Zur Homepage der Dissertation

ON THE ECOLOGY OF *ACER CIRCINATUM* PURSH:

A STUDY OF FACTORS THAT AFFECT THE DISTRIBUTION OF A SMALL HARDWOOD TREE WITHIN OLDGROWTH FORESTS IN SOUTHWESTERN BRITISH COLUMBIA, CANADA

Vom Fachbereich Biologie, Geo- und Umweltwissenschaften

der Carl von Ossietzky Universität Oldenburg

zur Erlangung des Grades einer

Doktorin der Naturwissenschaften

angenommene

Dissertation

von

Judit Gaspar

geboren am 1. Mai 1969 in Bad Godesberg

Oldenburg, April 2002

Erstreferent: Prof. Dr. Dietrich Hagen

Korreferent: Prof. Dr. Wolfgang Eber

Tag der Disputation: 5. 7. 2002

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LIST OF ABBREVIATIONS

#	number
A. circinatum	*Acer circinatum*
A. macrophyllum	*Acer macrophyllum*
A. plantanoides	*Acer plantanoides*
A. saccharum	*Acer saccharum*
A. rubrum	*Acer rubrum*
act	actual
ANOVA	analysis of variance
asl	above sea level
BC	British Columbia
BP	before present
CHIL	Chilliwack
COQ	Coquitlam
dbh	diameter at breast height
deg.	degree
DEM	digital elevation model
et al.	et alii
GVRD	Greater Vancouver Regional District
ha	hectare
IUGS	International Union of Geological Sciences
LAD	least absolute deviation
LED	light emitting diode
LSCR	Lower Seymour Conservation Reserve
max	maximum
min	minimum
N	North
n	number of cases
NY	New York
No.	number
OLS	ordinary least squares
ON	Ontario
OR	Oregon
p	probability of type I error
P. connectilis	*Phegopteris connectilis*
PAR	Photosynthetic available radiation
pers. comm.	personal communication
PVC	Polyvinylchloride
R. spectabilis	*Rubus spectabilis*
r^2	coefficient of determination
seedl.	seedling

SO	site openness
spec.	species
Tl	tree layer
TN	Tennessee
UBC	University of British Columbia
US	Upper Seymour
V. alaskaense	*Vaccinium alaskaense*
var.	variety
W	West
WA	Washington

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INTRODUCTION

The interaction of abiotic, biotic and historical factors combines with species characteristics to determine the distribution of a species (Hutchinson 1957, Begon et al. 1991, Frelich et al. 1993). Another factor that might influence species distribution, chance, is more commonly considered as the "null" factor, the background against which theories are tested. Which factors predominate in importance changes with the scale investigated (Reed et al. 1993, Ohmann and Spies 1998). The factors that affect the distribution of vine maple (*Acer circinatum*), a small hardwood tree, within oldgrowth forests in southwestern British Columbia are the subject of this study.

The most influential abiotic factor for the pattern of tree species distribution in the temperate coastal rainforests of British Columbia (BC) is climate (Green and Klinka 1994, Meidinger and Pojar 1991). On a smaller scale, variations in topography, soil, moisture, nutrient availability and light availability are frequently relevant (Krajina et al. 1982, Spies et al. 1990, van Pelt and Franklin 2000, Klinka et al. 1985, Klinka et al. 1996a, Bridge and Johnson 2000).

Though all abiotic factors are influenced, modified or even caused by the effects of living organisms, traditionally only direct interactions between species, including humans, and the effects of species characteristics are called biotic factors (Sitte et al. 1991). Above- and belowground competition between trees for resources, seedling predation and the presence of pathogens are examples of biotic influences that can shape tree distributions in the Pacific temperate rainforest (Oliver and Larson 1990, McKenzie et al. 2000, Fried et al. 1988, Perry et al. 1987, Tappeiner and Zasada 1993, Haeussler et al. 1990). Logging and planting are the most obvious form human influence takes. The exclusion of brush species, fire suppression and pathogen control are other examples (Oliver 1981, Messier and Kimmins 1991).

The effect of former abiotic or biotic influences on the present distribution of a species is subsumed under the term historical factors. Disturbance regimes are of particular importance (Klinka et al. 1985, Halpern 1989, Miles and Swanson 1986, Oliver et al. 1985, Lertzman et al. 1996, Lertzman and Krebs 1991). Species presence before stand disturbance, the pattern of invasion after a disturbance and the history of biotic interactions like the effects of previous competition all help shape the observable present distribution (Franklin and Hemstrom 1981, Messier and Kimmins 1991, Gagnon and Bradfield 1986).

The distribution of a small tree within a forest of taller trees is a special case of tree distribution. Vine maple is a deciduous shrub or tree usually less than 10 m tall within a forest dominated by long-lived evergreen conifers that can reach easily 50 or 60 m in height (Pojar and MacKinnon 1994, UBC Botanical Garden 1976). In the temperate rainforests of coastal British Columbia deciduous trees are disadvantaged by a climate of mild winters with heavy precipitation and warm and relatively dry summers (Waring and Franklin 1979). They often play pioneer roles or occupy habitats whose environmental features differ from the regional norm, for example avalanche chutes, old logging roads and riparian zones (Haeussler et al. 1990, Massie et al. 1994, McGhee 1996, Ohmann and Spies 1998).

Vine maple is an exception. It is an common understory shrub or small tree in both early and late seral stands in the Pacific region from northern California to southwest British Columbia (UBC Botanical Garden 1976, Krajina et al. 1982, Haeussler et al. 1990). Though vine maple is a common understory species, the ecology of vine maple in British Columbia has received little attention so far. How vine maple maintains its presence in the understory of the tall conifer forests in the forest is poorly understood, as are its pattern of distribution and the underlying causes for it.

Vine maple might be viewed as a model of a small tree growing in the understory of a coniferous forests. Other understory trees and shrubs who might follow similar growth strategies as vine maple might include salmonberry (*Rubus spectabilis*), Douglas maple (*Acer glabrum*), pacific yew (*Taxus brevifolia*) and cascara (*Rhamnus purshiana*). Vine maple is therefore an interesting species from the scientific as well as from a management perspective.

From the management perspective vine maple offers an opportunity to include a hardwood component and all the benefits associated with this in all stages of stand development. Forest stand development in British Columbia undergoes a predictable series of four developmental stages following a stand-destroying disturbance, according to the widely accepted succession model developed by Oliver (1981, detailed discussion in Oliver and Larson 1990). A stand initiation stage is followed by a stem exclusion, an understory reinitiation and finally an oldgrowth stage, if the development is not interrupted by another disturbance event. During stand initiation trees reestablish from seeds, suppressed saplings or through sprouting from stumps (Oliver and Larson 1990). Hardwoods, typically *Alnus rubra* and *Acer macrophyllum,* but also vine maple, may dominate the stand initiation stage until the taller conifers overtop or replace them (Franklin and Hemstrom 1981, Krajina et al. 1982, Haeussler et al. 1990, Tappeiner and Zasada 1993, Massie 1994, Pojar and MacKinnon 1994, Klinka et al. 1996b, McGhee 1996).

After several years of development, no new individuals are able to establish in the stand and some of the existing ones die due to competition (Oliver and Larson 1990). This stem exclusion stage is the least biologically diverse since severe light interception from the dense conifer overstory suppresses or excludes the understory (Klinka et al. 1996a, Qian et al. 1997, Lezberg 1998). Vine maple is able to survive in the understory during this stage (O'Dea 1992, McGhee 1996, Ogden 1996). Later the conifer canopy opens up again and the understory of forest floor herbs and shrubs and advance regeneration is reestablished (Oliver and Larson 1990, Tappeiner and Zasada 1993).

Much later the oldgrowth stage may be reached, when the death and subsequent replacement of single trees of the original cohort becomes the dominant form of stand dynamics (Spies and Franklin 1989, Oliver and Larson 1990, Lertzman et al. 1996, Lertzman and Krebs 1991). Oldgrowth stands in coastal British Columbia are characterized by a high structural complexity. The dominant conifers are long-lived, individual trees 600 to 1000 years old are not uncommon (Pojar and MacKinnon 1994). Natural stand-destroying disturbances like fires occur only with long intervals (Dale et al. 1986, Spies and Franklin 1989, Waring and Franklin 1979). Gap dynamics result in a wide variation in tree sizes, ages and the spacing of trees, multiple canopy layers and the accumulation of large sized dead standing and fallen trees (Lertzman and Krebs 1991, Lertzman et al. 1996). In oldgrowth stands multiple different habitats for plants, animal and fungi exist due to the heterogeneity in substrate, light and moisture availability that results from the structural complexity. The patchy, open canopy allows understory plants like vine maple to flourish. Coastal forests may need between 140 and 500 years to achieve oldgrowth characteristics (Harding 1994, Oliver 1981).

Commercial forest harvest in British Columbia manages forests for even aged stands of one to three conifer species on a harvest rotation of 80 - 140 years (Slaymaker 2000, Harding 1994, Qian et al. 1997). These forests will never reach the oldgrowth stage and the associated structural characteristics. Instead structurally homogeneous stands are created. In these stands biological diversity is reduced, since habitat requirements of less species are met (Qian et al. 1997, McGee et al. 1999). Bird species diversity, for example, is highly correlated with the number of canopy layers in a forest (Recher 1969).

About 190,000 ha forest were harvested per year in the 1990s, most of this through clearcutting (Slaymaker 2000). Within decades only small remnants of oldgrowth will be left in British Columbia (Harding 1994). Concern about the loss of biodiversity, especially of animal species dependent on oldgrowth characteristics like the spotted owl (*Strix occidentalis*) and marbled murrelet (*Brachyramphus marmoratus*), has heightened interest in ways to conserve biodiversity in managed stands in British Columbia.

The retention of a hardwood component throughout the cycle of cultivation enhances biodiversity through the addition of structural complexity and food and habitat for other species (Massie et al. 1994). The Biodiversity Guidebook to the Forest practices Code of British Columbia Act (BC Ministry of Forests and Environment 1995) therefore recommends that the proportion and distribution of the deciduous broadleaf stand components should be maintained during forest management.

Vine maple is particularly suited for this purpose, since it is a natural forest component throughout all stages of stand development (Haeussler et al. 1990, O'Dea 1992). Vine maple is an important food source and habitat for many animal species, including the Red-listed mountain beaver (*Aplodontia rufa rufa*) (Bailey and Poulton 1968) and the Blue-listed Roosevelt elk (*Cervus elaphus roosevelti*) (Singleton 1976, Haeussler et al. 1990, Harcombe et al. 1994). Species on the Red List are endangered with imminent extinction or extirpation throughout their range in British Columbia or likely to be endangered if factors affecting their vulnerability are not reversed. Species on the Blue List are considered to be at risk (Harcombe et al. 1994). Especially birds use the food supply and structural complexity vine maple clones offer (McGhee 1996, Hauessler et al. 1990). The deciduous leaf litter is decomposed to mull or moder humus forms instead of the mor humus forms prevalent under conifers (Tashe 1998, Ogden 1996), providing a divergent habitat for soil communities.

The presence of vine maple does not cause losses to site basal area, and with it timber production, in mature Douglas-fir stands, but increases the height of adjacent conifers (Wardman 1997). This increase in productivity is caused by additional nutrients provided by vine maple leaf litter. Vine maple leaf litter has higher nitrogen, phosphorus and micronutrient concentrations compared to conifer leaf litter (Tashe 1998, Ogden 1996).

1 Research objectives

This study attempts to determine factors that affect the distribution of vine maple within oldgrowth stands in British Columbia. An understanding of the ecology of vine maple will foster the understanding of forest dynamics and species distribution within the coastal temperate rainforests of British Columbia. Oldgrowth stands were chosen to eliminate confounding by human influence on vine maple distribution.

A sound ecological foundation is essential for proper forest management. The results of this study should provide foresters with the necessary ecological information to incorporate vine maple in forests management plans.

2 Vine maple characteristics and ecology

Vine maple is a deciduous multi-stemmed shrub or small tree of the pacific section *palmata* PAX of the genus *Acer* (van Gelderen et al. 1994). The stems are usually pale green, weak and slender and can reach up to 10 m in height. They emanate from a common root ball. In the shade the stems often grow in characteristic arching or crooked shapes that result in irregular clone crowns (Figure 1).

Figure 1: Vine maple stem displaying the characteristic arched shape. In the fore and middle ground additional vine maple stems are visible.

In the sun the stems are shorter, more erect and form a more compact and symmetric crown. Clones consist of uneven-aged stems, since stems are episodically replaced. The light-colored wood is dense and hard and rots quickly when in contact with the soil. The nearly circular opposite leaves have seven to nine sharply-toothed lobes. They are thin, lime green and can turn bright red in the fall if they are growing in a sunny spot. The root system is vigorous, but not invasive. No central tap-root is present (Haeussler et al. 1990, UBC Botanical Garden 1976).

Vine maple can propagate both sexually and vegetatively. The plant is monoecious, its seeds are double, winged samaras. Seed production is usually low (O'Dea 1992, UBC Botanical Garden 1976) as is seedling survival in both clearcuts and forests (Tappeiner and Zasada 1993, Russell 1974, Anderson 1967). Vegetative reproduction can occur through layering, root suckers and root sprouting. Layering occurs if stems or branches are pinned to the ground by fallen trees or branches, or simply if the stems become to long and heavy to remain erect. Sprout production is induced through mechanical damage, for example during logging (O'Dea 1992, Haeussler et al. 1990).

Following logging vine maple can quickly regenerate from surviving root or stem material, recreating the pattern of distribution found before the disturbance (O'Dea 1992, Drew 1968, Russell 1974, Anderson 1967). If residual stems are pinned to the ground by slash, they can layer and form extensive mats (O'Dea 1992, Haeussler et al. 1990). Vine maple is therefore believed to be a serious competitor to conifer establishment in clearcuts and routinely removed from managed stands. Vine maple control is recommended for up to ten years after logging, when conifers have overtopped vine maple (Krajina et al. 1982, Haeussler et al. 1990, Tashe 1998, Klinka et al. 1996b).

A bi-modal model of the life cycle of vine maple after clearcut logging was developed at the University of Oregon by Anderson (1967) and Russell (1974). After successful establishment of vine maple in a clearcut, it is abundant for the first 25 years after stand initiation, but is reduced to near extinction in the dense shade of the stem exclusion phase of stand development. When the stand has reached the oldgrowth stage, openings in the conifer canopy appear that allow vine maple to reestablish.

In the 1990s renewed scientific interest in vine maple has led to modifications of the bi-modal model. Vine maple occurrence in all stages of stand development was observed (O'Dea 1992). Throughout the critical time period of the stem exclusion and forest maturity phase vine maple is able to keep conifer canopy gaps open for at least 80 years (McGhee 1996) or perhaps even for 140 years (Spies et al. 1990). These gaps are not caused by more or less permanent surface features like rock outcrops or creeks (edaphic gaps sensu Lertzman et al. 1996). Two studies found no differences in soil gravel content, soil texture and soil pH in direct comparisons of the mineral soil below vine maple in these gaps and below adjacent conifers (Tashe 1998, Ogden 1996). These gaps are also not caused by the death of overstory trees (developmental gaps, the “classic” canopy gaps of for example Runkle 1985, Canham et al. 1990 and Brokaw 1985). Instead vine maple is believed to establish itself after logging and subsequently keep a gap open through its presence. The resulting vine maple gaps are termed priority gaps, since they result from priority effects early in stand development (McGhee 1996). Priority effects describe the following process: the colonists first to arrive on a site secure space and/or other resources and inhibit the invasion of subsequent colonists (inhibition model of Connell and Slayter 1977). This process may determine final species composition (Abrams et al. 1985, McCune and Allen 1985, Robinson and Edgemon 1988).

The existence of vine maple priority gaps implies that vine maple is able to hinder gap closure through conifers. Small canopy gaps can close through lateral expansion of the branches of adjacent conifers towards the gap center, larger gaps through the establishment of seedlings within the gap or the release of advance regeneration (Spies et al. 1990, Spies and Franklin 1989, Ehrenfeld et al. 1995, Whitmore 1989). Lateral expansion of branches was observed in conifers adjacent to vine maple priority gaps (Wardman 1997), the closure of small gaps can therefore not be prevented by vine maple. To keep larger gaps open vine maple has to repress conifer seedling establishment in the gap. Suspected mechanisms for this repression are the shading of conifer seedlings (McGhee 1996) and allelopathy of vine maple foliage to Douglas fir and other species (del Moral and Cates 1971). Vine maple is also known to rapidly deplete soil moisture (Drew 1968) and might prevent through this mechanism the establishment of conifer seedlings in the forest floor.

Edaphic and developmental gaps can also be occupied by vine maple, since they provide more light than the closed conifer canopy (Anderson 1967, Russell 1974, McGhee 1996). Vine maple is very shade tolerant, but vine maple growth is improved in canopy openings (Haeussler et al. 1990, Krajina et al. 1982, UBC Botanical Garden 1976). Vine maple survival might even depend on canopy openings or other areas of higher light availability, like forest edges and river terraces (Anderson 1967, Russell 1974, Drew 1968, Pojar and

MacKinnon 1994, Bailey 1966). In the absence of conifers on fragmental colluvial soils and block lava vine maple can dominate (Klinka and Krajina 1986, Klinka et al. 1989, Roach 1952). Both of these sediments are characterized by an absence of fine material that might pose an obstacle to conifer establishment. In two studies the light requirements of vine maple were quantified indirectly via overstory biomass and overstory cover (Russell 1974, McKenzie et al. 2000). In both studies an influence of these features on vine maple was observed. In one study the light environment below fully leafed vine maple was measured (McGhee 1996). No direct measurements of light availability to vine maple were realized so far.

As a second ecological requirement of vine maple besides high light availability a restriction of vine maple to fresh to wet sites is frequently mentioned (Haeussler et al. 1990, Pojar and MacKinnon 1994, Klinka et al. 1989, Krajina 1969). Creek beds, seepage areas and depressions are common habitats of vine maple (Haeussler et al. 1990, Parish and Thomson 1994, Lyons and Merilees 1995, Pojar and MacKinnon 1994, UBC Botanical Garden 1976). In Oregon vine maple has also been observed on xeric sites (Anderson 1967, Roach 1954). Therefore likely no physiological requirement of vine maple for high moisture availability exists. The two studies that compared edaphic properties of vine maple gaps to the surrounding conifer forest (Ogden 1996, Tashe 1998) indicated that vine maple is not dependent on comparatively wetter sites.

3 Hypotheses

This study is based on the assumption that vine maple distribution within a forest stand is not random. The pattern of distribution reflects the reaction of vine maple to environmental factors according to species characteristics.

Five factors were suggested by the literature as potentially influential on the distribution of vine maple within a stand: surficial geology (colluvial sediment and block lava), light availability, ground water levels, microtopography (creeks) and vine maple persistence (priority effects). Creeks are considered separately from ground water levels, since the often observed association of vine maple with creeks (Haeussler et al. 1990, Parish and Thomson 1994, Lyons and Merilees 1995, Pojar and MacKinnon 1994, UBC Botanical Garden 1976) might be due to other factors than improved moisture availability.

The following hypothesis about the influence of these factors on vine maple distribution were developed:

1. The presence of surficial sediments with little fine material will increase vine maple occurrence. Apart from edaphic differences caused by different surficial sediments, vine maple occurrence is not connected to soil type, texture or pH.
2. Vine maple distribution is directly light dependent. Vine maple performance will decline with a reduction in available light up to the exclusion of vine maple.
3. Contrary to common belief vine maple occurrence is not dependent on high ground water levels.
4. Vine maple occurrence is positively related to creeks.
5. Vine maple priority gaps persist into the old growth stage of forest succession. Vine maple can outcompete conifer seedlings for forest floor moisture and thus may prevent conifer seedlings from establishing in vine maple gaps.

Other factors that were included in this study are the response of vine maple to slope inclination and the time needed for habitat acquisition through layering. Steep slopes might reduce conifer canopy closure and therefore increase vine maple occurrence. Layering is the most important method of reproduction of vine maple in oldgrowth stands (O’Dea 1992). The time vine maple needs to reach new habitats can be estimated through the analysis of layering plants.

METHODS

1 Study sites

1.1 Lower Seymour Conservation Reserve

Location

In the Lower Seymour Conservation Reserve (LSCR), North Vancouver, BC, Canada, a stand was found that was suitable for this study. The LSCR was located in the Seymour Valley, a major valley running southwards within the Coast Mountains. The valley was 35 km long and opened into the Fraser Lowland. The Seymour watershed has provided drinking water to Vancouver since 1908, since 1936 the Seymour Valley was closed to the public for protection. In 1987 the area south of Seymour Falls Dam was opened to the public as the Seymour Demonstration Forest (now Lower Seymour Conservation Reserve). The area north of the dam is still closed to the public (Kahrer 1989). The study site was located close to Seymour falls dam, east of the Seymour River, approximately at 49°28'N and 123°42'W at an elevation between 360 and 470 m above sea level (asl) (Figure 2).

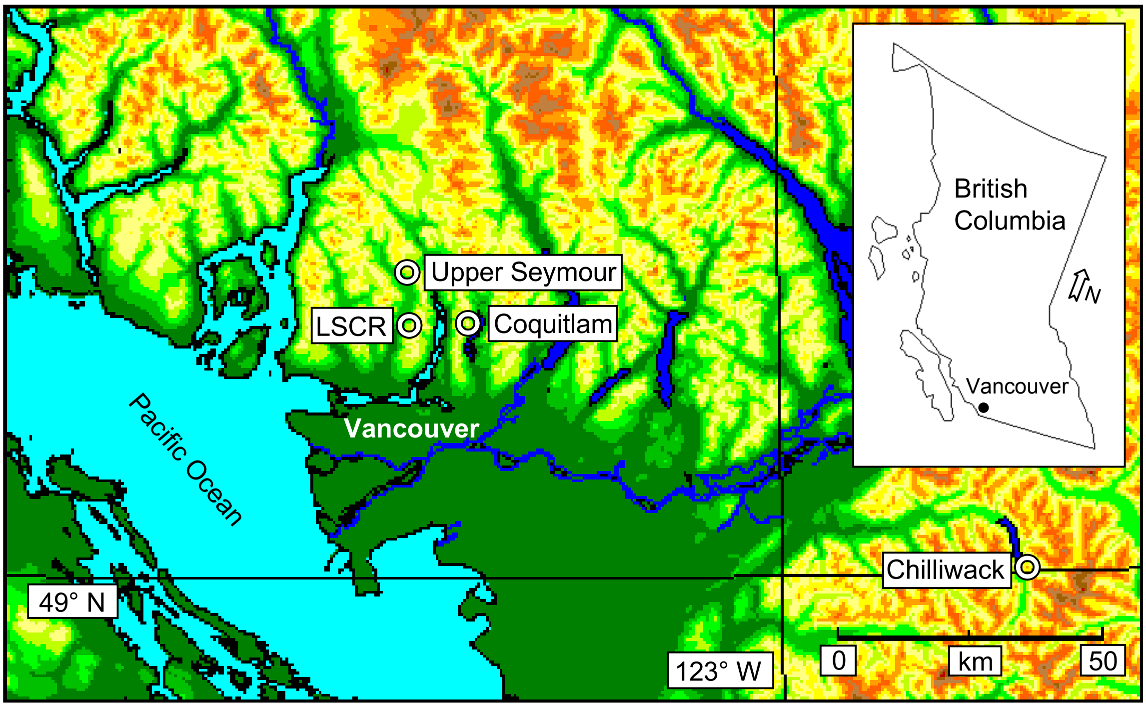

Figure 2: Location of the four study sites: Lower Seymour Conservation Reserve (LSCR), Upper Seymour, Coquitlam and Chilliwack. The map is based on a digital elevation model of the Georgia Basin (Environment Canada 2001a). Heights vary from 0 – 2500 m asl.

The study site covered an area of roughly 3.5 ha. The borders were determined to the west by a buffer zone of 40 m width to a gravel road, to the north and south by 10 m wide buffer zones to creeks. The eastern border was set to a distance of 250 m from the western border. The creek to the north of the study area was called Squamish Creek, the creek to the south had no name. Cliff sides (in the center along a precipice) and steep slopes with many fallen logs (in the southeast) were excluded from this area (Figure 3). The study site had a western exposition. Slopes in the site varied between five and 40 degrees.

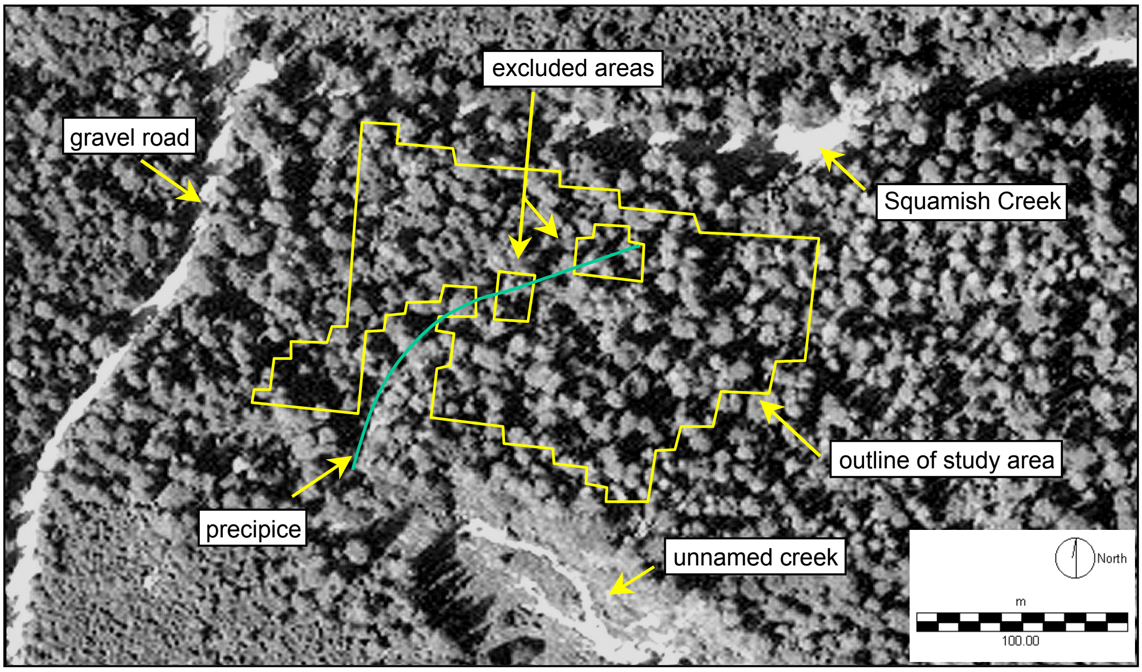

Figure 3: Position and outline of the LSCR study site superimposed on a detail of an aerial photograph of the lower Seymour Valley (30BCB92019 No. 19 from July 29th 1982). Photograph provided by the Greater Vancouver Regional District.

Quaternary history

The stratigraphy of the Fraser Lowland gives evidence to repeated glaciation cycles. The oldest named glaciations are the Westlynn and Semimahoo glaciations, separated by the Highbury nonglacial interval (Lian 1991). Both glaciations are probably equivalent to stades in the early part of the middle Weichsel - Wisconsinan (75,0000 - 25,000 BP, Andersen and Borns 1994, Lian 1991). Between 62,000 BP and 29,000 BP the Frazer Lowland was not covered by glaciers. This period was named Olympia nonglacial interval and ended with the onset of the Fraser glaciation (Lian 1991) in the late Weichsel - Wisconsinan (25,000 - 10,000 BP, Anderson and Borns 1994). The Fraser glaciation is recognized as the last glaciation in which glaciers occupied the mountains and lowlands of British Columbia. The Fraser ice sheet had receded from the Seymour Valley around 12,000 BP (Lian 1991).

As the ice retreated up the valley drift deposited on the valley sides was fluvially reworked and deposited as paraglacial alluvial fans and aprons. Some were deposited as prograding fans, others through debris or mud flows. These fans and aprons developed quickly after glaciation and became relatively stable within 2000 - 3000 years of deglaciation. The tributary streams started incising into these deposits shortly after this period (Lian and Hickin 1996).

The warm winters and high rainfall combined with steep relief still result in a very dynamic geomorphic environment. Deposition through mass movements and substantial local erosion due to flash floods of the tributaries to the Seymour River occurs frequently.

General geomorphology and geology

The Seymour Valley has formed since the late Cretaceous, by fluvial incision as the Coast Plutonic Complex began to rise above sea-level. Repeated ice sheet glaciations have resulted in an narrow U shaped valley, about 5 km wide with extensive valley fill forming a terrace at about 200 m asl in the area of the LSCR. The Seymour River is incised about 30 m into the surface of the valley fill in this area. The surrounding peaks rise up to a maximum of 1466 m asl. The bedrock in the study site consisted mainly of plutonic rocks formed in the Cretaceous, including quartz diorite, diorite, migmatite, granodiorite and granite (Lian 1991).

Climate

The study site had a humid climate with cool summers and mild winters. The majority of the precipitation (~75 %) occured during the winter months (October - March) with less than 15 % of the total precipitation falling as snow and frequently a hot, dry period in late summer. The annual precipitation averaged 4023 mm (average 1961 - 1990, Seymour Falls Climate Station, Environment Canada 2001b). Mean annual temperature was about 8 °C, with a mean temperature above 10° C for five months of the year (Meidinger and Pojar 1991).

Vegetation

The LSCR stand was located in the submontane very wet maritime biogeoclimatic variant, a variant of the Coastal Western Hemlock Zone (Meidinger and Pojar 1991). The dominant trees species were *Tsuga heterophylla*, *Thuja plicata* and *Abies amabilis* with average heights of 45 to 55 m (Seymour Watershed Forest Cover Map No. 6 1990). The stand was estimated to be at least 700 years old (oldgrowth) and showed a diversity of regeneration stages.

1.2 Other study sites

The validity of the results from the LSCR stand on the influence of surficial sediments and rockiness on the observed pattern of vine maple were checked in three other comparable oldgrowth stands. Despite extensive search of the accessible areas of BC with known occurrence of vine maple (Krajina et al. 1982) no further suitable study stands could be located. The difficulty in locating study stands was caused by the necessity to find low elevation oldgrowth stands in southern coastal BC located on slopes with less than approximately 45 degrees inclination to allow for safe working. Since these stands are easily accessible and close to human habitation, very little oldgrowth is left in these locations, usually in very small or otherwise marginal sites.

Remaining stands were found in the upper Seymour Valley (US), the Coquitlam watershed (COQ) and above the Chilliwack River Ecological Reserve (CHIL) (Figure 2). All three stands proved to be less suitable for research. They were very small and bordered either by steeper slopes (COQ, CHIL) or younger stands (US). Therefore only little data could be gathered from these sites.

1.2.1 Upper Seymour site

The stand in the Upper Seymour was located about 10 km north of the LSCR stand on the east side of the Seymour Valley. Vegetation, climate, geology and geomorphology closely resembled the LSCR stand. Exposition was northwest. The large cedars in the lower portion of the US stand showed scars from being used as mountings for towropes to remove stems from the stand located below.

1.2.2 Coquitlam site

The Coquitlam Valley was located ~15 km to the east of the Seymour Valley. It ran southwards and opened into the Fraser Lowland. The Coquitlam watershed has been used as a water supply for Greater Vancouver since 1892, and has been closed to the public since 1936 (Greater Vancouver Regional District 2000). Vegetation, climate and geology closely resembled the LSCR stand. The study site was located in the west of Coquitlam Lake with southeast exposition.

1.2.3 Chilliwack site

The Chilliwack study site was located in the Chilliwack Lake Park near the southern tip of Chilliwack Lake, close to the influx of the Chilliwack River into the lake. The floodplain of the Chilliwack River has been protected as an ecological reserve in the stretch between the lake and the United States border.

Chilliwack Lake was located ~100 km inland from the Pacific Ocean in the Cascade Mountains, part of the northern Canadian Cordilliera. The lake level was located at 650 m asl. The highest mountaintops of the area were generally of the order of 2100 - 2500 m asl. The study site was underlain by granitic batholiths from the mid-tertiary.

During the Fraser glaciation glacier ice filled Chilliwack Valley up to 2000 m asl. The valley displayed the classic glacially eroded cross section. During the vigorous paraglacial conditions after recession of the ice lateral glacier deposits had been rapidly deposited as valley fill, which modified the smoothness of the profile. Since the mid holocene geomorphic activity has been lower, but all types of mass movements are still active in the valley (Saunders 1985).

The Chilliwack Valley had a drier climate than the other three study sites. The closest climate station to the study site was located in Sardis, BC. Annual precipitation was only 1480 mm per year, 69 % of the precipitation occured in winter (average 1961 - 1990, Environment Canada 2001b). The exposition of the study site was northwest. The stand was located in the dry maritime biogeoclimatic variant, a variant of the Coastal Western Hemlock Zone (Meidinger and Pojar 1991). The dominant trees species were *Tsuga heterophylla* and *Thuja plicata* with average heights between 35 and 45 m (Forest Cover Map 92H.003 1996).

2 Sampling design

2.1 LSCR site

The LSCR site was divided into squares of roughly 100 m^2, resulting in a largely contiguous grid of 328 cells. Transects were established every 10 m along the baselines with compass and nylon tape measure. Flags marked the location along the transects every 10 m. Connections between these locations resulted in the cells (Figure 4). The cells were established in May 1998.

Vine maple distribution and sediment type were recorded for each cell. All other measurements were performed on a subset of the cells due to the often high expenditure of the measurements.

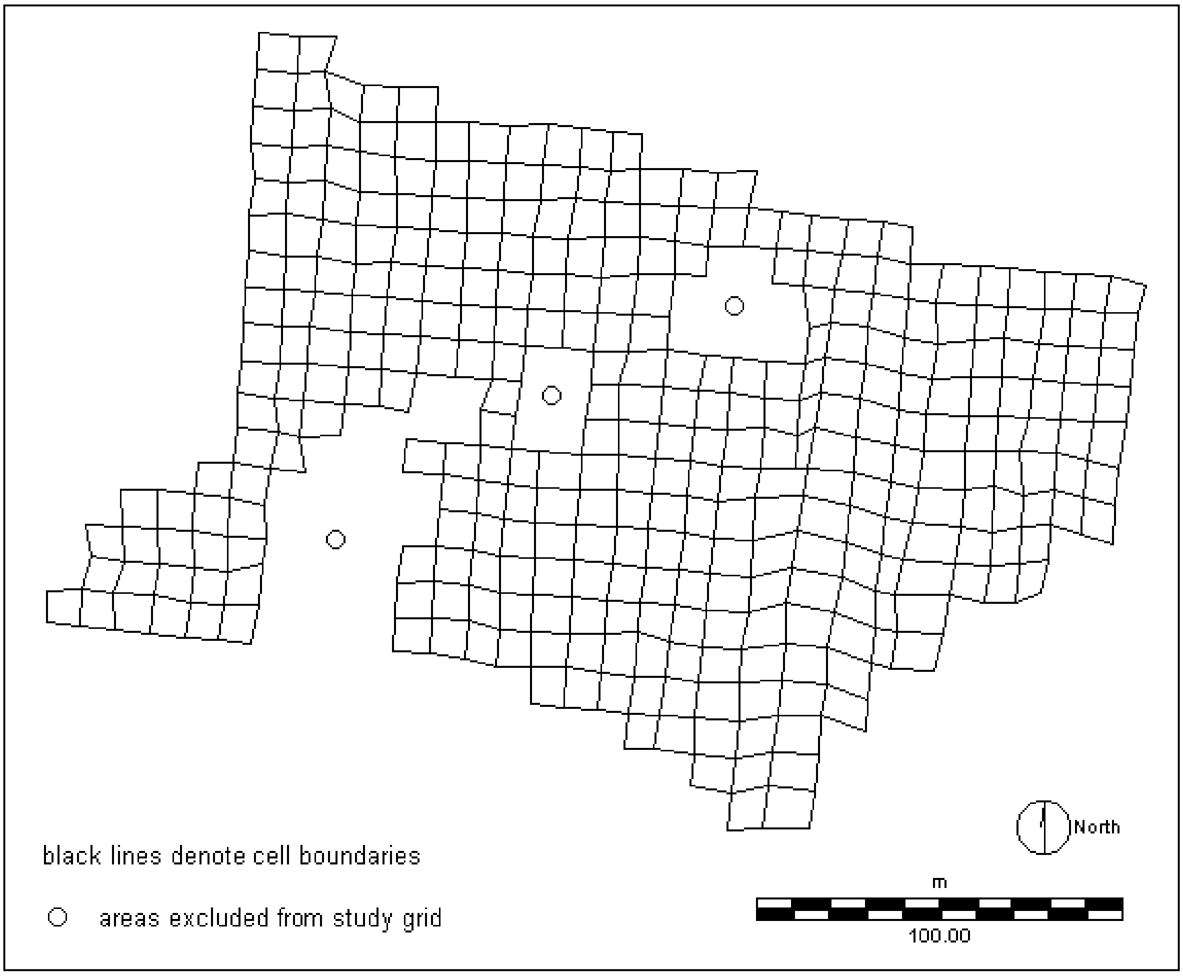

Figure 4: Layout of the cells in the LSCR site.

