frac{BA_i}{(BA_i + BA_j)} L_{ij}$$

where Lij is the distance from subject tree i to competitor j. Only those boundary lines closest to the tree are considered in defining a conifer's polygon (Fig. 2.3).

I recorded the DBH of each surrounding conifer larger than 20 cm in diameter at breast-height. I observed that stems smaller than this are young saplings and occur relatively infrequently in the study stands. All trees within 10 m of the subject tree were recorded. If an angle of greater than 90° was not occupied by a surrounding conifer, trees at a distance greater than 10 m were measured. I was careful to record all surrounding conifers whose foliage would define the gap created were the subject tree to be removed. I calculated the distance to the weighted bi-sector lines (W_{ij}) in Microsoft EXCEL and manually plotted the results. I then used a planimeter to measure the WAPA index (Fig. 2.3).

2.6.3 Basal Area Productivity

To determine the influence of the gap and canopy sites on the total BA present on a site or on net productivity, it is necessary to consider each tree's potential growing space. A mean value for *site BA* ($m^2 ha^{-1}$) was calculated by dividing each tree's BA by its WAPA index, and then deriving a site mean. Net productivity is generally defined as the increase in plant mass or volume per unit area per unit time (Wenger 1984; Kimmins 1988). However, to avoid error associated with converting tree dimensions to volumes (Kimmins 1988), I have represented *current BA productivity* ($m^2 ha^{-1} yr^{-1}$) as the mean annual increase of BA per unit ground area for the period of 1985 -1994.

2.7 Data Analysis

I analysed the data with SYSTAT software, versions. 5.0 and 6.0 (Wilkinson 1990, SPSS 1996). I tested differences between means using both parametric and non-parametric tests, depending on the observed distributions of the variables. Parametric tests are always preferable to non-parametric tests when the populations are normally distributed, as they are more powerful in detecting differences between means (Sokal and Rohlf 1981). However, non-normality is prevalent in ecological data sets and non-parametric statistics provide viable alternatives to parametric statistics when working with non-normally distributed populations (Potvin and Roff 1993). I used ranked order, non-parametric statistical tests when outliers were present in a data set, when data transformations were not possible to achieve normalcy (e.g. continuous or bi-modal distributions), or when it was doubtful whether the data set was normally distributed, given the small sample size (Potvin and Roff 1993). When the underlying population is not normally distributed, non-parametric procedures generally prove more efficient at detecting differences between means than their parametric counterparts (Potvin and Roff 1993). Mean values were calculated for each site in order to avoid pseudo-replication, a common problem in ecological studies (Hurlbert 1984). In determining whether site index was associated with the percentage of vine maple, individual trees formed the experimental unit.

2.7.1 Parametric Tests

In order to minimize variability due to inherent variation in the stand (Oliver and Larson 1990), I employed paired t-tests to test for differences between gap and canopy sites. I also used unpaired t-tests to compare between the Douglas-fir and western hemlock stands. Functional relationships were examined using model II linear regression (Sokal and Rohlf 1981). For all parametric tests, transformations were performed on data sets which were not normally distributed when checked with a normal probability plot (Wilkinson 1990). I used Pearson correlations to determine co-variance of linearized data.

2.7.1.1 Data Transformations

It is common for area measures to require transformations to achieve a normally distributed population (Lertzman *pers. comm.*). Gap size, BA and potential growing space (WAPA) required log transformations to achieve normality (Wilkinson 1990).

Crown volume was square root transformed (Wilkinson 1990). The percentage of vine maple was divided by 100 and then arc-sine square root transformed. Other variables either did not require transformations or were analysed with non-parametric tests, for which I retained the original form of the data set.

2.7.2 Non-Parametric Tests

For data sets that did not meet the assumption of normality, non-parametric tests were used. For paired analysis, I chose the Wilcoxon signed-ranks test. The Z stat (sum of signed ranks/ sum of squared ranks) is reported for Wilcoxon tests. To test for differences between chronological sequences, I employed the one sample Kolmogorov-Smirnov (KS) test. I used the two sample KS test to compare the distribution of tree ages for western hemlock (SPSS 1996).

2.7.3 Statistical Power

I used a standard significance level (α) of 0.05 for all the statistical tests in this thesis, minimizing my chances of rejecting the null hypothesis (H_0), when it is true (type I error). However, when a statistical test is unable to reject H_0, it does not necessarily mean that the two populations share the same mean. Differences between means may not have been detected due to low power ($1-\beta$), attributable to a small sample or effect size and/or a large sampling variability (Peterman 1990; Lertzman 1992). Statistical power was calculated for regressions with power analysis software (Borenstein and Cohen 1988).

Chapter 3

RESULTS

3.1 Site Characteristics

3.1.1 Expanded Gap Size

Expanded gap size in the Douglas-fir stand ranged from 53 m^2 to 187 m^2 with a mean of 90 ± 39 m^2 (Fig. 3.1a). Expanded gap size in the western hemlock stand ranged from 87 m^2 to 355 m^2 with a mean of 197 ± 80 m^2 (Fig. 3.1b). Priority gaps in the Douglas-fir stand were significantly smaller than priority gaps in the western hemlock stand ($t = 3.820$, $df = 18$, $p = 0.001$). The distribution of expanded gap sizes for Douglas-fir followed an exponential decay curve due to the high number of smaller priority gaps and relatively few larger priority gaps in the stand. Expanded gap sizes in the western hemlock stand were normally distributed about the mean.

3.1.2 Age Structure

I compared tree ages between paired sites to eliminate the possibility that observed responses were a result of inherent differences in age between gap and canopy sites. All sampled Douglas-fir regenerated within a narrow time frame. The ages of Douglas-fir on both sites were normally distributed around their means (~ 63 years for both sites; Table 3.2a). I did not detect significant differences for mean breast-height tree age between paired gap and canopy sites ($T = 1.51$, $df = 9$, $p = 0.17$; Fig. 3.2a). No veterans, large trees that are a legacy of the previous stand, were present on any Douglas-fir study sites.

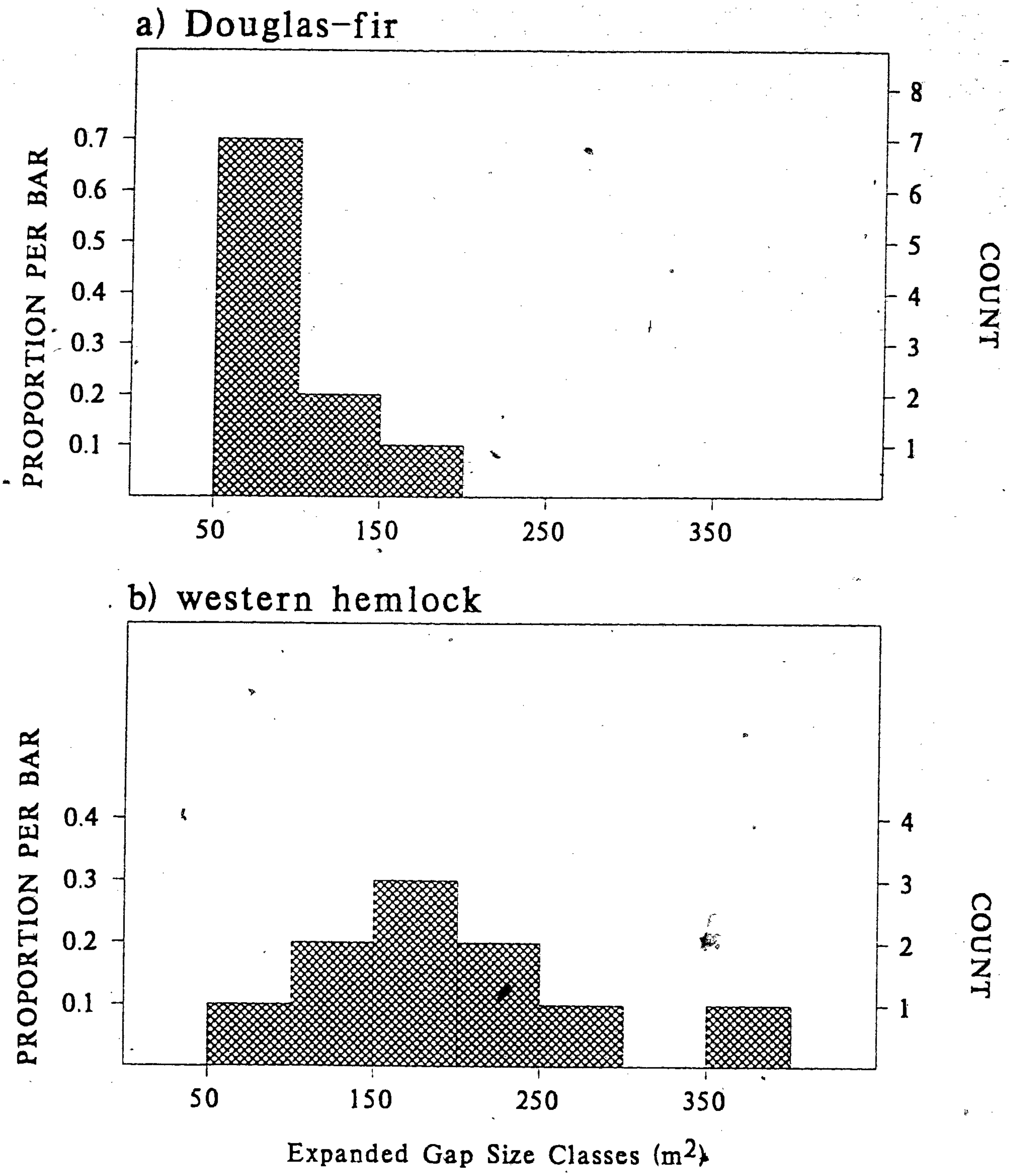


Figure 3.1. Distribution of expanded priority gap size on a) Douglas-fir and b) western hemlock gap sites (n = 10). Gap size in the Douglas-fir stand is significantly smaller than in the western hemlock stand (df = 18, p = 0.001).

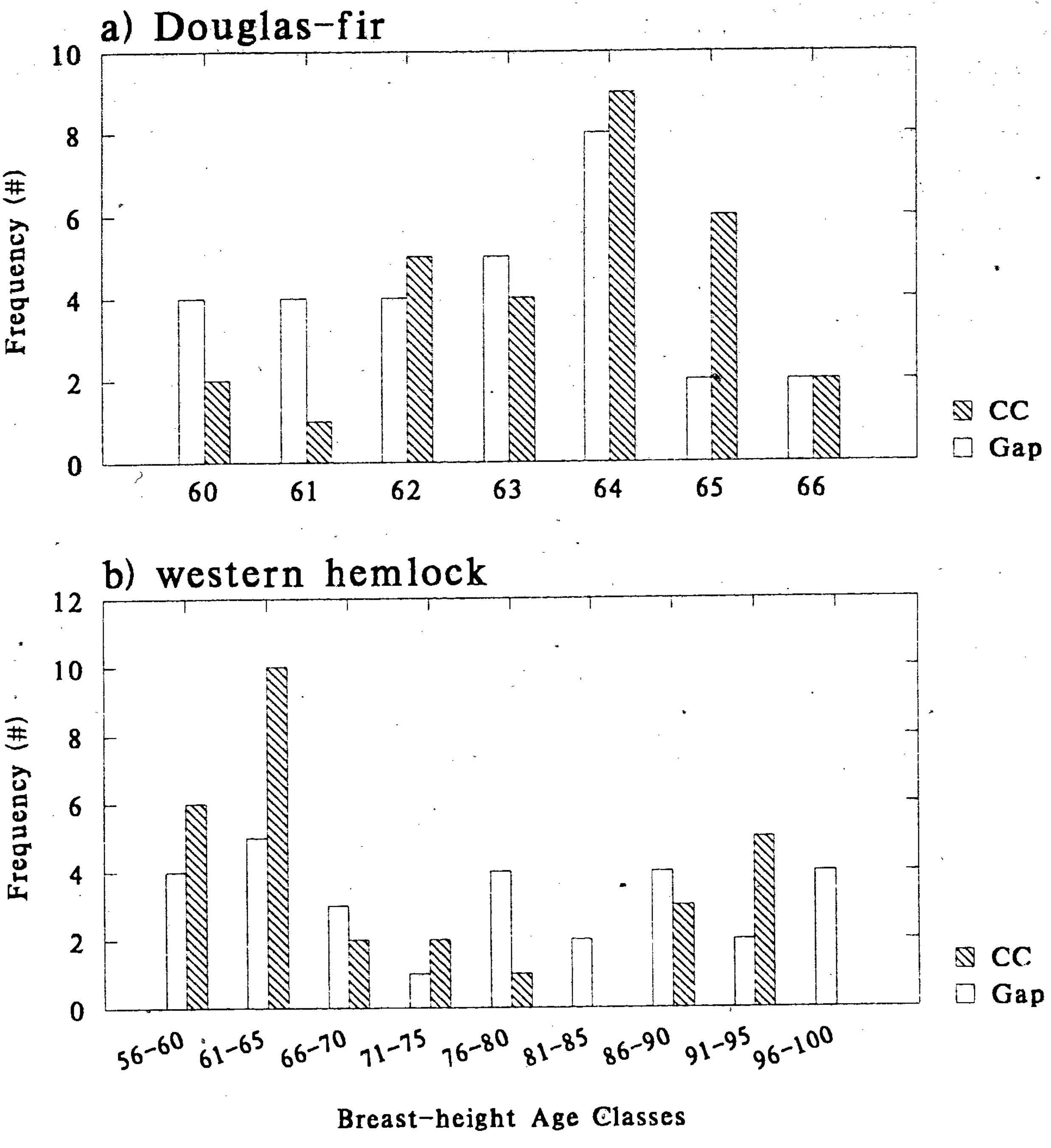


Figure 3.2. Distribution of breast-height age for gap and canopy a) Douglas-fir and b) western hemlock. All sampled trees are represented (n = 29 each for gap and canopy trees). No differences in mean site age between gap and canopy sites were detected for either species (Douglas-fir: T = 1.51, df = 9, p = 0.17; western hemlock: Z = 1.07, n = 10, p = 0.29).