2.2 Other study sites

In all three study sites belted transects were run straight uphill until the terrain became to difficult for a continuation. The base line of the transects started after a 40 m buffer zone to the nearest gravel road in the COQ and US sites and immediately above the last signs of human disturbance in the CHIL site. Cell size was chosen as 5 by 5 m, since the study in the LSCR stand indicated this to be the size best suited for the analysis of vine maple. Belted transects were placed 10 m apart in the CHIL and US sites and 20 m apart in the COQ site because of difficult terrain. Due to the small size of the sites, only two transects could be placed into each site, with varying length. This resulted in 13 cells in the US site, 28 cells in the COQ site and 20 cells in the CHIL site (Figure 5).

3 Vine maple distribution

For each cell total basal area and ground cover of vine maple were recorded.

Total basal area

The circumference of every vine maple shoot that emerged from at least the F-horizon and that was 3 cm or more in circumference was measured 20 - 50 cm from the exit point (Figure 6). Measurements included the pressed down moss layer. They were done with a nylon tape measure. In case of reemergence after layering, the measurement was taken only towards the distal end of the shoot. Several shoots emerging from one rootball, even if the point of divergence was up to 10 cm above ground, were measured individually. The basal area of all shoots in a cell was added up to the total basal area of a cell.

Ground cover

Ground cover of the complete vine maple biomass present in a cell was estimated on a Braun-Blanquet scale (Ellenberg 1998). The following cover classes were used:

0	no vine maple cover.	
1	< 5 %	vine maple cover
2a	5 - 10 %	“
2b	10 - 25 %	“
3	25 - 50 %	“
4	50 - 75 %	“
5	75 - 100 %	“

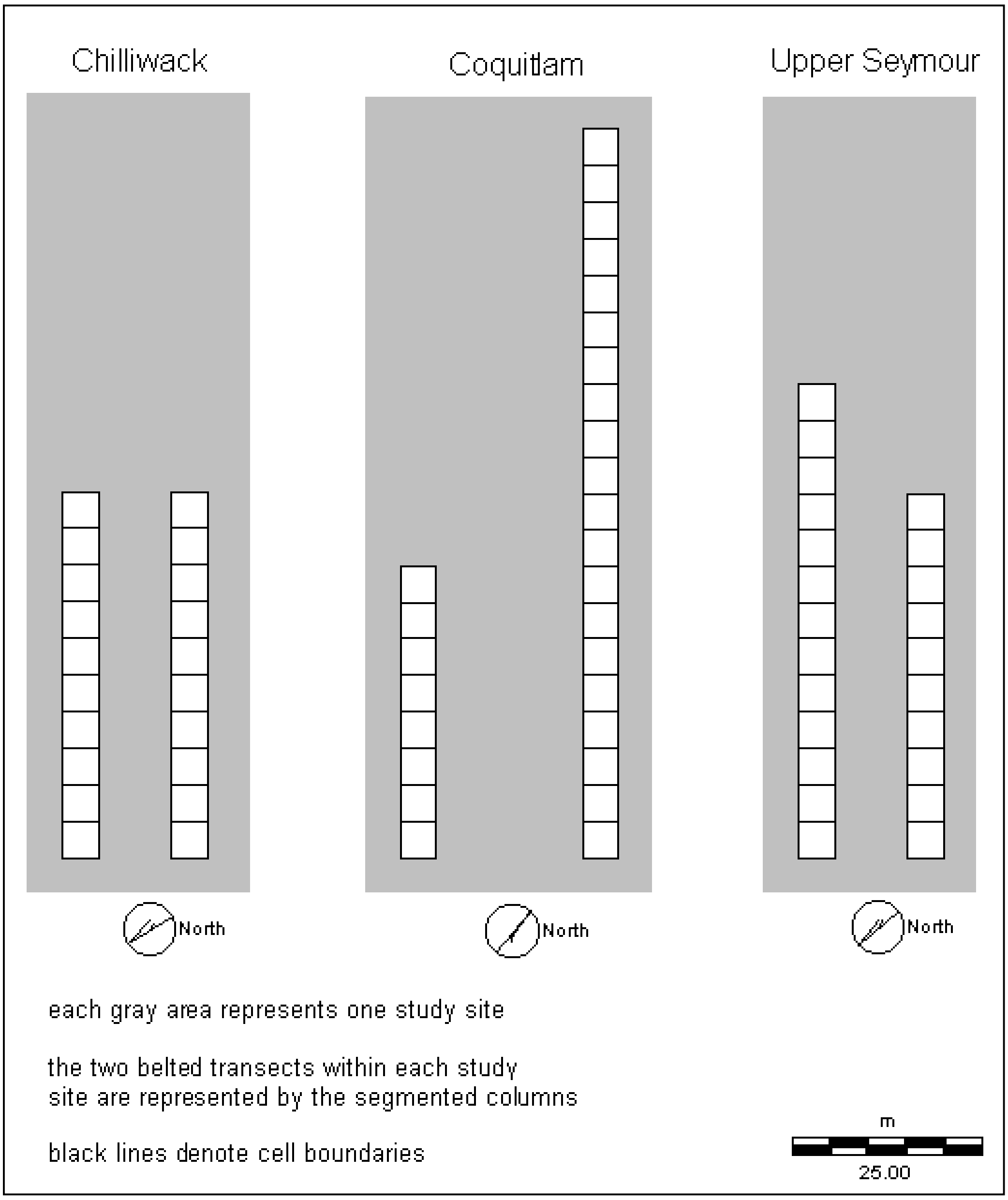

Figure 5: Layout of the cells in the Coquitlam, Upper Seymour and Chilliwack sites. Only the areas included in the belted transects were used for research.

Data analysis

To assess the degree and extent of spatial autocorrelation of vine maple cover and total basal area in the study stands all-directional Geary's C correlograms with Bonferroni-corrections (Legendre and Legendre 1998) were constructed with R-package 3.02 (Legendre and Vaudor 1997). The euclidean distance between the northeast corners of the cells was taken as geographic distance between cells.

LSCR site:

Distances were divided into 30 distance classes, each with a uniform width of 10.1 m. The data for vine maple cover and total basal area were log-transformed to improve normality of the data.

Other study sites:

The number of distance classes per site were chosen according to Sturge's rule (Legendre and Legendre 1998). Distances were divided into eight distance classes with a uniform width of 5.9 m in the CHIL site, nine distance classes with a uniform width of 10.9 m in the COQ site and nine distance classes with a uniform width of 6.9 m in the US site.

Figure 6: Multi-aged vine maple stems emanating from a common rootball.

4 Surficial geology

4.1 LSCR site

4.1.1 Surficial geology

To determine the influence of surficial geology on vine maple distribution, the surficial sediments of the study site were described and mapped. Squamish Creek, the creek that borders the LSCR study site in the north, has cut deeply into the surrounding sediments. Close to the gravel road which delimited the western border of the study site Squamish Creek flowed about 2 m below surface level. The depth of incision of the creek into the sediments increased within a distance of 400 m uphill to a depth of ca. 40 m where Squamish Creek flowed through a bedrock canyon. Four exposures were found and analysed along the creek bed. In addition to the four large sections found along Squamish Creek, two small sections created by creeks were found within the study site. They were analysed in the same way as the large sections.

Sections were logged in terms of the following properties:

Type of contact and thickness of units

All exposures were near-vertical. Direct measurement of sizes were obtained through measurement with a 25 m nylon tape measure. Contacts were classified as distinct or indistinct (conformable).

Texture

Size divisions followed the particle size classification of Wentworth (1922):

clay	< 2 µm
silt	2 - 62 µm
sand	62 µm – 2 mm
granule	2 - 4 mm
pebble	2 mm - 6.4 cm
cobble	6.4 - 25.6 cm
boulder	> 25.6 cm. Boulder sizes above 50 cm were noted separately.

Fine particles (sand, silt and clay) were hand textured (method after Luttermerding et al. 1990). Larger particles were classified according to the length of the longest axis. The roundness and material of the gravel was recorded. Particle roundness was estimated visually according to roundness classes depicted in Leeder (1982) (Figure 7). Petrography follows the IUGS igneous rock classification system (LeMaitre et al. 1989). All observations of sediment characteristics were made qualitatively in the field.

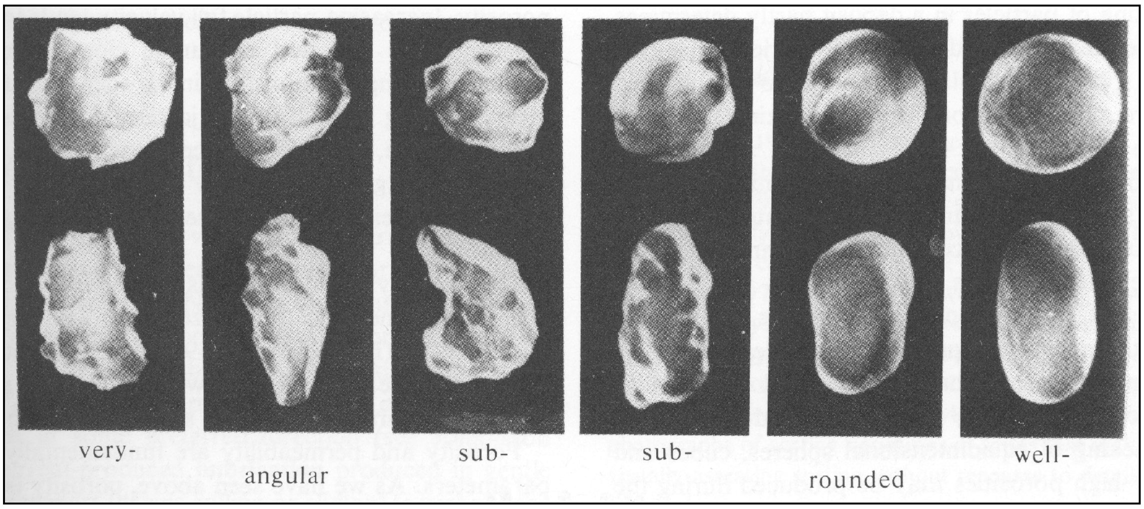

Figure 7: Chart of roundness classes. Figure taken from Leeder (1982).

Structure and fabric

The presence and kind of structure was always noted. The determination of fabric presented in most cases no difficulties and was therefore performed qualitatively. In one case a fabric analysis was performed to determine whether preferred clast orientation was present. The a - axis dip and dip direction were recorded for 50 elongate stones (a - c ratio larger 1.5) in a small part of the section, using a Brunton compass. Care was taken to execute the fabric analysis in undisturbed diamict on stones that were not in contact with each other.

The surface expression of each type of sediment was unique and easy to recognize. The material exposed by overturned trees, soil pits dug in the course of my study and frequent checks with a shovel gave additional information and aided in mapping the surficial geology. Each cell was assigned to the sediment type that underlay the majority of the cell.

Data analysis

Only three of the four recorded surficial sediment types occurred with sufficient frequency to allow a statistical analysis. A chi-square test was used to determine if vine maple cover was similar in all three sediment types. Spatial autocorrelation might have been present in the data. To avoid the associated problems a permutation chi-square test was chosen with 10,000 permutations derived through Monte-Carlo resampling. The test was performed with SPSS for windows 10.0.7 (2000).

4.1.2 Soil

Edaphic properties of the surficial sediments and their influence on vine maple distribution were investigated. In the course of an analysis of the relationship of vine maple occurrence to ground water levels 40 ground water wells were established (see Methods 6.1). Where it was impossible to auger ground water wells to a depth of 1 m wells were established by digging pits. The resulting 22 pits were used to gather data on the effect of soil properties on the distribution of vine maple. Thirteen soil pits were located in cells with vine maple, nine in cells without vine maple. A balanced design was not attempted.

Samples from 25 - 30 cm and, if possible, 65 - 70 cm depth were taken from each soil pit. Three pits were located on shallow soils (bedrock or highly compacted diamict within a depth of 19 - 76 cm). This reduced the sample size for sampling depth 65 - 70 cm to six samples in plots without vine maple and 13 samples in plots with vine maple. The soil properties type, texture, pH, skeletal content and rockiness were investigated.

Soil type

For each pit horizon depth and designation were recorded. If necessary, the depth to bedrock or to highly compacted substrate were measured. Soil classification followed the Canadian System of Soil Classification (Agriculture Canada Expert Committee on Soil Survey 1987).

Soil texture

Samples were air dried and passed through a 2 mm sieve. Soil texture was determined using two ASTM soil hydrometers 125H (Chase Scientific Glass, Inc., Rockwood, TN, USA) (method after Gee & Bauder 1986). Hydrometer readings were taken at three seconds, 60 seconds, three minutes, ten minutes, 90 minutes and, if there was still more than 5 % of the soil in suspension after 90 minutes, at five hours. No measurements were necessary beyond this point.

Soil pH

Soil pH in $CaCl_2$ solution was determined in a 1:3 soil:water suspension using a Fisher Scientific Accumet pH meter 10 (Fisher Scientific Ltd., Nepean, ON, Canada) (method after Gee & Bauder 1986).

Soil skeletal content

Percent coarse fragment (particles 4 mm to boulder size) was estimated visually for each depth in the soil pits. The proportion of granules (particle size 2 - 4 mm) in the total sample found after sieving the soil samples was calculated and added to the coarse fragment content of the sample for skeletal content.

Soil rockiness

A simplified method was used to gather data on skeletal content in 103 cells without digging soil pits. Measurement tapes were laid through the diagonals of 103 randomly chosen cells. Every 2 m along the tapes a metal rod 80 mm in diameter was pushed 50 cm deep into the soil. If the probe met resistance within 50 cm of the surface the kind of obstacle was determined. Two classes of obstacles were formed: rocks that were too large to be pushed away and “other”: tree roots and incompletely decayed dead wood. Rocks and tree roots or dead wood could be distinguished very clearly by sound and the kind of vibrations caused in the rod if the obstacle was tapped. If the obstacle was close to the ground visual inspection of the obstacle in the hole made by the probe always confirmed the previous classification. Rockiness of a cell was calculated as proportion of times rocks were hit in the cell.

Data analysis

Soil texture, pH, skeletal content and rockiness were compared between sediment types, between cells with vine maple and cells without vine maple and between combinations of sediment and vine maple cover. Depending on homoscedacity of the data, exact permutational t-tests, Mann-Whitney-U-tests, ANOVAs with Bonferroni corrections for multiple comparisons or Kruskal-Wallis tests were performed with Blossom statistical package W2001.05a (Cade and Richards 2001). In the case of rockiness 10,000 permutations were derived through Monte-Carlo resampling of the response variable.

4.2 Other study sites

Surficial geology

Experience gathered in the LSCR site allowed recognition of the types of sediments in the three additional study sites. Frequent checks of surface material exposed through the roots of toppled trees or mini-pits dug with a shovel verified the identification through the surface expression of the sediments. A measurable section through relevant sediments could only be found and documented at the Coquitlam site. Surficial geology was mapped in the same way as in the LSCR site.

Rockiness

Rockiness was measured in the same way as in the LSCR site. Due to the smaller size of the cells (5 m^2 instead of 10 m^2) measurements were performed every meter along the measurement tape instead of every 2 m.

Data analysis

Rockiness of the sediment types and vine maple response to rockiness were analysed the same way as in the LSCR site. Exact permutation tests were used because of the low number of cases.

5 Light

5.1 Absolute light requirements

To determine the amount of light a branch of vine maple requires to survive, a direct comparison of the photosynthetic available radiation (PAR) for living and dead branches on the same stem was conducted within six hours on August 1999. A Decagon Sunfleck PAR Ceptometer SF-80 (Decagon Devices, Pullman, WA, USA) was used to measure the average PAR flux density of 80 sensors in the 400 - 700 nm PAR region in mmol quanta m^{-2} s^{-1}. Fifteen to twenty measurements were averaged for each reading.

Forty cells were randomly chosen from all cells that had vine maple stems with a diameter above 3 cm in the cell. The cells were searched for stems that had both living and dead branches within arms reach. One hundred and twenty stems were found and sampled. The PAR was measured above the foliage at living branches, and above the dead twigs at dead branches.

Data analysis

The data was $\log_{10}$ transformed to improve normality. A paired student’s t-test was conducted with SPSS to determine if dead branches received significantly less light than living branches of the same stem.

5.2 Vine maple performance

Hemispherical photographs

To quantify the influence of light availability on the performance of individual vine maple stems and clones hemispherical photographs of 98 vine maple plots were taken in March and April 1999. The cells were chosen randomly from all cells containing vine maple biomass. The vine maple stem rooting closest to randomly chosen coordinates within the cell was marked. The camera was set up below the center of foliage of that stem. A specific stem within a clump was chosen because vine maple morphology is highly variable and often offers several potential “centers” of foliage within one clump.

Photos were taken with a Minolta XD 11 Camera with a Minolta MD Fish-Eye Rokkor-X 7.5 mm objective on Kodak elite 400 chrome slide film (Minolta Canada Inc., Mississauga, ON, Canada, Kodak Canada Inc., Toronto, ON, Canada). The camera was mounted on a tripod at breast height since vine maple is too large to shoot photos above the stems. The photos were taken before vine maple foliage emerged to reduce the error induced this way.

Hemispherical photographs were analysed for percent site openness (SO) with Gap Light Analyser 2.0 (Frazer et al. 1999). Percent site openness is the percentage of open sky seen from beneath a forest canopy given the influence of the effective horizon (mountain shading) (Frazer et al. 1997).

Photos of 48 plots without vine maple were taken in May and June 1999 to directly compare light levels at vine maple habitats to light levels in the surrounding forest. In the 48 randomly chosen cells without vine maple the camera was located on randomly chosen coordinates.

Vine maple performance

The stems chosen for hemispherical photographs were assessed for performance. Stem basal area and crown size were measured and the vitality of the stem was appraised through the proportion of dead branches, survival of the entire stem and the presence of flowers. These features were measured at the same time for the entire clone the stem was part of. Additionally the number of live and dead stems and sprouts (stems < 1.5 m height) of the clone were counted.

Clone definition

All stems that had a visible or through shallow digging discernible living connection to the marked stem were considered part of its clone. Since vine maple can propagate through root suckers and stems and roots might run for some distance underground there is no certainty that all stems in a clone were taken into account. Most clones had a sufficiently simple organization to ensure that the error introduced this way is not overly large.

Presence of flowers

Stems and clones were searched for flowers with binoculars in June 1999. All other measurements of clone and stem characteristics were conducted within two weeks in July 1999.

Summed basal area

The circumference of all living stems was measured 50 cm above ground. Layered stems were measured or, depending on size, counted again towards the distal end of the reemerged shoot. The basal area of all live stems in a clone was added up for the summed basal area.

Crown size

Stem crowns were considered to be roughly elliptical. The crown size of the stem was measured as the extent of the crown from the visual center of the foliage of the stem in directions north-south and east-west. The size of the crown was measured similarly, but additional visual centers of foliage were added if the crown proved to be very irregular in size.

Proportion of dead branches

The percentage of dead branches in stem and clone was classified into four categories:

Class 1: < 25 % dead branches
Class 2: 25 - 50 % “
Class 3: 50 - 75 % “
Class 4: > 75 % “

Data analysis

A Geary’s C correlogram was constructed with R-package 3.02 (Legendre and Vaudor 1997) to check % SO for spatial autocorrelation. The data was divided into 13 distance classes with an equal width of 23.3 m according to Sturge’s rule (Legendre and Legendre 1998). Four distance classes showed significant spatial autocorrelation: distance classes four, ten, eleven and twelve. The three largest distance classes were disregarded to exclude results based on few data pairs from locations solely at the edges of the study site. This left only two distance classes out of ten which displayed significant spatial autocorrelation. Spatial autocorrelation was therefore not considered to be a problem for statistical analysis and no remedial measures were taken.

Light availability to vine maple expressed in % SO at the 98 vine maple plots was compared to light availability in the surrounding forest with a student's t-test. The vine maple stems and clones assessed for performance were grouped into three categories:

1. dead and declining stems or clones: only dead stems or, if stems were still alive, more than 50 % of branches were dead
2. living stems or clones, neither declining nor flowering
3. stems or clones capable of producing flowers

Category two could not be divided into meaningful subcategories. Stem basal area, clone summed basal area and crown area were not linearly related and no "breaks" in the data suggested a meaningful subdivision. The data on % SO gained from the hemispherical photographs was compared among the three performance categories of vine maple stems and clones using an ANOVA with Bonferroni corrections after $\log_{10}$ transformation of the data (SPSS).

The clone parameters crown size, summed basal area, number of live stems and number of live sprouts were regressed against SO to assess the influence of light availability on these features (SPSS). Scatter plots of clone crown size and number of sprouts per clone showed a wedge shaped distribution pattern. Variance of the response variables increased up to 6 % SO for clone crown size and 8 % SO for number of sprouts per clone. Weighted least squares regression was used to account for the heteroscedacity. Variances in the response variables over four equal sized sections of the part of the wedge with increasing variances were calculated and a linear regression was fitted through the data points. Variances were calculated for each value of the predictor variable from this equation. The inverse square root of these variances was used as weights in the regression. Adjustments were made for values above 6 % SO for clone crown size and 8 % SO for number of sprouts per clone. Variance was not considered to increase beyond this point and was therefore kept constant. To avoid giving to much weight to the smallest value of the predictor variable this value was given the same weight as the next smallest value of the predictor variable.

Least absolute deviation (LAD) regression of the 90th quantile (Scharf et al. 1998) was used to estimate upper boundaries of the scatterplots in the areas with increasing variance with Blossom. Hypothesis testing for the LAD regressions was based on a scoring function of the sign of the residuals for the reduced parameter models to account for the heteroscedacity of the data (Cade and Richards 2000). One outlier was removed from the dataset for number of sprouts per clone prior to analysis.

The number of live stems and the summed basal area of the clone did not display systematic heteroscedacity as expressed in a linear increase in variance of the response variable over increasing values for the predictor variable. OLS regression was therefore used. No quantile regressions were performed.

The extent of the tree overstory depicted by hemispherical photographs was always larger than the portion just above the stem assessed for performance. In many cells the clone measured was a significant portion of the entire vine maple population of the cell. Therefore the association of different cover classes of vine maple to light availability as measured in % SO was investigated. The data for site openness was $\log_{10}$ transformed to ensure homoscedacity and ANOVAs with Bonferroni corrections for multiple comparisons were performed to compare cover classes (SPSS).

Light availability as measured in % SO was compared between sediment types. Lake sediment could not be entered into the statistical analysis due to the low sample size on this sediment. The data was heteroscedastic. A Kruskal-Wallis test was therefore performed (SPSS). Percent SO was compared between cells with high cover (> 25 %) and cells with low cover of vine maple (< 25 %) separately for each type of sediment with a student's t-test. A permutational version with 10,000 permutations derived through Monte Carlo resampling of the response variable was used (Blossom).

5.3 Leaf morphology

Vine maple leaf thickness might be related to the light levels present at the site of growth. If so, leaves collected during the summer could replace hemispherical photographs as a measure for light availability to vine maple. To test this possibility, leaves were collected from a subsample of 40 plots assessed for vitality in July 1999, after the extension growth for the year was largely finished.

Two branches were cut from the south side of the highest point in the outer crown of the marked stem. From each branch one leaf was taken from the branchlet with the longest internode. The center lobe of each leaf was cut out, including a wedge-shaped section ending at the leaf base. The leaf segments were stored immediately in formol acidic alcohol.

A portion of the leaf tissue from the lower third of ten leaf segments that were representative of different light regimes were analysed for thickness of the leaf lamina and of the leaf midribs. Leaf parts were prepared for thin sectioning through embedding in Technovit 7100 (Hereus Kulzer GmbH, Wehrheim, Germany). Thin sections were dyed with Toluidin-blue after Sakai (Gerlach, 1977). Leaf thickness was measured with the image analysis system Mini-Mop Version 2.0 (Kontron Elektronik, Eching bei München, Germany) in discrete mode. The remaining 70 leaves were hand cut and only the thickness of the midribs was measured with an eye piece graticule under a microscope.

Data analysis

Linear regression was used to determine if there is a relationship between the thickness of the midrib and available light, measured in % SO (SPSS). No correction for spatial autocorrelation was necessary since the results were non-significant.

5.4 Overstory tree densities

Overstory tree densities might provide another proxy measurement to direct light measurements that could replace hemispherical photographs. Overstory tree densities were therefore measured in 98 cells in August 1999.

The circumference of all conifers and deciduous trees (with the exception of vine maple) whose boles were at least half-way within the cell at breast height was measured. The number of conifer seedlings (< 25 cm high) and saplings (< 1.5 m high) per cell was recorded as well. The basal area of all measured trees in a cell was summed up to get the total overstory tree basal area.

Data analysis

Total overstory tree basal area and the number of trees, seedlings and saplings were compared between sediment types and vine maple cover classes. The data on total overstory tree basal area and seedling and sapling densities was $\log_{10}$ transformed and the data on number of overstory trees per cell was square root transformed to ensure homoscedacity. Permutational ANOVAs with 10,000 permutations derived through Monte-Carlo resampling of seedling densities were performed with Blossom.

6 Ground water

6.1 Ground water level

To determine if the depth of the ground water table has an influence on the distribution of vine maple, 40 ground water wells were established in the study site. Twenty wells were established in cells randomly chosen from those without vine maple and 20 in cells randomly chosen from those cells with vine maple total basal area above the median. Within each group of 20 cells, no two cells were allowed to border on each other in order to avoid redundant data. The wells in the plots without vine maple were placed as close to the center of the cell as possible, whereas the wells in the vine maple cells were placed as close to the highest density of vine maple stems in the cell as possible.

Where possible, a screw auger was used to establish the wells. Fourteen wells were established this way. The wells consisted of 1.5 cm diameter PVC pipe with holes, covered with nylon hose. The free spaces between the walls of the wells and the PVC tube were filled in with play sand to establish firm contact with the surrounding material. In 27 cells augering was impossible due to very stony soils.

To establish the remaining wells, pits were dug as deep as possible. In four cases the underlying parent material was reached, in the remaining cases the boulders got too large to be removed. The PVC pipes were inserted into the pits and the soil pits were then filled in with the original soil material. The wells vary in length from 53 cm up to 168 cm.

Acrylic tubes with an diameter of 1 cm of slightly longer length than the PVC tubes were inserted into the PVC tubes. Pieces of styrofoam, placed in the acrylic tubes, floated up with the rising ground water but tilted and got stuck when the water lowered, thereby recording the maximum ground water table within the measurement period. The styrofoam bits were replaced at the first sign of slippage.

The last wells were established at the beginning of August 1998 and the first measurement was taken on August 5th. The ground water table and maximum were recorded once every three weeks until August 28th 2000. In January 1999 and January and February 2000 no measurements were taken due to snow cover. In October and November 1998 measurements could only be taken at a portion of the wells, because 15 wells were destroyed by vandalism and had to be reestablished.

Data analysis

Complete data sets could not be obtained on any measurement date due to several reasons: Most wells fell dry during the summers of 1999 and 2000. This was in part due to not deep enough wells. In at least four cases, where wells extended to the parent material, it was due to a complete absence of ground water in the loose surface material at the site of the well. During October and November 1998 only the wells remaining after the vandalism could be used. Missing values occurred occasionally in the measurement of the ground water maxima because of slippage or sticking of the styrofoam bits. At ten dates less than six values were missing from the datasets for the ground water maxima and on three days from the datasets for the actual ground water tables. At all other measurement dates more values were missing, up to 38 values for the actual ground water table on September 16th 1998.

The thirteen data sets with up to six values missing were used for a comparison of the ground water level between plots with and without vine maple. Missing values were omitted. The data sets with higher amounts of missing data were not used for a statistical comparison because an imbalance in the number of dry wells would skew the outcome of the computations too strongly. The data for ground water maxima and actual ground water level were square root transformed and analysed separately using repeated measurement ANOVAs with Systat 8.0 (1998). Additionally, plots with vine maple and plots without vine maple were compared individually for each date using the student's t-test. No correction for spatial autocorrelation was necessary since the results were non-significant.

Wells were classified into five categories according to their hydrological status. The categories were defined according to how often ground water was found in the wells within 50 and 90 cm of the surface on the 32 measurement dates:

dry:	on zero days ground water within 50 cm of the surface, on zero days ground water within 90 cm of the surface
moderately dry:	on zero days ground water within 50 cm of the surface, on one to five days ground water within 90 cm of the surface
moderate:	on zero to five days ground water within 50 cm of the surface, on more than ten days ground water within 90 cm of the surface
moderately wet:	on five to ten days ground water within 50 cm of the surface
wet:	on more than ten days ground water within 50 cm of the surface

The distribution of wells of different hydrological status was compared between sediment types and cells with and without vine maple.

6.2 Vegetation analysis

To detect any changes in the vegetation due to water availability, 33 relevees were taken. For each relevee the cover of the vascular plants present was recorded in a modified Braun-Blanquet scale (Ellenberg, 1998):

r	single specimen, cover < 5 %
+	2 - 5 specimen, cover < 5 %
1	> 5 specimen, cover < 5 %
2a	cover 5 - 10 %
2b	cover 10 - 25 %
3	cover 25 - 50 %
4	cover 50 - 75 %
5	cover 75 - 100 %

The heights of the trees of the first and second tree layer were not recorded. The study site was uniform enough not to expect differences in tree height due to different nutrient levels and broken treetops and uneven age structure prevented a uniform height of tree layers. Shrubs were always recorded in the shrub layer, regardless of height. The study site was very rich in microsites, and boundaries, especially between woody debris and forest floor, were often not discernible. Microsites were therefore included in the sample plots, with the exception of epiphytes on standing dead or living trees. Bryophytes and lichens were not analysed in detail because their distribution was largely dependent on influences on a much smaller scale than the scale used in my study. Only the most common and abundant species of bryophytes were recorded: *Hylocomium splendens*, *Plagiothecium undulatum*, *Rhizomnium glabrescens*, and *Rhytidiadelphus loreus*. Because of the possible connection of their occurrence to high ground water levels, *Sphagnaceae* and thallic *Hepaticae* were also recorded as groups.

The vegetation relevees were sorted into vegetation units according to species characteristics mentioned in the literature (Klinka et al. 1989, Meidinger and Pojar 1991, Lyons and Merilees 1995, Pojar and MacKinnon 1994, Green and Klinka 1994). The resulting vegetation units were mapped in spring 2000 in the LSCR site and their distribution was compared to the data available on ground water levels in the study site.

Nomenclature

Scientific names for vascular plants follow Douglas et al. (1989-1994) and for bryophytes Anderson et al. (1990). Scientific names of birds and vertebrates used in the text follow Harding and McCullum (1994).

7 Microtopography

7.1 Growth adjacent to creeks

In August 1998 a topographical survey of the LSCR site was done with a Nikon D-50 total station (Nikon Inc., Melville, NY, USA) with a TDS HP-48-GX data collector (Tripod Data Systems, Corvallis, OR, USA). The position of all flags that denoted cell corners (with the exception of a few flags, which were already missing at that time or could not be reached), major elevation breaks and the course of major creeks were recorded. Separately the course of major and ephemeral creeks were mapped in relation to the position of the cells. Creeks were considered major as opposed to ephemeral if they were incised more than 10 cm into the topsoil, more than 50 cm wide and carried water for most of the year.

Data analysis

A digital elevation model (DEM) with a grid density of 1 m between nodes was constructed using Surfer 6.01 (1995). The DEM was calculated through kriging with an underlying linear variogram without nugget effect. The DEM was imported into IDRISI 32 Version 132.11 (2001).

The course of all major creeks was reconstructed from locations recorded with the total station and maps made in the field. Decisions were aided by an analysis of runoff patterns by IDRISI. For each cell the number of pixels that were identified as creek were counted. If a cell contained pixels identified as creek the cell was classified as “located in proximity to a creek”.

A one-tailed chi-square test was used to test for independence of vine maple occurrence and height of cover from a location in proximity to a creek. The test was done for all cells and additionally stratified after type of sediment. Spatial autocorrelation might have been present in the data. To avoid the associated problems a permutation chi-square test was chosen with 10,000 permutations derived through Monte-Carlo resampling (SPSS).

7.2 Slope angle

For each pixel of the DEM the slope was calculated by IDRISI in degrees, based on the elevation of the four directly adjacent neighbouring cells and the resolution of the DEM. Slopes were averaged for each cell.

Data analysis

Slopes were compared between vine maple cover classes and all cells with and all cells without vine maple. Permutational ANOVAs with 10,000 permutations were performed with Blossom. The display of slope inclination presented in the results section was constructed in Surfer.

8 Vine maple persistence and priority effects

8.1 Forest floor moisture

For a comparison of the water content of the forest floor between plots with and without vine maple, the water content was measured in 99 cells in the study site after a dry spell of several weeks. This was done within six hours on August 6th 1998.

The volumetric moisture content of the forest floor was measured with a ThetaProbe with an attached ThetaMeter Type HH1 (AT Delta-T Devices, Burwell, UK). Fifty cells were chosen randomly from all cells without vine maple stems, roots or foliage and 49 cells from all cells that contained at least one stem of vine maple with a stem diameter above 3 cm. This condition of minimum stem size was given to ensure that vine maple had a significant influence on the moisture content of the forest floor.

In each cell a focal point was chosen. Eight measurements were made in a circle with a 1 m radius around the focal point, a ninth was taken at the focal point. In cells without vine maple, the focal point was put two paces diagonally inwards from the northeastern corner of the cell. In cells with vine maple the focal point was located next to the stem of vine maple that was closest to the northeastern corner of the cell. Measurements were taken by inserting the metal rods of the ThetaProbe completely into the forest floor. Hindering dry branches on the ground were pushed to the side, but visible woody debris was not excluded from the measurement because it is an important seedling habitat.

Data analysis

The output in Volt given by the ThetaMeter was converted to moisture content in percent volume of the forest floor. The parameters for the conversion were taken from the ThetaProbe User Manual (1996). Parameters for organic soils were used. The nine measurements per cell were averaged and the means between plots with and without vine maple were compared using the student's t-test after square root transformation (SPSS). One randomly selected cell was removed from the dataset of cells without vine maple to get a balanced design. No correction for spatial autocorrelation was necessary, since the results were non significant.

8.2 Conifer regeneration

The influence of vine maple on conifer regeneration was assessed. During data collection on overstory tree densities (see Methods 5.4), the number of conifer seedlings (< 25 cm high) and saplings (< 1.5 m high) per cell were recorded as well. The number of conifer seedlings and saplings was compared between cells with and cells without vine maple using student's t-test. An ANOVA was performed to compare the mean number of seedlings and saplings between the different cover classes of vine maple. The data was $\log_{10}$ transformed to improve homoscedacity (SPSS). No correction for spatial autocorrelation was necessary since all results were non-significant.

8.3 Gaps

One hundred cells with vine maple and 100 cells without vine maple were surveyed for gaps. A gap was defined as a canopy opening of more than half the diameter of the crown of the neighboring trees. Canopy trees included all trees with a height above 2 m except vine maple. Canopy definitions that include only trees with a diameter at breast height larger than 22 or 25 cm (Spies et al. 1990, Lertzman & Krebs 1991) or trees with a minimum height larger than the average suppressed tree (Lertzman et al. 1996, Dahir and Lorimer 1996) were unsuitable for my study. The small size of vine maple causes many gaps of these definitions to be closed canopy in relation to vine maple. Gaps that expanded into more than one cell were only counted once, the first time they were encountered.

Gaps were classified as developmental, edaphic or independent:

developmental gaps: temporary gaps caused by the death of an overstory tree, identified by the presence of stumps or standing dead trees (Lertzman et al. 1996)

edaphic gaps: more or less permanent gaps caused by edaphic features like rock outcrops, standing water, creeks and cliff sides (McGhee 1996, Lertzman et al. 1996)

independent gaps: gaps without a visible developmental or edaphic origin.

Independent gaps included potential priority gaps (gaps caused by priority effects, McGhee 1996). Vine maple has been shown to cause gaps through priority effects in an 80 year old stand (McGhee 1996), but the time span vine maple can keep priority gaps open beyond that point in time has never been quantified.

Edaphic gaps were classified into two groups: caused by a creek or caused by bedrock outcrops. Creeks were only recorded if they had a creek bed more than 50 cm wide that was free of vegetation and fine material.

The state of decay of the remains of the tree or trees whose death appeared to be responsible for the formation of a gap was determined in all gaps encountered. Snags or, if they could be clearly attributed to a stump, logs were classified into seven different decay classes (modified after Graham and Cromack, 1982, Caza, 1993, and Lertzman and Krebs, 1991):

Class 0: Broken tree, still alive.

Class 1: Bark intact; current year twigs present; no invading roots; no vegetation on top; sound wood.

Class 2: Bark mostly intact; twigs absent; branch system entire; no invading roots; conifer seedlings germinate on top but do not survive; sapwood somewhat decayed but present, heartwood sound.

Class 3: Bark sloughing or absent; large branches present, longer than the log diameter; invading roots in sapwood only; saplings on top below 2 m in height, some shrubs and mosses; log supports own weight, sapwood decayed but some present, heartwood decayed but mainly sound.

Class 4: Bark detached or absent; branch stubs present, shorter than log diameter, can be pulled out; invading roots throughout wood; saplings on top less than 15 cm diameter at breast height (dbh), shrubs, mosses; heartwood rotten, does not support own weight, crumbling.

Class 5: Bark detached or absent; branches absent; invading roots throughout wood; trees on top larger than 15 cm dbh, shrubs, mosses; some sound wood of stumps still protruding above the forest floor.

Class 6: Bark detached or absent; branches absent; invading roots throughout wood; substantial growth of trees on top larger than 15 cm dbh, shrubs and mosses, wood powdery, visible only as mound on the forest floor, entirely covered by leaf litter and mosses.

For each gap the size of the canopy gap and of the extended gap were measured following the method described in Spies et al (1990). A canopy gap is the vertical projection of the opening in the forest canopy onto the ground. The boles of the trees whose canopies define the canopy gap define the boundary of the extended gap. With increasing latitude, and especially on slopes, an increasing amount of light enters a gap on angles less than

90 degrees. This results in light from a gap passing beneath the canopies of the trees bordering the gap. The extended gap is therefore a more appropriate measure of the effective opening than the canopy gap (Canham 1988). The projected area of the gaps was assumed to be roughly elliptical. Length and width were measured with a nylon tape measure.

Data analysis

The frequency of the occurrence of vine maple in gaps was compared to the frequency of gaps without vine maple. Gap origin, gap size and the elapsed time since the death of trees formerly present in the gap as represented in the decay class of the remains was compared between cells with and without vine maple to detect any priority effects of vine maple. A student's t-test was performed to test the significance of differences in canopy and extended gap size between gaps with vine maple and gaps without vine maple (SPSS). To improve homoscedascity of the data, the data was square-root transformed prior to analysis. The data was tested for spatial autocorrelation with Geary's C (R-package). Eleven distance classes with an equal width of 24.3 m were constructed according to Sturge's rule (Legendre and Legendre 1998). Only one single distance class (48 - 73 m) showed significant positive autocorrelation for the canopy gap data. The extended gap area showed no significant spatial autocorrelation at all. No remedial measures for spatial autocorrelation were therefore taken.

8.4 Minimum time of persistence

Vine maple clumps can replace aged shoots with young ones. It is therefore impossible to determine the age of a vine maple clump from aboveground material. To determine the minimum time period vine maple can persist in a gap the age of the rootball of a vine maple clump was measured. A clone in an old developmental gap was chosen. The stump of the tree whose death was responsible for gap creation was in decay class 5 (see Methods 8.3).

The oblong rootball was carefully excavated and sawed into 10 - 15 cm thick slices along the growth axis. The slices were sanded and the age of each slice determined through dendrochronology. Tree rings were counted twice along two different axes of the disk and recounted by a second person to ensure correct counts. Due to the irregular growth of the root no agreement could be found between different axes in several cases. In these cases it was assumed that the longer axis provided a more accurate count, since rings might be too crowded to distinguish in the more compressed axis.

9 Vine maple layering

Layering provides an opportunity to directly measure the average minimum time needed by vine maple to establish a rooted stem in a new location and the average distance spanned in the process. This allows an estimate of the maximum "speed" of the utilization of new habitats through vine maple, since vine maple propagates nearly exclusively through vegetative reproduction in oldgrowth forests (Anderson 1967, Russell 1974).

In June 1999 65 cells were randomly chosen out of all cells with vine maple and screened for layering. The stem emerging from the original rootball was termed "mother" stem, the stem reemerging after layering "daughter" stem (Figure 8). The distance between the roots of both stems was recorded.

Figure 8: Layering vine maple stems. The yellow arrow denotes the place where a mother stem enters the ground, the red arrow denotes where a daughter stem exits the ground.

Both the mother and the daughter stems had to be alive to allow dating through dendrochronology, since vine maple wood decays rapidly (UBC Botanical Garden 1976). Tree cores, or in the case of small stems, disks, were removed from mother and daughter as close to the point of rooting as possible.

Often, the mother stem was not the oldest stem emerging from a common rootball. There was no way of determining the age of the parent rootball, since older stems might have already been replaced. Therefore only the age difference of the actual mother and daughter stem was taken. This time period represents a minimum time needed to span the distance. To this minimum period an unknown time span between the establishment of a stem and the subsequent layering of another stem from the newly established rootball would have to be added for the true time lapse between the establishment of rootballs.

RESULTS

1 Vine maple distribution

1.1 LSCR site

Vine maple biomass was found in 205 (63 %) out of a total of 328 cells. Of the cells with vine maple 51 % had a vine maple cover of less than 5 % and only 11 % a cover of more than 50 %. The amount of vine maple present in the study expressed by cover was somewhat exaggerated through the coarse grid. A single vine maple at the corner of four cells caused four cells to be counted as vine maple cells.

Vine maple distribution was clumped. A high density and high cover of vine maple was found in four areas of the study site. Smaller clumps with mainly low cover and low total basal area were scattered between these areas (Figure 9 and Figure 10).

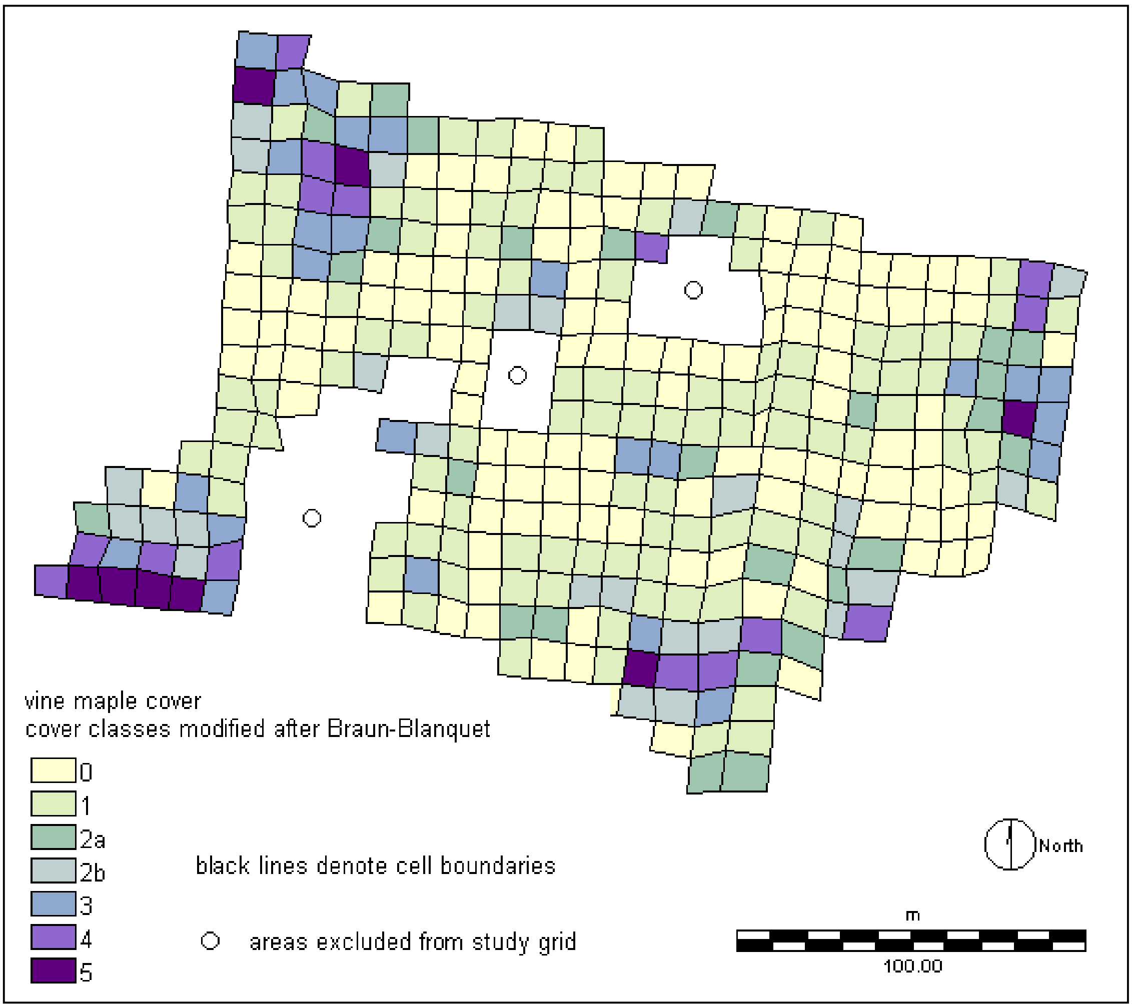

Figure 9: Display of spatial distribution of vine maple cover in the LSCR site

Rooted vine maple stems with a circumference above 3 cm were found in 155 cells. Altogether 1357 vine maple stems were counted, an average density of 416 stems/ ha. The number of stems counted in a cell varied from one to 43 with a median of six, resulting in a total basal area between one and 2993 cm^2 per cell. The median total basal area was 204 cm^2 per cell.

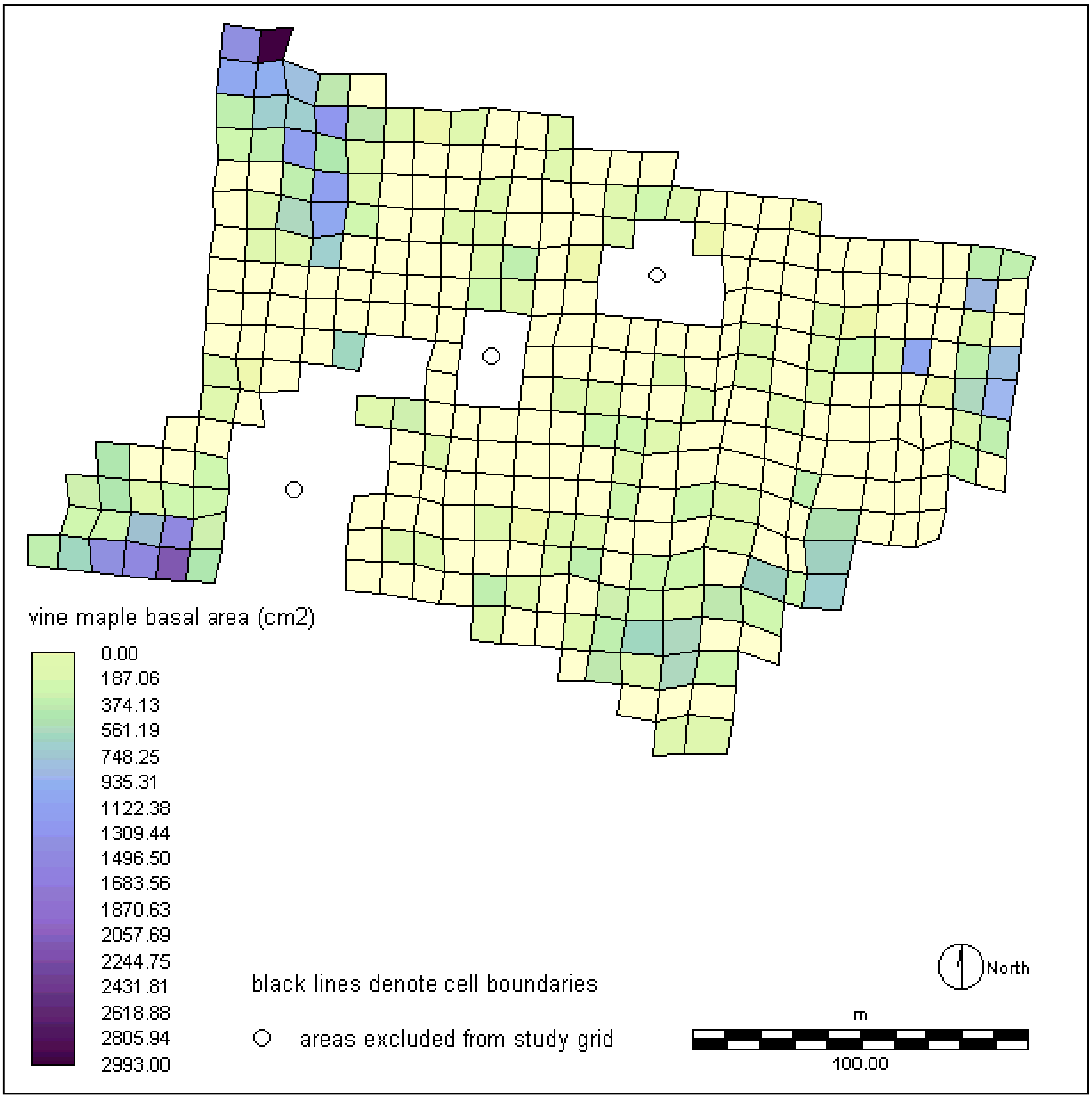

Figure 10: Display of spatial distribution of vine maple total basal area in the LSCR site

The Geary's C correlograms of vine maple cover and vine maple total basal area are very similar. Both display the pattern of a "false gradient" (Legendre and Legendre 1998) (Figure 11) Significant ($p < 0.05$) positive spatial autocorrelation is present up to distances of 131 m, significant negative autocorrelation at distances between 131 and 252 m between cells. The values for distance class nine in the correlogram of vine maple total basal area are not significant as are the values for distance class 13 and the four largest distance classes in both correlograms. Since the coefficients for the five largest distance classes are based on relatively few pairs of observations and could only be obtained from points located at the borders of the study site they will not be interpreted any further.

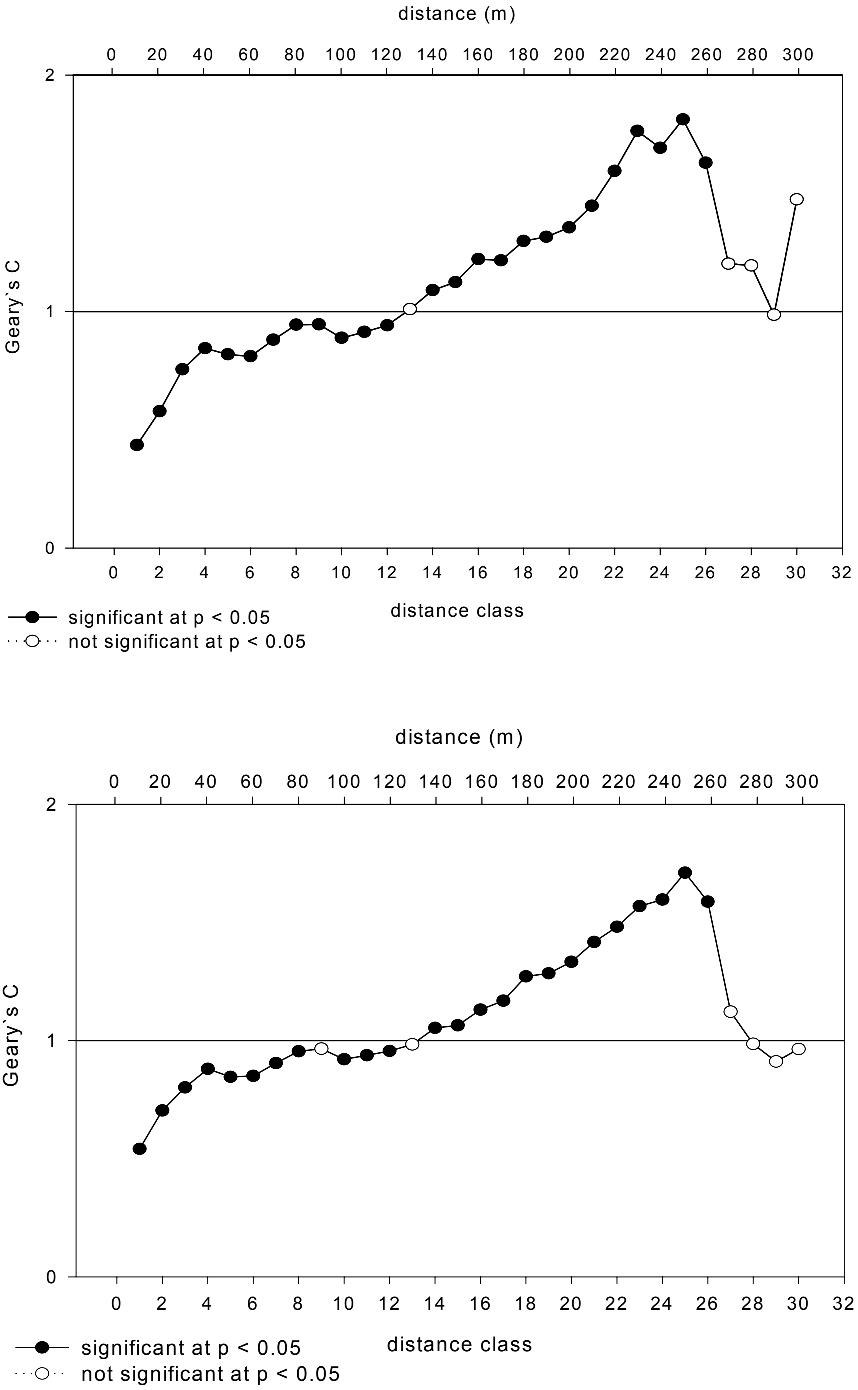

Figure 11: Geary's C correlograms of vine maple cover (upper graph) and total basal area (lower graph) in the LSCR site.

Positive spatial autocorrelation in both correlograms is relatively high only at distance classes one and two (upper boundaries 10.1 and 20.2 m) with values for Geary's C < 0.75. Negative spatial autocorrelation increases fairly linear from no spatial autocorrelation at a distance of 130 m up to values for Geary's C above 1.7 for distances around 240 m in both correlograms.

1.2 Chilliwack site

Of the 20 five by five meter cells in the study site, 15 contained vine maple. Forty percent of all cells with vine maple had a cover of less than 5 % and 47 % a cover larger 50 %. (Figure 13). Five cells contained rooted vine maple stems larger than 3 cm circumference with a total of 196 stems and 251 sprouts for all cells. Vine maple total basal area in these cells ranged from 3 cm^2 to 1741 cm^2 with a median of 998 cm^2.

The distribution of vine maple in the study site was highly clumped. The topmost located six cells of the study site contained all cells which had rooted vine maple stems and high vine maple cover. These cells were all located in the same large continuous area of high vine maple cover.

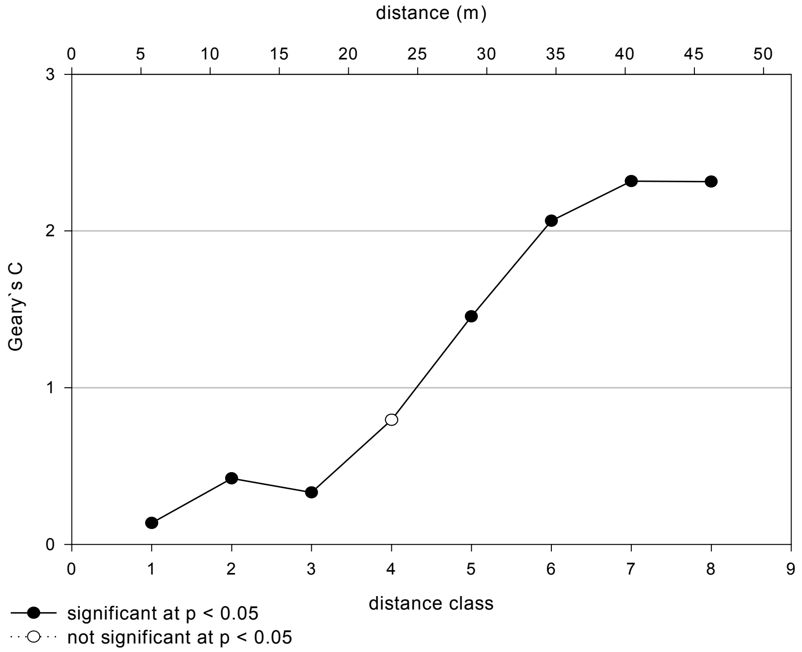

Figure 12: Geary's C correlogram of vine maple cover in the CHIL site.

This pattern of distribution is reflected in the Geary's C correlogram of vine maple cover of the site (Figure 12). In the first three distance classes, up to a distance of 17.8 m strong positive autocorrelation (Geary's C < 0.5) can be found. Geary's C for distance class four (upper boundary 23.7 m) is not significant. Distance classes five and six (23.8 to 35.6 m) show strong significant negative autocorrelation with Geary's C above 1.45. The last two distance classes should be disregarded since the results are based on few pairs of observations.

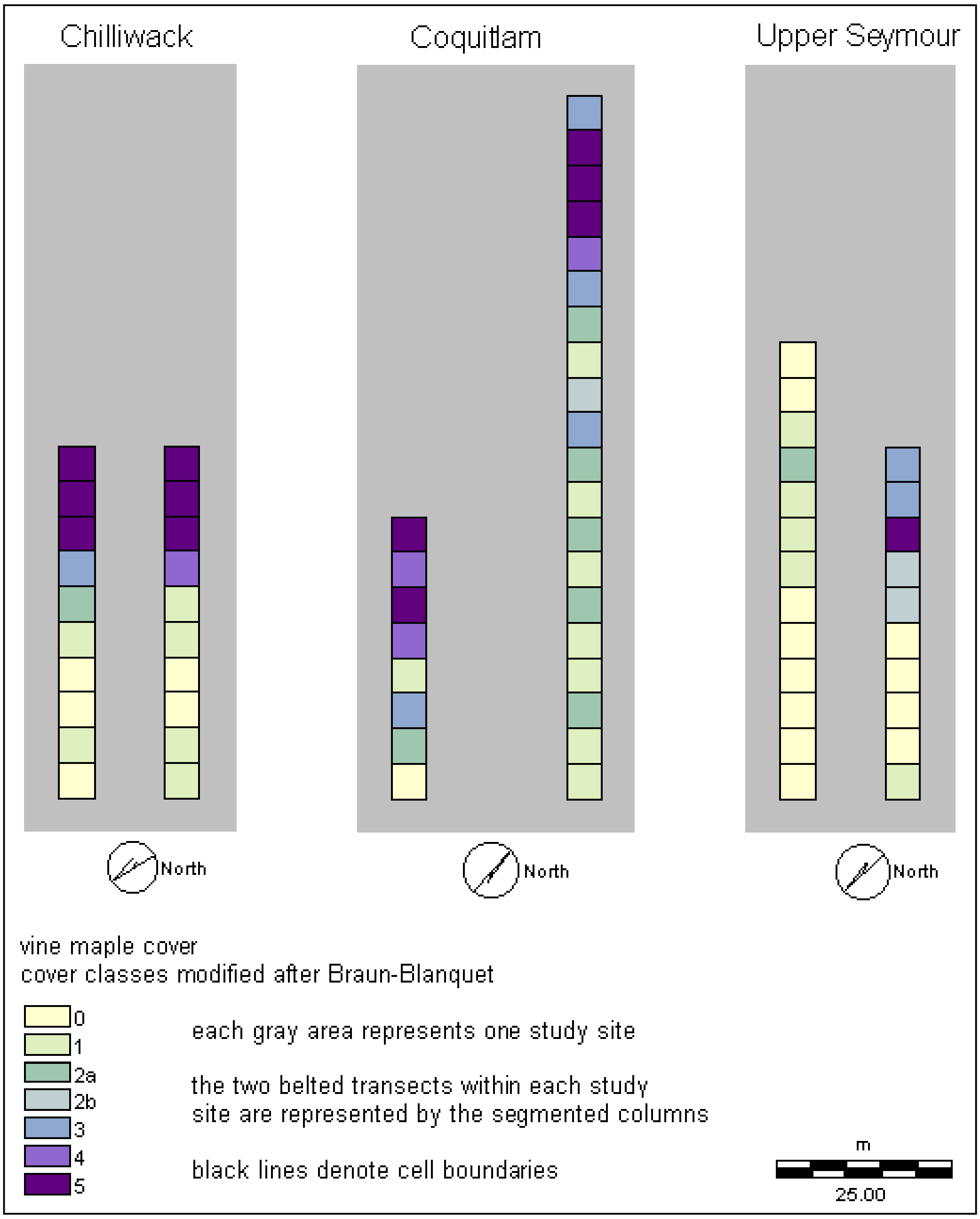

Figure 13: Display of spatial distribution of vine maple cover in the CHIL, COQ and US sites.

1.3 Coquitlam site

Twenty-seven of the 28 cells in the study site contained vine maple. Of those cells 30 % showed a cover of vine maple higher than 50 %, and 30 % a cover below 5 % (Figure 13). A total of 110 stems and 125 sprouts was found in 17 of the cells, amounting to a overall vine maple basal area of 3344 cm^2 with a median of 162 cm^2. Maximum total basal area found in one cell was 679 cm^2.

The Geary's C correlogram of vine maple cover (Figure 14) shows significant positive autocorrelation for the first two distance classes with a distance of 21.8 m. The third distance class with an upper boundary of 32.7 m shows significant negative autocorrelation. In the following three distance classes Geary's C is not significant. The seventh distance class with an upper boundary of 76.4 m shows again significant negative autocorrelation. The last two distance classes are not further interpreted since their result for Geary's C is based on too few pairs of observations.

The non-significant values for Geary's C in the middle distance classes are caused by the relative position of the transects to the continuous area of high vine maple cover. If the transects were positioned perpendicular to the large continuous area of high vine maple cover in the top portion of the study site instead of perpendicular to the slope of the mountain, the correlogram might have looked very similar to the one obtained from the Chilliwack data (Figure 12).

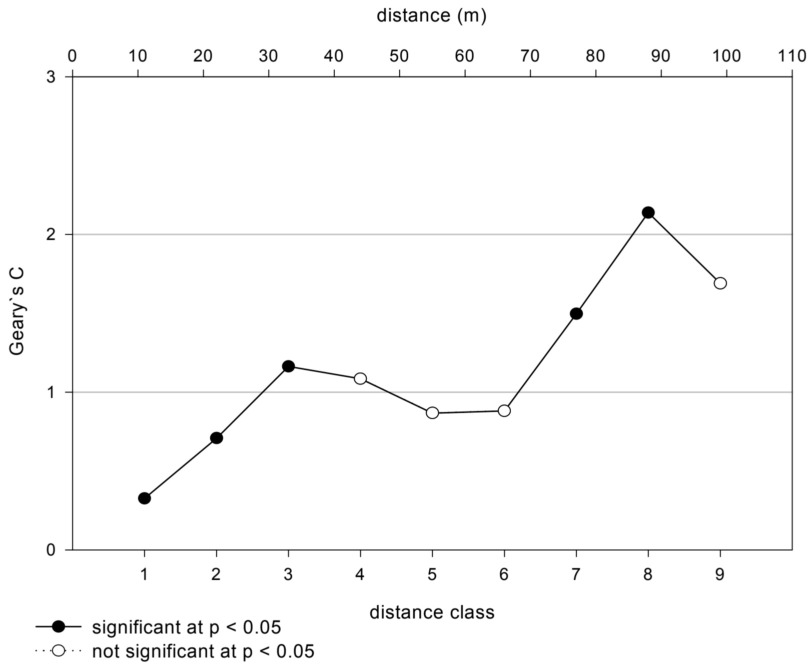

Figure 14: Geary's C correlogram of vine maple cover in the COQ site.

1.4 Upper Seymour site

The total amount of vine maple in the 23 cells of this site was much lower than in the COQ and CHIL sites. Only seven cells contained vine maple stems with a circumference above 3 cm and an additional four cells had vine maple biomass without rooting stems. Of these eleven cells only 9 % contained vine maple with a cover above 50 % and 45 % of the cells had less than 5 % vine maple cover (Figure 13). A total of five sprouts and 32 stems with a overall live basal area of 540 cm^2 were found. The highest vine maple total basal area found in one cell was 305 cm^2, the median total basal area over all cells with vine maple stems was 18 cm^2.

Throughout the longer belted transect of the study site vine maple cover was low or vine maple was completely absent. The shorter transect contained two small areas of higher vine maple cover. Several large clumps of vine maple were located on large rocks just outside of the shorter transect to the south. They were not accessible for measurement, but the portion of their stems that leaned towards the transect contributed to the cover of vine maple in that transect.

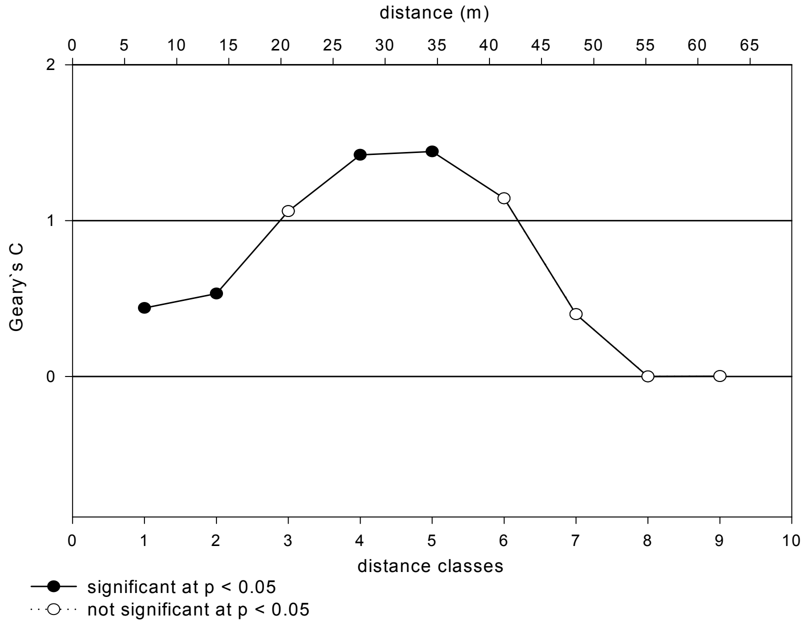

Figure 15: Geary's C correlogram of vine maple cover in the US site.

The Geary's C correlogram of the study site shows significant positive autocorrelation in the two smallest distance classes (upper boundaries 6.9 and 13.7 m), and significant negative autocorrelation in distance classes four and five (upper boundaries 27.5 and 34.4 m) (Figure 15). All other distance classes did not display significant autocorrelation. The two highest distance classes are again not further interpreted since their result for Geary's C is based on too few pairs of observations.

2 Surficial geology

2.1 LSCR site

2.1.1 Surficial geology

The surficial geology of the study site was dominated by mass movement sediments. Squamish Creek, the creek that forms the northern boundary of the LSCR study site has incised up to a depth of ca. 40 m into the terrain and has created four large exposures along the side of the study site. These sections (sections one to four) gave insight into the type and frequency of mass movement events that formed the surficial sediments of the study site. No complete stratigraphy of the study site could be constructed, nor was such a construction necessary for the purpose of the investigation. The sediments were therefore not assembled into stratigraphic units but named after their genesis.

The four measured sections found along Squamish Creek are presented schematically in Figure 20. Descriptions and interpretation of measured sections not appearing in Figure 20 can be found in the Appendix. The distribution of the surficial sediments of the site is presented in Figure 18.

2.1.1.1 Section one

Section one was composed of three beds, all with indistinct contacts. The lowest bed (bed one) was composed of unsorted, loose, clast supported cobble to large boulder (more than 1 m in diameter) gravel. It had a thickness of 1.5 m. Little fine material of fine to coarse sands filled the interstices between the dominantly angular to very angular rocks. The diamict of local granodiorite and granite showed no preferred orientation.

The second bed was only 60 cm thick and consisted of a clast supported, unsorted, loose pebble to boulder gravel with much smaller boulders (less than 40 cm in diameter) and more visible sandy fine material. Clasts were again predominantly angular to very angular granodiorites and granites.

The top bed was 3.50 m thick. The upper levels of this bed were free of fine material. Unsorted diamict of cobbles to large boulders (above 1 m in diameter) formed openwork gravel (Figure 16). In the lower levels interstices were filled by sandy fine material. The diamict showed the same angularity, lack of orientation and composition as in bed one.

Figure 16: Openwork gravel, detail of bed three in section one.

Beds one and three showed typical features of rockfalls. Squamish Creek had incised a four to five meter wide gorge with nearly vertical walls approximately 40 m deep into the granitic bedrock above the position of the study site. This canyon, or rather the former content of the canyon, formed a likely source of these sediments. The fine material in bed one was most likely derived from material deposited by the sediment visible in bed two.

Bed two is considered to be derived from a debris flow event. The smaller size of the clasts and the presence of a higher amount of fine material indicates a different genesis of this bed.

The surface expression of the bedrock sediment visible in the top layer of this section was dominated by large boulders. Interstices free of fine material were preserved beneath larger clasts where no fine material was washed in from surrounding sediments. The visible clasts were angular and their dark grayish surfaces were free of clay and silt. Mosses, coarse woody debris, humus and in depressions soil covered the clasts (Figure 17).

Figure 17: Surface expression of rockfall sediment.

Rockfall sediment underlay 18 cells in the northwest corner of the study area (Figure 18). The relief of this area suggests that Squamish Creek used to run along the eastern boundary of this sediment and united with the unnamed creek that forms the southern border of the study site near the center of the western boundary of the study site (see Figure 39). Subsequent development of Squamish Creek after the latest rockfall event documented in section one had rerouted Squamish Creek into its current bed.

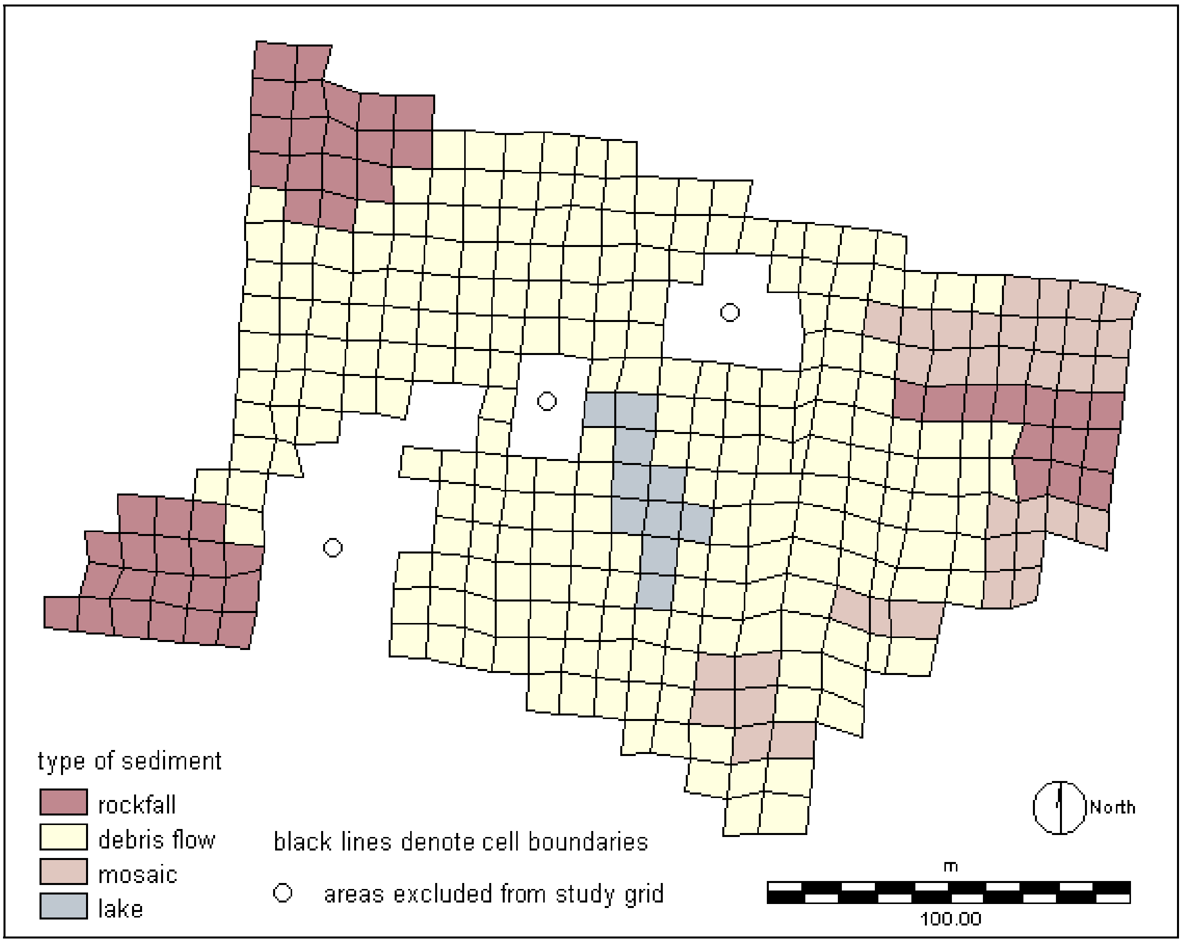

Figure 18: Display of the spatial pattern of surficial sediments in the LSCR site.

Similar surface expressions indicative of rockfall surficial sediments were found in two other areas of the study site. One area underlay 19 cells in the southwestern corner of the study site. The origin of the sediment is considered to be similar to the sediment found in the northwestern corner. The unnamed creek that formed the southern boundary of the study site had not formed a bedrock canyon. However, the creek ran in a snow avalanche chute. This gives evidence of the high energy relief that might just as easily form the path of rock avalanches. The main discharge of the unnamed creek now ran to the south of the study site. Deeply (one to two meters) incised channels give evidence that a larger volume of the water of the unnamed creek used to run through the study site and connect to Squamish Creek. These channels are now partly blocked by logs and rocks. This blockage was recent enough that the vegetation had not reclaimed the wide channels yet.