The range of breast-height ages for western hemlock was much greater than for Douglas-fir (Fig. 3.2a & b) -- 44 years (56 - 99 years) for western hemlock versus only 7 years (60-66 years) for Douglas-fir. I did not detect differences in mean site age between priority gap and canopy sites for western hemlock (Z = 1.07, n = 10, p = 0.29).

Western hemlock on closed canopy sites exhibited a bi-modal age distribution and tended to be either relatively young or relatively old. The age distribution for western hemlock on priority gap sites was relatively uniform across the age cohorts (Fig. 3.2b). I was unable to detect significant differences in the distribution of ages between western hemlock on gap sites versus canopy sites (KS, n = 10, p = 0.33).

3.2 Conifer Morphology

3.2.1 Bole Size

The mean DBH of trees on gap sites (Douglas-fir: 60.5 ± 6.2 yrs; western hemlock: 54.8 ± 8.9 yrs) was greater than trees on closed canopy sites (Douglas-fir: 49.8 ± 5.4 yrs; western hemlock: 42.5 ± 5.5 yrs) for both Douglas-fir (T = 4.46, df = 9, p = 0.002) and western hemlock (T = 4.12, df = 9, p = 0.003; Table 3.1). Linear increases in diameter resulted in exponential increases in BA (Wenger 1984). Diameters of Douglas-fir that were 21% greater on gap versus canopy sites resulted in mean BAs that were 46% greater for Douglas-fir on gap sites versus closed canopy sites (Table 3.1a). Mean

Table 3.1. Characteristics of gap and canopy a) Douglas-fir and b) western hemlock (means ± standard deviation, n = 10 each for gap and canopy for both Douglas-fir and western hemlock). Paired T-tests were used for all variables. The ratio denotes the value of the gap variable divided by the value of the closed canopy (CC) variable.

a) Douglas-fir

Characteristic	Gap	CC	Gap:CC	p values
Breast-height tree age (yrs)	62.8 ± 1.2	63.5 ± 1.1	0.99	0.166
Tree DBH (cm)	60.5 ± 6.2	49.8 ± 5.4	1.21	0.002
Tree BA (m^2)	0.29 ± 0.60	0.20 ± 0.43	1.46	0.002
Crown radius (m)	4.4 ± 1.2	2.9 ± 0.5	1.50	0.001
Crown depth (m)	22.0 ± 4.5	17.7 ± 3.3	1.24	0.026
Crown volume (m^3)	535 ± 154	190 ± 73	2.82	<0.001
Tree height (m)	48.4 ± 2.54	46.1 ± 1.86	1.05	0.055
Site index	42.6 ± 2.5	40.2 ± 1.9	1.06	0.047
Potential growing space (m^2)	44.0 ± 13.4	27.4 ± 6.8	1.61	0.007

b) Western Hemlock

Characteristic	Gap	CC	Gap:CC	p values
Breast-height tree age (yrs)	76.2 ± 12.0	71.5 ± 13.0	1.07	0.29
Tree DBH (m)	54.8 ± 8.9	42.5 ± 5.5	1.29	0.003
Tree BA (m^2)	0.25 ± 0.08	0.15 ± 0.04	1.69	0.002
Crown radius (m)	4.6 ± 1.7	3.5 ± 0.4	1.31	0.001
Crown depth (m)	23.7 ± 5.0	19.3 ± 3.3	1.23	0.01
Crown volume (m^3)	694 ± 300	299 ± 85	2.32	<0.001
Tree height (m)	40.3 ± 4.1	40.9 ± 1.8	0.99	0.69
Potential growing space (m^2)	45.8 ± 20.5	18.3 ± 7.3	2.50	<0.001

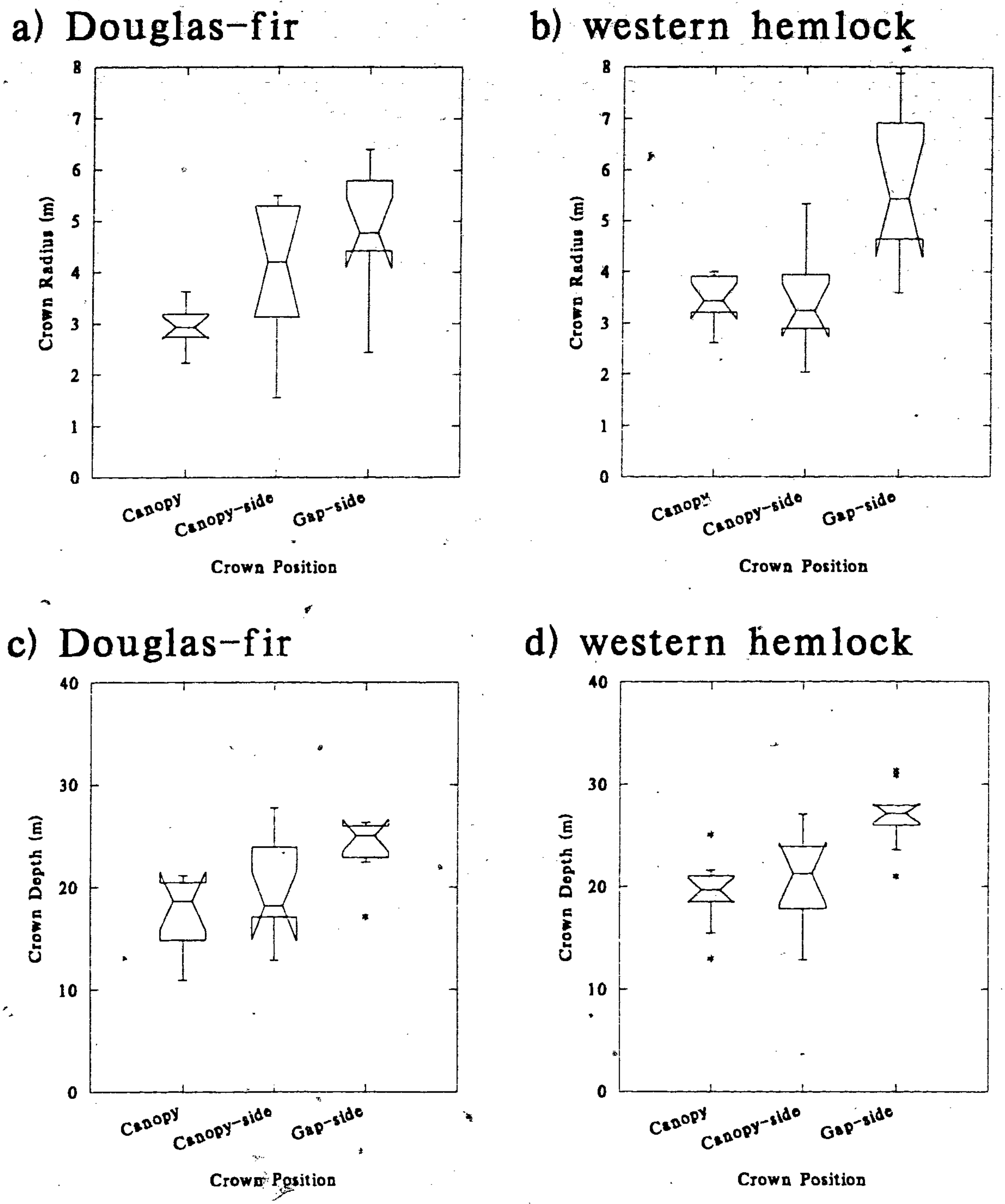
diameter differences of 29% for western hemlock on gap versus canopy sites resulted in mean BAs that are 69% higher for western hemlock gap versus closed canopy sites (Fig. 3.1b). Mean site BA was correspondingly higher on gap sites than the paired control sites for both species (Douglas-fir: T = 4.39, df = 9, p = 0.002; western hemlock: T = 4.17, df = 9, p = 0.002).

3.2.2 Crown Morphology

For Douglas-fir adjacent to gaps, I was unable to detect differences between the mean gap-side crown radius (4.7 ± 1.1 m) and mean canopy-side radius (4.1 ± 1.3 m; T = 1.21, df = 9, p = 0.26). However, both were significantly greater in length than the mean crown radius of closed canopy Douglas-fir (2.9 ± 0.5 m; gap-side: T = 5.07, df = 9, p = 0.001; canopy-side: T = 2.70, df =9, p = 0.02; Fig. 3.3a).

For western hemlock, however, the mean gap-side crown radius (5.7 ± 1.4 m) was significantly longer than the mean canopy-side radius (3.5 ± 1.1 m; T = 4.2, df = 9, p = 0.002) and the mean radius of closed canopy conifer crowns (3.5 ± 0.4 m; T = 5.48, df = 9, p < 0.001). I did not detect significant differences between the canopy-side crown radius and the closed canopy radius (T = 0.31, df = 9, p = 0.98; Fig. 3.3b).

Crown depth showed similar trends in both species. The gap-side crown was deeper (i.e. hung lower) than the canopy-side crown (Douglas-fir: T = 2.72, df = 9, p = 0.02; western hemlock: T = 4.93, df = 9, p = 0.001) and was also deeper than the mean



a) Douglas-fir

b) western hemlock

c) Douglas-fir

d) western hemlock

Figure 3.3. Box plots showing gap-side, canopy-side and mean closed canopy crown radii and crown depth for a) & c) Douglas-fir and b) & d) western hemlock. The central horizontal lines represent medians, and the point where the angled sides of the boxes reach full width are equivalent to the 95% confidence intervals around the medians. The upper and lower horizontal lines delimit the central 50% of the data, and the asterisks represent outliers (Wilkinson 1990; Lertzman 1992).

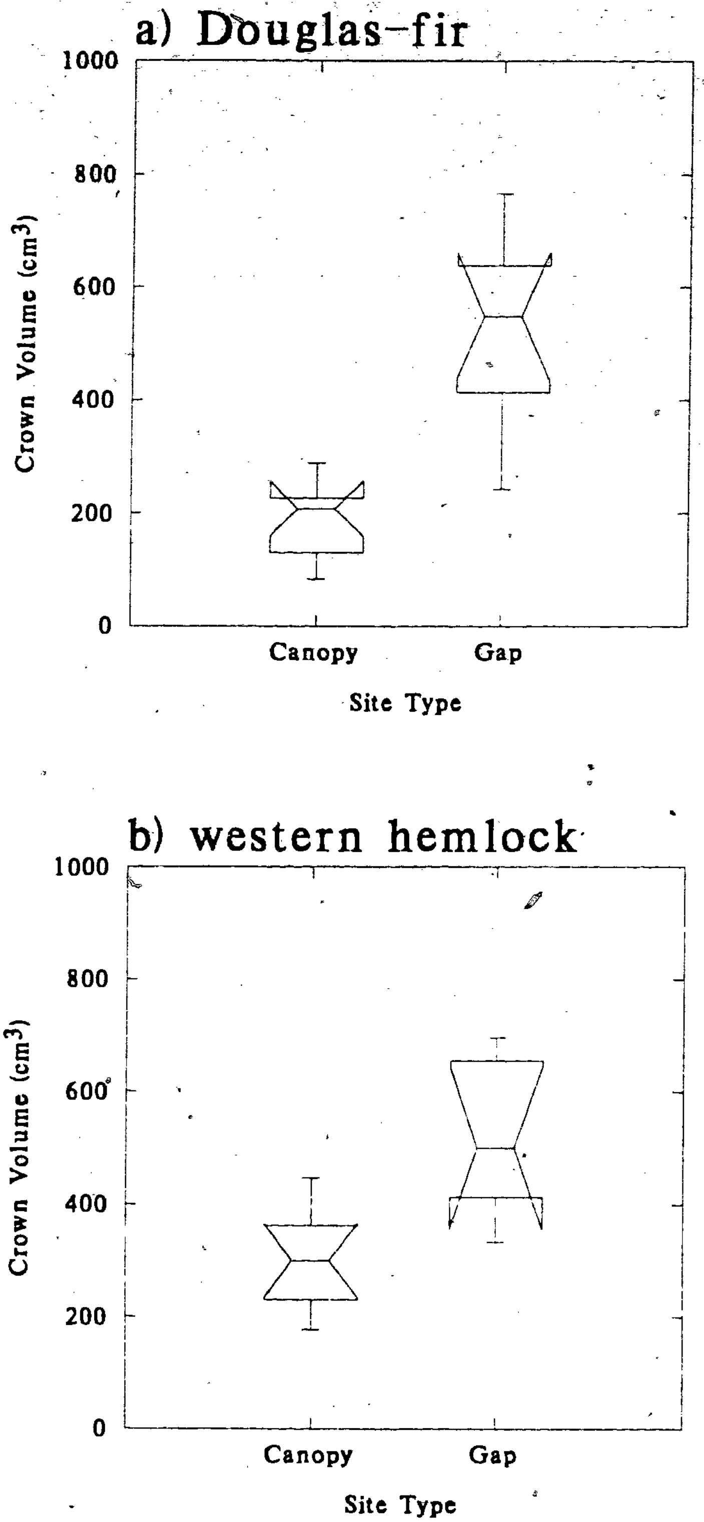


Figure 3.4. Box plots showing crown volume for a) Douglas-fir and b) western hemlock. Gap crown volume is significantly larger than canopy crown volume for both species.

closed canopy crown (Douglas-fir: T = 4.31, df = 9, $p = 0.002$; western hemlock: T = 5.89, df = 9, $p < 0.001$; Fig. 3.3c & d). I was unable to detect differences between the canopy-side crown depth and the closed canopy crown depth for either species (Douglas-fir: T = 1.10, df = 9, $p = 0.30$; western hemlock: T = 0.66, df = 9, $p = 0.53$; Fig. 3.3c & d).

The above relationships resulted in trees adjacent to gaps having larger crown volumes than trees in the closed canopy (Douglas-fir: T = 6.60, df = 9, $p < 0.001$; western hemlock: T = 7.02, df = 9, $p < 0.001$; Fig. 3.4a & b). The mean crown volume of Douglas-fir next to gaps was 2.82 times greater than the mean volume for closed canopy Douglas-fir (Table 3.1a). For western hemlock nest to gaps, mean crown volume was 2.32 times greater than mean crown volume for canopy western hemlock (Table 3.1b). Differences in crown volume were largely attributable to the greater crown radius and deep gap-side crown of trees adjacent to the gap.