The third rockfall area that was visible in the study site was located near the eastern boundary of the study site. Van-sized rocks were the most conspicuous aspect of the narrow lobe that underlay twelve cells. The source of these rocks was unclear, but the increasingly steep terrain above the study site will have provided enough potential sources.

2.1.1.2 Section two

Section two was a long section of a variable thickness of six to eight meters. One bed of loose very poorly sorted pebble to boulder gravel with random orientation was evident in the section. The diamict was mainly clast supported, in pockets matrix supported. The matrix consisted mainly of coarse sand with some silt and fine sand that showed some vague wavy bedding in pockets. Clasts were local rock, mainly angular.

The random orientation and poor sorting of the gravel indicates a thick debris flow sediment with fluvial components visible as pockets of wavy bedding. The main difference to the rockfall sediments that form the surface of section one was the increased presence of fine material. The rocks present in this type of sediment were always covered by yellowish-brownish fines.

The debris flow sediments formed a continuous surface between the position of section two and the rockfall sediments found in section one. Though the lower boundary of the older rockfall sediment in section one was not visible, the continuity and the thickness of the debris flow sediment found in section two indicate that the rockfall sediments found in section one were deposited on top of the debris flow sediment. This implies that at least two rockfall and one debris flow events have occurred since the deposition of the debris flow sediments found in section two (Figure 20).

The surface of the sediments that form the bed in section two was more even than the surface of the rockfall sediments. The main expression of the surface was a thick and relatively smooth layer of humus, coarse woody debris and soil. Smaller and larger rocks were visible on the surface of the sediment, either pulled up by toppled trees or because of their original proximity to the surface (Figure 19).

Debris flow sediments covered most of the study site (Figure 18). Through the center of the site a cliff formed a chain of bedrock outcrops. Where benches had formed in the face of the cliff the slope was level enough to allow sediment to accumulate in a thin layer of mainly finer material.

Figure 19: Surface expression of debris flow sediment.

2.1.1.3 Section three

Section three gave evidence of four depositional events. The sediments were exposed to a depth of 15 m. The topmost three beds were very similar to the sediment found in section two. Bed two contained some very large clasts (up to 3 m in diameter) and extended to a height of 12 m. Bed three was a pocket of ca. 1 m in height and 2 m in width between beds two and four with indistinct lower contact. It contained pebbles and coarse sandy granules in undulating horizontal bedding. The clasts were subrounded to subangular and showed no imbrication. Bed four was draped on top of the boulders of bed two. Bed four appeared most similar in clast size to the sediment in section two, but the possibility that instead bed two might have been deposited in the same debris flow event as the sediment in section two can not be ruled out (Figure 20). All three beds were interpreted as debris flow sediments. Bed three represents a fluvial component of a debris flow.

Bed one extended to a height of 2 m. The sediment consisted of a dark grey compact and massive cobbly pebble gravel, supported by matrix composed of all particle sizes. Some irregular horizontal bedding was observed but generally the sediment was very poorly sorted. Clasts were mainly subangular and predominantly granite and granodiorite with a small portion of basalt. No striations or snub scars were found on any of the clasts and the sediment functioned as an aquifer. However, the compactness, relatively small clast sizes and presence of non-local rocks (basalt) in the material made a glacial origin of the sediment possible. A fabric analysis was therefore performed. The clasts were randomly orientated. Lodgement till can therefore be ruled out as the origin of this sediment. The sediment might have been ablation till that was deposited higher up the valley side and reworked and redeposited as a mudflow. The high compaction and the position below 13 m of debris flow sediments designates this sediment as the oldest one found in the study site.

The sediment from bed one was found in several places of the study site below the loose debris flow sediments, in depths of less than 1 m. Proximity to bedrock in these places suggested that this sediment directly overlay bedrock. Due to the compactness of the material this remained speculative. Near the western boundary of the study site the sediment from bed one formed the surficial sediment in four cells. The former channel of Squamish Creek is presumed to run through this area. Erosion of the debris flow sediments on top of the sediments of bed one might have exposed this sediment. The near absence of large clasts marked the surface expression of the sediment in this area. Since this sediment is interpreted as a debris flow it is further subsumed under debris flow sediments.

2.1.1.4 Section four

Section four was located close to the bedrock canyon above the study site. Bedrock was exposed to a depth of ca. 18 m. The bedrock was capped by ca. 2 m of debris flow sediments that were similar in appearance to the top layer of sediment exposed in section three. No close examination of these sediments was possible. Due to the proximity of the sections this bed is considered to be of the same origin as the top layer of section three (Figure 20).

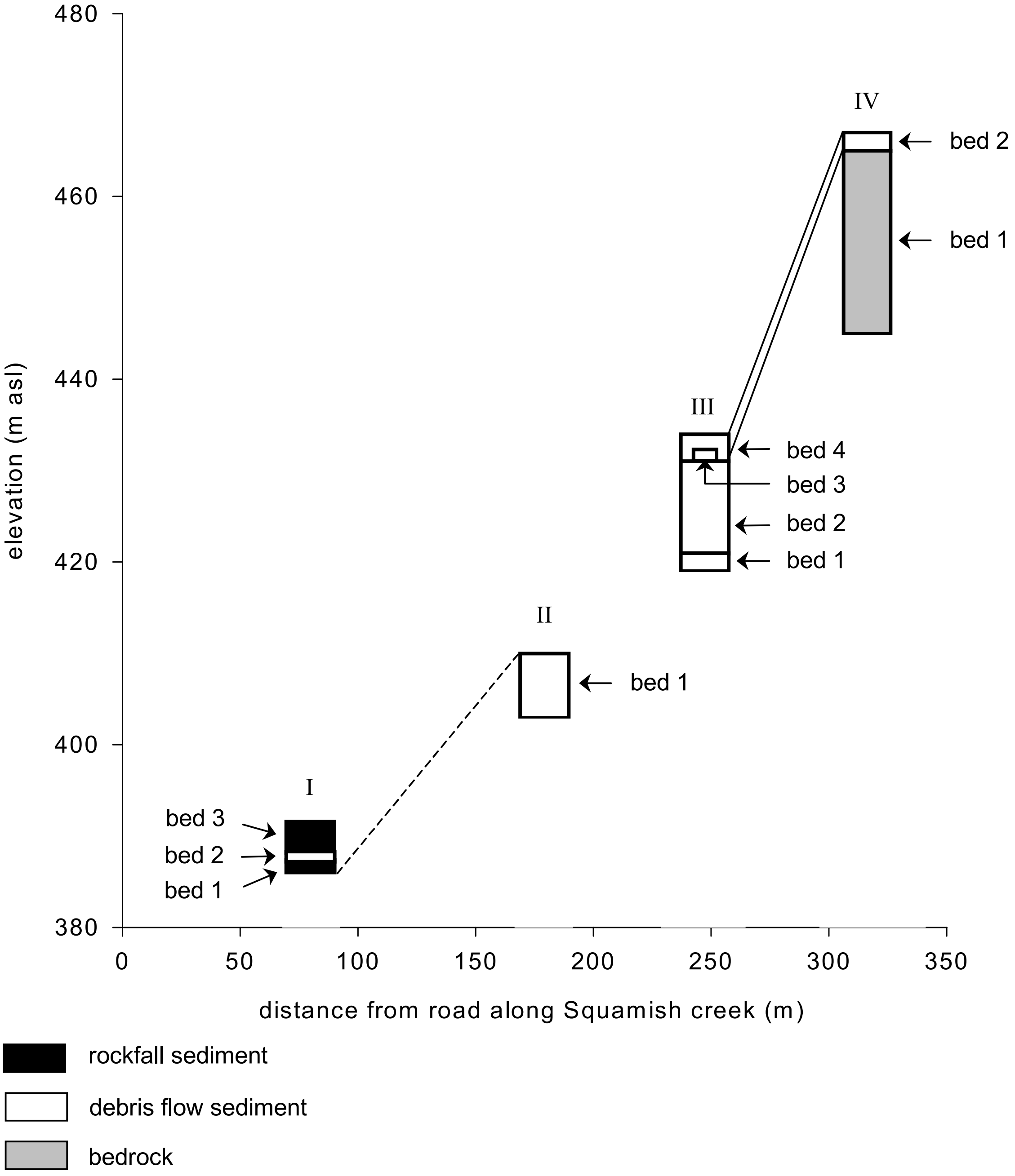

Figure 20: Diagram of sections found along Squamish Creek. Numbers of sections are located above each section in roman figures. Boxes represent beds. Beds were numbered bottom to top within each section. No complete stratigraphy of the study site could be constructed. The sediments were therefore not assembled into stratigraphic units. Instead they were named after their genesis. The two beds which belonged without doubt to a common horizon were connected by solid diagonal lines. Though the sediments evident in section two must have underlain the sediments found in section one, they were not exposed in section one. Their relative position is indicated by the slashed line.

2.1.1.5 Sediments not exposed in sections one to four

The four sections exposed by Squamish Creek gave evidence to repeated mass movement events. Debris flows formed the majority of depositional events and the majority of the surficial sediments. In the upper third of the study area bedrock was located relatively close to the surface. During mapping of the terrain, areas were observed which could not be clearly classified as one of the two sediments that were expected from the analysis of the sections in Squamish Creek. These areas contained rockfall snouts that could clearly be identified by color, the lack of fine material between the rocks and the size of the rocks. The tops of the snouts were covered by a layer of obvious debris flow sediment. This layer was thin enough to have flown around larger outcrops of rockfall boulders. The latest depositional event therefore was a debris flow. Since these areas showed characteristics of both rockfall and debris flow sediments in a small scaled mosaic pattern, they were mapped as a unique sedimentary unit. This unit is further referred to as mosaic sediment.

A deviation of the rockfall/ debris flow pattern was found in the center of the study site. Several larger and smaller holes were observed in the forest floor in this area. One good section of 1.20 m depth and 1 m width was found in one of these holes (section five). Deformed coarsely interlayered horizontal laminae of thick layers of clay and silty coarse sand of varying width (a few millimeter to 10 cm) formed the single bed of the section. Especially the clay layers were enriched in dark organic material. No grading or ripple marks were observed in the laminae. At the bottom of the hole, gravel and small boulders were found.

The holes were created by creek erosion. Several small creeks joined in this area and drained through a break in the bedrock cliff that intersected the study site. These creeks flowed both on the surface and below the surface. The holes were located in a wet and muddy flat area on top of the bedrock outcrops that formed the cliff. Scree was deposited at the foot of the break in the cliff through which the creeks drain. With the barrier of the cliff still intact, a pond would have formed in the resulting basin. Clay deposited in the pond alternated with sand deposited during rainstorms or similar events that increased sediment transport in the creeks that drained into the pond to form the laminae. When the barrier broke, the pond was emptied. The creeks had subsequently cut through the soft lake sediments to the debris flow material located beneath. This material formed the current surface of the creek beds. Ten cells were located on lake sediment (Figure 18).

Figure 21: Surface expression of mosaic sediment at former rockfall snout.

Figure 22: Surface expression of lake sediment.

2.1.2 Vine maple response to surficial geology

Vine maple showed a strong significant (p = 0.000) affinity to rockfall sediment in the study site. In 49 of the 50 cells classified as rockfall sediment vine maple was found. Twenty-nine of the total of 47 cells with vine maple cover above 25 % were located on this type of sediment. One and a half times the number of cells with vine maple cover between five and 25 % were located on rockfall sediment than could be expected if sediment type would not influence vine maple distribution. Cells without vine maple and cells with vine maple cover below 5 % were under-represented on this sediment type.

Debris flow sediment showed the opposite pattern: Cells with a high cover of vine maple were under-represented and cells with low or no vine maple cover were over-represented on this type of sediment. Vine maple response to mosaic sediment was intermediate between rockfall and debris flow sediment as might be expected from the intermediate characteristics of this type of sediment. A contingency table of the frequency the vine maple cover classes were found on different sediment types is given in Table 1.

Of the ten cells located on lake sediment three had no vine maple cover, five had a vine maple cover below 5 % and one had a cover of 12.5 to 25 %. Vine maple seemed to respond similarly to lake sediment as to debris flow sediment.

vine maple cover		type of surficial sediment			
		debris flow	mosaic	rockfall	sum
no vine maple	number of cases	103	13	1	117
	expected number of cases	*85.1*	*13.4*	*18.6*	
< 5 %	number of cases	82	10	7	99
	expected number of cases	*72.0*	*11.3*	*15.7*	
5 - 25 %	number of cases	31	8	13	52
	expected number of cases	*37.8*	*5.9*	*8.3*	
> 25 %	number of cases	13	5	29	47
	expected number of cases	*34.2*	*5.4*	*7.5*	
sum		229	36	50	315

Table 1: Contingency table of vine maple cover on debris flow, mosaic and rockfall sediment. Vine maple cover classes 2a and 2b were combined to a cover class 5 % - 25 % and cover classes 3, 4 and 5 were combined to a cover class > 25 %.

2.1.3 Soil characteristics of sediment types

The strong response of vine maple to sediment type in the study site could have been due to an edaphic characteristic of the sediment types. Differences in soil type, texture, skeletal content, rockiness and pH between the types of sediment and their influence on vine maple distribution were therefore investigated.

2.1.3.1 Soil type

Podzols were the dominant soil type of the study site and found on all sediment types. Twenty of the 22 sampled soils in the study site were classified as orthic ferro-humic podzols. Twelve of the podzols were located on debris flow sediment, three on mosaic sediment and five on rockfall sediment. In four plots the parent material (bedrock or highly compacted diamict) was found within 1 m of the surface. Even in the most extreme case (bedrock within 19 cm of the surface) a fully developed podzol had formed.

Two plots had an orthic sombric or orthic dystric brunisol soil type. The orthic sombric brunisol was found on rockfall sediment, the orthic dystric brunisol was found on debris flow sediment. Hemic folisols were found on large (the size of a van) boulders deposited by rockfall near the upper boundary of the study site but no folisols were sampled.

2.1.3.2 Soil skeletal content and rockiness

All soils studied were very coarse. The skeletal content (all particles larger than 2 mm) of the soil was in no plot below 20 % and was able to reach up to 98 %. Two depths were sampled: 25 - 30 cm and 65 - 70 cm. Soil pits were located in rockfall, mosaic and debris flow sediment. Soils that have developed on rockfall sediment averaged above 90 % skeletal content in both sampling depths, with a minimum of 75 % skeletal content. This is a significantly higher average skeletal content than the skeletal content found in the soil pits located on debris flow sediment (depth 25 - 30 cm: $p = 0.000$, depth 65 - 70 cm: $p = 0.009$). Details can be found in Table 2.

Not surprisingly the skeletal content of the soils that have developed on mosaic sediment showed an intermediate skeletal content between soils on rockfall and debris flow sediments. At the sampling depth closer to the surface the mean skeletal content of soils developed on mosaic sediment was not significantly different from the soils developed on debris flow sediment of the same depth ($p = 0.541$) but significantly different from the soils that have developed on rockfall sediment (p = 0.041). At the lower sampling depth the mean skeletal content of soils developed on mosaic sediment was 15 % higher than at the sampling depth closer to the surface. And the significant difference to soils that have developed on rockfall sediment has disappeared as well (p = 0.801). There was still no significant difference to the soils that have developed on debris flow sediment (p = 0.371). Since mosaic sediment was rockfall sediment thinly overlain by debris flow sediment a higher skeletal content at a greater sampling depth was to be expected.

Rockiness was a coarse measurement of skeletal content in the top 50 cm of the soil. It was used as a proxy of skeletal content in a study with a larger sample size of 103 cells to investigate the connection between the proportion of rocks in the soil and vine maple distribution. In four cells with soil pits rockiness was measured as well. A direct comparison of skeletal content of the samples from a depth of 25 - 30 cm and rockiness in these cells indicates a good correspondence of both methods (Figure 23). The value for rockiness was on average only 8 % below the value of skeletal content in the cells, the largest deviation was 12.5 %. Since the measurement method for rockiness ignored all smaller particles in the soil the lower value for rockiness is quite acceptable. Additionally the values for rockiness can be expected to be systematically lower than the direct measurement of skeletal content because of the number of live roots encountered. Large trees frequently occurred in the cells and in some cells encounters with roots formed a significant portion of the measurements.

In cells on lake sediment rocks were hit on average with the lowest frequency of all sediments sampled. In debris flow sediment rockiness showed a high variability. The average rockiness of debris flow sediment was with 47.5 % slightly, but not significantly, lower than the average rockiness of 53.8 % in mosaic sediment (p = 0.905). Variation was lower in mosaic sediment than in than in debris flow sediment, most likely due to the much smaller sample size of nine compared to 74 in debris flow sediment. The cells on rockfall sediment had the highest average rockiness with 76.0 % of all sediment types, significantly higher than rockiness in debris flow sediments (p = 0.000) and mosaic sediment (p = 0.008). This corresponds to the results for skeletal content at a sampling depth of 25 - 30 cm for these three sediment types. Details can be found in Table 2.

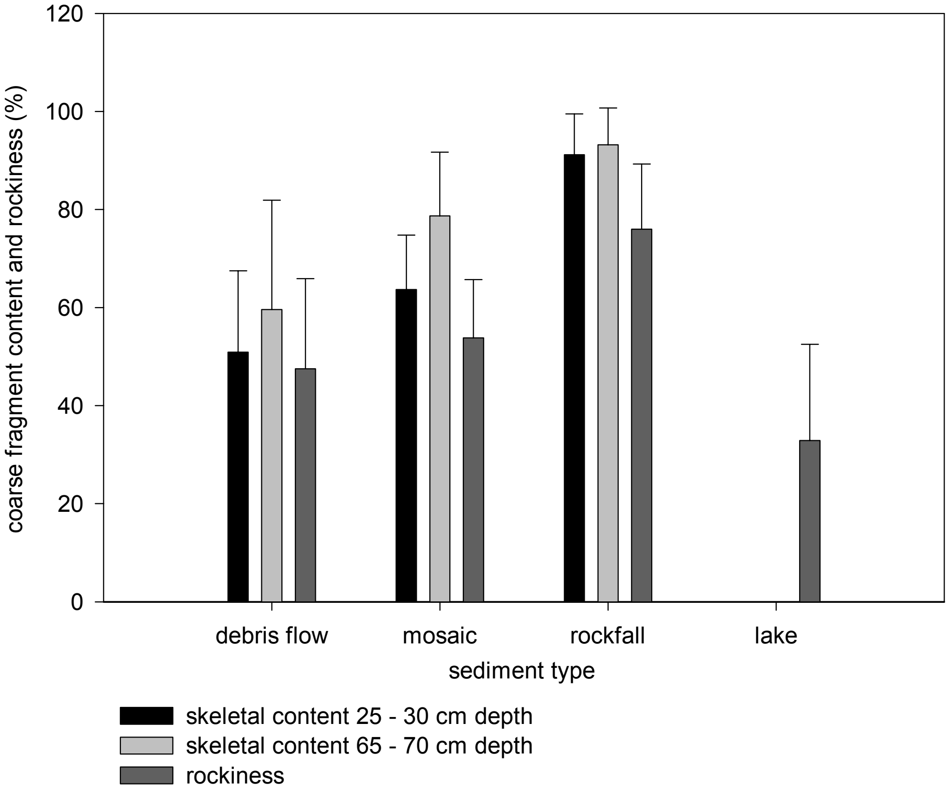

Figure 23: Skeletal content for two sampling depths and rockiness of debris flow, mosaic and rockfall sediment. On lake sediment only rockiness was measured. Error bars represent one standard deviation.

2.1.3.3 Soil texture

The clay content of the soil exceeded in no sample 1.3 % of the fine material and was below detection range in most samples, while the sand content varied from 65 to 91 %. Soil texture could be classified as coarse loamy-skeletal in nine samples, and sandy-skeletal in 32 samples. All but one loamy-skeletal soil textures were found on debris flow sediment. Since the sand content basically determines the texture class in the near complete absence of clay, the comparison of texture was simplified to a comparison of sand content.

Rockfall sediment had the highest average sand content of the three sediment types investigated in both sampling depths. However, the maximum difference to another sediment type was 7.7 % sand content and no difference was statistically significant (25 - 30 cm: $p = 0.091$, 65 - 70 cm: $p = 0.271$). Soil texture differences between the sediment types can therefore not be expected to be physiologically significant for vine maple. More details can be found in Table 2.

	sediment type	n	mean	standard deviation	minimum	maximum
skeletal content at 25 - 30 cm (%)	1	13	50.9	16.6	20	73
	2	3	63.7	11.1	52	74
	3	6	91.2	8.3	75	98
skeletal content at 65 - 70 cm (%)	1	10	59.6	22.3	31	92
	2	3	78.7	13.0	66	92
	3	6	93.2	7.5	78	98
rockiness (%)	1	74	47.5	18.4	7.1	84.6
	2	9	53.8	11.9	33.3	68.8
	3	16	76.0	13.3	53.3	100
	4	4	32.9	19.6	20	66.7
sand content at 25 - 30 cm (%)	1	13	73.0	6.1	65	85
	2	3	74.2	1.4	72.5	75
	3	6	80.2	8.2	68.75	90
sand content at 65 - 70 cm (%)	1	10	77.6	6.3	67.5	87.5
	2	3	80.0	7.5	72.5	87.5
	3	6	82.9	5.0	76.25	91.25
pH at 25 - 30 cm	1	13	4.38	0.3	3.73	4.68
	2	3	4.40	0.2	4.24	4.64
	3	6	4.32	0.1	4.20	4.44
pH at 65 - 70 cm	1	10	4.49	0.2	4.16	4.71
	2	3	4.70	0.2	4.47	4.84
	3	6	4.43	0.1	4.31	4.52

Table 2: Edaphic properties of debris flow sediment (sediment type one), mosaic sediment (type two), rockfall sediment (type three) and lake sediment (type four). n denotes the number of cases found on this sediment type.

2.1.3.4 Soil pH

Variation in the pH value of the samples was relatively low. All soils were acidic, the highest pH value found in any sample was 4.84, the lowest 3.73. Average pH values were lowest in rockfall sediment and highest in debris flow sediment in both sampling depths. More details can be found in Table 2. While there was no significant difference in the average pH between sediment types at a depth of 25 - 30 cm ($p = 0.826$) and 65 - 70 cm ($p = 0.055$), the averages at the depth of 65 - 70 cm were different enough to warrant closer inspection. The difference between mosaic and rockfall sediment was responsible for the low p value. Their averages were only 0.27 pH values apart. Even if only low sample sizes would have prevented significance, the difference would not be physiologically important to vine maple.

2.1.4 Vine maple response to soil characteristics

2.1.4.1 Vine maple response to soil type

Thirteen soil pits were located in cells with vine maple, nine in cells without vine maple. In 20 of these soil pits podzols were found, the two brunisols were found in cells with vine maple.

2.1.4.2 Vine maple response to soil skeletal content and rockiness

Vine maple sends roots through both sampling depths investigated and far deeper. Values for both sampling depths were therefore combined. Vine maple cover was used as the measure for response to edaphic factors because it is a generalized response to the conditions in the entire cell. Total basal area, for example, reflects the clumped nature of vine maple growth morphology much stronger and might therefore contort a comparison based on cell attributes.

If sediment type is ignored and skeletal content is compared between all plots with vine maple and all plots without vine maple mean skeletal contents did differ significantly ($p = 0.012$). The mean skeletal content was greater in plots with vine maple (mean: 76 %, range: 44 - 97 %) than in plots without vine maple (mean: 52 %, range: 20 - 83 %).

If the skeletal content of the soil is compared to vine maple abundance separately for each sediment type, the connection gets less pronounced. Statistics can only be done for debris flow sediment since all soil pits located on rockfall sediment were in cells occupied by vine maple, and only three pits were located on mosaic sediment in total. In debris flow sediment, vine maple still had a higher mean skeletal content of 61 % compared to the mean skeletal content of plots without vine maple of 48 %, but this difference was not significant any more ($p = 0.235$). In mosaic sediment the two plots located in cells with vine maple both had the same lower skeletal content of 65 % than the plot located in a cell without vine maple with a skeletal content of 83 %. In rockfall sediment no plots were located in cells without vine maple. Two soil pits were located in cells with low vine maple cover (cover less than 25 %). Those two cells had 77 and 97 % skeletal content, that averages to 87 %. Four pits were located in cells with high vine maple cover (cover more than 25 %). In these cells skeletal content averaged 95 % with a range of 93 to 97 %. More details can be found in Table 3. The data seems to indicate a trend towards a connection of vine maple distribution to skeletal content, but the investigation of rockiness showed that this trend is most likely due to low sample sizes.

The comparison of rockiness did not yield a significant difference between the 65 cells with vine maple and the 38 cells without vine maple sampled ($p = 0.196$). However, in cells with vine maple again the higher average value for rockiness (54.5 %) was found than in cells without vine maple (47.5 %). If cells are stratified after sediment types the connection between vine maple cover and rockiness disappears completely. On debris flow sediment 35 cells without vine maple were located and 39 cells without vine maple. The average rockiness of all cells without vine maple was with 47.2 % nearly identical to the 47.7 % mean rockiness in cells with vine maple, not a significant difference ($p = 0.908$). On mosaic sediment only ten cells were located in total. The averages of cells with vine maple are with 55.4 % slightly higher than the averages of cells without vine maple with 50.7 %, not a significant difference ($p = 0.643$), and both are higher than the averages from debris flow sediment.

On rockfall sediment 16 cells were located, all with vine maple. Therefore two combined cover classes of vine maple were created to investigate the possibility that high vine maple cover is connected to high rockiness of the soil. Vine maple cover classes 1, 2a and 2b and cover classes 3, 4 and 5 were combined to two new cover classes < 25 % and > 25 % cover, both with eight cases. Average rockiness was higher in cover class < 25 % than in cover class > 25 %, but not significantly so ($p = 0.354$). For more details see Table 3.

	number of cells	mean rockiness (%)	standard deviation	minimum (%)	maximum (%)
all cells					
no vine maple	38	47.5	17.6	7.1	84.6
vine maple	65	54.5	21.5	12.5	100.0
debris flow sediment only					
no vine maple	35	47.2	17.8	7.1	84.6
vine maple	39	47.7	19.1	12.5	81.3
mosaic sediment only					
no vine maple	3	50.7	17.8	33.3	68.8
vine maple	6	55.4	9.5	42.9	68.8
rockfall sediment only					
vine maple cover < 25 %	8	79.1	14.0	60.0	100.0
vine maple cover > 25 %	8	72.8	12.7	53.3	87.5

Table 3: Vine maple response to rockiness, for all cells and stratified after sediment types.

Three of the cells located on lake sediment had a vine maple cover of 1 at an average rockiness of 37.2 % and one cell located on that sediment type had a vine maple cover of 4 at a rockiness of 20 %.

These results indicate that rockiness of the soil is not the factor that determined vine maple distribution in the study site. While the skeletal content of the soil was one of the major differences between the sediment types in the study area, it was not this feature of the sediments that caused the strong response of vine maple to sediment type.

2.1.4.3 Vine maple response to soil texture

Vine maple was indifferent to texture of the fine fraction of the soil, too. The sand content of the fine material varied from 68.2 % to 86.8 % in all plots with vine maple. In all plots without vine maple the sand content varied from 65.0 % to 83.8 %. The mean sand content of the fine material was with 78.7 % slightly higher in plots with vine maple than in plots without vine maple with a mean of 74.5 %, not a significant difference ($p = 0.094$).

The difference in the mean sand content of plots with vine maple and plots without vine maple located on debris flow sediment was also not significant ($p = 0.363$), but plots with vine maple still had a slightly higher mean of 76.0 % (range: 68.1 - 78.8 %) compared to 74.1 % (range: 65.0 - 83.8 %) in plots without vine maple. In the plots located on rockfall sediment the cells with a high cover of vine maple also had a slightly higher average sand content (82.2 %, range: 74.4 - 86.3 %) than the plots with low cover of vine maple (80.31 %, range: 76.9 - 86.9 %). And the sand content of the plot located in a cell without vine maple on mosaic sediment was with 77.5 % intermediate between the values of 72.5 and 81.25 % sand content for plots with vine maple on mosaic sediment.

2.1.4.4 Vine maple response to soil pH

The average pH of the soils from all pits located in cells with vine maple was 4.40 (range: 3.95 - 4.56), slightly lower than the average pH of 4.46 (range 4.22 - 4.60) in plots without vine maple. This is not a significant difference ($p = 0.420$). This pattern stays fairly constant if the data is stratified after sediment types. The average pH values of plots with vine maple (mean: 4.36, range: 3.95 - 4.56) was only 0.09 units lower than in plots without vine maple (mean: 4.45, range: 4.22 - 4.60) ($p = 0.207$) in plots located on debris flow sediment. The average pH was nearly identical between vine maple plots (4.56, 4.56) and plots without vine maple (4.54) in mosaic sediment. And in rockfall sediment no real difference existed between cells with a low cover of vine maple (mean: 4.40, range: 4.33 - 4.57) and those with a high cover of vine maple (mean: 4.37, range: 4.29 - 4.38).

2.2 Chilliwack site

2.2.1 Surficial geology and rockiness

Eight cells in the top section of the study site were located on sediment deposited in one rockfall event. Only folisols had developed on the large boulders that were characteristic for this type of sediment. Lichens were still predominant on many rock surfaces and higher vegetation was mainly present in gaps between the boulders. No trees have been able to establish themselves, shrubs and bushes dominated (Figure 24). Species like *Cystopteris fragilis*, *Lycopodium annotinum*, *Rubus ursinus*, *Carex deweniana*, *Goodyera oblongifolia* and *Platanthera orbiculata* attested to the open, rocky and relatively dry character of this site. The measured rockiness of this sediment was with 65.1 % on average (range: 33 - 94 %) fairly high.

Twelve cells in the lower section of the study site were located on debris flow sediment. On this sediment mature oldgrowth forest on fully developed podzols were extant (Figure 25). Rockiness of this sediment was significantly lower ($p = 0.017$) than in rockfall sediment, with an average rockiness of 35.9 % and a variation from zero to 75 %. A display of the distribution the sediment types in the study site can be found in Figure 26.

2.2.2 Vine maple response to surficial geology and rockiness

Vine maple response to surficial geology of the study site was extreme. As in the LSCR site a scatter of vine maple with (mainly) low cover was found on debris flow sediment while high cover of vine maple was found on rockfall sediment. On rockfall sediment large vine maple bushes with many relatively thin stems had developed. Up to 86 stems with a total basal area of 1222.4 cm^2 were counted in one 5 by 5 m cell. Vine maple cover above 75 % was found in five cells, cover class 4 was found twice and cover class 3 once. No cell had a lower cover than 25 % vine maple. On debris flow sediment five cells had no vine maple cover. Six cells with a cover below 5 % and one cell with cover class 2a were found.

Figure 24: Chilliwack site: Vine maple on rockfall sediment.

Figure 25: Chilliwack site: In the foreground debris flow sediment, in the background vine maple on rockfall sediment is visible through the tree trunks.

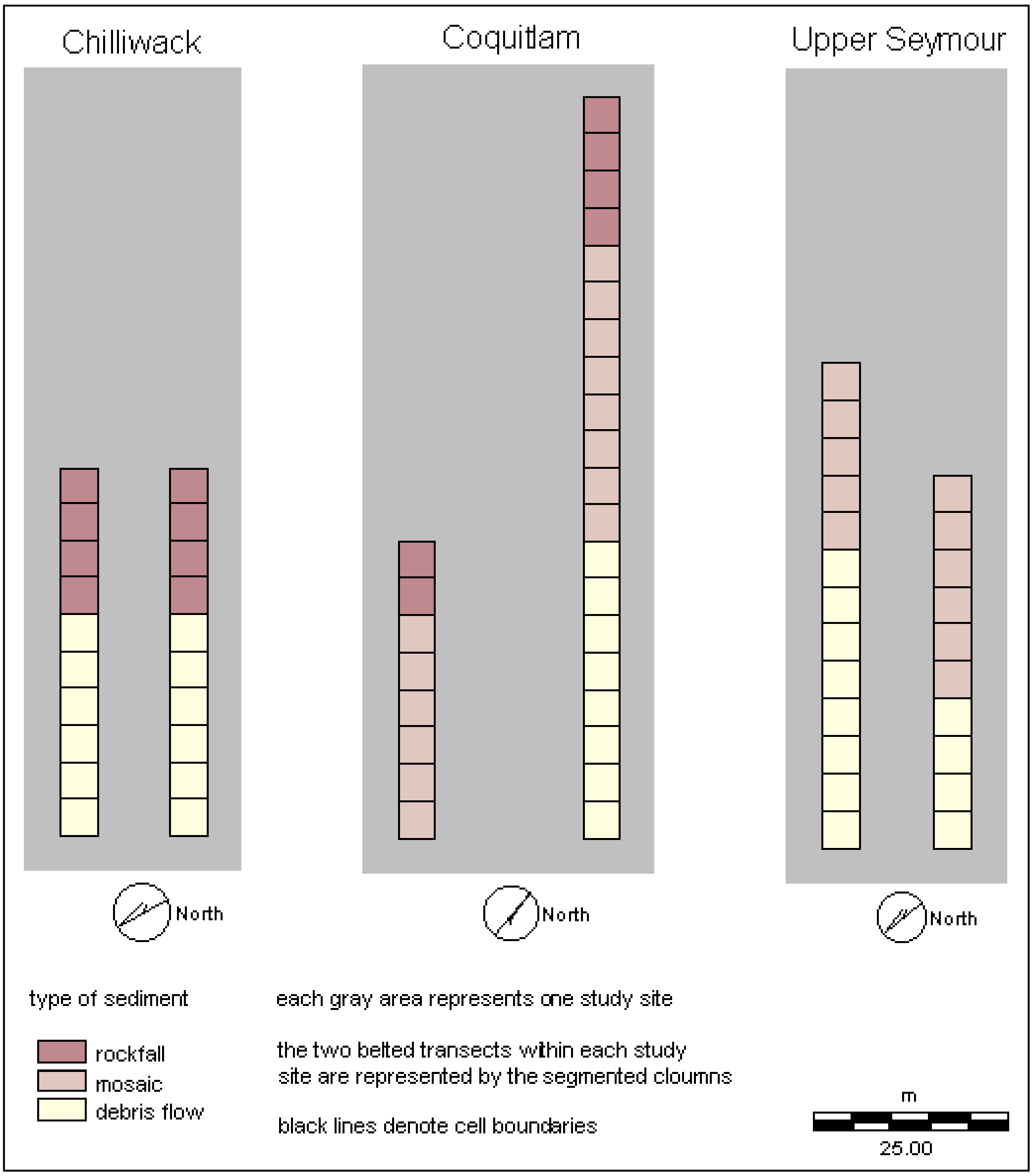

Figure 26: Surficial geology of the Chilliwack, Coquitlam and Upper Seymour study sites.

Vine maple response to rockiness was indifferent, as in the LSCR site. A comparison between cells with no vine maple cover, low cover (cover classes 1, 2a and 2b) and high cover (cover classes 3, 4 and 5) gives a nearly significant result ($p = 0.054$). This reflects the differences in rockiness between sediments since all cells with high vine maple cover were located on rockfall sediment. If the cells with low vine maple cover and the cells without vine maple, all located on debris flow sediment, are compared, no significant differences are found ($p = 1$). Average rockiness of these cells was nearly identical, with 36.0 % rockiness in cells without vine maple (range: 20 - 60 %) and 35.9 % in cells with vine maple (range: 0 - 75 %). The constantly high cover of vine maple on rockfall sediment was located on soil with a range of rockiness from 33 to 94 %.

2.3 Coquitlam site

2.3.1 Surficial geology and rockiness

A long section exposed by the construction of the road that passed below the study site gave evidence to repeated debris flow events that overlay the granodiorite bedrock. A description of the section can be found in the Appendix. Eight cells in the southeast of the study site, low on the slope, were located on debris flow sediment. Rockfall sediment overlay these sediments uphill from this point. The rockfall lobe reached further down the slope in the west of the study site. This rockfall sediment was overlain by a thin veneer of debris flow sediment and formed a mosaic with this type of sediment. Fourteen cells were classified as mosaic sediment. Both mosaic sediment and the debris flow sediment supported mature old growth forest.

Material from another rockfall event was deposited on top of the mosaic sediment higher up the slope. The rocks were covered by mosses and lichens. Shrubs dominated the vegetation. No trees had established yet on the folisols. Six cells were classified as rockfall sediment. A display of the distribution of the sediment types in the study site can be found in Figure 26.

On rockfall sediment a significantly higher rockiness of 65.4 % on average was measured than on mosaic sediment ($p = 0.025$) and debris flow sediment ($p = 0.017$). On debris flow and mosaic sediment the measured average rockiness of 38.7 and 39.9 % was very similar ($p = 1$). The smallest value obtained for rockiness was 53.3 %, much higher than the minimum values of 6.3 % for mosaic sediment and 13.3 % for debris flow sediment. The maximum values were closer together: 85.7 % for rockfall sediment, 73.3 % for mosaic sediment and 56.3 % for debris flow sediment.