3.2.3 The Influence of Priority Gap Size

3.2.3.1 Douglas-fir Priority Gaps

On Douglas-fir gap sites, relationships between gap size and BA ($r^2 = 0.01$, n = 10, $p = 0.78$, power = 0.06), recent BAI ($r^2 = 0.06$, n = 10, $p = 0.49$, power = 0.09), or crown volume ($r^2 = 0.11$, n = 10, $p = 0.35$, power = 0.01) could not be detected. Low power in these regressions was attributed to the small sample and effect size (Peterman 1990). Given the small r^2 values, if a relationship does exist, it is likely not a strong one. The size of the expanded priority gap was statistically related to potential growing space

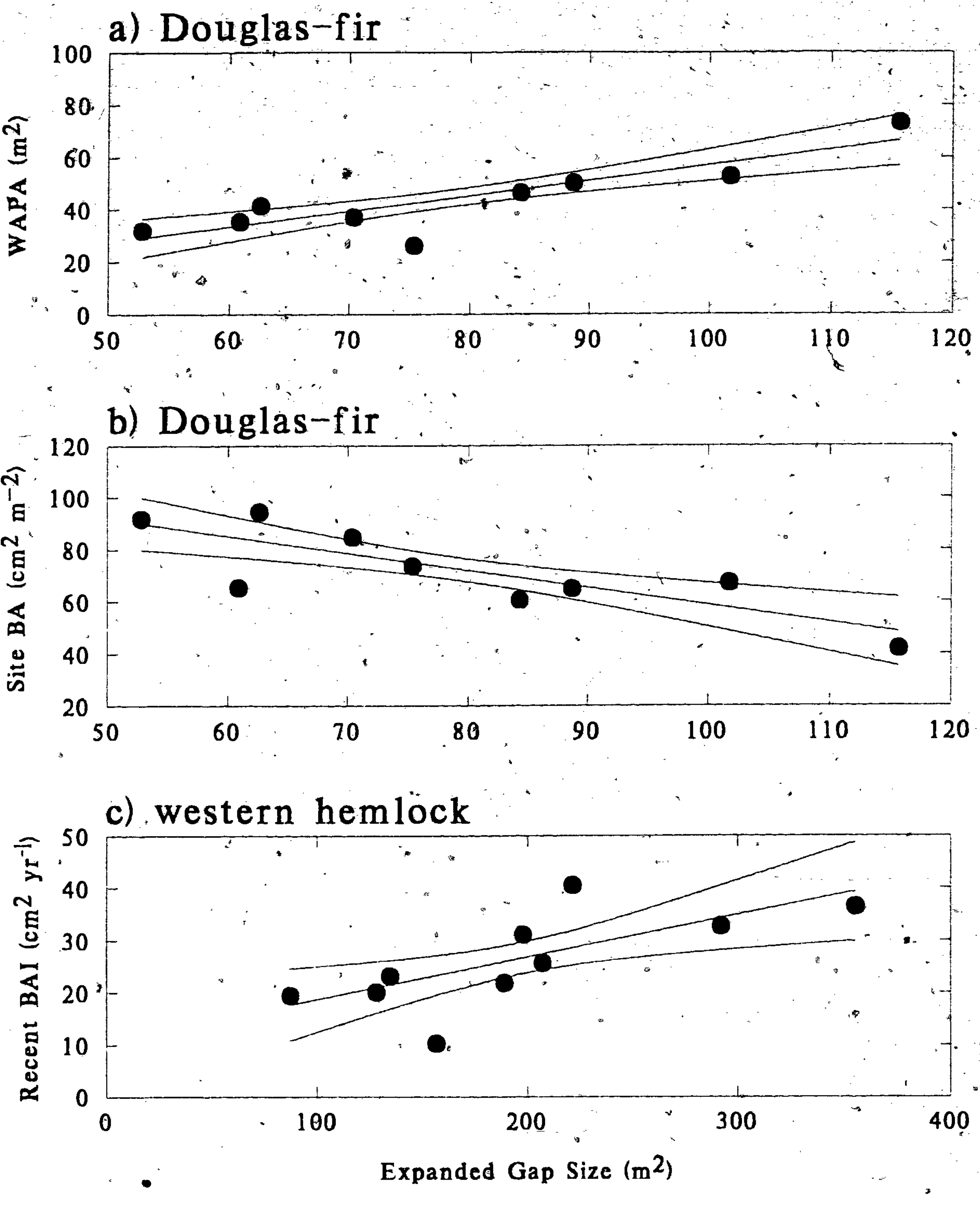


Figure 3.5. Significant regressions on Douglas-fir and western hemlock gap sites. a) Potential growing space (WAPA) vs expanded gap size for Douglas-fir on gap peripheries ($r^2 = 0.68$, $n = 9$, $p = 0.006$) and b) site BA ($r^2 = 0.60$, $n = 9$, $p = 0.01$) vs expanded gap size in the Douglas-fir stand. The largest expanded gap was left out of both of the above analyses due to its very large influence on the regressions. c) Mean annual basal area increment (BAI) of western hemlock for the past decade (1985-94) vs expanded gap size ($r^2 = 0.49$, $n = 10$, $p = 0.03$).

($r^2 = 0.68$, $n = 9$, $p = 0.006$; Fig. 3.5a) and to site BA ($r^2 = 0.60$, $n = 9$, $p = 0.01$; Fig. 3.5b), but I was unable to detect a statistical relationship between gap size and current BA productivity ($r^2 = 0.34$, $n = 9$, $p = 0.01$, power = 0.31). The largest gap was removed from the three latter analyses due to the large influence it had on the regressions (Wilkinson 1990).

3.2.3.2 Western Hemlock Priority Gaps

On western hemlock gap sites, an influence of gap size on BA ($r^2 = 0.01$, $n = 10$, $p = 0.38$, power = 0.11), crown volume ($r^2 = 0.16$, $n = 10$, $p = 0.38$, power = 0.02), potential growing space ($r^2 = 0.03$, $p = 0.63$, $n = 10$, power = 0.07), current BA productivity ($r^2 = 0.15$, $n = 10$, $p = 0.27$, power = 0.15) or site BA ($r^2 = 0.004$, $n = 10$, $p = 0.86$, power = 0.06) were not detected. Recent BAI was the only variable statistically related to gap size ($r^2 = 0.49$, $n = 10$, $p = 0.03$; Fig. 3.5c).

3.3 Site Chronologies

3.3.1 Douglas-fir Sites

During the earliest stages of stand development, from 1932-1945, approximately 7 years after seedling establishment and until the saplings were about 20 years in total age, there was no detectable difference between the radial growth chronologies in Douglas-fir adjacent to gaps and those in the canopy (KS, $n = 14$, $p = 0.18$; Fig. 3.6a). The ratio of radial growth of Douglas-fir on canopy sites to Douglas-fir on the edge of the gap during this time period was approximately 1.0 (Fig. 3.6b). As the canopy continues to grow and

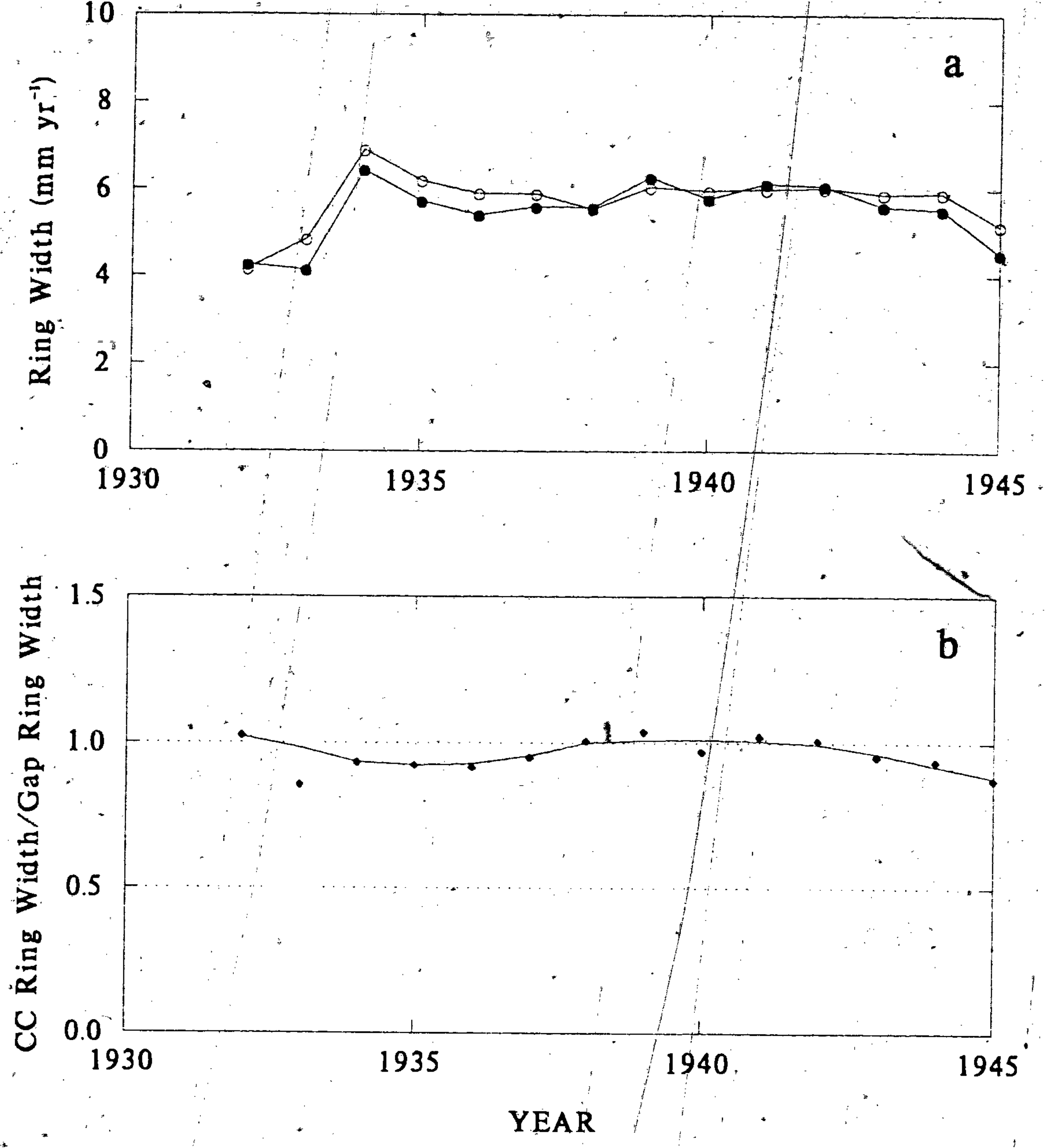


Figure 3.6. a) Mean radial growth of Douglas-fir saplings on priority gap (O) and closed canopy sites (●) (n =10 each for gap and canopy sites), and b) the ratio of mean closed canopy (CC) radial growth to mean gap radial growth. A Lowess smoothing function with a tension of 0.4 was applied to the data (Wilkinson 1990).

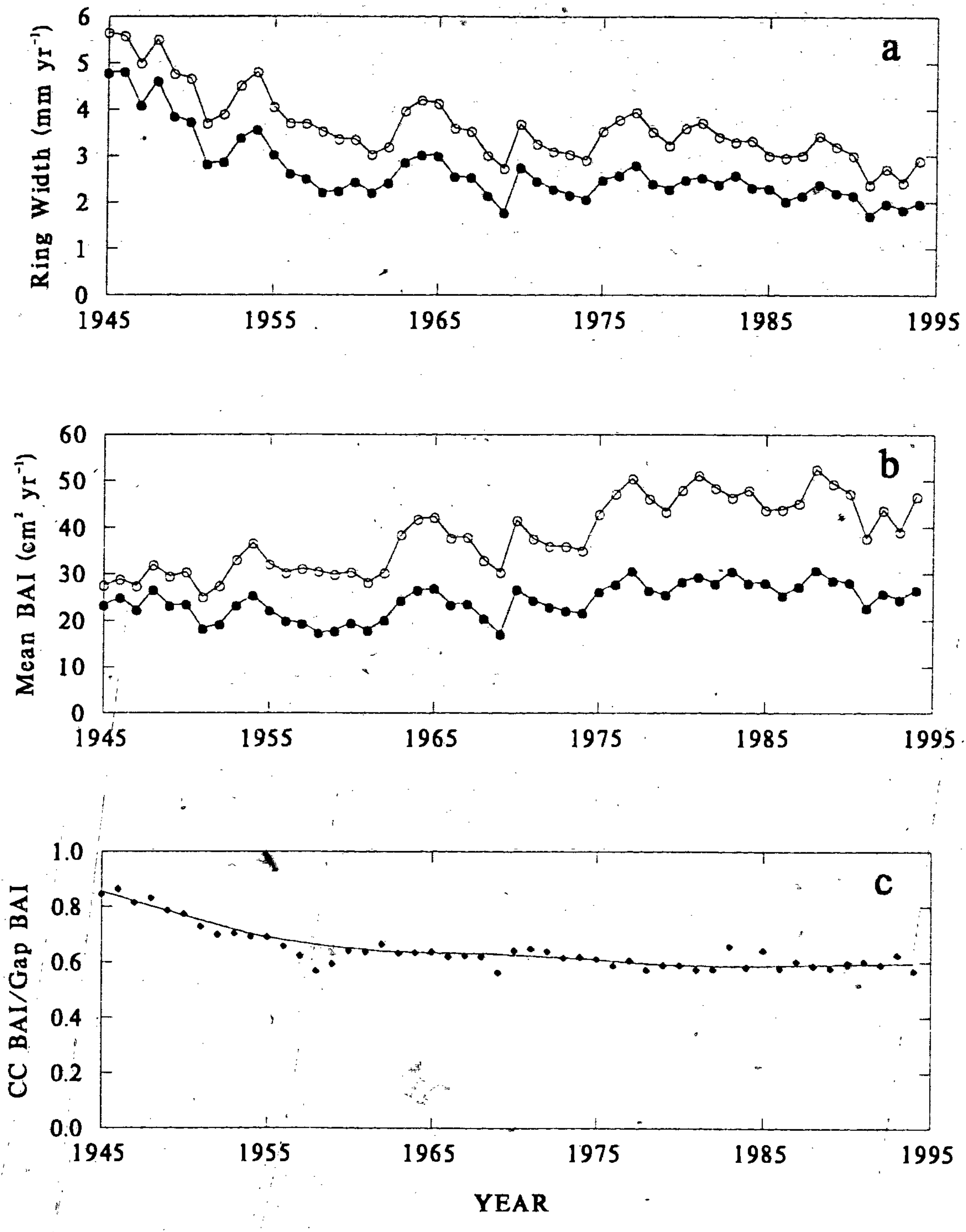


Figure 3.7. Chronologies of a) radial growth and b) basal area increment (BAI) for gap (O) and canopy (●) Douglas-fir for 1945-1994 and c) the ratio of mean canopy BAI to mean gap BAI. The numbers of cores representing each data point = 58 (29 trees). A Lowess smoothing function with a tension of 0.4 was applied to the data (Wilkinson 1990). Chronosequences in b) are statistically different (KS, n = 50, $p < 0.001$).

begins to close in the years after 1945, Douglas-firs adjacent to the gap increasingly outgrow those in the closed canopy (Fig. 3.7a & b). The chronology of BAI for Douglas-fir adjacent to the gap was different from the BAI chronology of closed canopy Douglas-fir (KS, $n = 50$, $p < 0.001$), as BAIs were consistently higher throughout the chronology for Douglas-fir on the edge of the gap compared to those in the closed canopy (Fig. 3.7b). The ratio of canopy BAI to gap BAI decreases as stand age increases (Fig. 3.7c). In 1945, the BAI ratio was 0.84. This value continually decreased with time, reaching a minimum of approximately 0.60 in 1994 (Fig. 3.7c).