2.3.2 Vine maple response to surficial geology and rockiness

Vine maple dominated the vegetation on rockfall sediment as in the CHIL site. All cells on this sediment supported a vine maple cover above 25 %, in four cases a cover above 75 %. The clumps were composed of fewer stems than in the CHIL site. A maximum of 13 stems with a total basal area of 679 cm^2 was found in one cell.

The other extreme was found on debris flow sediment. No cell had a vine maple cover above 7.5 % but all cells had some cover of vine maple. The most divergent cover was found on mosaic sediment. All cover classes and one cell without vine maple were found on this sediment.

High cover of vine maple (> 25 %) was significantly (p = 0.003) connected to high values for rockiness (mean: 57.8 %, range: 28.6 - 85.7 %) if compared to low cover of vine maple (mean: 37.3 %, range: 6.3 - 68.7 %). The single cell without vine maple had the very low value of 6.7 % rockiness. On rockfall sediment only cells with a high cover of vine maple were found, on debris flow only cells with a low cover of vine maple. The only within sediment comparison can be performed on mosaic sediment. The seven cells located on this type of sediment with a low cover of vine maple (< 25 %) had a lower average value for rockiness of 35.7 % (range: 6.25 - 68.8) than the six cells with a high cover of vine maple (> 25 %) of 50.2 % rockiness (range: 28.6 - 73.3 %). And the single cell without vine maple with the low value for rockiness was located on this type of sediment as well. The difference between the averages for cells with low and cells with high vine maple cover are not significant (p = 0.173). Since the effects of rockiness and sediment can not be clearly distinguished for most types of sediment in this site an effect of rockiness on vine maple cover can not be ruled out.

2.4 Upper Seymour site

2.4.1 Surficial geology and rockiness

In the US site only two types of sediment were found: debris flow and mosaic sediment. Debris flow sediment covered the lower section of the study site down to the road that determined the lower boundary of the study site. Material exposed along this road gave evidence to a thick layer of debris flow sediment. Twelve cells in the northwest of the study site were covered by this type of sediment.

A rockfall lobe that reached further down the slope in the west of the study site was found on top of the debris flow sediment towards the southeast of the study site. The rockfall snout was clearly visible and the sediment was typically expressed near the snout. The rockfall lobe was covered by a thin layer of debris flow sediment that increased in thickness towards the southeast of the study site. Since both rockfall and debris flow characteristics were present in this part of the study site, this sediment was mapped as mosaic sediment. Eleven cells were located on mosaic sediment.

The average value for rockiness was with 52.0 % (range: 14.3 - 86.7%) slightly but not significantly (p = 0.456) lower in debris flow sediment than in mosaic sediment (mean: 58.2 %, range: 20.0 - 86.7 %).

2.4.2 Vine maple response to surficial geology and rockiness

Vine maple occurred in three of the twelve cells located on debris flow, always with a cover below 5 %. On mosaic sediment vine maple occurred in eight of eleven cells, five cells with vine maple cover below 25 % and three cells with vine maple cover above 25 %. A wide range of cover classes occurred on mosaic sediment in the LSCR site as well.

When the rockiness of cells without vine maple, cells with a low cover (< 25 %) of vine maple and cells with a high cover (> 25 %) of vine maple was compared no significant difference was found (p = 0.557). Cells without vine maple had the same average rockiness of 53.2 % as cells with low vine maple cover, and the range of values found was with 14.3 to 86.7 % for cells without vine maple and 28.6 to 71.4 % for cells with a low cover of vine maple high in both cases. Cells with a high cover of vine maple had on average a value of 66.7 % for rockiness, with a smaller range of 62.5 to 75.0 %. The average value for rockiness was highest in cells with a high cover of vine maple, but the highest value for rockiness was found in a cell without vine maple. No connection between rockiness and vine maple cover can therefore be assumed for this study site.

3 Light

3.1 Absolute light requirements

The assessment of the absolute light requirements of vine maple branches to survive on a stem did yield a clear connection of survival to light level. Light levels above dead branches, measured in photosynthetic available radiation, were 8 % lower than light levels above living branches on the same stem (p = 0.000). This relationship was relatively constant throughout the entire measurement period. However, the light requirements for the survival of a branch varied considerably between stems. Measurements within one cell, which were done within minutes of each other, yielded light levels for live branches on some stems which were below light levels for dead branches on other stems. Therefore no absolute lower boundary for the survival of branches was obtained.

3.2 Vine maple performance in response to light

3.2.1 Light levels in vine maple plots compared to the surrounding forest

Vine maple was clearly not confined to gaps or even to high light levels. The minimum value of percent site openness (SO) encountered at vine maple plots was 1.7 %, which is lower than the minimum value found at plots without vine maple (2.9 %). The average SO was with 5.94 % in plots with vine maple nearly identical to 5.92 % in plots without vine maple (p = 0.962).

The forest canopy seemed to provide mainly habitats with a SO between 3.6 and 8.8 % SO (10th and 90th percentiles). Vine maple occurred in more sites with light availability above 8.8 % SO and in the sites with the largest SO (Figure 27). Twelve percent of the plots with vine maple had a SO larger than 8.8 % compared to 6 % of the plots without vine maple. The maximum SO in a plot with vine maple was 12.5 % compared to 10.5 % in a plot without vine maple.

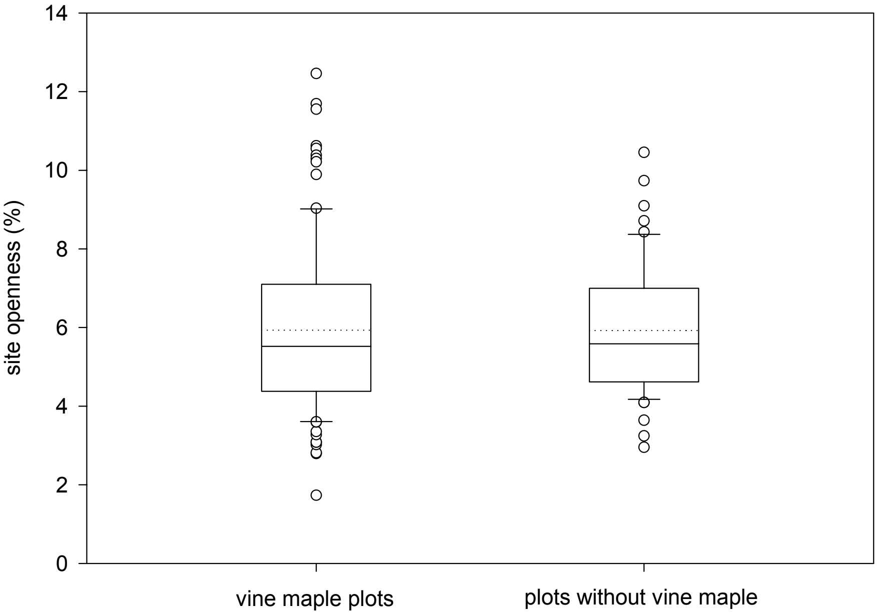

Figure 27: Percent SO at plots with (n = 99) and without (n = 48) vine maple. Boxes are defined by median, 25th and 75th percentile, whiskers plot the 10th and 90th percentile. Circles represent outliers, dotted lines represent means.

The connection between vine maple cover of the cells the hemispherical photograph were taken in and available light as measured in % SO was significant. An ANOVA that compared % SO between cover classes of vine maple did get a significant result (p = 0.006), but individual comparisons between cover classes did not attain statistical significance (all p > 0.05). Therefore an ANOVA was performed with combined cover classes to increase the number of observations per class. Vine maple cover classes 0 and 1 were retained, cover classes 2a and 2b and cover classes 3, 4 and 5 were combined to two new cover classes: 5 - 25 % and > 25 %. The ANOVA with combined cover classes showed significant differences between cover classes 1 and > 25 % (p = 0.002) and 5 - 25 % and > 25 % (p = 0.002). All other comparisons were non-significant.

In cells with vine maple cover class 1 the average SO was 5.3 %, just slightly lower than the average SO of 5.4 % in cells with cover class 5 -25 % and of cells without vine maple (5.92 %). Cells with cover classes 3, 4 and 5 all had average SO values above 7 %, on average in cover class > 25 % 7.2 % SO. More details are shown in Table 4.

High vine maple cover (> 25 %) was therefore connected to high levels of light availability, while cells with low vine maple cover (< 25 %) were not connected to higher light levels than cells without vine maple. Since a high cover of vine maple was already found at comparatively low light levels (minimum value for cover class > 25 %: 3.1 % SO), light levels are clearly not the only limiting factor for vine maple cover.

vine maple cover class	n	mean % SO	minimum % SO	maximum % SO	standard deviation
0	48	5.9	3.0	10.5	1.7
1	33	5.3	1.7	9.9	1.8
2a	15	5.0	2.8	8.8	1.6
2b	18	5.7	2.8	11.6	2.2
5 - 25 %	33	5.4	2.8	11.6	2.0
3	14	7.1	4.5	12.5	2.5
4	14	7.2	3.1	11.7	2.7
5	5	7.5	4.6	10.3	2.3
> 25 %	33	7.2	3.1	12.5	2.5

Table 4: Percent site openness (SO) for different cover classes of vine maple. n denotes the number of cases per cover class.

3.2.2 Light levels on different types of sediment

High vine maple cover showed a strong connection to rockfall sediment. If light availability differed between sediment types, a higher light availability on rockfall sediment might explain vine maple response to rockfall sediment.

Light availability as measured in % SO was not significantly different between sediment types (p = 0.363). On debris flow sediment light availability was on average lowest (mean: 5.7 %) and highest on rockfall sediment (mean: 6.4 %). The average light availability on mosaic sediment was with 6.2 % intermediary between these two values, as usual. More details can be found in Table 5. Only two plots were located on lake sediment. Light availability in these two plots was with 4.1 and 6.1 % SO relatively low. The positive response of vine maple response to rockfall sediment can not be explained with a generally higher light availability on this type of sediment.

sediment type	n	mean	standard deviation	minimum	maximum
debris flow	101	5.7	1.7	1.7	10.6
mosaic	15	6.2	2.7	3.1	11.6
rockfall	35	6.4	2.5	2.8	12.5

Table 5: Percent site openness for debris flow mosaic and rockfall sediment. n denotes the number of plots on each type of sediment.

Within sediment variation of vine maple cover on all types of sediment might have been connected to light availability. Reduced cover classes of vine maple cover < 25 % and vine maple cover > 25 % were used to test this possibility. Significant differences between these two cover classes were found for rockfall sediment (p = 0.004) and debris flow sediment (p = 0.043), but not for mosaic sediment (p = 0.212). Only eleven plots were sampled on mosaic sediment, with no less variation than on the other types of sediment. Significance might have been prevented by the high variance in the data. On all three types of sediment cells with a high cover of vine maple had the higher average light availability, higher maximum values for % SO and in two out of three cases also higher minimum values. Details can be found in Table 6. Light availability to vine maple can not explain vine maple response to rockfall, but some of the within sediment variation in vine maple cover.

vine maple cover	n	mean	standard deviation	minimum	maximum
debris flow sediment only					
< 25 %	50	5.3	1.7	1.7	9.9
> 25 %	8	6.7	2.0	4.5	10.6
mosaic sediment only					
< 25 %	7	4.9	1.7	3.6	7.8
> 25 %	4	7.2	3.3	3.1	10.6
rockfall sediment only					
< 25 %	15	5.1	1.8	2.8	8.7
> 25 %	21	7.7	2.7	4.1	12.5

Table 6: Percent site openness for cells with a low cover of vine maple (< 25 %) and cells with a high cover of vine maple (> 25 %) on debris flow, mosaic and rockfall sediment. n denotes the number of cases in each category.

3.2.3 Vine maple stem and clone performance

3.2.3.1 Stem performance

Vine maple stems assessed for performance showed much variability. Stems had a wide span of stem sizes (basal area ranged from 0.1 to 223.5 cm^2 with a mean of 42.2 cm^2), and crown sizes ranged from 0.5 to 83.2 m^2 with a mean of 9.7 m^2. Stems could be dead or alive, flowering or not and belong to a large or small clone or be solitary.

The stems were grouped into three categories:

1. dead and declining stems (n = 22)
2. living stems, neither declining nor flowering (n = 51)
3. stems capable of producing flowers (n = 25).

Dead and declining stems showed a significant difference in % SO (p = 0.001) to stems with enough resources to produce flowers. The average % SO for dead and declining stems had a value of 4.8 % (range: 2.8 - 10.6 %), lower than the average values for categories three (6.9 %, range 4.2 - 12.5 %) and two (5.9 %, range 1.7 -11.7 %). Death or decline of a stem therefore was associated with low light levels, while the ability to produce flowers was connected to higher light levels. No significant difference existed between stems capable of producing flowers and other live stems (p = 0.163) or between categories one and two (p = 0.060).

Category one contains two outliers: plots 106 and 279. Both have very high values for % SO (10.6 and 10.2 %), while all other plots in category one show values between 2.8 and 5.8 % SO. If the two outliers are removed a significant difference exists between categories one and two ($p = 0.003$). The clone associated with plot 106 had a relatively large crown size of 39.9 m^2 and was capable of producing flowers while the stem in plot 279 had no other stems associated with it. While within-clone competition for light could explain the death of the stem in plot 106, the decline of the stem in plot 279 clearly was not related to or caused by light levels.

While the death and decline of a stem was connected to low light levels, low light levels alone did not cause the death and decline of the vine maples in category one. Light levels as low as found in category one were found in plots with healthy or even flowering stems and the lowest % SO measured in the study site was found in a plot with a living vine maple stem. However, low light levels could add enough additional stress to otherwise weakened or damaged vine maples to impede survival.

3.2.3.2 Clone performance

The variability of the clones assessed for performance was even higher than the variability of the stems. Vine maple clones consisted of one to 48 stems (mean: five) and zero to 89 sprouts (mean: eleven), had a summed basal area of one to 813 cm^2 (mean: 134 cm^2) and a crown area of 0.3 to 98.6 m^2 (mean: 25 m^2).

The clones were grouped into the same three categories as the stems:

1. dead and declining clones (n = 14)
2. living clones, neither declining nor flowering (n = 30)
3. clones capable of producing flowers (n = 54).

Altogether clones performed better than the stems that were part of them. Eight clones with dead or declining stems assessed for performance were not declining and an additional 29 clones were capable of producing flowers. The worse shape of individual stems within the clone might have been due to within-clone competition or any factor that might have affected only a single stem, for example old age, ungulate browsing or unfavorable direction of growth.

The response of the entire clone to different light level was similar to the performance of single stems. The average % SO for dead and declining clones was on average the lowest of the three categories (mean: 4.5 %, range: 2.8 - 10.2 %). Category two had a mean of 5.8 % (range: 1.7 - 9.9 %), lower than the average value for category three (6.4 %, range 3.0 - 12.5 %). And again the only significant difference (p = 0.007) between categories was between dead and declining stems and stems with enough resources to produce flowers. The declining clone in plot 279 remains as an outlier in category one, while the clone in plot 106 that formed an outlier in the comparison of stems belongs now to category three. All other clones in category one had between 2.8 and 5.8 % SO. If the outlier is removed, categories one and two show significantly different light levels (p = 0.03).

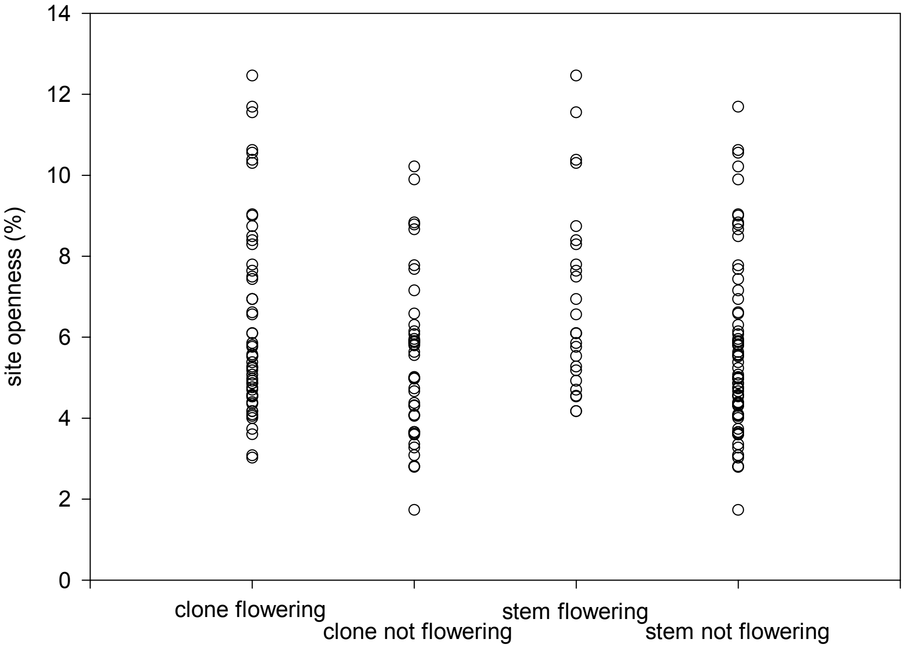

Figure 28: Percent site openness at plots with flowering stems and clones and plots without flowering stems and clones. Each circle represents one plot.

Death or decline of an entire clone therefore was also associated with low light levels while the ability to produce flowers was connected to higher light levels. Sexual reproduction did not occur in clones located on sites with less than 3.02 % SO and all vine maple found at sites with more than 10.21 % SO were producing flowers (Figure 28). No significant difference existed between clones capable of producing flowers and other clones (between categories two and one: p = 0.137, between categories two and three:

p = 0.683). And while light availability does explain some variation in the performance of clones, it does not explain all of it. The lowest SO was found at the site of a clone of category two and flowering clones were found at light levels as low as 3.02 %.

The number of living stems and sprouts per clone, the size of the crown and the summed basal area of the clone were compared directly to light levels to assess if these features were directly influenced by light availability to the clone. None of these features showed a strong relationship and some no relationship at all to light availability. The high variation in all datasets gives evidence that other factors besides light availability influenced these features as well.

The size of the crown of a clone was the only investigated clone characteristic to show a significant linear relationship to % SO ($p = 0.011$), but the relationship was very weak ($r^2 = 0.065$). The regression equation can be found in Figure 29. The linear relationship indicates that for every additional % SO one can expect to find an increase in clone crown size by 2.7 m^2. However, small crown sizes could be found at any light level and a crown size of 92.2 m^2, the second largest crown overall, was already found at 5.6 % SO.

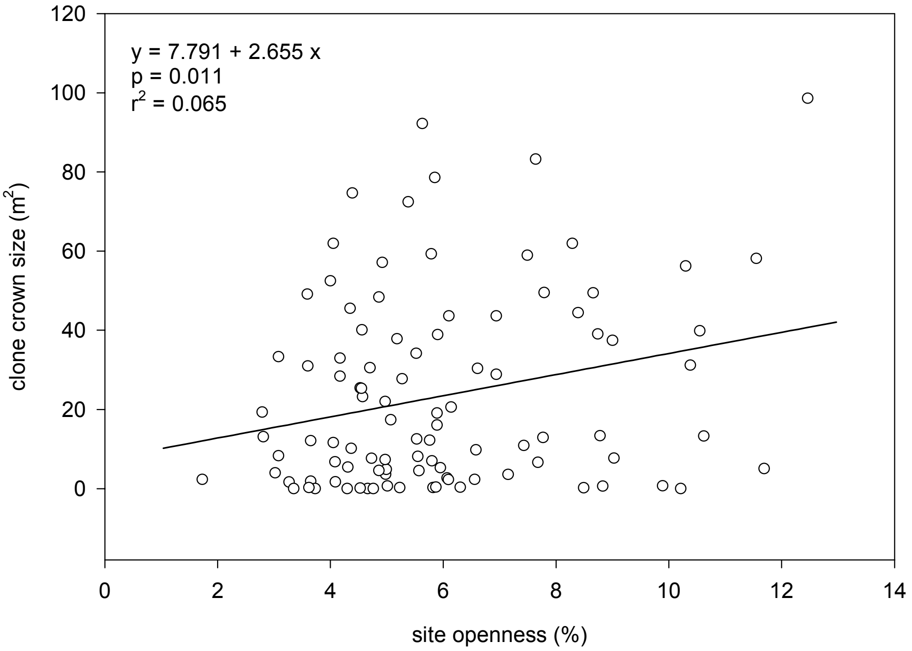

Figure 29: Scatter plot and plot of linear regression line of clone crown size against percent site openness. The regression equation is given in the upper left corner of the graph.

Though the scatterplot of crown size against % SO indicates a limiting influence of light availability on crown size at least up to 6 % SO and though crown size was correlated enough with light availability to produce systematic heteroscedacity in the data set, the limiting effect of light on crown size was not strong enough to produce a statistically significant upper edge through lest absolute deviation regression (LAD) of the 90th quantile (p = 0.09).

The number of live sprouts found in a clone had no significant linear relationship to % SO (p = 0.100). Again clones with low numbers of sprouts were found at all light levels and the overall variability of the data was high. Therefore it is more informative to regard light levels as a limiting factor to maximum production of sprouts in a clone. Visual inspection of the scatter plot of number of sprouts per clone against site openness indicated that light availability might have been a limiting factor to sprout production up to light levels of 8 % SO.

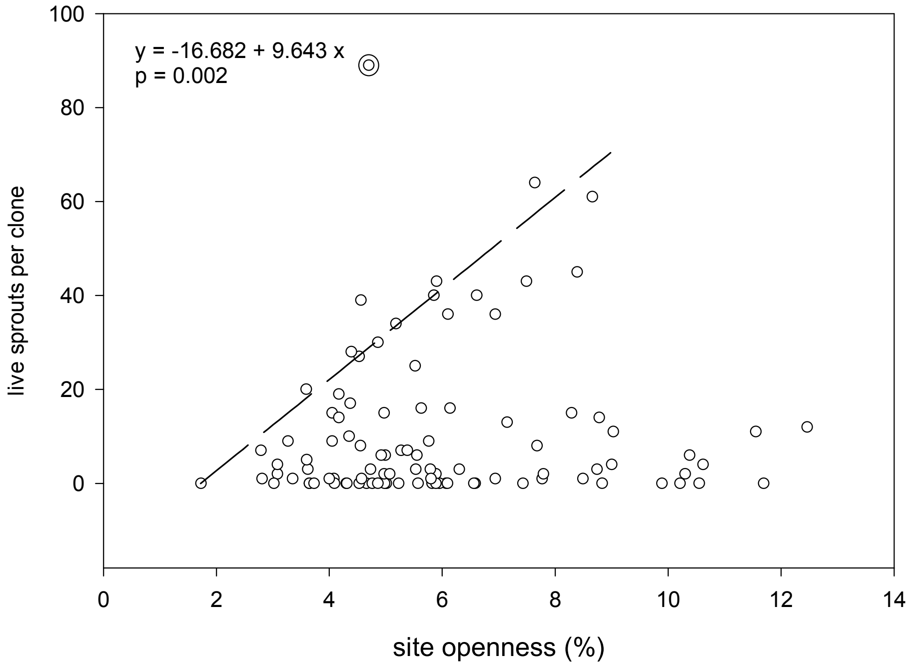

Figure 30: Scatter plot of the number of live sprouts per clone against percent site openness. The outlier is marked by a double circle. A LAD regression of the 90th quantile was plotted with a dashed line. The regression equation is given in the upper left corner of the graph.

Beyond 8 % SO no further increase in number of sprouts per clone occurred, in fact the number of sprouts stayed low. Since there is no reason to suspect that high light availability should result in a low number of sprouts this was considered to be a chance effect of low sampling size. LAD of the 90th quantile of sprout numbers of clones located at sites with less than 8 % SO did yield a significant upper limit to sprout production ($p = 0.002$). The regression equation indicates that with an increase of 1 % SO a maximum of ten additional sprouts can be expected. The regression equation can be found in Figure 30. The upper limit is not stringent. One clone had produced 98 sprouts at 4.7 % SO. This might be a true outlier, a clone that simply does not behave like all other clones, or it might indicate that the limiting effect of light availability observed in the data set is incidental. Only further studies can validate either possibility.

Both the number of live stems per clone and the summed basal area of the clone did not show any significant relationship to light levels (live stems: $p = 0.056$, summed basal area: $p = 0.300$). The p value for the number of stems per clone seems to indicate at least a trend in the data, but the r^2 is only 0.04. Even if there truly is a relationship between number of stems per clone and light level it is to weak to be of any importance. Most clones at all light levels had few stems and the highest numbers of stems in a clone (48) was found at medium light levels (6.1 and 6.9 % SO). Light availability did not seem to limit the maximum number of stems per clone as measured by LAD ($p = 0.365$) or measured as a linear increase in variance of number of stems over light availability (Figure 31).

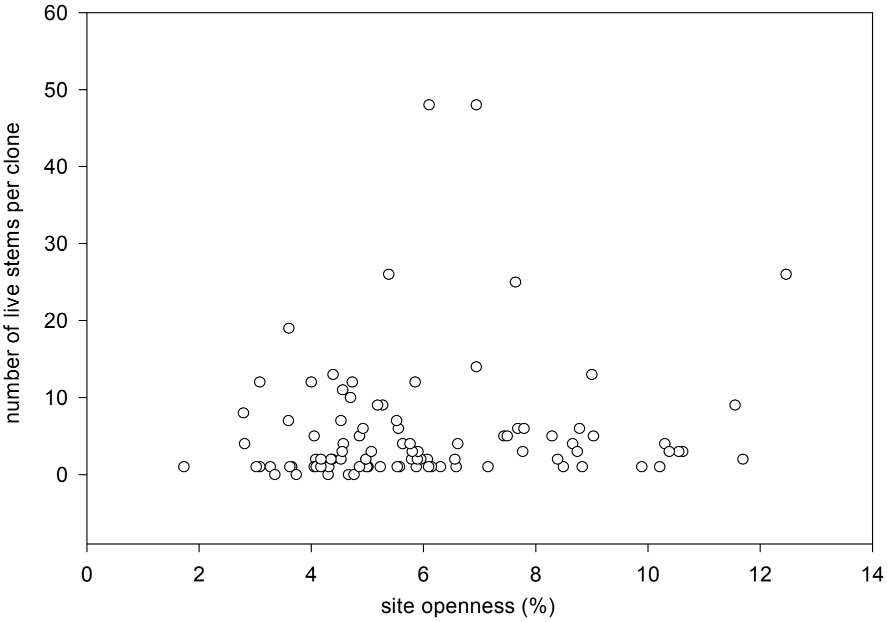

Figure 31: Scatter plot of the number of live stems per clone against percent site openness.

The scatterplot of summed clone basal area did not even indicate that a limiting relationship to light might exist (Figure 32). The clone with third largest summed basal area (215 cm^2) found was located at a site with only 3.7 % SO. No LAD regression was therefore attempted.

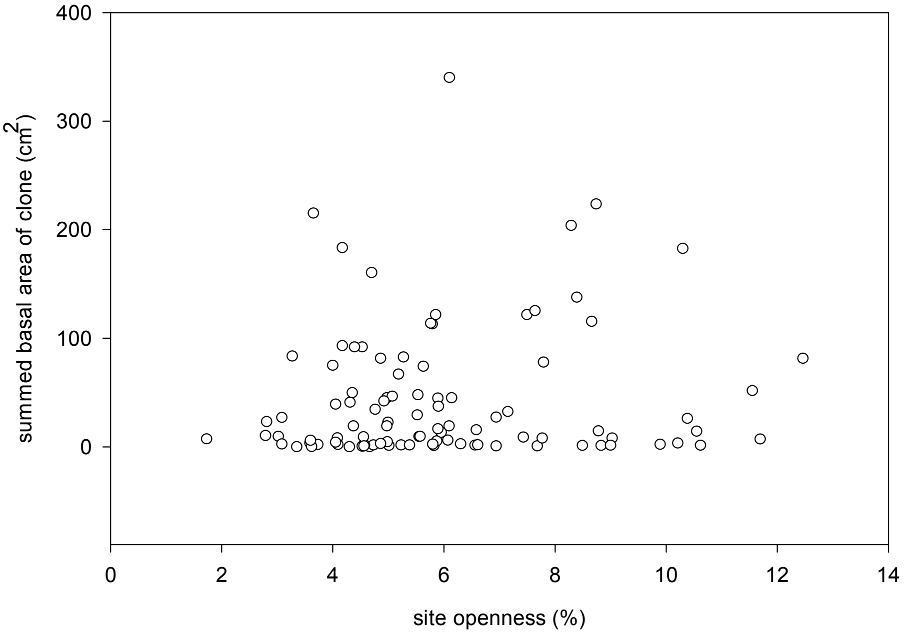

Figure 32: Scatter plot of the summed basal area per clone (upper graph) and the number of live stems per clone (lower graph) against percent site openness.

3.2.4 Leaf morphology

The vine maple leaves sampled showed characteristic features of shade leaves. The palisade parenchyma was only one cell layer thick and the leaf lamina was only 0.067 mm thick on average with a range from 0.055 to 0.079 mm. In the leaves representative of low light levels the palisade parenchyma had funnel-shaped, loosely-spaced cells. Palisade cells in leaves from higher light environments were more densely packed, but the overall thickness of the leaf lamina did not change with light levels in the five samples representing different light regimes (Figure 33).

The thickness of the vascular system of a leaf can change with light levels. Therefore the thickness of the middle rib was measured as well. The thickness of vine maple leaf midribs ranged from 0.35 to 0.82 mm. The thickness of the midrib of the ten leaves chosen for a preliminary analysis did correlate well with light levels. The analysis of the entire sample of 80 leaves from 40 plots showed that this was a chance effect of the low sampling size. There is no significant (p = 0.138) correlation of thickness of the midrib to % SO in the analysed leaves (Figure 34). Leaf or midrib thickness therefore cannot replace the direct measurement of light availability to vine maple.

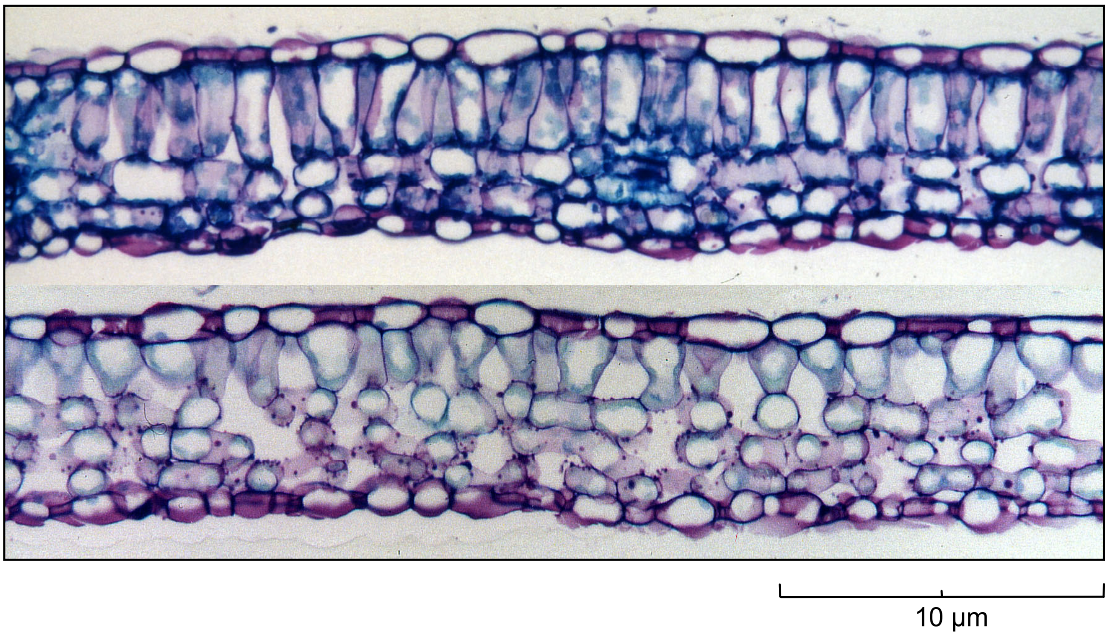

Figure 33: Cross sections of vine maple leaf laminae. Upper section from plot with 11.69 % SO, lower section from plot with 3.02 % SO.

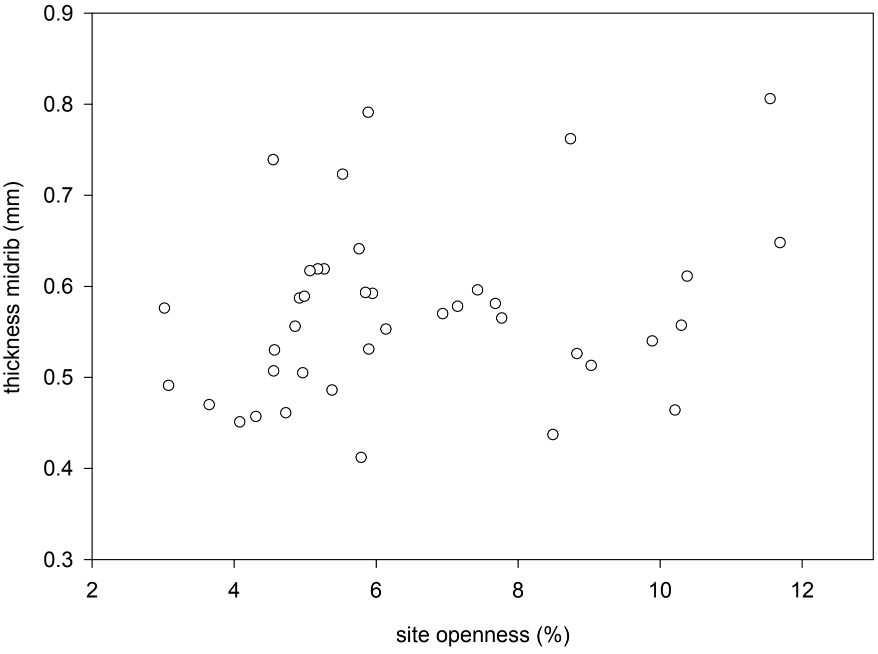

Figure 34: Thickness of the midrib of vine maple leaves plotted against percent site openness.

3.3 Overstory tree density

In 106 cells 1730 trees, 2782 saplings and 8082 seedlings were counted. Variation in the data was high: the largest number of seedlings found in one cell, for example, was 437 while several cells contained no seedlings at all.

Vine maple presence or absence and vine maple cover were not connected to overstory tree densities. The average number of overstory trees in the 100 m^2 cells with vine maple was 16.36 with a range of three to 43. This was nearly identical to the average number of trees in cells without vine maple of 16.27 with a range of four to 38. There was also no significant difference between cover classes of vine maple. The number of trees in cells with high vine maple cover (cover classes 3, 4 and 5; combined mean: 15.8 range: 7 to 32), for example, was not significantly lower than in cells with vine maple cover below 5 % (mean: 17.0 range: 3 - 43) ($p = 0.982$).

Total overstory tree basal area had a slightly but not significantly lower mean of 10.3 m^2 (range: 0.04 - 55.2 m^2) in cells with vine maple compared to a mean of 12.3 m^2 (range: 0.05 - 102.9 m^2) in cells without vine maple. The variations in total overstory tree basal area between cells with different vine maple cover classes were quite high but show no systematic pattern. The mean total overstory basal areas of cover classes 1 to 5 were in order of increasing cover: 7.7 m^2, 18.1 m^2, 11.1 m^2, 3.0 m^2, 18.9 m^2 and 3.3 m^2. The highest total basal area was found in cover class 2a, the lowest in cover class 4. High variation in the data of each cover class prevents statistical significance for these differences ($p = 0.248$). Vine maple response to higher light levels can not be attributed to a reduced canopy closure within a cell.

Overstory tree densities might have differed between sediment types. While the mean number of trees per cell was slightly higher on debris flow sediment (16.9 trees per cell) than on mosaic (16) and rockfall sediment (twelve), the difference was not statistically significant due to the high variation in the data ($p = 0.240$). There was also no statistically significant difference in the total basal area of the overstory trees per cell between different sediment types ($p = 0.180$). Cells on mosaic sediment had the highest average total basal area per cell (24242.5 cm^2), followed by cells on debris flow sediment (mean: 10338.5 cm^2). And, like the number of overstory trees per cell, the total basal area was lowest on rockfall sediment (mean: 7168 cm^2). More details can be found in Table 7.

Sapling densities continued the pattern. The number of saplings per cell was lowest on rockfall sediment (mean: 10.5), highest on mosaic sediment (mean 34.1) and somewhat lower in cells on debris flow sediment (mean 27.4). This difference was again not significant (p = 0.061).

Seedling densities were significantly lower in cells located on rockfall sediment than on debris flow sediment (p = 0.028). The average number of seedlings on debris flow sediment was 88.6, on mosaic sediment 53.8 and on rockfall sediment 28.2. The mean number of seedlings per cell in mosaic sediment was not significantly different from either debris flow (p = 0.868) or rockfall sediment (p = 0.849).