For Douglas-fir gap sites, decadal BAIs were greater than decadal BAIs for canopy trees for all decadal segments: 1945-54 ($Z = -1.99$, $n = 10$, $p = 0.05$); 1955-64 ($Z = -2.81$, $n = 10$, $p = 0.005$), 1965-74 ($Z = -2.70$, $n = 10$, $p = 0.007$), 1975-84 ($Z = -2.70$, $n = 10$, $p = 0.007$), and 1985-94 ($Z = -2.70$, $n = 10$, $p = 0.007$). Mean decadal BAI increased as stand age increased for both gap and canopy sites (Fig. 3.8a).

Differing magnitudes of BAI between the sites led to different cumulative BA (CBA) curves. Mean CBA for Douglas-fir increased at a greater rate than the CBA of closed canopy Douglas-fir (Fig. 3.9a), resulting in the BA differences in Table 3.1a. By calculating the CBA chronosequence from the core data, the width of the bark at the time of sampling is not included, resulting in proportionally lower values of BA than when I compared BA using field measurements, which did include bark width.

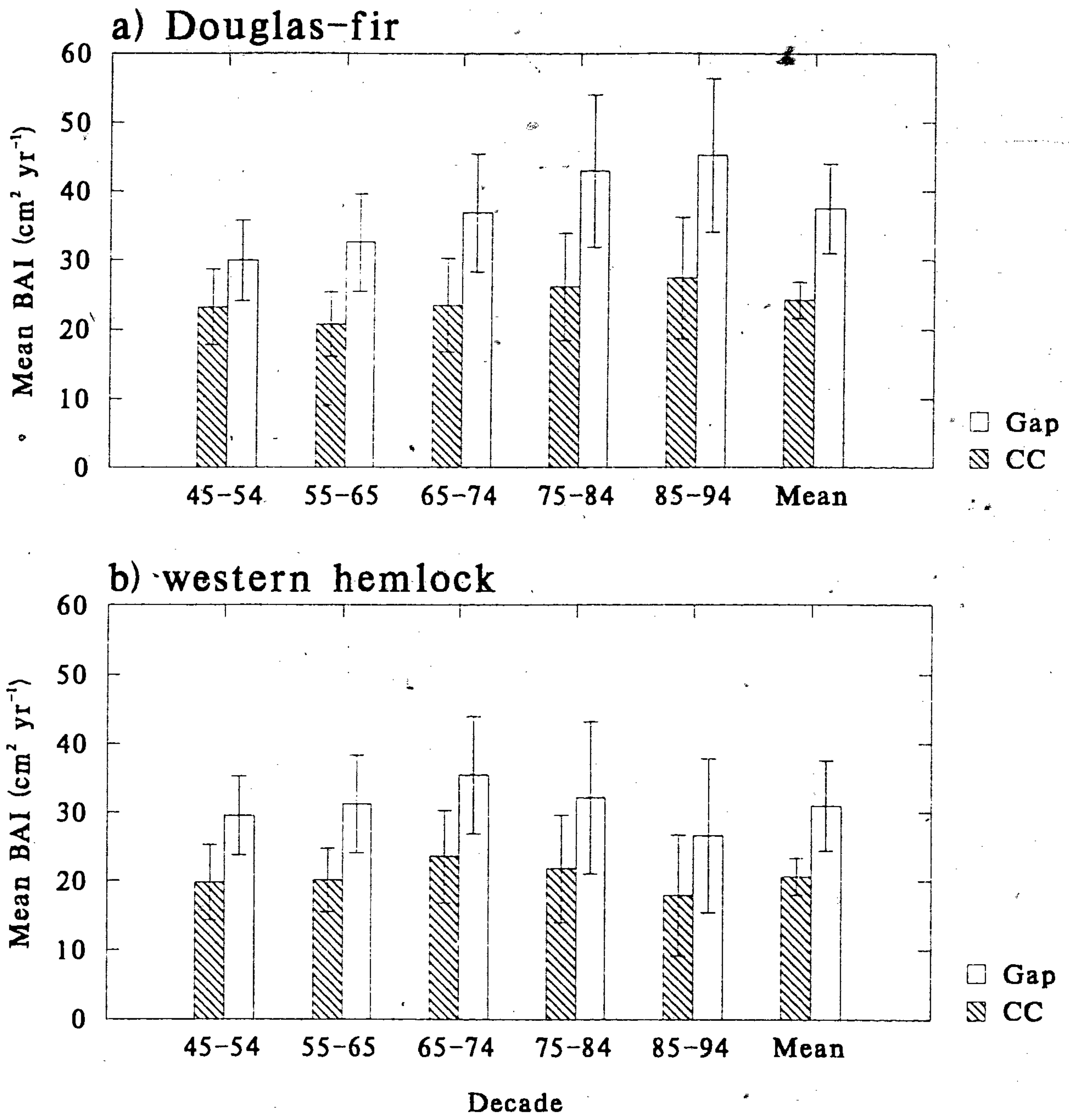


Figure 3.8. Mean annual BAI for the last 5 decadal periods (1945-1994) for a) Douglas-fir and b) western hemlock gap and canopy sites (n = 10 each for gap and canopy (CC) sites). All paired decadal BAIs are significantly different ($p < 0.05$) except the 1945-1954 decadal period for western hemlock. Error bars represent 1 standard deviation from the mean.

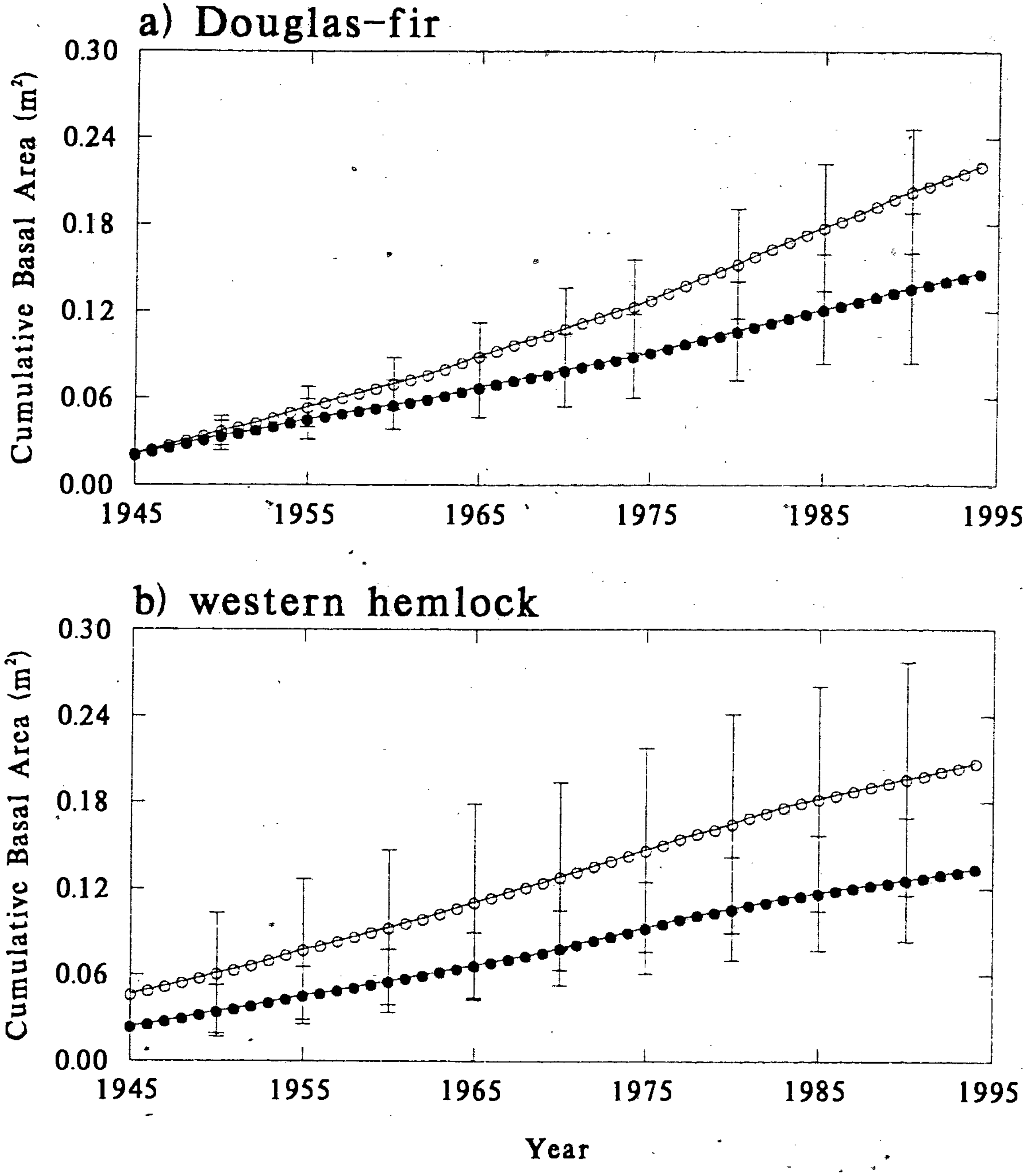


Figure 3.9. Cumulative basal area of a) Douglas-fir and b) western hemlock on gap (O) and canopy (●) sites. Number of trees representing each data point equals 29 on 10 sites. Error bars represent 1 standard deviation from the mean.

3.3.2 Western Hemlock Sites

During the earliest stages of stand development, from 1932-1945, I could not detect a difference between the radial growth chronologies of western hemlock adjacent to gaps and those in the canopy (KS, n = 14, p = 0.13; Fig. 3.10a). The ratio of radial growth of western hemlock on canopy sites to western hemlock on the edge of the gap during this time period ranged from 0.62 to 1.31 (Fig. 3.10b).

The BAI chronology for western hemlock on the gap is significantly different from the canopy western hemlock chronology (KS, n = 50, p < 0.001) due to the consistently higher BAIs on gap versus canopy sites from 1945-1994 (Fig. 3.11a). However, the difference between gap and canopy BAI did appear to widen with time as it did with Douglas-fir (Figs. 3.7b and 3.11b), and annual ring widths on gap sites did not appear to exceed ring widths on canopy sites by the same magnitude as in the Douglas-fir stand. Mean annual ring widths for both sites appear to be relatively equal until approximately 1950, when gap sites begin to outgrow canopy sites (Fig. 3.11a). The ratio of the ring width of closed canopy western hemlock to western hemlock adjacent to the gap is relatively low (0.61; Fig. 3.11c), though there is no evidence in the 1932-1945 radial chronosequence that indicates why the mean BAI is higher on gap sites in 1945 (Fig. 3.10a). The ratio of canopy to gap BAI between 1945-1994 was relatively constant and showed no distinct trend, starting and ending the recorded time period at approximately 0.70 (Fig. 3.11c).

For the 1945-54 decade, I did not detect differences in decadal BAI between gap

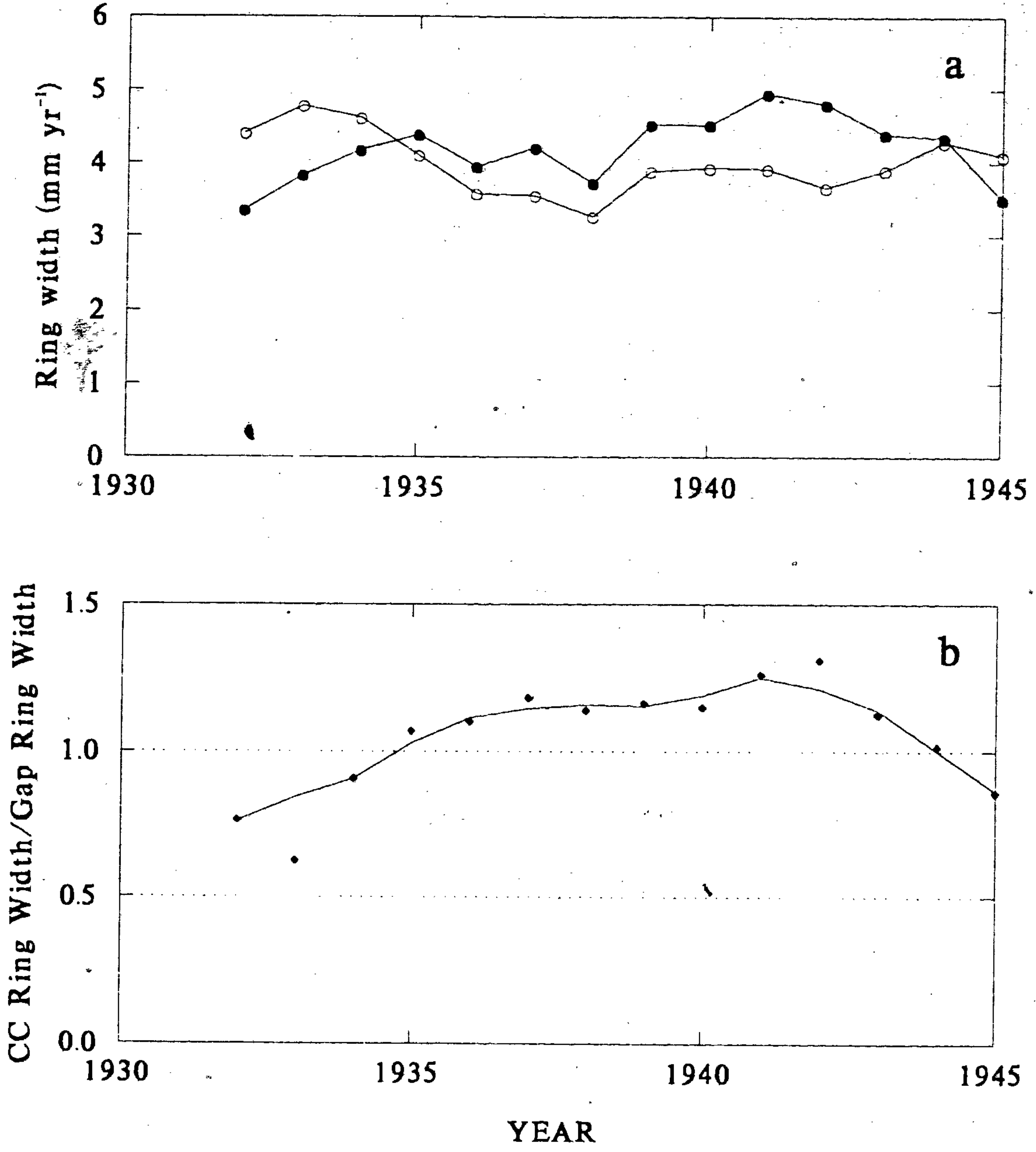


Figure 3.10. a) Mean radial growth of western hemlock saplings on priority gap (O) and closed canopy sites (●) (n=5 each for gap and canopy sites), and b) the ratio of mean closed canopy (CC) radial growth to mean gap radial growth. A Lowess smoothing function with a tension of 0.4 was applied to the data (Wilkinson 1990).

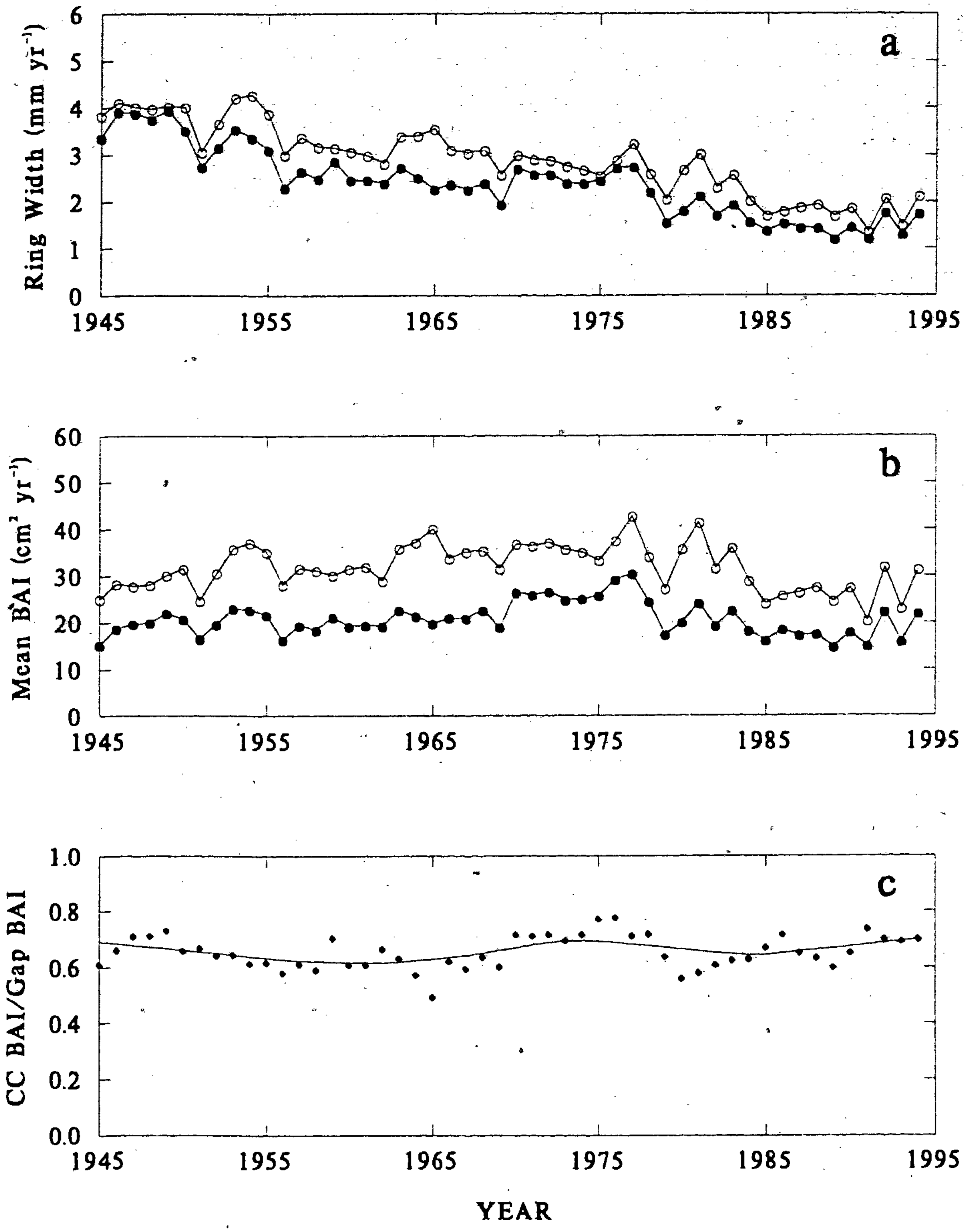


Figure 3.11. a) Radial growth and b) basal area increment (BAI) chronologies for gap (O) and canopy (●) western hemlock for 1945-1994 and c) the ratio of mean canopy BAI to mean gap BAI. The numbers of cores representing each data point = 58 (29 trees). A Lowess smoothing function with a tension of 0.4 was applied to the data (Wilkinson 1990). Chronosequences in b) are statistically different (KS, n = 50, $p < 0.001$).

and canopy sites for western hemlock (Z = -1.68, n = 10, p = 0.09; Fig. 3.8b). All other decadal segments had significantly higher mean annual BAI on gap sites compared to canopy sites (Fig. 3.8b): 1955-64 (Z = -2.29, n = 10, p = 0.02), 1965-74 (Z = -2.19, n = 10, p = 0.03), 1975-84 (Z = -2.09, n = 10, p = 0.04), and 1985-94 (Z = -2.29, n = 10, p = 0.02). Mean decadal BAI increased as stand age increased until the 1975-85 decade, when decadal BAI declined (not significantly). BAI significantly declined for the most recent decade of growth (1985-94) compared to the previous decade (1975-84) for both western hemlock next to gaps (Z = -2.24, n = 10, p = 0.02) and in the closed canopy (Z = -2.60, n = 10, p = 0.01; Fig. 3.8b).

Mean CBA for western hemlock next to gaps increased at a greater rate than the CBA of closed canopy western hemlock (Fig. 3.9b), resulting in the BA differences in Table 3.1b. By calculating the CBA chronosequence from the core data, the width of the bark at the time of sampling is not included, resulting in proportionally lower values of BA than when I compared BA using field measurements, which did include bark width.

3.4 Site Productivity

3.4.1 Site Index

The estimated mean site index for the Douglas-fir stand was 41.4 m. This represents the upper range of site index for Douglas-fir in the coastal forests of B.C. (Thrower and Nussbaum 1991). Site index was significantly higher for Douglas-fir adjacent to priority gaps (42.6 ± 2.5 m) than those in the closed canopy (40.2 ± 1.9 m; T = 2.26, df = 9, p = 0.05; Fig. 3.12a).

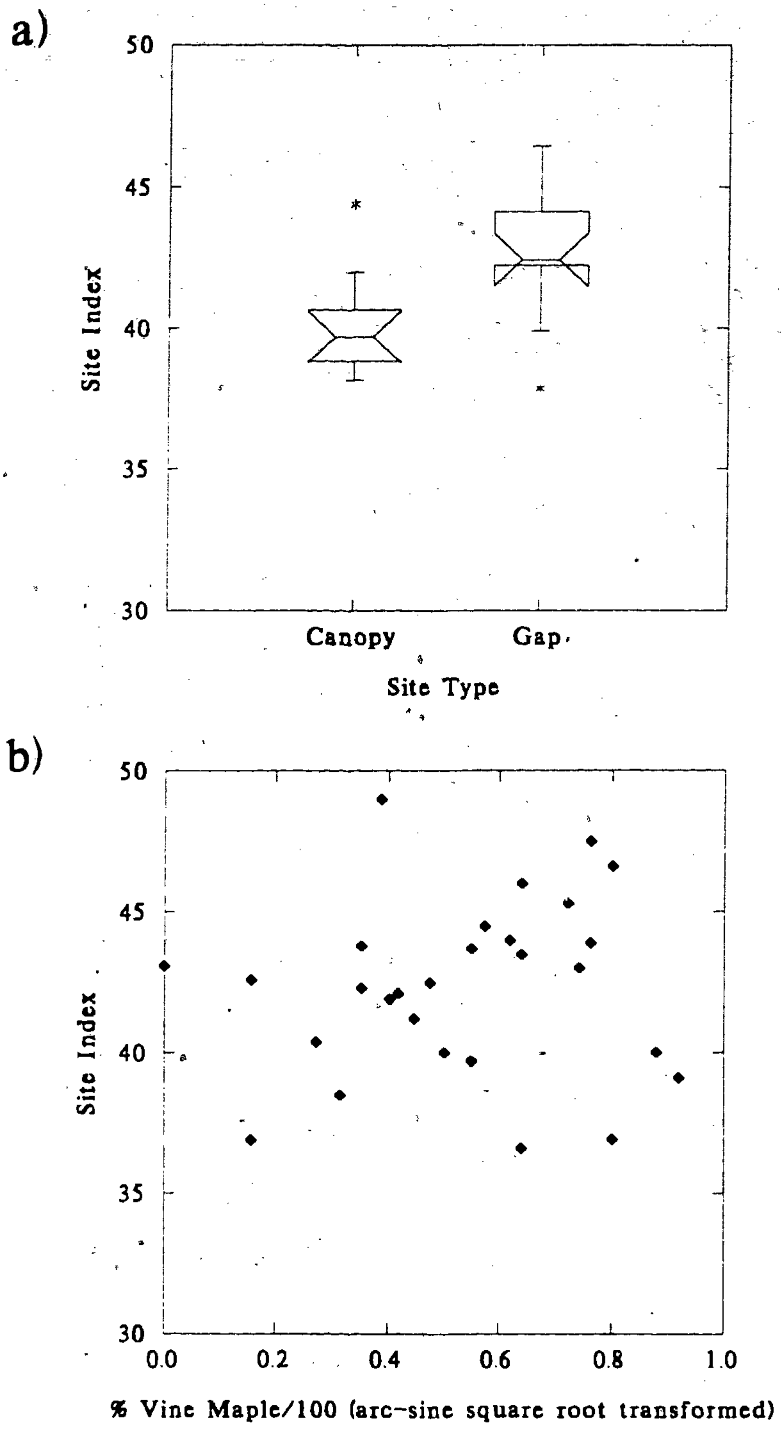


Figure 3.12. a) Site indices for gap and canopy Douglas-fir sites, analysed with a paired t-test (p = 0.050, n = 10 each for gap and canopy), and b) a plot showing the non-significant correlation of percent cover of vine maple within 5 m of each subject Douglas-fir and site index (r = 0.18, n = 29, p = 0.34). Both gap and closed canopy sites are associated with a high site index for coastal Douglas-fir in B.C. (Thrower and Nussbaum 1991).

The percentage of vine maple within a 5 m radius of Douglas-fir adjacent to the gap ranged from 0 to 75 % with a mean of 32.1 ± 21.8 % (Fig. 3.12b). Site index was not significantly correlated with the transformed percentage of vine maple cover within a 5 m radius ($r = 0.18$, $n = 29$, $p = 0.34$; Fig. 3.12b). However, several outliers did occur in the data set which may explain why significant results were not obtained, even though the trend was an increase in site index as the percentage of vine maple increased. Three of the outliers occurred on a single site. When this site was removed from the analysis the correlation was significant ($r = 0.41$, $n = 26$, $p = 0.04$).

3.4.2 Potential Growing Space

The mean potential growing space for Douglas-fir on the edge of gaps ranged from 27.0 m^2 to 74.1 m^2 with a mean of 44.0 ±13.4 m^2 and on canopy sites values ranged from 19.4 m^2 to 39.4 m^2 with a mean of 27.4 ± 6.8 m^2. For western hemlock adjacent to the gap, mean potential growing space ranged from 24.3 m^2 to 78.5 m^2 with a mean of 45.8 m^2 (± 20.5 m^2) and on western hemlock canopy sites, values ranged from 5.6m^2 to 28.2m^2 with a mean value of 18.3 m^2 (± 7.3 m^2). Potential growing space was significantly greater on gap sites versus canopy sites for both species (Douglas-fir: $T = 3.45$, $df = 9$, $p = 0.007$; western hemlock: $T = 5.74$, $df = 9$, $p < 0.001$; Table 3.1).