Two of the cells sampled were located on lake sediment. In these cells 16 seedlings, 39.5 saplings and 24.5 overstory trees with a total basal area of 1939.9 cm^2 were found on average. High overstory tree regeneration can therefore be assumed on this type of sediment.

	sediment type	number of cells	mean	standard deviation	minimum	maximum
number of seedlings	1	80	88.6	105.8	0	473
	2	11	53.8	59.7	0	196
	3	13	28.2	37.2	1	115
number of saplings	1	80	27.4	32.2	0	134
	2	11	34.1	35.6	1	121
	3	13	10.5	10.8	0	39
number of trees	1	80	16.9	9.9	3	43
	2	11	16.0	6.9	5	28
	3	13	12.0	6.4	4	26
total basal area of (cm^2)	1	80	10338.5	15104.2	4.9	59537.0
	2	11	24242.5	33944.3	534.3	102912.0
	3	13	7168.9	4722.8	153.1	15851.0

Table 7: Overstory tree response to debris flow sediment (sediment type one), mosaic sediment (type two) and rockfall sediment (type three).

4 Ground water

4.1 Ground water level

The majority of the 40 wells used in my study fell dry over the summer but carried ground water over most of the winter. One well with a depth of 124.5 cm was dry over the entire measurement period and in the driest period of the summer 1999 only three wells carried water. The ground water table fluctuated in many cases quite strongly within the measurement period. The largest recorded difference between the actual ground water table and the maximum ground water table in a measurement period was 101.5 cm.

Wells were classified into five categories from dry to wet according to their hydrological status. Five wells could be classified as dry, nine as moderately dry, eight as moderate, five as moderately wet and eleven as wet. Two wells could not be classified. The wells were only 60.5 and 69 cm deep and carried on no measurement date water within 50 cm of the surface.

Six wells were located in rockfall sediment: all five dry and one moderately wet well. Ground water levels below rockfall sediment might have been comparatively low because of the preponderate lack of fine material in the sediment that could draw water closer to the surface through capillaries. Debris flow and mosaic sediment were not connected to a specific level of ground water. Wells of all categories from moderately dry (eight wells) to wet (nine wells) over moderate (five wells) and moderately wet (four wells) were found in debris flow sediment. Five wells were located in mosaic sediment. Of these wells one each were classified as moderately dry and wet, the remaining wells as moderate. One well was located in lake sediment. It was classified as wet. A display of the distribution of well categories on different sediment types can be found in Figure 35.

Within the study site vine maple distribution was not dependent on high ground water levels. While vine maple was of course present at the site of all five wells in rockfall sediment that were classified as dry, vine maple was also found at four moderately dry, four moderate , one moderately wet and six wet wells. A comparison of the mean depth to ground water of the 13 data sets that allowed a direct comparison between sites with and sites without vine maple confirmed that vine maple was not influenced by the range of ground water levels that occurred in the study site.

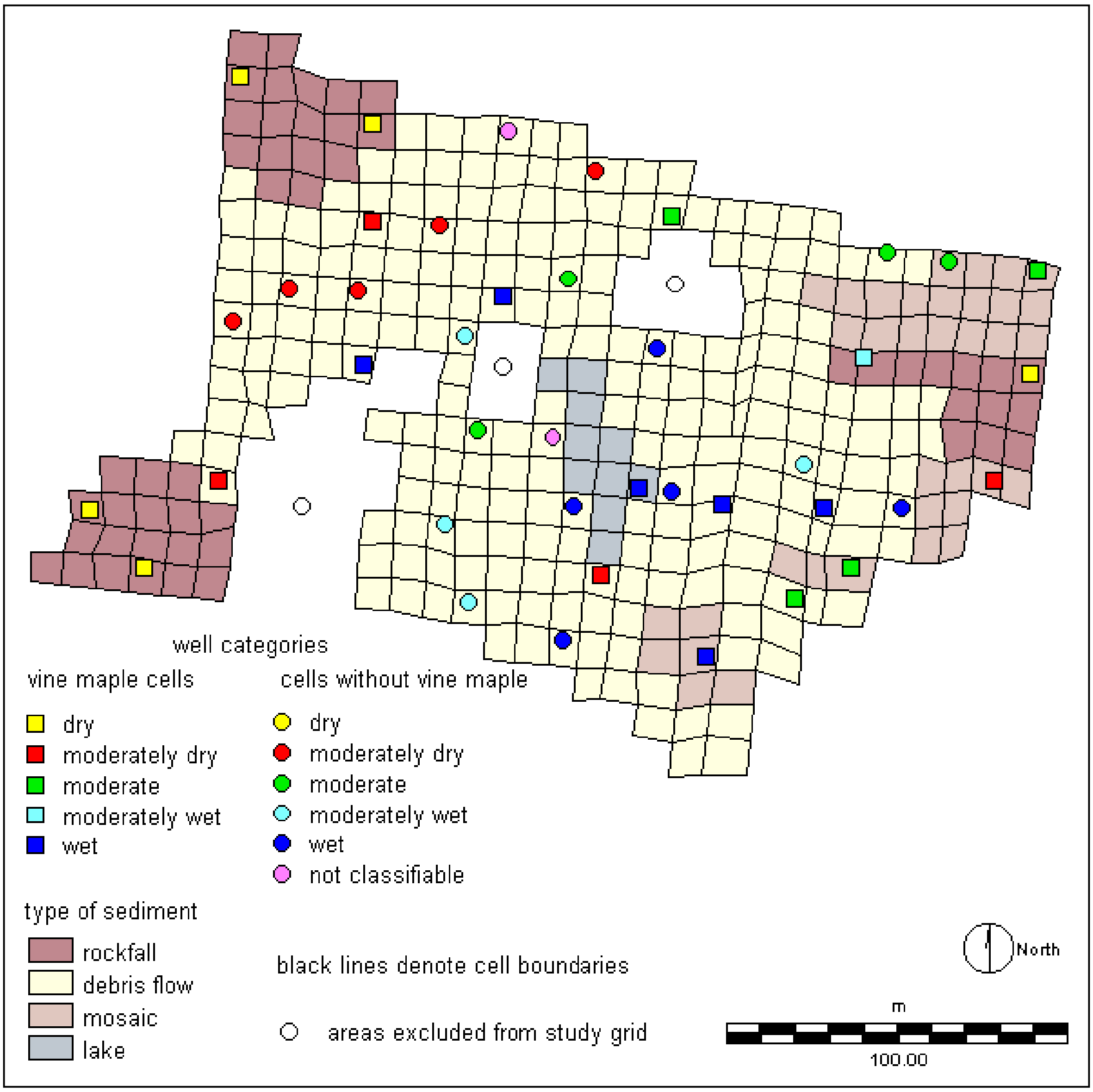

Figure 35: Position and hydrological status of the 40 wells located in the LSCR site.

The mean depth to ground water in plots without vine maple was actually higher (but not significantly) than in plots with vine maple in eleven out of the 13 computed data sets. In plots with vine maple the means for the ground water depth maxima ranged from 31 cm (19.1.1999) to 60 cm (9.5.2000) and the means for the actual ground water depth ranged from 61 cm (19.1.1999) to 71 cm (9.5.2000). On plots without vine maple the means for the ground water depth maxima ranged from 35 cm (19.1.1999) to 49 cm (9.5.2000) and the means for the actual ground water level ranged from 51 cm (19.1.1999) to 63 cm (9.5.2000) (Figure 36).

Neither the comparison of the means of the actual ground water level nor of the means of the ground water maxima between plots with vine maple and plots without vine maple showed significant differences in repeated measurement ANOVAs (actual: p= 0.514, maximum: p= 0.730). The same holds true for all individual dates (p > 0.41 in all cases).

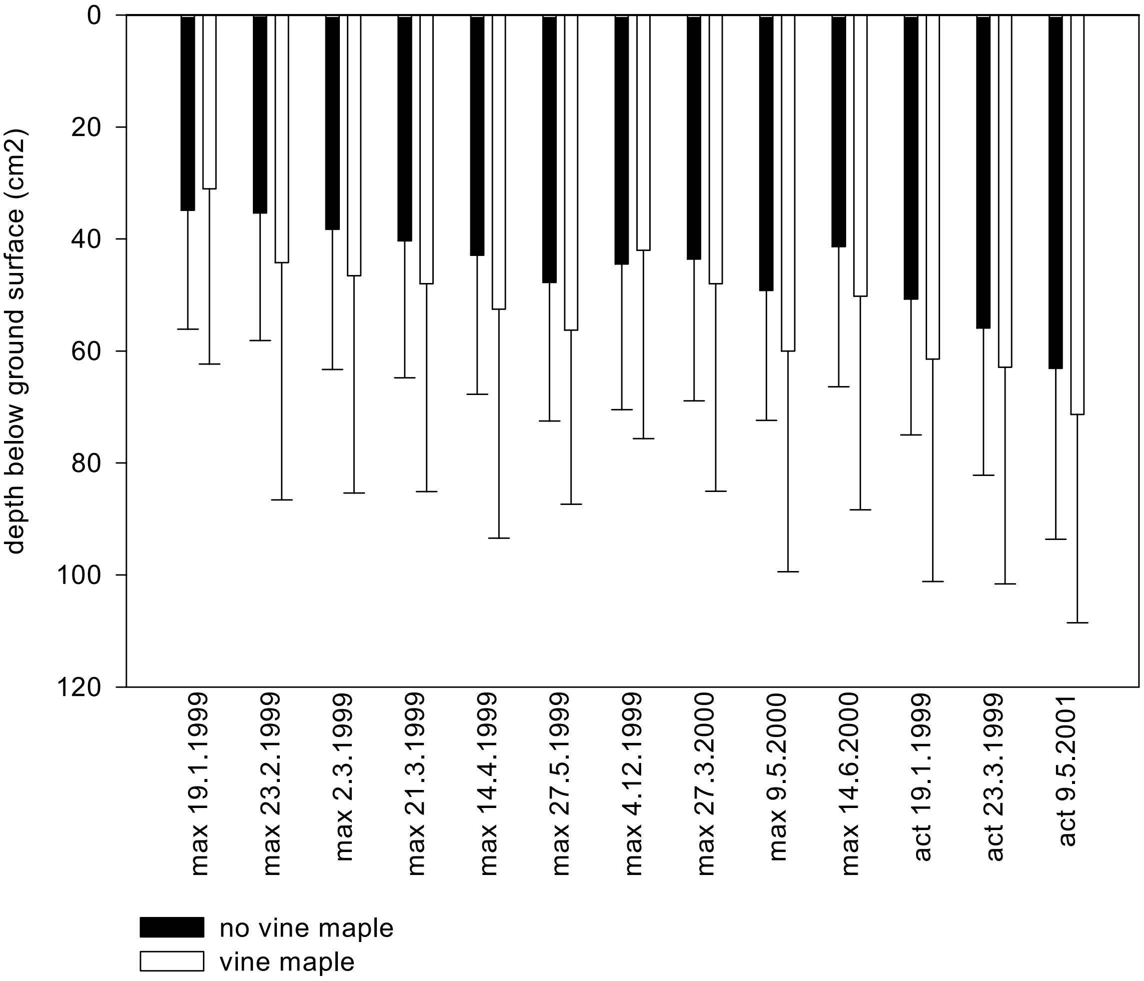

Figure 36: Mean maximum (max) or actual (act) depth to ground water on 13 measurement dates for plots with vine maple and plots without vine maple. Error bars represent one standard deviation.

4.2 Vegetation analysis

Thirty-three vegetation plots were surveyed. Two vegetation units were synthesized out of the relevees, with one unit subdivided into two subunits (Table 8). The first tree layer in almost all plots was dominated by *Thuja plicata* and *Tsuga heterophylla* and had a cover of between five and 70 %. *Tsuga heterophylla* was usually present in the second tree layer, together with the less frequently found *Abies amabilis*, *Taxus brevifolia* and *Thuja plicata*. The second tree layer had a cover between three and 90 %. Some of the plots had a very open canopy, with low covers in both tree layers, while others showed a nearly complete tree cover. The often very prominent shrub layer contained in almost all surveys tree regeneration of *Tsuga heterophylla* and, more seldomly, *Thuja plicata* and *Abies amabilis*. The most common companions in the herb layer were *Dryopteris expansa*, *Tiarella trifoliata* var. *trifoliata* and var. *unifoliata* (both subspecies frequently occurred together in the same relevees and were subsequently lumped in the analysis), *Blechnum spicant*, *Vaccinium parvifolium* and *V. alaskaense*, *Cornus canadensis*, and *Tsuga heterophylla* seedlings. *Plagiothecium undulatum*, *Rhizomnium glabrescens* and *Hylocomium splendens* were present in the moss layer of most plots.

The vegetation unit that covered most of the area in the study site was defined by the presence of *Rubus spectabilis*, *Acer circinatum, Athyrium filix femina*, *Streptopus amplexifolius* var. *americanus*, and *Polystichum munitum*. It was named *R. spectabilis* unit. A subunit of this unit was characterized by *Phegopteris connectilis*, *Sambucus racemosa* ssp. *pubens*, *Opoplanax horridus*, *Boykinia elata*, *Ribes bracetosum*, *Smilacena racemosa* and *Tolmiea menziesii*. It was found along creeks and in seepage zones, on large boulders and in other similarly disturbed sites on debris flow and mosaic sediment. The *Phegopteris connectilis* subunit was located on sections of all areas of the LSCR site with rockfall sediment. The rockfall lobe in the west of the study site was even nearly completely covered with this subunit.

Three wells were located in the *P. connectilis* subunit. Two of them were classified as dry, one as wet. There is no indication that the subunit was connected to any particular ground water level in the study site. Photos of this subunit are shown in Figure 22 and Figure 37.

A second subunit of the *R. spectabilis* unit lacked the diagnostic species of the *P. connectilis* subunit. This typical subunit covered most of the study site on all sediment types and therefore represented the dominant forest vegetation. Thirty-one wells were located in this subunit. Ground water levels at these wells included the highest and lowest levels found in the study site and well classifications from dry to wet. Photos of this unit are shown in Figure 17, Figure 19 and Figure 21.

Small areas (20 to 50 m^2) of a nudum unit were scattered through the matrix of the *R. spectabilis* unit (Figure 38). This unit lacked the diagnostic species of the *R. spectabilis* unit and most other understory plants. Four wells were located in this unit, classified as moderately dry, moderate, moderately wet and wet. The nudum unit was never found on rockfall sediment and only one small patch was located on mosaic sediment.

Figure 37: *Phegopteris connectilis* subunit on rockfall sediment. In the middle ground vine maple is visible. One stem is growing decumbent over a boulder.

Figure 38: Nudum unit.

units	1																														2		
subunits	1.1							1.2																									
relevee #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
hydrological status of wells				d	d	md					w		w		m	w	m		mw	d		m	mw	d	m			mw	m	m	w	d	
sediment type	1	1	3	3	3	2	3	5	4	1	1	3	2	1	4	1	1	1	1	1	1	2	1	3	2	1	1	1	1	1	1	1	1
inclination	5	0	20	17	40	45	3	30	50	12	10	5	30	25	30	25	8	9	40	10	10	35	5	20	40	20	15	20	25	30	25	25	25
tree layer 1 cover (%)	3	40	10	5	15	5	55	3	15	70	15	6	20	4	40	30	5	60	45	5	30	5	70	8	20	4	30	10	15	2	30	60	6
tree layer 2 cover (%)	7	20	20	3	6	70	4	15	/	20	40	6	4	50	55	10	10	10	40	80	40	70	26	60	40	75	55	51	20	90	80	20	15
shrub cover (%)	10	85	10	90	50	15	10	60	40	10	20	90	60	65	20	40	70	35	10	8	40	6	4	30	60	30	10	20	70	2	9	30	90
herb cover (%)	50	20	85	60	90	50	50	15	30	30	35	75	50	25	45	40	30	30	30	45	40	20	30	35	25	5	30	40	30	5	5	4	2
bryophyte cover (%)	90	20	40	40	30	60	50	80	90	40	50	50	30	20	60	30	30	40	40	90	20	50	30	85	25	5	50	60	50	15	5	7	20
diagnostic species unit 1																																	
Rubus spectabilis	1	2b		2a	1	1	+	1	1	r	r	+	2a	1		1	r	+		+	+	r						1	1				
Acer circinatum	1	+	2a	5			r	3	r	1	1	5	3			3			1		1	1	r	2b	3	2b	1		3	r			
Athyrium filix-femina	2b	+	3	2b	2b	3	2b	2a	r	+	2b	2a	2a	1	1	2b	2a	2a	1	2a	2a	1	2a	r		r	2a	2a	1	+			
Streptopus amplexifulius	1	+	+	1	+	+	+	1	1	+	+	+	+	r	1	+	+	1	+	+	1	1	+	+	1	+	+	1	1	r	+		
Polystichum munitum	1	+	2b	2b	3		1	1	r		+	1	1			2b		+			+			2b			r						
Viola glabella	+		1		1			1		+	1		+			+	+										1	1	1				
diagnostic species unit 1.1																																	
Phegopteris connectilis			2a	+	1	+	1								1												1						
Acer macrophyllum (Tl 1)				r			2b																										
Alnus rubra (Tl 1)							r																										
Sambucus racemosa	1	r				+	1					1	r																				
Ribes bracetosum	1			r			1																										
Opoplanax horridus		r					2a							r																			
Boykinia elata	2a	1	+																														
Smilacena racemosa					+	r																											
Tolmiea menziessi	1			2a			1																										
accompanying species																																	
tree layer 1																																	
Tsuga heterophylla	1	3		+		r	3	+	1	4	2		2a		3	2a		4		1	r		2a	1	2a		3	2a	1	r	2b	2a	+
Thuja plicata		2a	2a	r	2b	+		r	1		2b	2a	2a	+	1	2b	1	1	3		3	1		1	2b	3	r	r	2a	+	2a	4	r
Abies amabilis										1										1													
tree layer 2																																	
Tsuga heterophylla	2a	2b		+	r	4	r	2b		2b	3	2a		3	2a	2a	2a	2a	3	4	3	3	3	4	3	4	3	4	2a	5	5	2b	2b
Abies amabilis								+						2b			1		2b	3		3					+		2b	2a			
Thuja plicata			2a												1								4		2a								
Taxus brevifolia								r					2a						r		2a					1							
shrubs																																	
Tsuga heterophylla	1	3	1		2a	2b		2b	2b	2b	2b	+	1	3	2a	2b	2b	2b	1		3	1		2a	2a	2b	1	2a	1		2a	3	5
Vaccinium parvifolium	1	2b	1	+	1	1	1	2a	2a	1	2a		1	2a	2a	2a	1	1	1		2a	1	1	1	1	1	1	2a	3	1	1	1	1
Vaccinium alaskaense	1	2b			1	1	1		2a	1	1	2a	1	2a	2a	1	3	1	1	2a	1	1	1	1	+	1	1	1	2b	+		1	
Menziesia ferruginea	r		r		r	r			+		+		r	r	+	r			r		+				+		r	+	r				
Abies amabilis		+						r						2b											r		+		2a				
Thuja plicata	r	1			r	r		+	+					+			2a												+				
Vaccinium ovalifoilium	1	+		1			1	1		1	+	+		1				1		1	1			r			1					r	
Rubus parviflorus		r															r																
Galtheria shallon	+	2a				1		r				+							1				r		1	1							
Rubus pedatus		1				1		1	1					1						1			1					+					
Taxus brevifolia		+	2b		2a						2b				2a												2a						
Ilex aquifolium				r								+			r			r								+			r				
Rosa gymnocarpa					1																			r									
herbs																																	
Dryopteris expansa	2a	1	+	2b	2a	1	2b	1	2a	2a	2b	3	1	2a	1	1	2a	2a	2a	2b	1	1	1	2a	1	1	1	1	2	1	+	1	1
Tiarella trifoliata	2a	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	+
Blechnum spicant	1	2b	3	1	1	2a	1		1	2a	2b	2a	2b	2b	3	2a	2a	2a	2b	2a	2b	2a	2b	2a	2b	1	2b	3	2	1	1	1	1
Cornus canadensis		1	+		1	1		1	1	1	1			1	1	1		1	1	1	1	1	1			1	1	1	1			r	1
Tsuga heterophylla seedl.		1			1	1			1	1	1	1		1	1		+	1		1		1	1	+	+	1	1		1	+		+	
Gymnocarpus dryopteris	1		1	1	1	+		1	1		1		1	1		+		1			+	1		+			1	1	1				
Streptopus roseum	r				r	r		+	+		+			+	+			r	+			+				1	+	+	+	r	1		+
Thuja plicata seedlings		1			r			r	1		+	1		1	+		1							r	r				1	+			
Huperzia miyoshiana									1		1															1	+	+	1	+			
Luzula parviflora	r			1					1			1																					
Abies amabilis seedl.										r					+								r									r	
Polypodium glycirhizza			+						1				+																				
Melica subulata	+			1												+																	
Linnea borealis		1														1																	
mosses																																	
Hylocomium splendens	1	r		2a	2a	r	r	r	r	1	r	1	r		r	r	1	1		r	r	1		3	1		r	1		r		r	
Plagiothecium undulatum	2b	1	1	2a	1	2a	2a	1	r	2b	2a	2b	1	2a	3	1	1	2a	3	2a	2a	2d	2a	3	2a	1	1	1	2a	1	1	2a	2a
Rhizomnium glabrescens	2a	1	1	1	1	1	1	1	2b	2a	2b	2b	1	1	2a	2a	2a	2b	2b	3	2a	2b	2a	2a	2a	r	2a	3	2a			1	r
Rhytidiadelphus loreus	1	2a			2a		1	r		1	1		1	2a	1		1	1	1	1	r	1	r	2b	1				r				
Pogonatum spec.	3	2a	2b	1	1	2b	2a	3	2a	1	1	r		1	r	1	2a	1		1					2a		2b	2a	1			r	
Sphagnum spec.	2a							2a	1											2b							1	1					
thallic hepaticae	r		r		r			2a				r	1	r	r	r	r	r		1	r	r											

additionally occur: relevee 1: Poa palustris 1, relevee 2: Acer macrophyllum seedlings r, relevee 5: Lactuca muralis r, relevee 20: Gymnocarpum disjuncta 1

Unit 1: *Rubus spectabilis* unit
Unit 1.1: *Rubus spectabilis* unit, *Phegopteris connectilis* subunit
Unit 1.2: *Rubus spectabilis* unit, typical subunit
Unit 2: Nudum unit

Table 8: Vegetation relevees from the LSCR site. Abbreviations for hydrological status of wells and types of sediment used are given in brackets: dry (d), moderately dry (md), moderate (m), moderately wet (mw), wet (w), debris flow (1), mosaic (2), rockfall (3), lake (4).

5 Microtopography

5.1 Growth adjacent to creeks

A major creek ran through 86 of the 325 cells of the LSCR study site (Figure 39). Sixty-two of these cells were occupied by vine maple, that were 30.2 % of all cells with vine maple. The remaining 25 cells comprised 20.8 % of all cells without vine maple. Cells with vine maple were over-represented in cells that were located in proximity to a creek and under-represented in the other cells, a significant difference (p = 0.042). Details can be found in Table 9.

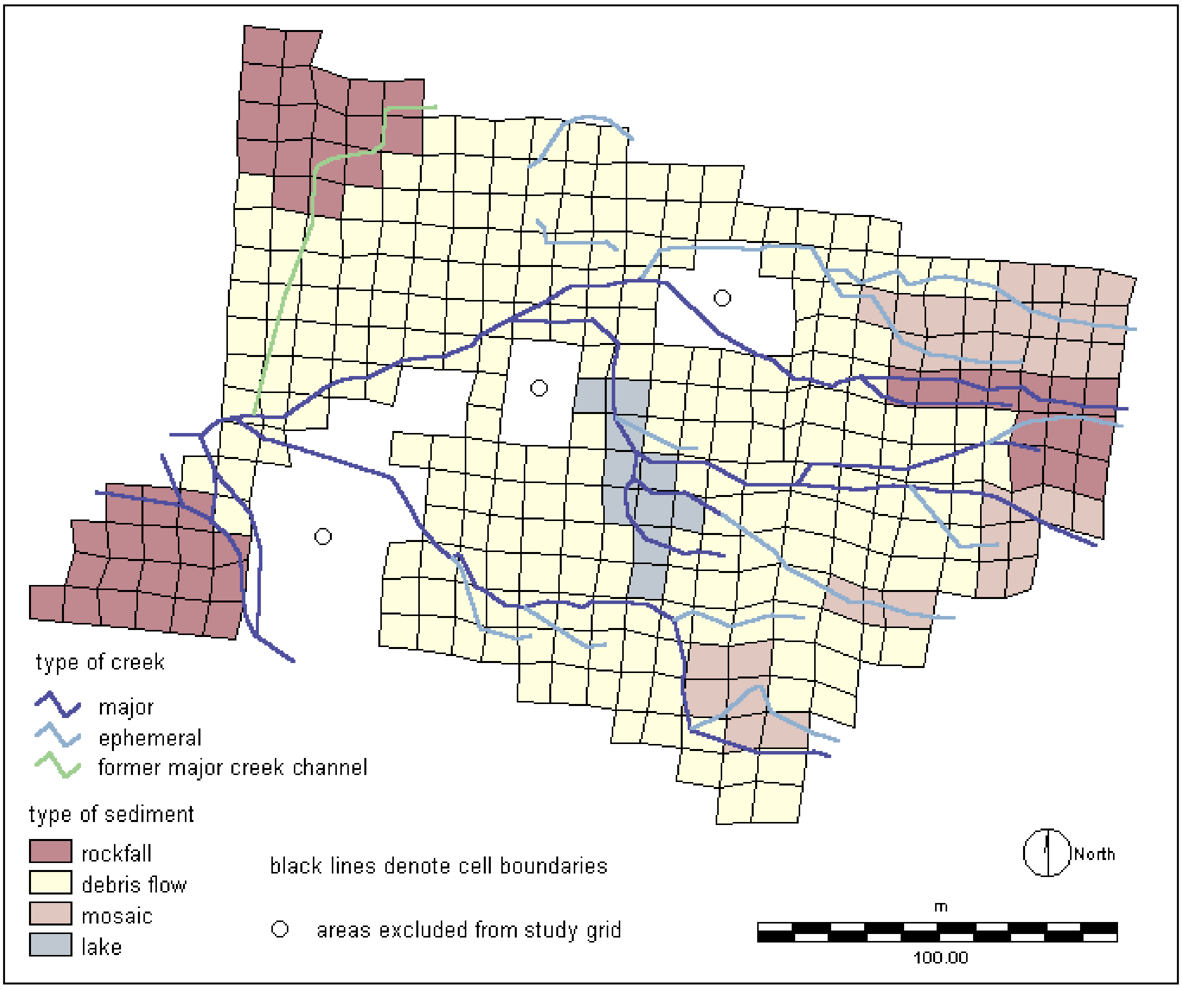

Figure 39: Position of the creeks that ran through the LSCR study site. Creeks were considered major as opposed to ephemeral if they were incised more than ten cm into the topsoil, more than 50 cm wide, and carried water for most of the year. The former major creek channel and sediment types were added to this map as an illustration for chapter 2.1.1.1.

The occurrence of vine maple in cells located at a creek was investigated separately for the four different sediment types. The pattern of significant over-representation of cells with vine maple in cells located at creeks and under-representation in the other cells was reproduced only on debris flow sediment (p = 0.012). On mosaic (p = 0.605) and lake sediment (p = 0.467) vine maple occurrence was independent of position to creek. Sample sizes for lake sediment were very low (n = ten). On mosaic sediment only five out of 36 cells were located in proximity to a major creek. The independence of vine maple of proximity to a creek on these types of sediment should therefore be viewed with caution. Only one cell without vine maple was located on rockfall sediment. No sensible investigation of vine maple occurrence in proximity to major creeks was therefore possible.

vine maple occurence		cells not at creek	cells at creek	sum
all types of sediment				
vine maple	number of cells	143	62	205
	expected number of cells	*150.1*	*54.9*	
no vine maple	number of cells	95	25	120
	expected number of cells	*87.9*	*32.1*	
debris flow sediment only				
vine maple	number of cells	89	41	127
	expected number of cells	*94*	*33.1*	
no vine maple	number of cells	84	19	103
	expected number of cells	*76.1*	*26.9*	
mosaic sediment only				
vine maple	number of cells	20	3	23
	expected number of cells	*19.8*	*3.2*	
no vine maple	number of cells	11	2	13
	expected number of cells	*11.2*	*1.8*	
lake sediment only				
vine maple	number of cells	2	5	7
	expected number of cells	*1.4*	*5.6*	
no vine maple	number of cells	0	3	3
	expected number of cells	*0.6*	*2.4*	
all types of sediment				
cover < 25 %	number of cells	109	47	156
	expected number of cells	*109.4*	*46.6*	
cover > 25 %	number of cells	34	14	48
	expected number of cells	*33.6*	*14.4*	

Table 9: Contingency table of the number of cells with and without vine maple (rows) and location in proximity to a major creek or not in proximity to a major creek (columns). Sections for all cells, debris flow, mosaic and lake sediments only are divided by thin lines. The rows of the lowest section, divided by a thick line from the sections above, presents the number of cells with low (< 25 %) and high (> 25 %) cover of vine maple over all types of sediment.

The presence of a major creek in a cell was associated with a higher occurrence of vine maple, at least on debris flow sediment, but not with a higher cover of vine maple. The height of vine maple cover expressed as low (< 25 %) or high (> 25 %) cover was independent of proximity to creek over all sediment types (p = 0.526).

5.2 Slope angle

Average slopes per cell in the LSCR site as measured by IDRISI varied from 5.3 to 38.2 degrees. The study site did contain much steeper slopes, for example the sheer rock outcrops in the center of the study site. Those cliffs were excluded from the area covered by the cells for safety reasons. A contour map of the LSCR site is presented in Figure 40.

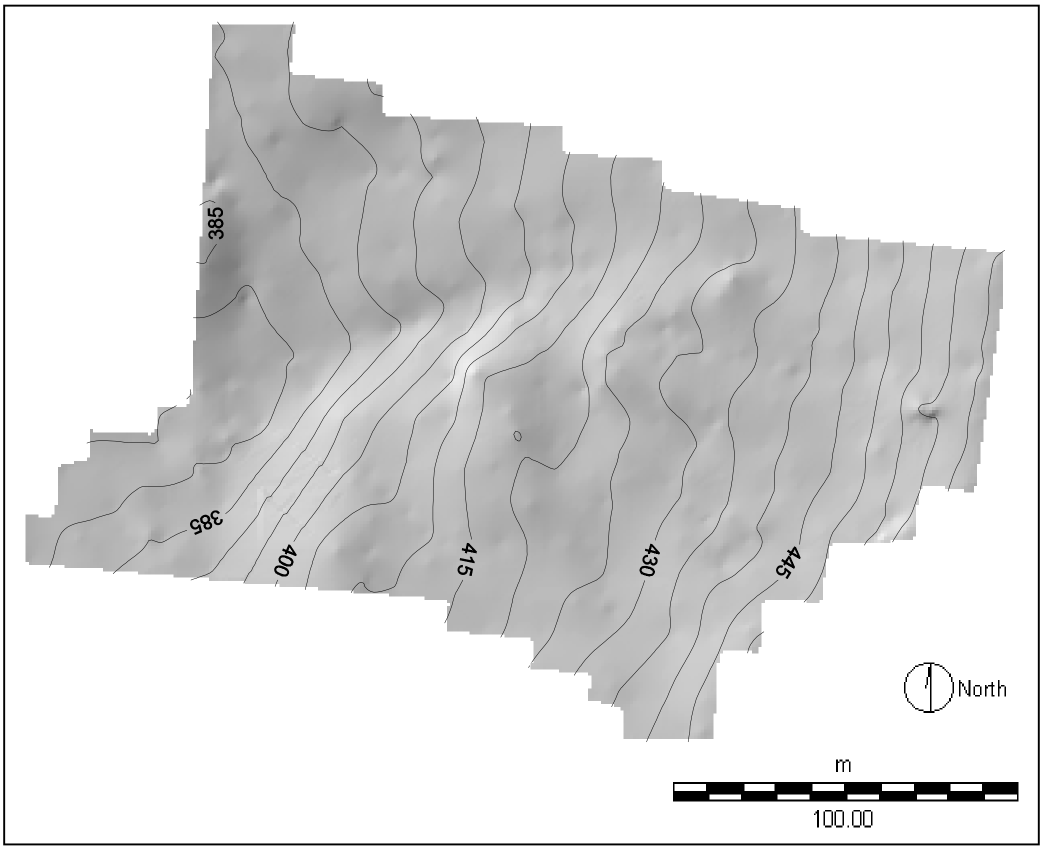

Figure 40: Contour map of the LSCR site. Contours are placed 5 m apart. Height is given in meters above sea level. To improve visualization of slope inclination analytical hillshading was used. The light source was placed in the north-west.

Vine maple showed no preference towards a particular angle of inclination. Vine maple cells were located on average on slopes of 19.3 degrees with a minimum of 5.3 and a maximum of 33.6 degrees. This was not statically different from the cells not occupied by vine maple: the average slope of cells without vine maple was 20.4 degrees with a range from 8.3 to 38.2 degrees. There was also no statistical difference (p = 0.198) or linear trend in slope position between different cover classes of vine maple. Cells with vine maple cover class 5 were located on a very similar angle to cells with cover class 1 (cover class 5: 18.1 degrees, cover class 1: 18.8 degrees). More details can be found in Table 10.

vine maple cover class	n	mean slope (degrees)	minimum slope (deg.)	maximum slope (deg.)	standard deviation
0	120	20.4	8.3	38.2	6.3
1	105	18.8	7.2	33.6	5.8
2a	26	21.7	14.2	33.1	5.5
2b	26	20.1	10.7	31.3	6.1
3	25	18.5	10.0	33.6	6.5
4	15	18.9	5.3	29.5	7.2
5	8	18.1	13.6	26.8	4.2

Table 10: Vine maple response to slope inclination. n denotes the number of cells in each cover class.

6 Vine maple persistence and priority effects

6.1 Forest floor moisture

Plots without vine maple had a lower mean water content (16 %) in the forest floor than plots with vine maple (20 %). The variability of the measurements was very high, both within plots and between plots. The standard deviation of within cell sample means was on average 43 % of the cell mean and reached up to 94 %. The average within cell values for plots without vine maple ranged from five to 42 % and for plots with vine maple from three to 46 % water content. No significant difference was found for forest floor moisture content between plots with and plots without vine maple (p = 0.171). Vine maple suppression of conifer seedling establishment through desiccation of the forest floor was not supported by the data.

6.2 Conifer regeneration

Conifer seedling and sapling density was compared between cells with vine maple and cells without vine maple to check for a repression of conifer seedling establishment through vine maple. There was no significant difference (p = 0.067) between the number of seedlings in cells with vine maple (mean: 62) and without (mean: 93). The same held true for the number of saplings in cells with vine maple (mean: 22) compared to cells without vine maple (mean: 31) (p = 0.392). More details can be found in Table 11.

The p-value for the number of seedling is fairly low. A further investigation of conifer seedling and sapling density at different cover classes of vine maple was therefore conducted. The rationale was that, if vine maple had an effect, more vine maple should have had more of an effect. There was no significant difference in the number of seedlings (p = 0.179) and saplings (p = 0.314) in different cover classes of vine maple. The mean number of seedlings was lower in cells with a cover of vine maple above 50 % than in cells with cover below 12.5 %, but high variation in the data and small sample sizes in high cover classes might have prevented the data from showing significant differences. The cells with medium vine maple cover (classes 2b and 3) did not show any clear trend.

vine maple cover class	n	mean	standard deviation	minimum	maximum
conifer seedlings					
0	51	91.0	102.8	0	416
1	26	71.7	84.5	2	297
2a	7	132.9	171.0	1	473
2b	9	18.0	31.8	2	102
3	6	47.3	47.6	1	132
4	4	17.3	9.2	8	30
5	3	44.0	43.5	0	87
all cells with vine maple	55	62.6	90.5	0	473
conifer saplings					
0	51	30.7	35.4	0	134
1	26	22.7	31.6	0	121
2a	7	23.3	23.3	0	69
2b	9	9.9	12.7	0	42
3	6	41.3	24.6	9	66
4	4	14.3	6.7	7	23
5	3	22.0	15.4	9	39
all cells with vine maple	55	22.1	26.2	0	121

Table 11: Number of conifer seedlings and saplings found in cells with different vine maple cover classes. n denotes the number of cells analysed.

The number of conifer saplings per cell was less correlated with the amount of vine maple in a cell than the number of conifer seedlings. The mean number of conifer saplings in cells with vine maple cover above 75 % was 22, just one less than in cells with vine maple cover below 5 %. The lowest mean sapling count per cover class found was ten in cover class 2b, the highest was 41 in cover class 4.

6.3 Gaps

Vine maple priority effects in oldgrowth forest might be detected through an analysis of canopy gaps. In 200 cells of the LSCR site 44 gaps of varying sizes were found, 28 of them occupied by vine maple and 16 of them without vine maple. Fifty-eight percent of all cells contained no gaps, 61 % of those cells were cells without vine maple. This implies that 45 % of all cells with vine maple sampled did not contain a gap compared to 71 % of all cells without vine maple sampled.