Crown volume and bole size were highly correlated with potential growing space. All of these variables were positively correlated (significantly) with recent BAI growth for both species. Greater spacing between boles produced trees with larger crowns and boles and higher rates of BA growth (Table 3.2). The high degree of correlation between crown and bole size, recent BA growth and the potential growing space lends validity to the WAPA index as an accurate indicator of growing space (Table 3.2).

3.4.3 Basal Area Productivity

The ratio of current BA productivity of Douglas-fir on gap sites versus canopy sites is 1.05 (Table 3.3). The ratio of site BA is 0.91 (Table 3.3). For Douglas-fir sites, site BA (Z = -0.76, n = 10, p = 0.45) and current BA productivity (Z = -0.46, n = 10, p = 0.65) did not significantly differ between gap and canopy sites (Table 3.3 and Fig. 3.13a & c). Douglas-fir on the gap periphery occupy 161% of the growing space of Douglas-fir in the closed canopy (Table 3.1a), and the greater growing space was utilized by Douglas-fir to increase its BA.

The ratio of current BA productivity of gap versus canopy western hemlock was 0.62. The ratio of site BA is 0.64 (Table 3.3). Western hemlock on the edge of the gap had significantly lower site BA (Z = 2.29, n =10, p = 0.02; Fig. 3.13b) and lower current BA productivity (Z = 2.50, n = 10, p = 0.01; Fig. 3.13d) than western hemlock on closed canopy sites. Even though western hemlock adjacent to the gap had a mean BA that was 69% larger than western hemlock in the closed canopy, western hemlock adjacent to the gap occuppied 150% more growing space than closed canopy trees (Table 3.1b), and this value may be underestimated (see discussion).

Table 3.2. Pearson correlation values and probabilities showing the interdependance of conifer characteristics for a) Douglas-fir and b) western hemlock. Crown volume (CV), breast-height diameter (DBH), mean annual basal area increment (BAI) for 1985-94, and potential growing space (WAPA) all positively co-vary for both species.

Pearson's Correlation Matrix - Douglas-fir

	DBH	CV	BAI (85-94)
CV	0.881 (0.000)	----	
BAI (85-94)	0.564 (0.010)	0.634 (0.003)	----
WAPA	0.895 (0.000)	0.904 (0.000)	0.562 (0.010)

Pearson's Correlation Matrix - Western hemlock

	DBH	CV	BAI (85-94)
CV	0.797 (0.000)	----	
BAI (85-94)	0.909 (0.000)	0.728 (0.002)	----
WAPA	0.616 (0.023)	0.666 (0.008)	0.662 (0.009)

Values in matrices represent Pearson coefficients. Values in brackets represent Bonferroni probabilities.

Table 3.3. Summary of the site basal area (BA) and current BA productivity (1985-94) for gap and canopy (CC) sites for Douglas-fir and western hemlock (mean ± standard deviation, n = 10 each for gap and closed canopy; Wilcoxon signed-ranks test). The ratio represents the gap value divided by the canopy value.

Basal Parameter	Gap	CC	Gap:CC	p
Douglas-fir site BA (m^2 ha^{-1}).	69.7 ± 15.7	76.9 ± 23.4	0.91	0.45
Current BA productivity (Douglas-fir) (m^2 ha^{-1} yr^{-1})	1.07 ± 0.28	1.02 ± 0.31	1.05	0.65
Western hemlock site BA (m^2 ha^{-1})	58.1 ± 13.0	91.5 ± 35.8	0.64	0.02
Current BA productivity (western hemlock) (m^2 ha^{-1} yr^{-1})	0.66 ± 0.30	1.07 ± 0.40	0.62	0.01

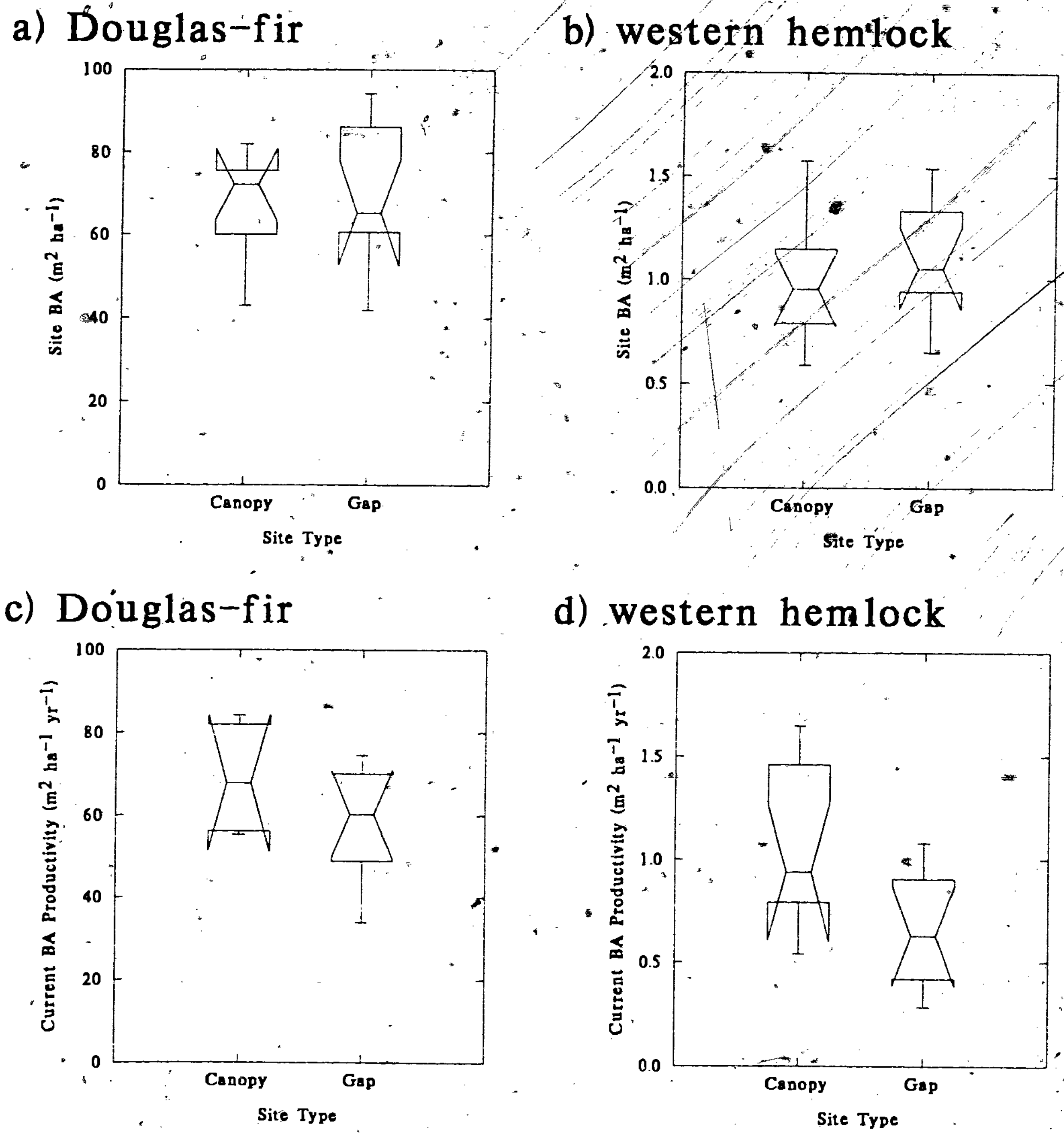


Figure 3.13. Site basal area (BA; n = 10) for a) Douglas-fir and b) western hemlock and current BA productivity for c) Douglas-fir and d) western hemlock. Productivity measures are not significantly different between gap and canopy sites for Douglas-fir but are significantly different for western hemlock (p = 0.01 for b, and 0.02 for d).

Chapter 4

DISCUSSION

In Chapter 1, I established two *a priori* hypotheses based on the expected responses of Douglas-fir and western hemlock to the presence of a priority gap. My first hypothesis stated that an increase in growing space would be observed for conifers adjacent to gaps resulting in increases in a variety of biophysical conifer characteristics. Douglas-fir and western hemlock adjacent to priority gaps did have significantly greater potential growing spaces than trees in the adjacent closed canopy (Table 3.1). Since one of the primary controlling mechanisms for above-ground, net primary productivity in temperate forests is light availability (Mitchell 1975; Law et al. 1992), the wider spacing of conifer stems (Table 3.1) associated with the presence of a priority gap would result in greater light interception for trees adjacent to the gap (Oliver and Larson 1990). The greater the interception of light, the larger the crown that is able to develop, the greater the photosynthate that is produced, and the greater the addition of xylem to the stem (Table 3.2). Therefore, Douglas-fir and western hemlock on the edge of the gap, though similar in age to the same species in the closed canopy, have developed deeper and wider crowns (Fig. 3.3) and larger crown volumes (Fig. 3.4) than conifers on closed canopy sites. Greater crown volumes generate greater radial growth and BAIs (Pacala et al. 1994; Long and Smith 1984; Oliver and Larson 1990; Table 3.2; Figs. 3.7b and 3.11b), which resulted in the larger diameter stems on priority gap sites (Table 3.1). Basal growth rates for Douglas-fir next to priority gaps did largely compensate for the increased growing space, resulting in site BAs that were similar between gap and canopy sites (Table 3.3). Western hemlock next to gaps could not compensate for the 150% increase in growing space and site BA was lower for western hemlock on gap sites compared to canopy sites (Table 3.3).

My second hypothesis was associated with the finding that vine maple adds a rich supply of bases to the forest floor (Krajina et al. 1982; Ogden 1996), which may increase the site index associated with the priority gap environment in the Douglas-fir stand. The site index was significantly higher for Douglas-fir adjacent to priority gaps (Fig. 3.12a). But, I was unable to detect a significant relationship between site index and the percentage of vine maple cover around a stem (Fig. 3.12b). However, outliers were present, and their influence on the correlation is addressed in section 4.3.

Expanded priority gap size was significantly smaller in the Douglas-fir stand compared to the western hemlock stand (Fig. 3.1). The differing mean gap size associated with stands dominated by Douglas-fir and those dominated by western hemlock (Fig. 3.1) can be explained by the canopy characteristics of each species. Stands dominated by Douglas-fir have a higher degree of interstitial spacing among trees than stands which are dominated by western hemlock, allowing for more penetration of light to the forest floor (Haeussler et al. 1990). Increased diffuse light, which filters in from the surrounding canopy, eliminates the need for a large gap opening that would otherwise be required to achieve sufficient light levels for the survival and persistence of the vine maple. Stands composed dominantly of western hemlock form the densest canopies of any tree species in the coastal temperate rainforests, making it difficult for understory vegetation to survive beneath them, particularly in middle-aged (30-80 years) stands (Pojar and MacKinnon 1994). The lack of light filtering in through the canopy of stands which are dominated by western hemlock means that only vine maple clones in larger gaps are able to survive and hold the gap open through the stem-exclusion phase. McGhee (1996) did not detect differences in insolation, at 1.3 m above the forest floor, between priority gap and canopy sites. However, her hemispherical photographs were taken below the fully leafed foliage of vine maple clones during the summer and light levels *above* vine maple clones in gaps would likely be higher than those measured below the foliage. Also, clones with a significantly greater number of stems occur on gap sites compared to sites in the canopy that have recently closed due to crown expansion (McGhee 1996), indicating the availability of light on gap sites is likely greater than in the closed canopy.

Given the height of surrounding canopy trees in these stands (~ 40-50 m), vine maple's ability to persist in relatively small gaps is quite remarkable. In modelling understory light levels in single-tree developmental gaps (75 m^2), Canham et al. (1990) found that single-tree gaps in Douglas-fir -- hemlock stands had little effect on understory light levels beneath the gap and suggest that a gap size of 528 m^2 would be required to create understory light levels comparable to those in single-tree developmental gaps in northern hardwood forests. The size of the gaps in my Douglas-fir stand are similar to the size of single-tree developmental gaps reported by Spies et al. (1990) in mature coastal Douglas-fir forests. Spies et al. (1990) found that single-tree developmental gaps dominate in these stands, where the median canopy gap size is 19 m^2, with most less than 50 m^2. The gaps in the stand dominated by western hemlock are similar in size to persistent gaps in the New Jersey Pinelands where canopy openings range in size from $22m^2$ to $223m^2$ (Ehrenfeld et al. 1995) and to several-tree developmental gaps in coastal old-growth forests, reported by Lertzman and Krebs (1991; median expanded gap size 203 m^2) and Spies et al. (1990; median canopy gap size 85 m^2).

All sampled Douglas-fir regenerated within a narrow, 7 year time frame; whereas, the ages of western hemlock have a range of 43 years. Differences in the age structure of stand dominants between Douglas-fir and western hemlock stands result from the relative shade-tolerance of each species. Arsenault and Bradfield (1995) conducted research in the coastal watersheds of southwestern B.C. on the species composition of temperate rainforests. They found mature stands were characterized by active regeneration of western hemlock in the understory and that Douglas-fir only occurred in the larger size-classes in these stands. Douglas-fir would not have been present in the understory prior to logging due to its shade-intolerance (Carter and Klinka 1992). In my study, Douglas-fir established immediately after logging, in the early 1920's (Fig. 3.2a). Upon harvesting, many of the western hemlock that existed under the pre-logging canopy must have remained relatively uninjured by logging and were released afterwards. The rest of the western hemlock established after logging, contributing to the large range in age for this species (Fig. 3.2b).

Only well established western hemlock saplings which were present at the time of logging, and vigorous, newly established seedlings have become dominants in the western hemlock closed canopy (Fig. 3.2b). Previously suppressed seedlings may have experienced initially slow growth upon the removal of the canopy by logging. As they adjusted to full sunlight conditions (Oliver and Larson 1990), trees on closed canopy sites were likely overtopped and outcompeted by vigorous, newly established seedlings and larger, pole-sized trees. Western hemlock in all age cohorts (55 - 100 years breast-height age) occur on the periphery of the gap, as competition between conifers is less (potential growing space; Table 3.1b) around the gap. Western hemlock that may not have survived stem exclusion in the canopy have been able to on the edge of the gap.