Edaphic causes (creeks and cliff faces) were not sufficient by themselves to form a gap with one exception: a gap formed by a single huge boulder. The death of one or more trees close to a creek or cliff face will often cause a gap that is larger and possibly harder to close than the gap resulting from the death of a tree away from those features. A creek might not be wide enough to cause a (linear) gap, but will force tree boles to be positioned a certain distance away from the creek, causing larger crowns in the adjacent trees. And no trees can establish themselves in the creek or on the cliff face to act as gap fillers after an opening in the canopy occurred. Seventeen gaps showed evidence of both edaphic and developmental origins, 14 of them along creeks and three near cliff faces. Of the 14 gaps near creeks eight contained vine maple. One of the three gaps near cliff faces contained vine maple. On debris flow 14 of the gaps with edaphic origin were located, one on mosaic and two on rockfall sediment. Since debris flow sediment underlay most of the study site no clear connection to sediment type was indicated by this proportion.

Eighteen gaps were caused solely by the death of one or more trees. Eleven of these gaps contained vine maple. Five developmental gaps were located on rockfall sediment, the remaining 13 on debris flow sediment.

The remaining nine gaps showed no clear evidence of their origins (independent gaps). Though tree stumps were found in some of these gaps, they were either very small or located only in one corner and could not account for the size of the gap. Of these nine gaps eight contained vine maple. Four of the independent gaps were located on rockfall sediment, three on mosaic sediment and only two on debris flow sediment.

On average about the same number of remains of dead trees was found in gaps occupied by vine maple and other gaps (3.5 for gaps with vine maple, 3.3 for gaps without vine maple). The average gap size for vine maple was 3.1 times larger for canopy gaps (significant difference, $p = 0.034$) and 2.1 times larger for extended gaps (significant difference, $p = 0.033$) than for gaps without vine maple. Vine maple occupied more and larger gaps, some of them very large (see Figure 41). The average size of a vine maple canopy gap was 68 m^2, the largest gap measured 417 m^2, five times larger than the largest gap without vine maple. The average size of a canopy gap not occupied by vine maple was 22 m^2. Vine maple extended gaps measured 161 m^2 on average, while extended gaps not occupied by vine maple had an average size of 78 m^2. More details can be found in Table 12.

	gap cause			size of canopy gaps (m^2)			size of extended gaps (m^2)		
	edaphic	developmental	independent	mean	min.	max.	mean	min.	max.
cells with vine maple	9	11	8	68	7	417	161	40	807
cells without vine maple	8	7	1	22	6	83	78	48	117

Table 12: Sizes of canopy gaps and extended gaps and number of edaphic, developmental and independent gaps for cells with vine maple and cells without vine maple.

The four largest gaps with canopy gap sizes above 100 m^2 were all located on rockfall sediment. Conifer regeneration was weak on this type of sediment. This might have led to the exceptional size of the gaps.

Dead trees of the decay classes 5 and 6, the classes with the strongest indicators of decay, were strongly represented in both gaps with vine maple (35 % of all dead trees found in gaps occupied by vine maple) and gaps without vine maple (48 % of all trees found in gaps not occupied by vine maple). 45 % of dead trees found in gaps with vine maple belonged to decay classes 3 and 4 but only 20 % of dead trees in other gaps belonged to these decay classes. Trees of the decay classes 0 to 2, the most recently dead trees, were found more frequently in gaps without vine maple (32 %) compared to 21 % in gaps occupied by vine maple.

In vine maple gaps more dead trees of decay classes 3 and 4 and less recently dead trees were found than in gaps not occupied by vine maple. This indicates a delay of gap closure through vine maple: gaps without vine maple close while the gap makers are still in decay class 0 to 2. The death of the trees whose remains were now in decay classes 5 and 6 was in no case the cause of a gap. Tree boles and stumps take centuries to completely disintegrate, most likely much longer than the time span needed for gap closure. Very decayed stumps of decay classes 5 and 6 were also found under closed canopy. The presence of these stumps and logs in the gaps is no indicator of the time since gap development.

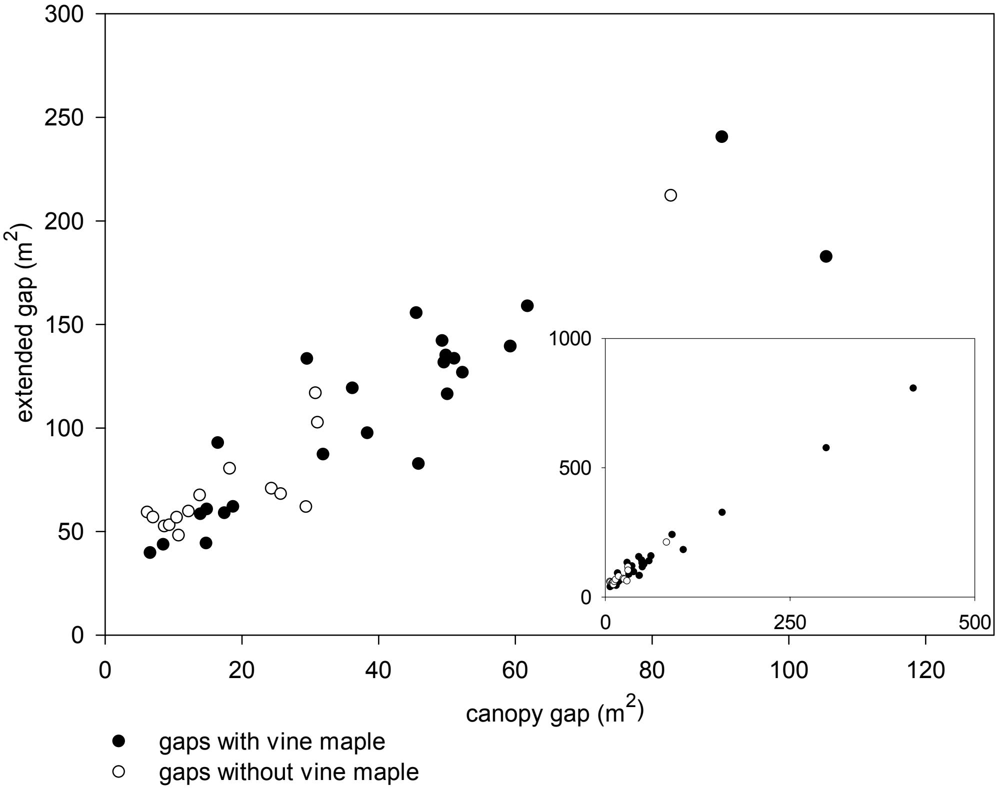

Figure 41: Canopy gap and extended gap size of gaps with and without vine maple. To enable a good depiction of smaller gaps the y-axis was truncated at 300 m^2 and the x-axis at 130 m^2. The same graph without truncation was set into the truncated graph as a smaller inset to enable the display of the three largest gaps (all vine maple gaps).

6.4 Minimum time of persistence

Vine maple can not be aged through the wood of its stems, since new stems are continually grown while old stems may die back. To determine the minimum time of persistence of vine maple in one location, it was therefore attempted to age a rootball instead. The rootball excavated was 97 cm long and had an average diameter of 20 cm. One large shoot emerged from one end of the rootball, while numerous smaller shoots and large and small roots emerged from the sides. The largest emerging shoot was 118 years old. About 25 cm away from its point of emergence began the oldest section of the rootball, with an age of 136 years. For 70 cm the age of the rootball stayed constant (with a counting error of about five years). Only the last 10 cm of the rootball furthest away from the largest emerging shoot showed a lower age of 117 years.

No evidence of the origin of the rootball was found. If a vegetative connection to a mother vine maple plant once existed no traces of it are left. Similarly no evidence of seedling establishment was found. The rootball developed quite rapidly, growing 70 cm in length within one or a few years and did not expand much further beyond that point. Dead vine maple wood decays quite rapidly. Consequently it was impossible to follow dead roots or shoots for more than a few centimeters. It was impossible to definitely attribute any dead wood to vine maple, foiling any attempt at ^{14}C dating to discover a minimum time of persistence.

7 Vine maple layering

In 19 out of the 65 cells checked layering from a live mother to a live daughter was found. In those 19 cells, 37 incidents of layering were measured. The distance between the roots of the mother and the daughter was on average 3.9 m with a range from 1.2 to 7.3 m. The mothers were on average 60 years old, with a range of 24 to 131 years. The daughters were on average 13 years old, the oldest 69 and the youngest one year old. The difference in age between mothers and daughters was on average 47 years with a range of three to 97 years. A conservative estimate of the time needed for the establishment of a rootball and growth to a mature clone might be 20 years. This is the time needed by vine maple clones to fully regenerate after logging to their previous size (Halpern 1989). If this time is added to the 47 years average age difference in mother and daughter stems, on average 67 years will have lain between layering events. This translates into an average distance spanned of 5.8 cm per year or 17.2 years per meter.

Layering occurred predominantly down slope. In 27 instances the daughter was 45 degrees or more down slope from the mother. In eight instances the daughter was at about the same height as the mother and in only two instances was the daughter within 45 degrees upslope of the mother.

DISCUSSION

1 Vine maple distribution

The distribution of species is usually not uniform or random in space. Instead patchiness or organization along gradients are common. This inhomogeneity of distribution can be attributed to the inhomogeneity of the environment and to biotic processes and interactions (Legendre and Fortin 1989, Thomson et al. 1996, Legendre 1993). In all study sites vine maple distribution was patchy, especially the high cover classes seemed to occur clustered. Therefore the dependency of vine maple distribution on some factors other than chance alone can be assumed.

Positive autocorrelation of vine maple cover was always present at the smallest distance classes, in three cases up to a distance of ~20 m, in one case (US site) only up to a distance of 13.7 m. Negative autocorrelation occurred in the higher distance classes of all four study sites. Most vine maple occurred in small clumps. Between 30 and 50 % of all cells with vine maple showed a cover of less than 5 %. Total basal area was also relatively low in most cells, but achieved very high values in a few cells. The highest vine maple total basal area per square meter was found in the CHIL site.

The clustering of cells with high vine maple cover and total basal area suggests that vine maple distribution has not only been caused by the tendency of clonal species to occur in clusters, but as a response to other factors.

In the LSCR site 416 vine maple stems per hectare were counted. This was a considerably lower density of vine maple than found by Peck and McCune (1998) in a study in northwestern Oregon where vine maple averaged between 3035 and 3940 stems per hectare. Vine maple reaches the northernmost edge of its habitat in southwest BC, due to its intolerance of late frosts, mean annual temperatures below 5 °C and probably heavy snow accumulation (UBC Botanical Garden 1976, Krajina et al. 1982). Lower densities and a more restricted distribution of spaces where all vine maple habitat requirements are met is the result (Virgos and Casanovas 1999, Brown 1984).

2 Surficial geology

Mass movements like debris flows, rock falls, slides and dirty snow avalanches are common features in the Coast Mountains. They are caused by a combination of steep slopes, heavy seasonal rainfall and the presence of an impermeable till or bedrock substratum in many valley sides. The Seymour Valley is no exception (O'Laughlin 1972, Miles and Swanson 1986). In the LSCR site rockfall, debris flow and mosaic sediment were found, the latter being a label for a thin veneer of debris flow sediment on rockfall sediment. In a small area lake sediments formed the surface sediment.

In a study of the surficial geology of the lower Seymour Valley Lian (1991) describes thick paraglacial sediments, deposited by all sorts of mass movements. He mapped the surface sediments of this area. The lower part of the LSCR site was mapped as paraglacial fan or apron. This part is most likely identical to the areas described as rockfall sediment in this study. Since Lian used a unique signature for rockfall sediment, he apparently thought the sediments to be of alluvial or debris flow origin. Lian most likely did not know the exposures along Squamish Creek. They are not mentioned in his thesis and the maximum thickness of paraglacial sediments found by him is 10 m, 5 m less than the thickness of section three at Squamish Creek. The surface of the rockfall sediments in the LSCR site did not deviate strongly from the surface expression of debris flow or alluvial material. Since the focus of Lians study was several kilometers downstream of the LSCR site, the small change in surface expression might have escaped Lian.

The surface sediment of the upper part of the LSCR site was mapped as bedrock by Lian. It is likely conform with the areas above the precipice identified as debris flow, mosaic sediment and rockfall sediment in this study. The presence of bedrock outcrops visible in most of the neighbouring stands, the LSCR site and upper parts of tributary creeks might have been the cause for this misclassification.

In all four study sites used in the present study the height of vine maple cover was connected to the type of sediment encountered. Rockfall sediment was connected to a high cover (> 25 %) of vine maple. On debris flow sediment cells without vine maple and cells with a low cover of vine maple (< 25 %) were found most often. Vine maple response to mosaic sediment held an intermediate position between these two types of sediment and the response to lake sediment was similar to the response to debris flow sediment.

A connection between vine maple and colluvial and alluvial sites is mentioned in the literature (UBC Botanical Garden 1976, Klinka et al. 1989, Haeussler et al. 1990, Bailey and Poulton 1968). In these studies the terms colluvium and alluvium are used in the broad sense laid down in the Canadian System of Soil Classification (Agriculture Canada Expert Committee on Soil Survey 1987). Colluvium may designate any unsorted sediment whose components have reached their present position by direct gravity-induced movement. The term alluvium indicates a fluvial origin of the sediment. No information about the kind of colluvium or alluvium or about causal connections to edaphic conditions, frequency of disturbance or any other factor is provided in any of these studies.

In the LSCR site variations in soil type, texture and pH did not explain the response of vine maple to sediment type. Twenty of the 22 sampled soils were podzols. In both the Coast and the Cascade Mountains humo-ferric or ferro-humic podzols and regosols dominate, except on poorly drained sites (Fonda and Bliss 1969, O'Laughlin 1972, Saunders 1985, Pojar et al. 1991). The conifer species in the study sites are able to thrive on these soils as well as vine maple (Pojar et al. 1991, Klinka and Krajina 1986, Lertzman and Krebs 1991, Ogden 1996, Klinka and Krajina 1986). In two sample plots under vine maple brunisols were found. The occurrence of vine maple on the only two brunisols sampled points towards a connection of vine maple to younger soils. However, the predominance of podzols under both vine maple and conifers rules out that soil type was responsible for high vine maple cover on rockfall sediment.

Soil texture in the LSCR site was either coarse loamy-skeletal (in nine samples) or sandy-skeletal (in 32 samples), without physiologically important differences between sediment types. No significant differences were found between plots with vine maple and plots without vine maple. Conifers can grow on loamy skeletal and sandy skeletal soils (Pojar et al. 1991, Klinka and Krajina 1986). Texture classes that can support vine maple range from clays and silty clays over clayey, silty, sandy and skeletal loams to sands, loamy sands and skeletal sands (Anderson 1967, Drew 1968, Klinka and Krajina 1986, Bailey and Poulton 1968, Ogden 1996). No physiological limit to either vine maple or conifer occurrence was reached in the LSCR site. Ogden (1996) did a comparison of edaphic properties of vine maple gaps to the surrounding conifer matrix. She found no differences in sand or gravel content.

Soil chemistry is usually not of primary importance for vegetation patterns in western mountain systems (Ohmann and Spies 1998). Soil pH in the LSCR site varied from

3.73 to 4.84. No physiologically significant differences were found between sediment types. Under vine maple slightly higher mean pH values were found than in plots without vine maple, but these differences are neither significant nor large enough to be physiologically important. Vine maple litter is known to have a higher content of bases than conifer litter (Haeussler et al. 1990) which results in higher pH levels in the forest floor under vine maple. This difference may translate into slightly but not significantly higher pH values in the mineral soil below vine maple compared to plots without vine maple (Ogden 1996, Tashe 1998).

The most conspicuous difference between rockfall and debris flow sediment is the amount of fine material in the sediment. In this study rockiness was used as an inverse measure for the amount of fine material. In all three study sites in which both types of sediment were present, rockfall sediment was significantly rockier than debris flow sediment. The rockiness of mosaic sediment showed always intermediary values between those of rockfall and debris flow sediment. In the LSCR lowest values for rockiness were found in lake sediment. But the amount of fine material, measured inversely as rockiness, did not influence vine maple distribution by itself, since variation in rockiness within the sediment had no influence. An influence of the distribution of fine material between the rocks, for example the frequency of air-filled interstices, is conceivable instead and would have escaped detection.

High cover of vine maple on extremely rocky sites was also observed by Roach (1952), Anderson (1967) and Klinka and Krajina (1986). Roach (1952) described an *Aceretosum circinati lavetosum* dominated by vine maple in a study of 460 to 600 year old lava flows. He described the substrate as bare expanses of large black block basalt with large air crevices between the blocks. Vine maple was able to establish itself in pockets of wind blown organic and inorganic material accumulated in depressions and crevices between the rocks. Conifer seedlings dried out and conifers were subsequently unable to establish themselves on this substrate. In Douglas-fir forests adjacent to the block lava Roach found vine maple as well. The substrate below the forest differed in only one respect. On these sites the blocks were smaller and the larger interstices were almost absent. Roach attributed the difference in the vegetation to the larger amount of fine material.

Anderson (1967) observed that, where rock outcrops, rock bluffs or talus slopes occurred, vine maple was invariably found. He attributed this observation to a restriction of tree growth on these positions due to shallow soils. Permanent edaphic gaps were formed that ensured the survival of vine maple because it was never shaded out. Both Roach and Anderson believed in a more or less permanent dominance of vine maple on these rocky sites due to edaphic properties.

Klinka and Krajina (1986) described an *Acer circinatum - Ribes lacustre* plant association on fragmental soils in a Coast Mountain forest. They classified this association as an early stage in the primary succession on talus. In other words, they believe vine maple dominance on these sites to be time limited. The occurrence of vine maple thickets on talus slopes has also been observed in the Northern Cascades, Washington (Oliver et al. 1985).

For rockfall sediment, a limited time period of vine maple dominance due to succession seems more likely than a permanent edaphic difference. After all, conifers were able to establish on rockfall sediment in the LSCR site and now dominate on this type of sediment. Vine maple might play a classic successional role on rockfall sediment. It can establish on rockfall sediment, while neither "classic" pioneer species like *Alnus rubra* and *Acer macrophyllum* nor conifers seem to be able to do so. *Alnus rubra* could be observed in avalanche scars directly adjacent to the study sites. After logging, late-seral species like *Tsuga heterophylla* or *Abies amabilis* can regenerate promptly without interplay of pioneer tree species (Klinka et al. 1985, Franklin and Hemstrom 1981). After shallow landslides in the Cascades in western Oregon *Pseudotsuga menziesii*, *Tsuga heterophylla*, *Thuja plicata*, *Alnus rubra* and *Acer macrophyllum* had reestablished within six to 28 years on the new sediments while vine maple played only a very minor role (Miles and Swanson 1986). Even in areas only recently deglaciated conifer establishment was not impeded (Oliver et al. 1985). There was no shortage of seed sources for any of these species near the rockfall areas in the study sites.

Which adaptations enable vine maple to grow on relatively fresh rockfall sediment are unknown. The root system must develop very quickly after germination to reach the often low ground water table before the seedling dries out, because capillary water is scarce in rockfall sediment. Very little is known about the root system of vine maple. It has been described as fibrous and vigorous, with several taproots (UBC Botanical Garden 1976, O'Dea 1992), most likely similar to the often shallow and rapidly branching root system of other species of the genus *Acer* (Köstler et al. 1968). How it differs from the root system of *A. macrophyllum* to give it a competitive advantage over this pioneer species is unknown. A known advantage are the green stems, which allow vine maple to photosynthesise in the mild and wet winter. The shrub size and high morphological plasticity will also be of benefit. How far primary succession has to have progressed before vine maple can establish itself is unknown as well. There are virtually no published observations on the course of primary succession on rockfall and talus sediment in southwest British Columbia (Karel Klinka, pers. comm. 20.11.2001).

Once vine maple has established itself on rockfall sediment it should eventually improve the edaphic properties of the sediment enough to allow conifer establishment. Vine maple roots and stems will conserve material that the wind blows in. It is known to add nutrients to the soil through its abundant leaf litter (Haeussler et al. 1990, Tashe 1998, Russell 1974) and ameliorates the microclimate below its foliage until it resembles closed conifer canopy conditions (Ogden 1996, McGhee 1996). Dead vine maple stems or broken rootballs may form a seedbed for hemlock, which regenerates nearly exclusively on dead wood (Roach 1952, van Pelt and Franklin 2000, Franklin and Hemstrom 1981, Spies and Franklin 1989) and grows only on sites with significant organic content of the soil (Pojar and MacKinnon 1994).

The dominance of vine maple on rockfall sediments in the CHIL and COQ sites and the absence of a tree layer might have been due to a more recent formation of the rockfall sediments in these sites compared to the LSCR site. No dates for the age of the sediments were obtained in this study. The rockfall sediments were too overgrown by mosses and higher vegetation to allow lichonometry. No suitable organic material for ^{14}C dating was found in the sections, and the size of the boulders that would have had to be moved to access deeper layers made a search for dateable material impossible. If vine maple truly acts as a nurse crop for conifers and how long the succession to a closed conifer forest might take can only be determined through further research on rockfall sediments of known age.

3 Light

A connection between vine maple cover or its occurrence and light availability has frequently been mentioned in the literature. Anderson (1967) called vine maple shade intolerant and restricted to canopy openings in the forest. He postulated a cyclic development of vine maple: after logging or fire has removed the overstory, vine maple expands to a peak in cover in the 20th year after the disturbance. When the overstory closes vine maple declines due to light limitation until, after 50 years, the forest canopy opens up and vine maple can again increase in cover.

Russell (1974) investigated vine maple biomass changes during early succession. Though he only studied stands seven to 22 years and one stand 450 years old, he repeats Anderson's hypothesis of vine maple abundance depending on successional status as his own. His "bi-modal" cycle of vine maple abundance has been fairly influential. It was cited by Wardman (1997), Ogden (1996) and the important reference Haeussler et al. (1990). The conviction that vine maple is restricted to canopy openings and light spots can also be found by Bailey (1966), Drew (1968) and Pojar and MacKinnon (1994).

Contrary to this conviction, O'Dea (1992) used in her study on the demography of vine maple only clones under closed canopy in stands of all ages. She found the largest clones in stands 35 - 47 years of age. In a study of McGhee (1996) about priority effects of vine maple in mature 60 - 80 year old stands, 18 % of the clones were found under closed canopy. Those vine maple had on average fewer stems, but were not declining.

In the LSCR site vine maple was not confined to canopy openings. Light availability was not generally lower below the closed conifer canopy than in small canopy openings (Figure 42). Small gaps have little or no effect on understory light levels beneath the gap. This is a consequence of the extremely high ratio of tree height to crown width in conifer forests (Canham et al. 1990). Forests do not consist of a uniformly dark closed canopy punctuated by bright openings. The effects of larger canopy openings can extend a considerable distance beyond the projected outline of the gap, especially to the north of the gap, since the study sites are located at northern latitudes (Canham et al. 1990, Spies et al. 1990). This results in a continuum of light levels from gaps to the closed canopy (Lieberman et al. 1989).

Light availability in gaps was not explicitly measured in this study. Vine maple occurred in two thirds of the gaps investigated. Most gaps were relatively small. Despite little increase in light availability in small gaps, they might offer a free space that enables vine maple to grow without mechanical damage or obstruction through conifer branches. This could explain the frequent occurrence of vine maple in gaps that most likely do not offer better light availability.

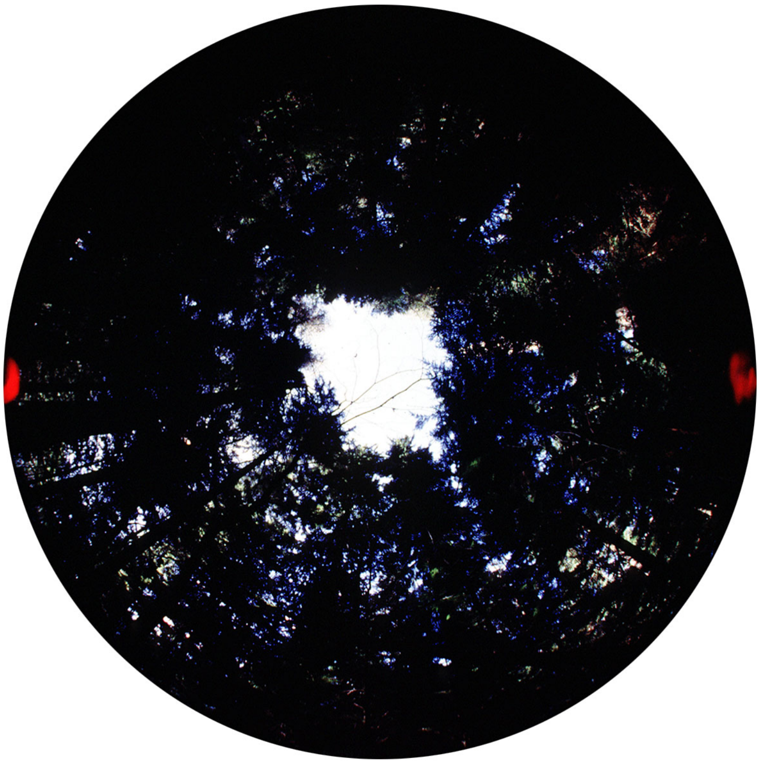

Figure 42: Top photograph: vine maple gap, 4.92 % SO. Bottom photograph: vine maple under closed canopy, 4.98 % SO. Red dots were caused by LEDs that were attached to the camera to delimit the horizontal extent of the photographs.

Three attempts were made so far to quantify vine maple response to light availability. Russell (1974) and McKenzie et al. (2000) used indirect methods to quantify light availability to vine maple. McGhee (1996) used hemispherical photographs.

Russell (1974) used overstory biomass as a proxy for light availability. He reported an inverse relationship of vine maple stem frequency and biomass to overstory biomass and concludes that vine maple stem frequency and biomass is light limited. Russell's data do not support his conclusions. They will therefore not be discussed any further.

McKenzie et al. (2000) investigated overstory influences on the understory of mature (70 - 140 year old) forests in Washington, USA. They found that vine maple cover was correlated negatively with canopy cover, as was total shrub and total herb cover. Canopy cover in their study ranged from 0 to 98.1 %, with averages of 64.8 to 83.3 %. No further details about this relationship were given in the study.

McGhee (1996) attempted to compare light availability to vine maple clones of different demographic status. To this end she measured light availability beneath fully leafed vine maple canopies in the summer. She found no difference in light availability below vine maple and below conifers, with one exception. Below clones she had classified as declining significantly less light was available than below either conifers or other vine maple clones. Due to the used methodology her results do not allow any conclusions about a connection between light availability to vine maple and vine maple demography.

No direct light measurements that determine light influence on vine maple were made before the present study. In the LSCR site, vine maple could be shown to be very shade-tolerant. Vine maple was able to survive in the entire range of understory light availability in the study site, 1.73 to 12.4 % SO, and it was clearly not confined to gaps. Light levels as low as these limit the growth of *Thuja plicata*, *Tsuga heterophylla* and *Acer macrophyllum* seedlings (Carter and Klinka 1992, Fried et al. 1988).

The ability of vine maple to persist in the low light levels under the conifer canopy was not due to an excessively open conifer canopy in the LSCR site. The canopy closures found in this study were even fairly high. Klinka et al. (1996a) reported an average canopy cover of 61.5 % for early seral stands of the *Abies amabilis - Thuja plicata - Rubus spectabilis* association, a similar association to the vegetation units found in the study site. In 60 - 80 years old mixed *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata* stands McGhee (1996) reported an average of 35 % SO under closed canopy. The gap sizes observed in the LSCR site were comparable to the gap sizes and gap size distributions observed in other coniferous forests of various ages (McGhee 1996, Wardman 1997, Lertzman and Krebs 1991).

In the LSCR site vine maple was able to reproduce sexually and to attain high cover and large crown sizes at relatively low light levels. Some clone characteristics were even independent of light availability within the range of light levels measured in the study site. These characteristics included the number of stems in a clone and their summed basal area and the thickness of leaf laminae and leaf midribs.

The number of stems in a vine maple clone might be dependent on light availability, but only at stronger variations in light availability than was encountered in the study site. Vine maple demography changes during succession (O'Dea 1992). In clearcuts vine maple grows in dense clumps with many erect stems. During succession the number of stems decreases, while their diameter increases. In oldgrowth forests clones consist of few, often decumbent or rambling stems. This is considered to be an adaptation to changes in light availability (O'Dea 1992). On the open rockfall area of the CHIL site clones had the highest number of stems per rootball found in this study. Summed stem basal area might display the same relationship to strong changes in light availability. It might also stay fairly constant at different light levels due to an increase in diameter of the fewer stems at low light levels.

The missing response of leaf lamina thickness to changes in light availability in the LSCR site might also have been due to altogether too small variations in light availability. The dorsiventral leaves of many deciduous trees and shrubs possess both shade and sun adapted leaves. Sun adapted leaves have, next to physiological adaptations, taller palisade cells or even several layers of palisade cells, increasing leaf lamina thickness (Sitte et al. 1991, Troll, 1973, Goulet and Bellefleur 1986).

No such effect could be observed in the vine maples sampled. All leaves had the characteristic funnel-shaped cells of shade adapted leaves, with a somewhat denser packing of palisade cells in plants exposed to higher light levels. The same was observed for *Acer rubrum*, while *A. plantanoides* and *A. saccharum* possess thinner shade leaves than sun leaves. This difference was attributed to *A. rubrum* being a pioneer species and the other two maples being climax species (Goulet and Bellefleur 1986). This explanation is not likely applicable to vine maple, since it can be both pioneer and climax species. Either vine maple does not react to increased light levels with a thicker palisade parenchyma, or light levels did not vary enough to trigger a response. A comparison to leaves from vine maple growing on open sites might provide an answer.

While vine maple was found at even the lowest light levels measured in the LSCR site and some clone characteristics were independent of light levels, vine maple cover, clone crown size, sexual reproduction and sprout production were influenced by light availability. Within stem branch survival depended on the availability of light to the branch. Only 8 % less available light separated, on average, dead branches from live branches.

In the LSCR site high light levels gave rise to a high cover of vine maple (> 25 %). Low light levels increased the likelihood of death and decline for vine maple and even a moderate increase in light availability increased vine maple survival. In the absence of overstory trees vine maple was able to attain high cover over large areas on rockfall sediment in the CHIL and COQ sites. Improved growth in canopy openings with their higher light availability despite the high shade tolerance of vine maple was also observed by other authors (Tappeiner and Zasada 1993, UBC Botanical Garden 1976, O'Dea 1992). Similar claims were made about *Acer japonicum* and *Acer sieboldianum*, both in the section *palmata* PAX like vine maple, in Japanese cool temperate forests (Akashi 1996, Yamamoto and Nishimura 1999, Yamamoto et al. 1995). The influence of light on vine maple distribution is quite typical for understory plants. In forests the competitive effects of overstory trees often determine, in large part, the distribution and abundance of subcanopy trees, shrubs and herbs (Beckage et al. 2000, McKenzie et al. 2000, van Pelt and Franklin 2000, Klinka et al. 1996a, Tappeiner and Alaback 1989, Eber 1972).

In the LSCR site sexual reproduction occurred more frequently at high light levels. The same observation was made by O'Dea (1992). In clonal herbs and shrubs the production of flowers depends on the amount of available resources (Eber 1986, Pitelka 1980, Hibbs and Fisher 1979). Sexual reproduction of vine maple might therefore be viewed as a luxury that was enabled through a resource surplus due to increased isolation.

One form of vegetative reproduction of vine maple is sprout production. In the LSCR sprout production might have been light limited at light levels below 8 % SO. At higher light levels no limiting influence of light availability on sprout production was found. In the bright light environment of clearcuts, vine maple stems form mainly through sprouting whereas after conifer crown closure the number of sprouts is greatly reduced (O'Dea 1992, Russell 1974, Anderson 1967). A reduction in sprout production at low light levels would be ecologically useful because it would hinder the production of new stems at disadvantageous sites. Layering would instead establish a clone at a different spot. Stems tend to grow towards the light (Anderson 1967). They might therefore layer in the direction of lean either due to their instable ratio of height to diameter or because they are pinned to the ground by debris falling from overstory trees (O'Dea 1992). The clone could "wander" (Tappeiner and Alaback 1989) towards the light in this way, if the light spot is not located upslope. Layering occurred in this study predominantly down slope or across slope, as was also observed by Anderson (1967).

Variability in vine maple response to light availability was high for all characteristics measured in this study. The limiting influence of light was strongest at lower light levels. Above ~8 % SO other factors than light seem to have limited vine maple. Nutrient limitation is one likely factor. Much of the competition among plants takes place belowground as root competition for moisture and nutrients. It can reduce plant performance more than aboveground competition for light (Casper and Jackson 1997, Riegel et al. 1995, Leuschner et al. 2001, Coomes and Grubb 2000). Moisture availability had no influence on vine maple distribution in the study site. However, a nutrient limitation of vine maple growth and performance is plausible. In the coastal forests of British Columbia the major growth-limiting nutrient is nitrogen (Edmonds et al. 1989). The nutritional requirements of vine maple are high for nitrogen, calcium and magnesium (Krajina et al. 1982). Vine maple roots are concentrated near the surface (Drew 1968), like the roots of *Tsuga heterophylla* and *Thuja plicata*, the dominant forest species (Schütt et al. 1994). Direct competition for nutrients by those and other species in the same soil volume might have influenced vine maple performance as strongly as light availability.

Infection by pathogens, grazer activity, historical factors and genetic variation are examples of other factors that might have contributed to the variability in the data. Several pathogens attack vine maple stems and leaves (Haeussler et al. 1990, UBC Botanical Garden 1976). Most vine maple in the LSCR site were infected by a leaf spot fungus, probably *Phleospora aceris* (LIB.) SACC. (UBC Botanical Garden 1976). Browsing by deer was observed in the LSCR site, but a variety of other species utilize vine maple as well, ranging in size from caterpillars to moose (*Alces alces*) (Haeussler et al. 1990, McGhee 1996).

Part of the high variability in the data might have been caused by the methodology used. A reaction of vine maple to recent changes in the light environment due to the death of an overstory tree will occur delayed. Small clones take time to grow into large ones if new light resources become available. This delay was not reflected by the light measurements and can result in a decoupling of clone parameters and measured light availability.

Overstory tree density might be considered as a proxy for direct light measurements. But despite a connection between vine maple cover and light availability, vine maple cover in the LSCR site was not connected to overstory tree density. This might have been an unusual feature of the LSCR site. In other studies in the Pacific Northwest increased stand density was correlated with reduced vine maple stem growth (O'Dea 1992), cover (McKenzie et al. 2000) and number of stems (Anderson 1967). The unusual decoupling of light availability and overstory tree density might have been due to the topography and stand age of the LSCR site. The LSCR was located on relatively steep slopes. Increased lateral influx of radiation caused by the uneven tree heights and thin crowns of oldgrowth forest on the sloped terrain of the study site could have resulted in increased light availability independent of the density of the conifer canopy within the cell.

In the LSCR site total conifer basal area per cell also had no influence on vine maple cover. Similar results were found by McKenzie et al. (2000). Anderson (1967) even found a positive effect of increased conifer total basal area on vine maple cover and abundance. Larger total basal area occurs in older stands and in patches of older trees in oldgrowth forests. In these stands or patches crowns will be more irregular in height and size than in younger stands. Total overstory tree basal area is therefore not a good proxy for light availability to the understory.

Light availability to vine maple was similar on all types of sediment found in the LSCR site. Therefore the high cover of vine maple on rockfall sediment can not be simply attributed to higher light levels on this type of sediment. However, the influence of large gaps on vine maple distribution on rockfall sediment might have been underestimated in the study. The four largest canopy gaps investigated in the LSCR were located on rockfall sediment. These gaps ranged in size from 105 to 807 m^2 and were all occupied by a high amount of vine maple. All three clones investigated that grew in these gaps were located on gap borders due to a chance effect of the random sampling scheme. With values of 8.39 %, 10.21 % and 10.30 % SO light availability was high for the three clones, but did not reflect conditions in the gap center.

4 Ground water

Vine maple has a high tolerance of low moisture conditions. It is able to grow on xeric sites with an average annual precipitation as low as 66 cm (Haeussler et al. 1992) with most of the precipitation falling during winter. Even on sites with higher annual precipitation low precipitation is often found in the summer causing moderate growing season moisture stress for vine maple (Anderson 1967, Roach 1952, Fonda and Bliss 1969, Russell 1974, Ohmann and Spies 1998).

Despite this high tolerance of xeric conditions, vine maple has sometimes been described as occurring only on fresh to wet sites (Pojar and MacKinnon 1994, Klinka et al. 1989, Krajina 1969, Klinka et al. 1985). This misconception might, to some extent, be due to the frequent observation of vine maple along creek beds (Haeussler et al. 1990, Parish and Thomson 1994, Lyons and Merilees 1995, Pojar and MacKinnon 1994, Anderson 1967, UBC Botanical Garden 1976).