Orwig and Abrams (1994) noticed a similar age stratification between shade-tolerant blackgum and shade-intolerant tulip poplar in a mature, mixed stand in Virginia. Most of the blackgum in the stand originated prior to logging and was released after the disturbance; whereas, most of the tulip poplar established post-logging.

4.1 Conifer Morphology

I expected the size of the boles to be larger adjacent to priority gap sites because of the greater space between conifer stems surrounding the gap compared to the relatively close proximity of conifers in the canopy. The spacing between boles largely determines the rate of basal growth and consequently the basal size of conifers (Oliver and Larson 1990). With greater potential growing space for conifers on the gap edge (Table 3.1) comes larger basal sizes (Table 3.2) compared to trees in the closed canopy. To clarify this point, I draw upon summary data of conditions for 7 pre-thinned plots which contained greater than 80% Douglas-fir (Marshall 1996). The number of boles in each plot ranged from 5500 to 13720 stems ha^{-1}, but the BA ha^{-1} ranged from only 30.0 to 40.7 m^2 ha^{-1}, with a stem density of 6840 stems ha^{-1} having the highest BA ha^{-1}. These data show that the BA of individual trees must be larger on low density plots, because the total BA between plots remains relatively constant, even though the number of stems differs greatly between plots.

Typically, as canopies close, lower branches do not receive adequate light levels to be sustained and these branches die (Oliver and Larson 1990). This has not occurred to the same degree for conifers on the edge of gaps compared to those in the closed canopy. The retention of lower branches and the subsequent development of deep crowns (Fig 3.3) indicates the gap has existed for a significant period of time. Large gap-side crown radii (Fig. 3.3a & b) are a result of the lateral expansion of the crowns into the gap, which is a primary way that gaps are filling. Seedlings and saplings, common in developmental gaps (Runkle 1982; Veblen 1986; Brokaw and Scheiner 1989; Spies et al. 1990; Lertzman 1992), are rarely present in priority gaps (McGhee 1996). The gap offers room for the development of deep and wide crowns, resulting in significantly larger crown volumes for trees adjacent to the gap (Table 3.1 and Fig. 3.4).

I expected, *a priori*, that increasing gap size would result in increasing bole and crown size, and BAI, due to the expected increase in potential growing space on sites with larger expanded gaps. However, crown volume, BA, and recent growth for Douglas-fir on the gap edge varied little with gap size. Perhaps the relatively small range of gap size (~50-120 m^2, with one gap being 187 m^2; Fig. 3.1a) in the Douglas-fir stand did not allow for a significant increase in light between sites to increase crown and bole growth on larger gaps. Because growing space increased as gap size increasesd (Fig. 3.5a) but BA did not, site BA for gap sites surrounded by Douglas-fir declined as gap size increased (Fig. 3.5b).

On gap sites in the western hemlock stand, crown volumes, potential growing space, BA, and recent growth varied little with increasing gap size. Growing space did not vary with gap size because, I found while plotting the WAPA index, with larger gaps the potential growing space for conifers is defined not by the trees across the gap but by those adjacent to the subject tree. Therefore, increasing the gap size, which is the same as increasing the distance to trees across the gap, would have little effect on the measured WAPA index. Because of this, potential growing space is likely increasingly underestimated as gap size in the western hemlock stand increases. Poulson and Platt (1989) report that light levels in gaps in temperate forests increase as gap size increases. Therefore, trees on the edge of larger priority gaps likely intercept more insolation than those on smaller gaps. Law et al. (1992) report that the degree to which canopies intercept light is related to above-ground net primary productivity. This is likely why western hemlock adjacent to larger priority gaps were associated with greater recent BAIs than seen on the edge of smaller gaps (Fig. 3.5c).

4.2 Site Chronologies

In Douglas-fir stands, radial growth differences between gap and canopy sites are not seen until approximately 1943 to 1945 (Figs. 3.6a and 3.7b). Radial growth increments on western hemlock gap and canopy sites do not show a marked difference until after 1950 (Figs. 3.10a and 3.11a). Tappeiner and Zasada (1993) believe that vine maple does not likely interfere with conifer regeneration in clearcuts. However, their observation is not consistent with other studies, as vine maple clearly inhibits the establishment of conifers on many sites it occupies (Spies et al. 1990; McGhee 1996), otherwise priority gaps could not be established and maintained. However, in my study, the vine maple did not appear to affect negatively the radial growth of Douglas-fir on the edge of priority gaps during stand initiation (1932-45; Fig. 3.6).

The initial stage of development of an even-aged, single-species stand is characterized by small trees that grow without competitive interaction (Oliver and Larson 1990). As the trees grow and begin to interact, this marks the onset of canopy closure and the growth rate of individual trees is reduced relative to their potential in the absence of intra-specific competition (Long and Smith 1984; Little et al. 1995). As I was unable to detect any differences in radial growth between sites prior to 1945 for Douglas-fir (Fig. 3.6a) and radial growth increments were remarkably similar for western hemlock until 1950 (Figs. 3.10a and 3.11a), it is these times that mark the likely onset of canopy closure.

Rates of basal growth of Douglas-fir adjacent to gaps in my study exceed the growth rates for Douglas-fir in other second-growth stands. In several stands in southwestern Oregon, Little et al. (1995) report BAIs for dominant Douglas-fir, similar in age to my study, that peak at 25-35 $cm^2 yr^{-1}$, depending on the stand. Comparatively, their results show that the trees in the stands they studied outperformed Douglas-fir in other second-growth stands in southwestern Oregon and were more indicative of sites that have been thinned and (or) fertilized. The mean BAI for Douglas-fir adjacent to gaps on my sites has leveled off in recent years at approximately 45-50 $cm^2 yr^{-1}$ (Figs. 3.7a and 3.8a), much higher values than those reported by Little et al. (1995). In their chronologies, decadally averaged BAIs tended to level off at a relatively early stand age (~ 30-40 years), similar to the chronology for Douglas-fir in the closed canopy that I recorded. However, in my study, BAIs for Douglas-fir on the edge of gaps continue to rise as the stand develops (Figs. 3.7a and 3.8a).

I found the difference in BAIs between western hemlock gap and canopy sites in the year 1945 puzzling (Fig. 3.11b). The differing values cannot be attributed to differences in the radial growth of newly regenerating seedlings during early stand development (1932-45; Fig. 3.10a & b). If any growth differences did exist between sites during this time, and were not detected, it would appear that the radial growth of western hemlock on canopy was higher than that of western hemlock trees on the gap sites (Fig. 3.10a). Two alternative hypotheses could account for this initial difference in BAI between gap and canopy sites. The first hypothesis is that, immediately after logging, the radial growth of already established seedlings and saplings adjacent to vine maple was much faster than stems on future closed canopy sites, perhaps due to the improved nutrient status associated with vine maple clones (Ogden 1996). Western hemlock adjacent to vine maple would then be able to establish larger diameter stems by 1945 than trees on closed canopy sites. However, because the newly regenerated seedlings did not experience greater radial growth than the closed canopy seedlings, I would not expect the radial growth of established western hemlock to be greater.

My second hypothesis is that a higher number of older stems do occur on the edge of the gap compared to the closed canopy in the western hemlock stand, even though no significant differences were detected between mean tree age (Fig. 3.2b). Nineteen western hemlock adjacent to the gap were biological legacies, defined as trees greater than 65 years breast-height age, whereas only 13 western hemlock in the closed canopy were (Fig. 3.2b). These legacies were already established at stand initiation and would obviously have larger boles than newly regenerating seedlings. As boles with larger diameters are associated with greater BAI, differences in age structure between sites would result in the differences in BAI between sites in 1945 (Fig. 3.11b).

If my second hypothesis is true, then the difference in BAI between western hemlock on the periphery of gaps and those in the closed canopy, is partly a result of inherent differences in tree age and size as well as differences in radial growth attributable to western hemlock's adjacency to the gap. Though apparent differences in radial growth do occur after the years of suspected canopy closure in the western hemlock stand, they are not of the same magnitude as seen between Douglas-fir sites (Figs. 3.7a and 3.11b), nor do the differences between BAI widen with time (Figs. 3.7b & c and 3.11b & c).

Competitive interactions between vine maple and conifers were not measured in my study. However, given the decline in radial growth rates following canopy closure for trees on closed canopy sites compared to trees adjacent to vine maple (Figs. 3.7 and 3.11), it is likely that competition between conifers is much stronger than vine maple--conifer interactions, even at this early age. This is consistent with studies that suggest that competition for light is one of the driving forces behind radial growth responses of conifers (Mitchell 1975; Law et al. 1992; Pacala et al. 1994). Since vine maple remains in the understory, it does not compete with adult conifers for light. Similar patterns of conifer growth around understory hardwoods occur in central Arizona. Competition between Ponderosa pine and Gambel oak, a shrubby hardwood, is minimal, even on dry sites, when Gambel oak remains in the understory (Biondi et al. 1992). The oak naturally spaces the pine, decreasing intra-specific competition, and increasing the radial growth of pine as the percentage of Gambel oak in the understory increases.

The radial growth releases associated with the formation of a developmental gap have been documented in several ecosystems and are based on suppression and release patterns. In temperate deciduous forests, Henry and Swan (1974) found that a 150% increase in tree-ring width for a period of at least four years marked a release from suppression. This same definition was also used by Veblen (1986) in a temperate spruce-Douglas-fir forest. In developmental gaps, growth responses last from several years to several decades (Clinton et al. 1993; Orwig and Abrams 1994), but gap resources are eventually utilized by species colonizing the gap, or crown expansion eventually closes the canopy opening (Runkle 1982; Frelich and Martin 1988). The size of priority gaps in my study is large enough to have resisted canopy closure by crown expansion for more than 70 years (McGhee 1996) and the benefits of increased basal growth around gap sites have been seen for approximately 50 years. Chronologies for Douglas-fir show little indication that the trend in BAI will change in the near future (Fig. 3.7), though growth differences between gap and canopy sites for western hemlock appear to be declining in recent years (Fig. 3.11).

In the stands that I studied, the trend in BAI for Douglas-fir is to increase with time (Fig. 3.8a). However, for western hemlock, the last decade (1985-94) has resulted in a significant decline in BAI on both gap and canopy sites (Fig. 3.9b). While Douglas-fir stems are still relatively young (Fig. 3.2a), some stems in the western hemlock stand are approaching 100 years breast-height age (Fig. 3.2b). Growth in older stems slows relative to younger stems (Oliver and Larson 1990) and these stems exert an influence on the overall mean, resulting in decadal BAIs that are declining on these sites (Fig. 3.8b).

4.3 Site Productivity

4.3.1 Site Index

In the stand dominated by Douglas-fir, I found the site index for trees adjacent to the gap to be higher than for Douglas-fir in the canopy (Fig. 3.12a). When all sampled Douglas-fir were included in the analysis, I did not detect a significant relationship between site index and the amount of vine maple foliage within 5 m of Douglas-fir stems (Fig. 3.12b). In an eastern hemlock (<u>Tsuga canadensis</u>) -- tulip poplar (<u>Liriodendron tulipifera</u>) stand in eastern Kentucky, Boettcher and Kalisz (1990) found that the soil landscape is a mosaic which reflects the nutrient cycling characteristics of the ground cover and tree species present on a site. Similarly, vine maple appears to be establishing areas of influence. The presence of vine maple increases the concentration of several bases in the priority gap environment (Ogden 1996) and this may be the reason for the improved site index (Fig. 3.12a).

The presence of hardwoods is not always associated with increasing the nutrient status of soils. Results obtained by Perry et al. (1987) in conifer stands with and without hardwoods showed that total nitrogen levels and mineralizable nitrogen were lower in the stands with hardwoods. Perry et al. (1987) attributes this effect to the fact that conifers cycle nitrogen differently when hardwoods are not present in the stand. Binkley (1995), states that studies suggesting hardwood species improve the soil is based on weak evidence, and that no study has proven that any single species positively or negatively influences soil properties. Therefore, attributing differences in site index between sites in a stand to a single species must be conducted with caution.

The percentage of vine maple within a 5 m radius of a subject tree was not significantly associated with site index (Fig. 3.12b). However, three of the four Douglas-firs with low site indices, but with a high percentage of vine maple within their 5 m radius, all occurred on one, steeply-sloped site (21°). Steep slopes are subject to erosion which can decrease the quality of a site (Swanson et al. 1989). When this priority gap site was not included in the analysis, the trend of increasing site index with increased percentage of vine maple became significant (Fig. 3.12b). This suggests that significant results may have been obtained had site factors been constant throughout the stand. These results are consistent with results obtained in the mixed Ponderosa pine -- Gambel oak stand in Arizona, where increases in the density of Gambel oak is correlated with increasing nitrogen concentrations in the organic layer and upper soil horizons (Lefevre and Klemmedson 1980).

Though the trend in my results suggest that the percentage of vine maple in the understory may have a positive influence on site index (Fig. 3.12b), Ogden (1996) found that the size of the clone did not affect the total amount of nutrients deposited on the forest floor. However, Ogden admits that differences may not have been detected given vine maple foliage represents a very small proportion of the total weight of litter entering the system, and her statistical power was low.

4.3.2 Basal Area Productivity

Site BA and current BA productivity are not significantly different between gap and canopy sites in the Douglas-fir stand, but are significantly lower for canopy sites in the western hemlock stand (Table 3.3). Douglas-fir is able to compensate for the 61% greater growing space it occupies around gaps by utilizing this space to increase its BA by 46% over Douglas-fir in the closed canopy (Table 3.3 and Fig. 3.13a & c). As radial growth for Douglas-fir on priority gap sites continues to exceed radial growth for Douglas-fir in the closed canopy (Fig. 3.7a), there is no indication that site BA for Douglas-fir in the closed canopy will become significantly greater than site BA on priority gap sites in the future.

Western hemlock on the gap periphery are unable to compensate for the increased amount of growing space imposed by the large size of the expanded priority gaps in the western hemlock stand (Fig. 3.1b). Though western hemlock adjacent to gaps have mean BAs that are 69% greater than closed canopy hemlock, the potential growing space for western hemlock adjacent to gaps is 150% greater than in the canopy. This results in the lower site BA and current BA productivity on gap sites (Table 3.3 and Fig. 3.13b & d). There is no indication that western hemlock adjacent to gaps can compensate for this difference in the near future, as the ratio of current BA productivity for western hemlock adjacent to gaps to those in the closed canopy (0.62) is actually lower than the ratio of site

BA (0.64). This is attributable to the declining difference in radial growth rates and BAIs between gap and canopy sites in the past decade (1985-94; Fig. 3.11). If the western hemlock stand persisted well into the mature stage, I would expect the differences between site BA between gap and canopy sites (Table 3.1) to decline; not because of increased basal growth rates around gaps, but because as dominant stems in the canopy grow larger and require a greater growing space (Oliver and Larson 1990), they will likely cause the mortality of adjacent trees and increase their own potential growing space. As the patchiness of the stand increases through the mature stage (Oliver and Larson 1990), dominant western hemlock in the canopy may eventually occupy potential growing spaces similar to western hemlock adjacent to gaps.

4.4 The Distinctness of Vine Maple Priority Gaps

Vine maple is distinct because it is a deciduous tree species that is shade-tolerant which persists in the understory of conifer stands. Other deciduous species in southwestern B.C., for example red alder and bigleaf maple, are less shade-tolerant and are part of the canopy layer in young to middle-aged stands they occupy (Haeussler et al. 1990). For priority gaps to develop, an understory species must be able to prevent the establishment of conifers at stand initiation and through several successional stages. The understory species must also be shade-tolerant enough to persist through the dense stem-exclusion phase. Salmonberry (Rubus spectabilis) is an understory shrub species which Tappeiner et al. (1991) suggest persists in the understory of west coast conifer stands, preventing the establishment of even shade-tolerant conifer species and holding open a gap in the canopy for many years.

Because vine maple remains in the understory, it does not compete for light with mature conifers, and light is one of the major limiting factor to growth in temperate rainforests (Mitchell 1975; Law et al. 1992). Thus, trees around vine maple priority gaps are able to accumulate basal wood faster than trees in the adjacent canopy (Fig. 3.9). As potential growing space was highly correlated with BA in my stands (Table 3.2), I would not expect similar rates of basal growth to occur where conifers are adjacent to overstory hardwood species, such as red alder or bigleaf maple, instead of the priority gap.

Chapter 5

CONCLUSIONS

5.1 Summary of Findings

The recent discovery of priority gaps offered an excellent opportunity to quantify the impact of vine maple priority gaps on the development and growth of conifers on the periphery of priority gaps compared to conifers in the adjacent forest matrix. My research goal was to determine the influence of vine maple priority gaps on the morphology, basal growth, and productivity of Douglas-fir and western hemlock within the coastal temperate rainforest of British Columbia.

Median expanded priority gap size was significantly smaller in the Douglas-fir stand (80 m^2) than in the hemlock stand (197 m^2). Priority gaps in the Douglas-fir stand were similar in size to the single tree developmental gaps measured by Spies et al. (1990) in coastal Douglas-fir stands; whereas, priority gaps in the western hemlock stand were similar in size to the gaps measured by Spies et al. (1990) in old-growth temperate rainforest and to old-growth sub-alpine forests in southwestern B.C. (Lertzman and Krebs 1991). The higher degree of interstitial spacing in stands dominated by Douglas-fir enables more diffuse light to reach the vine maple clone than in stands dominated by western hemlock, requiring a relatively smaller gap size to allow enough light to reach the clone to ensure its survival.

Douglas-fir and western hemlock on the periphery of priority gaps utilized the increased spacing associated with the gap to increase their crown volume and bole size. The larger crown volumes of gap conifers were a result of deep crowns and crown expansion into the gap. Crown expansion in developmental gaps is an important means of gap filling (Frelich and Martin 1988; Spies and Franklin 1989). Developmental gaps often fill by advanced regeneration or seedling establishment, but this rarely occurs on priority gap sites (McGhee 1996).

Trees of both species on the edge of priority gaps had significantly greater BAIs than trees in the closed canopy. No differences in radial growth patterns during the earliest stages of stand development (1932-1945) were detected for either species. The canopy of the Douglas-fir stand likely began to close in the years after 1945, initiating a decrease in the ratio of canopy BAI to gap BAI, which continued to decline to a value of approximately 0.6 in 1994. In the western hemlock stand, differences in annual ring width do not occur until approximately 1950. The ratio of closed canopy BAI to gap BAI for hemlock has been relatively steady between 1945-1994, fluctuating between 0.6 and 0.7.

Douglas-fir on the periphery of vine maple priority gaps had a significantly higher site index than Douglas-fir in the forest matrix. An increasing percentage of vine maple within a 5 m radius of Douglas-fir was significantly positively correlated with site index only after 3 outliers, which all occurred on a steeply-sloped priority gap site, were removed from the analysis. The high concentration of bases in vine maple litter (Krajina et al. 1982; Ogden 1996) may be responsible for the higher site index measured around priority gaps. This relationship has important implications on the long-term health and productivity of forest ecosystems where vine maple is present in the understory (Edmonds et al. 1989).

In the stand where Douglas-fir was the dominant canopy tree, site BA and current BA productivity were not significantly different between vine maple priority gaps and paired closed canopy sites. The BA of Douglas-fir on the edge of priority gaps was 46% larger than Douglas-fir in the canopy and this largely compensated for the 61% greater spacing between conifer stems associated with the presence of the priority gap. For western hemlock on the edge of the priority gaps, the BA was 69% greater than trees in the canopy, but this was not large enough to compensate for the 150% greater potential growing space that western hemlock on the gap occupy.

Managing for biodiversity means ensuring that distinct habitat niches, such as vine maple priority gaps, remain an integral part of forest stands. Vine maple is an important species in west coast ecosystems, and its shade-tolerance offers an opportunity to retain hardwood species, and their beneficial effects, in the understory of conifer stands. Integrating vine maple priority gaps into stand management practices promotes the development of stands that are rich in biological and structural diversity while still meeting the socio-economic needs of our society.

5.2 Management Implications

The body of new knowledge being generated by ecologists has given scientists and managers an appreciation for the enormous complexity of forest ecosystems. Simple forest practices, such as clearcutting, that create uniform, even-aged stands that lack both biological and structural diversity are being abandoned for more ecologically responsible alternative forest practices (Coates and Steventon 1994; Lippke 1996; Kohm and Franklin 1997). The emerging theme of ecosystem management is to manage for the long-term integrity of the whole ecosystem and not only for the production of merchantable timber (Lertzman et al. 1997). Timber production is now often a secondary objective for many forest managers:

> Today, multiple objectives typically include maintenance of specific levels of ecosystem processes, including habitat for elements of biological diversity. Tree regeneration and its subsequent growth are often still concerns, although these objectives -- especially for rapid growth of regeneration -- often are subordinate to other goals. ...Recent research on forest ecosystems has clarified the importance of structural complexity to forest ecosystem functioning and the maintenance of biological diversity. (Franklin et al. 1997)

Tappeiner et al. (1997) believe that two management philosophies will begin to emerge in forestry over the next few decades. One system would manage for the retention of old-growth characteristics, while the second management philosophy would aim to produce high yields of wood while still incorporating "considerable habitat diversity and other values." Based on my analysis of priority gaps and adjacent conifer species, I have identified two main recommendations from my research and provide the rationale behind these recommendations:

1) Silvicultural practices should enhance the diversity of stand structure and wildlife habitats, particularly during earlier successional stages, by incorporating vine maple priority gaps within a matrix of continuous forest cover.

The inclusion of vine maple priority gaps in earlier successional stages helps managers develop stands that are diverse in structure (Tappeiner et al. 1997) and ensures that distinct habitats are retained in B.C. coastal forests. Vine maple is distinct in that it is an understory hardwood species that is shade-tolerant. It has the ability to persist in the understory of conifer stands, even through the dense stem-exclusion stage (Russel 1973; O'Dea et al. 1995). By preventing the establishment of conifers on sites that it occupies (McGhee 1996), vine maple plays an important role in adding structural diversity in the young to middle-aged stands of B.C.'s west coast forests. McGhee found only 6.3% of the forest area in stands emerging from stem exclusion was influenced by developmental expanded gaps, but 19.7% of the forest area was influenced by expanded priority gaps.

Stands with a diversity of tree species will support more wildlife than a stand with only one tree species (B.C. Ministry of Forests and B.C. Environment 1995b). Vine maple and vine maple priority gaps can aid managers in meeting habitat and biodiversity objectives, as vine maple is important to a variety of wildlife. Vine maple is an important species for deer and elk populations (Brown 1961; Miller 1968; Singleton 1976; Tappeiner and Zasada 1993), which browse on its leaves and twigs. Mountain beavers forage on vine maple, climbing several meters to cut off small limbs (Harestad 1983). Vine maple communities provide excellent habitat for rabbits (Haeussler et al. 1990). In the Pacific Northwest, large trees with extensive large-diameter branching systems, like the trees with deep crowns that grow adjacent to priority gaps (Figs. 3.3 and 3.4), are important to species such as marbled murrelets and northern spotted owls (Franklin et al. 1997). Pacific-slope flycatchers also use the deep conifer crowns adjacent to the gap for a perch from which to hawk for insects above vine maple foliage (Lertzman et al. *unpubl.*). Lertzman et al. (*unpubl.*) also found that the number and diversity of bird species is significantly higher within the vine maple gap than in the adjacent closed canopy, and attribute this to the diversity of resources associated with vine maple gaps.

2) Forest managers should promote the development of vine maple priority gaps through all successional stages due to the benefits of long-term site productivity that are associated with vine maple and vine maple priority gaps.

The positive influence of vine maple in terms of the high concentrations of nutrients in its foliage (Ogden 1996) suggests that vine maple may play an important role in enhancing the productivity of a stand through many rotations (Edmonds et al. 1989). Its ability to colonize on most sites within a stand (Haeussler et al. 1990; Tappeiner and Zasada 1993; McGhee 1996; Ogden 1996) would give managers the flexibility to allow vine maple to propogate on relatively nutrient poor sites, thus replenishing soil nutrients and retaining high levels of productivity through successive rotations. With the increased site quality (Table 3.1 and Fig. 3.12a) associated with vine maple priority gaps also comes greater height growth, adding to the greater bole volume that would be associated with greater basal size for trees adjacent to the gap (Nyland 1996).

Other implications of the benefits of vine maple priority gaps arise from my research. Allowing vine maple to regenerate naturally reduces the need to control vine maple. This should help minimize stand management costs, particularly during the earliest stages of stand development when vine maple is considered to be most competitive with conifer species (Haeussler et al. 1990). Ideally, vine maple should be left to propogate, which would likely result in the occurrance of priority gaps through stem exclusion and later successional stages. However, in some coastal forests in Washington and Oregon, vine maple is very prolific and can form dense thickets, preventing merchantable conifers from regenerating (Haeussler et al. 1990). In cases where vine maple is a significant competitor, vine maple could be manually controlled to prevent the establishment of very large priority gaps. The natural priority gap size distribution in a stand would likely vary with slope, aspect, latitude, overstory species and site index, and the priority gaps I measured are likely only representative of stands with very similar site characteristics to those in my study. In order to ensure that priority gaps persist through the dense stem-exclusion stage, vine maple clones need to become firmly established prior to canopy closure, as propogation of vine maple rarely occurs during stem-exclusion (Russel 1973; O'Dea et al. 1995).

Site BA and current BA productivity do not significantly differ between Douglas-fir priority gap sites and sites in the adjacent canopy (Fig. 3.13a & c), suggesting biodiversity and stand structural objectives in these stands can be met without significant losses in timber production. However, the value of the wood, and therefore the economic returns from the stand, may differ between sites. Without an extensive analysis of the value of timber harvested on gap and canopy sites, this question can only be addressed qualitatively, by inferring potential economic returns from the characteristics of gap and canopy trees and from general guidelines which determine timber value.

In general, large trees with straight boles command the highest returns to producers:

> Large trees are increasingly scarce, as natural forests are progressively 'creamed', and short-rotation managed crops become more dominant in timber supply.... A large tree or log commands a higher delivered price per cubic meter than a small one. It is also less costly per cubic meter to harvest: felling several small trees requires a repeated sequence of operations needed only once for a large one; debranching a large tree is substantially faster than the equivalent volume of small ones; attaching extraction wires, chains or ropes may take no longer for a large log than a small one.... Economies of handling large logs continue in processing, and the larger the log, the higher percentage conversion to final products. (Price 1989)

Large diameter stems can be worth several times the price per cubic meter than small diameter stems (Nyland 1996), depending on market trends and the quality of the wood produced. The largest diameter stems in the two stands occur adjacent to priority gaps (Table 3.1) and this may increase the value of the trees harvested. However, wood value is also a function of quality, and wood quality decreases as the percentage of knots, particularly in the main trunk portion increases (Nyland 1996). Nyland (1996) reports that the most valuable trees have no branches on the lower part of the bole, or only small diameter branches, and that these are usually found in the closed canopy. The deep and wide crowns that develop adjacent to gaps (Fig. 3.3) likely result in more and larger knots in the lower boles for conifers located next to a gap. Though significant trade-offs in timber production are associated with priority gaps in stands dominated by western hemlock (Fig. 3.13b & d), the retention of vine maple priority gaps in these ecosystems is still important, as "forests function to sustain the whole, not to produce any one part. Every part is essential, but no part is more or less important than another" (Hammond 1991).

5.3 Suggestions for Future Research

Several areas of vine maple research remain unexplored. Though the role of vine maple as a 'weed' or 'pest' has been well documented in the literature (Haeussler et al., 1990), only recently has research into the beneficial influence of vine maple on the health and productivity of forests been conducted. The influence of priority gaps on the quality and value of wood produced on the edge of these gaps needs to researched. Also, studies addressing whether the presence of vine maple decreases conifer seedling mortality due to ungulate browsing should be undertaken. Finally, controlled, long-term vine maple studies which can accurately address whether vine maple is responsible for increasing site quality and sustaining long-term site fertility need to be conducted.

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