In the LSCR site vine maple distribution was not influenced by the depth of the ground water table. Vine maple existed on plots without measurable ground water within 125 cm from the surface throughout the entire year as well as on plots with ground water levels which were close to the surface from November until March. There was no significant difference in ground water levels between sites with and sites without vine maple. This is consistent with observations by Ogden (1996). In her study of vine maple priority gaps, Ogden compared the ground water level under six vine maple gaps paired with six closed canopy plots. Ogden did not find any significant difference between plots with and plots without vine maple.

The indifference of vine maple to the range of ground water levels found in the LSCR site was corroborated by the results of a vegetation survey in this site. Two vegetation units were found. A *Rubus spectabilis* unit covered most of the LSCR site. It was subdivided into a *Phegopteris connectilis* subunit and a typical subunit. Small areas occupied by a nudum unit were found scattered within the area occupied by the *R. spectabilis* unit. The nudum unit lacked the rich understory vegetation of the *R. spectabilis* unit, including vine maple.

No connection between the vegetation units in the study site and ground water levels was found. Since vine maple was one of the diagnostic species of the *R. spectabilis* unit, this result implies that no connection between vine maple distribution and ground water levels existed. Most diagnostic species for the *R. spectabilis* unit function as indicator plants for fresh to wet and nitrogen rich soils (Klinka et al. 1989).

The *R. spectabilis* unit seems to correspond to both the *Tsuga heterophylla* - *Blechnum spicant* and the *Thuja plicata* - *Tiarella trifoliata* association of Klinka and Krajina (1986). These two associations are floristically very similar, with the exception of the degree of dominance of *Tsuga heterophylla* and *Thuja plicata*. Krajina and Klinka use a system based on a combination of degree of dominance of tree species, predicted climax species and characteristic combination of species which reuses diagnostic species on different levels of the system. It was not possible to make an unequivocal fit to their classification system. In British Columbia the biogeoclimatic ecosystem classification of Green and Klinka (1994) is in wide use. Their hierarchical classification system is based on topography, climate, soil moisture and nutrient status. The most commonly used units are called site series. These site series can support a particular type of climax forest or successional stages. The site series with the closest similarity to the vegetation units found in the study site is the *Abies amabilis* - *Thuja plicata* - *Rubus spectabilis* site series. This site series is characterized by nutrient rich to very rich and moist to very moist sites. Fonda and Bliss (1969) proposed a forest classification system for comparable lowland and montane forests of the Olympic Peninsula, Washington. Their community types are based on dominant tree species. A tentative fit to their *Abies amabilis* - *Tsuga heterophylla*/ *Oxalis* community type might be made. The systems used by Klinka and Krajina (1986), Green and Klinka (1994) and Fonda and Bliss (1969) do neither offer differentiation on the level of subunits nor a distinction of depauperate units.

The *P. connectilis* subunit was found on special habitats like large boulders, along creeks and in seepage zones. The presence of *Alnus rubra*, *Acer macrophyllum*, *Sambucus racemosa*, *Boykinia elata* and *Ribes bracetosum* in this subunit suggests that the time that has passed since the last disturbance might have been a factor for the presence of the *P. connectilis* subunit (Klinka and Krajina 1986). The subunit also covered a large part of the rockfall sediments. This suggests that on parts of this sediment the vegetation had not reached the climax stage yet. The strong vine maple presence on rockfall sediment could therefore have been a relic of the successional role vine maple might play on rockfall sediment.

Areas occupied by the nudum unit were only found on debris flow sediment. They consisted of relatively even aged younger trees. It is likely that these trees have established in a very dense patch. Where *Tsuga* saplings form such a dense patch the forest floor is almost void of any herbaceous growth due to restricted light levels (Anderson 1967). No vine maple was found in the nudum unit. Strong patchy conifer regeneration that resulted in a reduction of the understory was therefore able to influence vine maple distribution. However, current light levels were not low enough to eliminate vine maple. The hemispherical photographs taken in the nudum unit displayed on average 5.6 % SO. Vine maple was able to survive and even flower at this light level. The current absence of vine maple from nudum patches might therefore have had historical reasons: previously lower light levels had excluded vine maple and it has not been able to reestablish itself yet.

A temporal explanation of the absence of vine maple from nudum units is related to the idea of Connell's "ghost of competition past" (Connell 1980), and can therefore not be proved. Of course other explanation models for the exclusion of most understory species, including vine maple, from the nudum unit are conceivable. Small scale edaphic variations or the presence of a soil pathogen that attacks only angiosperms are possible explanations. Although no such factors were found in this study, only further research can exclude this possibility.

5 Microtopography

Vine maple is often described as preferring creek beds and depressions. This is usually attributed either to increased moisture availability or to increased light levels along creeks (Haeussler et al. 1990, Parish and Thomson 1994, Lyons and Merilees 1995, Pojar and MacKinnon 1994, Anderson 1967, UBC Botanical Garden 1976). In the LSCR site vine maple grew on debris flow sediment with a significantly often in proximity to major creeks. Low sample sizes on rockfall, mosaic and lake sediment prevented statistical analysis or significance.

Increased moisture availability along major creeks was likely not the cause of the frequent growth of vine maple at major creeks on debris flow sediment. There has been no indication that vine maple responds positively to high moisture levels in the study site. Increased light availability along the creeks is a more likely explanation. Even a moderately higher light availability prevented vine maple death and decline. No measurements of light availability along major creeks were made in this study. Likely the increase in light availability provided by the edaphic gaps major creeks can cause was only moderate. There was no connection between the height of vine maple cover and occurrence in proximity to a creek. A high cover of vine maple would have resulted from high light availability along major creeks.

Many authors report slope angle or slope position in their description of plant associations which contain vine maple, or in studies on vine maple (Klinka and Krajina 1986, Ogden 1996, Wardman 1997, Bailey and Poulton 1968, McKenzie et al. 2000, Drew 1968). Reported slopes which can support vine maple range from 9 % (McKenzie et al. 2000) to more than 100 % (Bailey and Poulton 1968). No consistent pattern for a connection between vine maple and slope inclination can be found in the literature. This was also true for the LSCR site. Vine maple distribution was independent of slope inclination.

6 Vine maple persistence and priority effects

The ability of vine maple to persist in the understory of coniferous forests has puzzled many authors and different mechanisms of persistence have been proposed (Ogden 1996, McGhee 1996, Wardman 1997). One mechanism proposed was allelopathy to conifer seedlings. Vine maple is reported to interfere with Douglas-fir establishment through the presence of phenolic compounds in its leaf litter (del Moral and Cates 1971). However, while Tinnin and Kirkpatrick (1985) affirm the presence of allelopathic compounds in vine maple leaf litter, they reported the allelopathic effect to be minimal under field conditions. The importance of the allelopathic relationship in situ is therefore unclear.

Excessive moisture depletion by vine maple might be another mechanism of vine maple persistence. Growing-season water deficit is a problem for conifer seedling establishment. Hemlock regenerates exclusively on dead wood because its water holding capacity is higher than that of mineral soil (Qian et al. 1999, Roach 1952, van Pelt and Franklin 2000, Franklin and Hemstrom 1981, Spies and Franklin 1989). Drew (1968) investigated the influence of species abilities to deplete soil moisture on the course of secondary succession in clearcuts. He found that vine maple more rapidly depletes soil moisture during July and August than several grasses, herbs and small shrubs. He also observed that less precipitation reached the forest floor beneath vine maple than beneath the other species. He concluded that these properties make vine maple a serious obstacle for conifer establishment in clearcuts. In mature forests precipitation and soil moisture were not lower below vine maple than below conifers (Ogden 1996). In the LSCR site forest floor moisture content was not different under vine maple than under conifers. The low size of vine maple compared to the surrounding conifers indicates already that it is unlikely that vine maple depletes soil moisture stronger than conifers do. The persistence of vine maple in the LSCR site could not be attributed to excessive moisture depletion.

A third proposed explanation for vine maple persistence was the repression of conifer seedlings through shading of the forest floor (Wardman 1997), as known from other understory species (Huenneke 1987, Beckage et al. 2000, Lorimer et al. 1994, Klinka et al. 1996a, Spies and Franklin 1989). McGhee (1996) compared light availability below fully developed vine maple canopies and conifer canopies. She found no difference. Vine maple does repress conifer seedlings through shading as much as mature conifers do, at least in the summer. Contrary to gaps without vine maple, vine maple gaps therefore do not offer improved regeneration opportunities to conifer seedlings.

The worse regeneration opportunities for conifers under vine maple than in gaps without vine maple was evident in the delay of gap closure by vine maple observed in the LSCR site. In gaps occupied by vine maple a higher proportion of further decayed stumps and logs were found than in other gaps. This indicates that more time has passed since gap formation. Vine maple gaps were also on average larger than gaps not occupied by vine maple.

How long the delay of conifer regeneration through vine maple presence in a gap might last is unknown. The direct determination of the age of vine maple clones is frustrated by the ability of vine maple to continually renew the aboveground biomass through sprouting. The oldest stem present might be much younger than its rootball. The trial excavation of a rootball in the course of this study did not shed new light on the time vine maple can persist in one spot. The rootball excavated was 138 years old. This was not much older than the oldest stem cored in the LSCR site with an age of 131 years and younger than the oldest known age of a vine maple stem of 142 years (Anderson 1967). Since it is impossible to distinguish old from young rootballs prior to excavation, the choice of the rootball might have just been unlucky. But it is also possible that rootballs have a limited life span that does not exceed the age of the stems. Some rootballs which were broken apart were observed in the study sites.

An indefinite delay of conifer regeneration is implied in oldgrowth priority gaps. Vine maple forms gaps at stand initiation and can keep them open for at least 80 years

(McGhee 1996, Ogden 1996), possibly even for 140 years (Spies et al. 1990). Priority gaps have no other origin than vine maple presence (McGhee 1996).

In the study site eight vine maple gaps were found that had no edaphic or developmental origin (independent gaps). Four of them were located on rockfall sediment and three on mosaic sediment. Only one was located on debris flow sediment, though this type of sediment covered the majority of the study site. Because of this disproportion the existence of true vine maple priority gaps on debris flow sediment can be ruled out.

The independent gaps on rockfall and mosaic sediment might have been true priority gaps. They might have been remnants of the successional stage on rockfall sediment dominated by vine maple before conifer establishment. However, some unrecognized edaphic factor might have been responsible for the independent gaps as well. This edaphic factor might have impeded conifer regeneration on rockfall sediment. Conifer seedlings occurred with a significantly lower density on rockfall sediment than on debris flow sediment. This effect could not be attributed to a statistically measurable influence of the high vine maple cover on rockfall sediment. However, the absence of statistical significance might have been caused by high variability in the number of seedlings per cell instead. The data does no clearly support or refute the existence of true priority gaps in the LSCR site.

If the independent gaps on rockfall and mosaic sediment were true priority gaps, there is no reason to believe that conifers will not eventually occupy these gaps. While vine maple does repress conifer regeneration, it can not do so indefinitely. Successful conifer regeneration below vine maple was observed by Klinka and Krajina (1986), Wardman (1997) and McGhee (1996). Rockfall and mosaic sediment support conifers in the LSCR site. Overstory tree density and total basal area were even as high on these types of sediment as on debris flow sediment.

7 Vine maple layering

In oldgrowth forests vegetative reproduction is the dominant form of reproduction for vine maple (Anderson 1967, Haeussler et al. 1990, O'Dea 1992). The observed distribution of vine maple in the study sites therefore reflected a historical pattern of vine maple distribution as well as the current site conditions. The occurrence of suitable sites not occupied by vine maple ensued from the uneven potential of sites for colonization dependent on their distance from existing clones.

Layering is one form of vegetative reproduction used by vine maple (O’Dea 1992, Anderson 1967). Successful vine maple vegetative reproduction through layering recently occurred in the LSCR site in one third of the investigated cells. To establish a new rootball 10 m distant from the mother plant vine maple needed 170 years. This time span includes a lag of 20 years between the establishment of a daughter stem and the start of the growth of the future new mother stem. The only other account given of the time needed for such a “movement” is the description of a 115 years old clone with a child one half this age 25 m apart (Anderson 1967). In that case vine maple had needed 75 years for 10 m.

A time span of 170 years for 10 m implies that vine maple layered twice in the same direction. Though this is of course only one possibility, this assumption is not entirely unreasonable. The light spot vine maple was leaning to before the first layering event might well still be present when the daughter plants starts to layer. Intervals between stand-replacing disturbances might exceed 1000 years on many sites in the coastal temperate rainforest (Spies and Franklin 1989). The dominant conifer species have lifespans of 400 to 1000 years (Waring and Franklin 1979). Therefore, the small scale, low intensity disturbance typical for these forests leads to extremely long turnover times of 350 - 950 years (Lertzman et al. 1996). When a tree falls to the ground and produces a gap, a long time can pass until it is decayed enough to serve as a nurse log for hemlock, the most common regenerating species. Between 480 and 580 years are believed to be necessary to eliminate 90 % of an 80 cm diameter *Pseudotsuga* log. The large *Thuja* logs are even more decay resistant than those of *Pseudotsuga* (Franklin and Hemstrom 1981). Compared to these time frames the establishment of vine maple ramets through layering in a new location is a relatively fast process. Layering might therefore be a good evolutionary adaptation to the slowly but constantly shifting mosaic of the conifer canopy.

CONCLUSION

Vine maple distribution in the study sites was influenced by abiotic, biotic and historical factors. One abiotic factor, the type of sediment, was of overriding importance. Over areas of hundreds of meters it broadly determined the frequency of vine maple occurrence and magnitude of vine maple cover. All other investigated factors that were found to exert influence on vine maple did so mainly on the scale of single clones. They explained some of the variability in vine maple cover and occurrence within one type of sediment. Abiotic factors active on this scale were light availability and proximity to a major creek. No influence of soil properties, slope, and ground water level on vine maple distribution was found in the study sites.

The influence of the abiotic factors was modified by biotic and historical factors: the ability of vine maple to delay conifer regeneration at its growth location and its ability to colonize new sites. Vegetative reproduction is the near exclusive form of reproduction in oldgrowth forests (O'Dea 1992). New sites can only be utilized by vine maple if they are located near to an existing clone nearby. The current distribution of vine maple therefore reflected a historical distribution of vine maple.

Vine maple distribution might have also been influenced by the historical distribution of light availability in the study sites. The absence of vine maple in areas with denudated undergrowth might have been caused by formerly low light levels in these areas. Similarly, increased vine maple occurrence at major creeks might have been caused by increased light availability along creeks. Though both factors might be indirect expressions of the influence of the abiotic factor light availability, they need to be considered as independent factors in my study because their connection to light availability has not been proven.

The factors that were identified in my study explained the broad pattern and some of the small scale variation of vine maple distribution in the study sites, but part of the variation in the cover and clone characteristics of vine maple remained without explanation. Root competition for nutrients, infection by pathogens, grazer activity and genetic variation might have contributed to the variation. Investigation of these factors would further the understanding of vine maple ecology. Other areas of interest for future research are an investigation of the role vine maple plays in primary succession on rockfall, talus and related sediments in British Columbia, and of the morphological and physiological adaptations that allow vine maple to thrive on these types of sediment.

Any discussion of vine maple ecology has to take current forestry practices into account, since nearly all vine maple habitat in British Columbia is in second-growth forests. By 1972 clear-felling had been carried out in most of the valleys draining into Howe Sound and Burrard Inlet below altitudes of 1220 m (O'Laughlin 1972). Foresters have viewed vine maple traditionally as a weed species, a strong competitor to conifers, because it might form thickets after logging, and long lists of herbicides for the destruction, termed control, of vine maple are available (Haeussler et al. 1990, Krajina et al 1982, Massie et al. 1994, Klinka et al. 1996b). The current practice is to remove vine maple from managed stands in Washington, Oregon and British Columbia (Tashe 1998, Haeussler et al. 1990).

The dreaded vine maple thickets form mainly through unsuitable silvicultural practices. Thickets form where stems left standing after logging layer because they were pinned to the ground or buried by slash (O'Dea 1992, Haeussler et al. 1990). If vine maple stems are cut during logging, the probability of thicket formation is much reduced. High vine maple cover and therefore a high danger of thicket formation were found on rockfall sediment. Rockfall sediment and the structurally similar talus are common sediments in the Coast Mountains. Those sites will not be more conductive to conifer regeneration after logging than before logging, and full occupancy of a stand following logging can not be expected. Unusually high cover of vine maple might even be used as a warning sign that conifer regeneration will be impeded in a site.

The usual vine maple proportion and distribution on sites favorable to conifer growth found in my study were a scatter of mainly small vine maple clones with an overall low cover. If vine maple is allowed to regenerate after logging from roots in this pattern, vine maple will help reduce the erosion and decrease the likelihood of landslides caused by clearcutting on sloped terrain (O'Laughlin 1972, Slaymaker 2000) through its fast development (Krajina et al. 1982). The survival of soil organisms might be enhanced through the continuity of the root system throughout the logging period and with it subsequently conifer seedling survival (Perry and Maghembe 1989). The natural spacing provided by vine maple will reduce competition between the conifers of a stand. Intra-specific competition between conifers can reduce conifer growth stronger than inter-specific competition with brush species (Biondi et al. 1992, Oliver and Larson 1990).

In Douglas-fir forests vine maple presence does not reduce stand productivity, and with it profit from timber harvests (Wardman 1997). Vine maple litter is richer in nutrients than conifer litter, especially in the limiting nutrients nitrogen, boron and magnesia.

Conifers adjacent to vine maple have higher nitrogen concentrations in their leaves than other conifers (Ogden 1996, Tashe 1998). Greater height, increased total basal area and larger crowns for Douglas-fir and western hemlock are the result (Wardman 1997). Since the current productive capacities of the forest soils of British Columbia result from thousands of years of shifting mosaics of coniferous and hardwood vegetation on the land (Fried et al. 1989) the long term effects of an elimination of vine maple on soil productivity are incalculable.

Vine maple presence increases biodiversity in a stand, particularly during the least diverse stand initiation phase of forest development (McGhee 1996, Tashe 1998, Oliver and Larson 1990). It adds structural complexity, deciduous leaves and leaf litter that results in nutrient rich humus and thus unique habitat and food to the conifer dominated forests (Tashe 1998). Several birds and mammals use vine maple as an important food source and habitat. These include the Red-listed mountain beaver, the Blue-listed Roosevelt elk, the black-tailed deer (*Odocoileus hemionus*), moose, rabbits (*Lagomorpha* spec.), the winter wren (*Troglodytes troglodytes*), Swainson`s thrush (*Hylocichla ustulata*) and Pacific Slope flycatcher (*Empidonax difficilis*) (Bailey and Poulton 1968, Singleton 1976, Miller 1968, Haeussler et al. 1990, McGhee 1996, Harcombe et al. 1994). Under vine maple mull or moder humus forms instead of the mor humus prevalent under conifers (Tashe 1998, Ogden 1996), providing a divergent habitat for soil communities.

Increased ecological concern has led to a new recognition of the need to preserve biodiversity, most notably codified in the United Nations Convention on Biological Diversity (1992), which was signed and ratified by Canada. The will to preserve biodiversity is also set forth in the preamble of the Forest Practices Code of British Columbia Act (BC Ministry of Forests 2001). The Biodiversity guidebook of the Forest Practices Code of British Columbia Act (BC Ministry of Forests and Environment 1995) recommends to this end that the proportion and distribution of the deciduous broadleaf components of stands should be maintained within the range found in unmanaged stands within the landscape unit. The retention of vine maple in managed stands is simple, helps maintain site productivity, may reduce costs associated with spacing, fertilizing, and herbicide use and enhances biodiversity.

Therefore vine maple should be incorporated into forest management plans in southwest British Columbia as a natural and valuable forest component. To this end the following recommendations ensue from my study:

On debris flow sediment and other types of sediment with good conifer regeneration vine maple stems should be cut during logging to eliminate the danger of thicket formation. Vine maple should not be destroyed by treatment with pesticides to allow regeneration. If necessary cutting of the stems can be repeated before replanting with conifers to reduce competition by vine maple with the planted seedlings. Vine maple will reestablish in the characteristic scatter of small clones.

Rockfall, talus and related sediments are not suitable for clearcut logging. The composition of these types of sediment indicates a high danger of erosion of the fine material after clearcutting. Erosion would further reduce the fertility of these sites and with this future timber production. Vine maple is strongly present and might easily dominate. Partial cutting regimes, ideally single-stem extraction, are preferable harvesting regimes. The continuous presence of a conifer overstory should prevent soil loss and unwanted spread of vine maple.

SUMMARY

Vine maple (*Acer circinatum* Pursh) is a deciduous small tree or shrub component of the pacific temperate rainforest of southwest British Columbia (BC), Canada. The pattern of vine maple distribution within the predominantly coniferous forest might be caused by the interaction of a variety of abiotic, biotic and historical factors. The influence of surficial geology, light availability, ground water levels, aspects of the microtopography and of vine maple persistence, priority effects and layering on this pattern were singled out for investigation.

The majority of the study was conducted in the Lower Seymour Conservation Reserve (LSCR) in the Coast Mountains, BC. The results from the study on surficial geology were validated in three study sites in the Coast and Cascade Mountains, BC. All study sites were located in oldgrowth forests.

In a survey of the surficial geology of the LSCR site four types of surficial sediments were found: debris flow and rockfall sediment, a small-scale mosaic of rockfall sediment thinly overlain by debris flow sediment termed mosaic sediment, and lake sediment. In the other three study sites only the mass-movement sediments were found. The type of sediment had a strong influence on vine maple distribution. It broadly determined the frequency of vine maple occurrence and magnitude of vine maple cover. All other investigated factors that were found to exert influence did so mainly on the scale of single clones. They explained some of the variability in vine maple cover and occurrence within one type of sediment.

In all study sites high vine maple cover was significantly correlated with rockfall sediment, low vine maple cover significantly with debris flow sediment. Mosaic sediment held an intermediate position and on lake sediment mainly low cover of vine maple was found. Differences in soil type, texture, pH and coarse fragment content were not responsible for this effect, despite a significantly higher coarse fragment content of rockfall sediment. High vine maple cover on rockfall sediment might have been a remnant of vine maple presence during primary succession.

The level of light availability was responsible for some of the variability within rockfall and debris flow sediment, but did not cause the positive response of vine maple to rockfall sediment. A high cover of vine maple and an increased incidence of sexual reproduction were significantly connected to higher light levels. Branch demography was also

significantly influenced by light. Vine maple proved to be very shade tolerant, but its chance of survival was reduced by low light levels. Low light levels might have also been limiting to the maximum sprout production per clone. Other clone characteristics, like the number of living stems, the size of the crown and the summed basal area of a clone as well as leaf lamina thickness, showed only weak or no relationships to light levels.

On debris flow sediment increased vine maple occurrence was significantly associated with growth in proximity to major creeks. This can not be attributed to increased moisture provided by the creeks, since vine maple distribution and cover were independent of ground water levels. Increased light availability along major creeks might have been responsible instead. Slope inclination had no effect on vine maple. A vegetation survey showed vine maple to be part of the dominant vegetation unit of the LSCR site. It was absent in a vegetation unit lacking nearly all understory species due to previous exclusion through dense conifer regeneration.

The influence of these abiotic and historical factors was modified by the ability of vine maple to delay but not completely repress conifer regeneration in gaps it occupied. On debris flow sediment priority effects by vine maple could not be detected while on rockfall and mosaic sediment their existence could not be ruled out. The delay of gap closure by conifers was not due to excessive desiccation of the forest floor by vine maple. Vine maple distribution was also influenced by the limitations imposed by the predominantly vegetative mode of reproduction in oldgrowth forests.

An understanding of the ecology of vine maple will foster the comprehension of forest dynamics and species distribution within the coastal temperate rainforests of British Columbia. The results of this study should provide foresters with the necessary ecological information to incorporate vine maple in forest management plans.

DEUTSCHE ZUSAMMENFASSUNG

Die primären Wälder British Columbias (BC) werden von langlebigen und oft über 50 m hohen Nadelbäumen beherrscht (Pojar und MacKinnon 1994, UBC Botanical Garden 1976). *Acer circinatum* ist ein Laubbaum oder -busch, der zumeist weniger als 10 m hoch wird. Er ist innerhalb seines Verbreitungsgebietes häufig sowohl in frühen Stadien als auch in Klimaxstadien der Bestandessukzession anzutreffen.

Die Faktoren, welche die Verbreitung von *A. circinatum* innerhalb primärer Wälder in Südwest BC bestimmen, sind der Inhalt dieser Studie. Der Einfluss von sechs Faktoren wurde untersucht: Oberflächengeologie, Licht, Grundwasser, Mikrotopographie, die Fähigkeit von *A. circinatum* seinen Standort zu behaupten und die Rametenbildung durch Bewurzelung von Stammabschnitten.

Der Einfluss dieser Faktoren wurde in einem etwa 3,5 ha großen Studiengebiet in der Lower Seymour Conservation Reserve (LSCR), North Vancouver, BC, untersucht. Der Einfluss der Oberflächengeologie wurde an drei weiteren Standorten überprüft: im oberen Tal des Seymour River (US), am Coquitlam Lake (COQ) und am Chilliwack Lake (CHIL).

1 Die Verbreitung von *A. circinatum* in den Studiengebieten

A. circinatum trat in allen Untersuchungsgebieten deutlich geklumpt auf. Kleinere Bereiche mit hoher Deckung von *A. circinatum* lagen neben größeren Bereichen mit niedriger Deckung und insgesamt kleineren Klonen von *A. circinatum*.

2 Oberflächengeologie

Die Oberflächengeologie des LSCR wurde überwiegend von Lockersedimenten bestimmt, die aus Erdrutschen und Felsstürzen hervorgegangen waren. Das im Untersuchungsgebiet in drei Bereichen an der Oberfläche liegende Felssturzmaterial bestand aus einem unsortierten, nicht eingeregelten Korngemisch mit weitem Größenintervall aus lokalen Tiefengesteinen. Das wenige Feinmaterial füllte die Zwischenräume zwischen dem kantigen Grobmaterial, das über einen Meter im Durchmesser erreichen konnte, nicht aus.

Aus Erdrutschen hervorgegangenes Material lag an der Oberfläche weiter Bereiche des LSCR. Dieses Material wies einen deutlich höheren Anteil an Feinmaterial auf als das Felssturzmaterial, überwiegend Sande, und außerdem Anzeichen fluviatilen Einflusses.

Das Grobmaterial bestand aus den gleichen lokalen Tiefengesteinen wie bei das Grobmaterial der Felsstürze, allerdings in kleineren Blöcken.

Im Zentrum des LSCR fand sich ein kleiner Bereich, dessen Oberflächenmaterial durch Ablagerung von Feinmaterial in einem kleinen Teich gebildet wurde. Dieses Oberflächenmaterial wird im folgenden limnisches Material genannt. Bereiche, in denen die Oberfläche ein enges Mosaik der Charakteristika von Felssturz- und Erdrutschmaterial aufwies, wurden als von Mosaikmaterial bedeckt bezeichnet. In den drei zusätzlichen Untersuchungsgebieten COQ, US und CHIL wurden nur Felssturz-, Erdrutsch- und Mosaikmaterial aufgefunden.

Das Verbreitungsmuster von *A. circinatum* in den Untersuchungsgebieten wurde maßgeblich von der Oberflächengeologie bestimmt. Über Flächen von mehreren hundert Quadratmetern bestimmte diese maßgeblich den Deckungsgrad und die Häufigkeit von *A. circinatum*. Hohe Häufigkeiten und insbesondere hohe Deckungsgrade von *A. circinatum* traten signifikant auf Felssturzmaterial auf, während niedrige Deckungsgrade und ein insgesamt selteneres Auftreten von *A. circinatum* signifikant mit Erdrutschmaterial verbunden waren. Niedrige Deckungsgrade von *A. circinatum* im LSCR traten nicht signifikant auch auf limnischem Material auf. Auf Mosaikmaterial fand sich die gesamte Bandbreite der Deckungsgrade von *A. circinatum*.

Im LSCR wurden auf allen Oberflächenmaterialien überwiegend saure Podsole mit lehmig-sandiger oder sandiger Textur gefunden. Dabei traten keine Unterschiede in Bodentyp, -pH oder -textur zwischen Standorten mit und Standorten ohne *A. circinatum* auf. Diese Bodeneigenschaften hatten also keinen Einfluss auf die Verbreitung von *A. circinatum.*

Der auffälligste Unterschied zwischen den Oberflächenmaterialen war der Anteil an Feinmaterial, invers als Skelettanteil gemessen. Zwischen dem Skelettanteil von Erdrutschmaterial und dem Skelettanteil von Felssturzmaterial bestand in allen Untersuchungsgebieten ein signifikanter Unterschied, der sich auf *A. circinatum* übertrug. Variationen des Skelettanteiles innerhalb eines Materiales blieben stets ohne Einfluss auf *A. circinatum*. Der erhöhte Skelettanteil war daher nicht Ursache des gehäuften Auftretens von *A. circinatum* auf Felssturzmaterial.

Eine gehäuftes Auftreten von *A. circinatum* auf Kolluvium und Alluvium oder spezifisch auf Felsschutt wird häufig in der Literatur erwähnt (UBC Botanical Garden 1976, Klinka et al. 1989, Haeussler et al. 1990, Klinka und Krajina 1986, Bailey und Poulton 1968, Oliver et al. 1985, Anderson 1967). Klinka und Krajina (1986) beschreiben *A. circinatum* als Teil der Primärsukzession auf Felsschutt. Die hohe Deckung von *A. circinatum* auf Felssturzmaterial in den vier Untersuchungsgebieten lässt sich wahrscheinlich darauf zurückführen, dass das Klimaxstadium eines von Nadelbäumen dominierten Waldes auf diesem Material erst in Teilbereichen erreicht wurde.

Durch seine Ansiedlung auf Felssturzmaterial verbessert *A. circinatum* das Mikroklima, fügt dem Boden Biomasse und Nährstoffe zu, hält mit seinen Wurzeln Feinmaterial fest (Haeussler et al. 1990, Tashe 1998, Russell 1974, Ogden 1996, McGhee 1996) und ermöglicht so schließlich die Ansiedlung der Nadelbäume der Klimaxvegetation. Im LSCR fanden sich auf Felssturzmaterial signifikant weniger Keimlinge der dominanten Nadelbäume als auf Erdrutschmaterial. Diese geringere Anzahl lässt vielleicht auf immer noch schlechte Wuchsbedingungen für Nadelbäume auf Felssturzmaterial schließen. Die hohe Präsenz von *A. circinatum* auf Felssturzmaterial kann ebenfalls zu der niedrigen Zahl von Koniferenkeimlingen beigetragen haben. Präsenz oder Deckungsgrad von *A. circinatum* hatten zwar keinen statistisch nachweisbaren Einfluss auf die Zahl der Koniferenkeimlinge, allerdings war dies möglicherweise durch hohe Schwankungen in der Zahl der Keimlinge bedingt.

3 Licht

Innerhalb der von der Oberflächengeologie gesetzten Grenzen erklärten andere Faktoren einen Teil der Schwankungen in der Häufigkeit und Deckung von *A. circinatum*. Diese Faktoren nahmen zumeist Einfluss in der Größenordnung einzelner Klone. Einer dieser Faktoren war die Stärke des Lichteinfalls.

Die innerklonale Demographie von *A. circinatum* wurde wenigstens zum Teil von der zugänglichen Lichtmenge bestimmt. Tote Äste konnten im Durchschnitt über signifikant weniger Licht verfügen als der nächste lebende Ast am gleichen Stamm. Ein absoluter minimaler Lichtbedarf für das Überleben von Zweigen konnte nicht gefunden werden.

Hohe Deckung (über 25 %) von *A. circinatum* war signifikant mit hohem Lichteinfall verbunden, geringe Deckung (unter 5 %) von *A. circinatum* signifikant mit geringem Lichteinfall. Der Lichteinfall an Standorten mit einer geringen Deckung von *A. circinatum* unterschied sich statistisch nicht von dem Lichteinfall an Standorten ohne *A. circinatum*.

Es bestand kein signifikanter Unterschied im Lichteinfall zwischen den Oberflächenmaterialien. Unterschiede im Lichteinfall können daher nicht für den starken Einfluss der Oberflächengeologie auf die Verbreitung von *A. circinatum* verantwortlich gemacht werden. Die großen Bestandeslücken auf Felssturzmaterial wurden allerdings in dieser Untersuchung nicht ausreichend berücksichtigt.

Die Auswirkungen des Lichteinfalls auf das Überleben und die Leistungsfähigkeit von Stämmen und ihrer Klone wurde ebenfalls untersucht. Die Fähigkeit zur sexuellen Reproduktion war bei Stämmen und ganzen Klonen an einen signifikant hohen Lichteinfall gebunden. Geringer Lichteinfall war mit dem Tod oder Niedergang von Stämmen und Klonen verbunden. Statistisch ließ sich dieser Zusammenhang allerdings wegen Ausreißern im Datensatz nicht nachweisen. Es bestand ein sehr schwacher linearer Zusammenhang ($r^2 = 0.065$) zwischen der Größe der Krone eines Klons und dem Lichteinfall. Die maximale Anzahl der kleinen (< 1,5 m) neuen Sprosse pro Klon wurde an Standorten mit geringerem Lichteinfall durch die verfügbare Lichtmenge begrenzt. Eine solche Begrenzung wäre ökologisch sinnvoll, um die Produktion neuer Sprosse an einem ungeeigneten Standort zu verhindern.

Sowohl die Anzahl der lebenden Stämme pro Klon als auch die Gesamtgrundfläche des Klons und die Dicke des Blattquerschnitts und der Mittelrippe äußerer Kronenblätter der untersuchten Stämme waren unabhängig von der Stärke des Lichteinfalls. Dies kann durch die relativ geringen Schwankungen des Lichteinfalls im LSCR bedingt gewesen sein.

Insbesondere in der älteren Literatur findet sich die Überzeugung, dass *A. circinatum* schattenintolerant ist (Bailey 1966, Drew 1968, Anderson 1967, Russell 1974 und Pojar und MacKinnon 1994). Andere Autoren bezeichnen *A. circinatum* als sehr schattentolerant, aber mit verbessertem Wachstum in Bestandeslücken (Haeussler et al. 1992, Tappeiner und Zasada 1993, UBC Botanical Garden 1976, O'Dea 1992). Zu diesem Ergebnis kommt auch diese Studie. Allerdings war erhöhter Lichteinfall und nicht die Präsenz von Bestandeslücken verantwortlich für Steigerungen in Deckungsgrad, Häufigkeit und Eigenschaften von *A. circinatum*. Lateraler Lichteinfall aufgrund der Hanglage des LSCR und die unregelmäßige Höhe der Baumkronen entkoppelten im LSCR den Lichteinfall von der Anordnung der dominanten Bäume am Wuchsort von *A. circinatum* (Canham et al. 1990, Spies et al. 1990). Daher zeigte sich auch die Deckung von *A. circinatum* unabhängig von der Dichte der dominanten Koniferen. Diese eignet sich daher nicht als Messmethode für den Lichteinfall.

Die Höhe des Lichteinfalls konnte nur einen Teil der Schwankungen in der Häufigkeit, der Deckung und in den Kloneigenschaften von *A. circinatum* erklären. Insbesondere bei hohem Lichteinfall ließ sich kein begrenzender Einfluss von Lichtmangel auf Kloneigenschaften von *A. circinatum* mehr feststellen. Wurzelkonkurrenz, pathogene Organismen oder Fraßfeinde könnten die verbleibenden Schwankungen erklären.

4 Grundwasser

Es ließ sich keine Zuordnung von *A. circinatum* zu trockeneren oder feuchteren Standorten vornehmen. Die Höhe des Grundwasserspiegels unterschied sich nicht zwischen Standorten mit *A. circinatum* und Standorten ohne *A. circinatum*. Die in der Literatur häufige erwähnte Beschränkung von *A. circinatum* auf frische bis nasse Standorte ließ sich daher nicht bestätigen (Pojar and MacKinnon 1994, Klinka et al. 1989, Krajina 1969, Klinka et al. 1985). Diese Beobachtung stimmt mit zahlreichen Beschreibungen von *A. circinatum* an Standorten, an denen zumindest im Sommer Wasserstress auftritt, überein (Haeussler et al. 1992, Anderson 1967, Roach 1952, Fonda und Bliss 1969, Russell 1974, Ohmann und Spies 1998).

Die im LSCR auftretenden Vegetationseinheiten waren ebenfalls unabhängig von der Höhe des Grundwasserspiegels. Da *A. circinatum* charakteristischer Teil der Vegetationseinheit war, die den Großteil des LSCR bedeckte, impliziert dies die Unabhängigkeit von *A. circinatum* vom Grundwasserspiegel.

Die Untersuchung der Vegetationseinheiten des LSCR ergab zusätzlich Hinweise auf andere Faktoren, die einen Einfluss auf A. circinatum ausübten. Eine Untereinheit der dominanten Vegetationseinheit mit zahlreichen Störungszeigern (Klinka and Krajina 1986) bedeckte weite Teile des Felssturzmaterials. Dies legt nahe, dass die starke Präsenz von *A. circinatum* auf Felssturzmaterial zumindest zum Teil noch sukzessionsbedingt war.

Eine denudierte Vegetationseinheit entstand auf Erdrutschmaterial aus kleinen Bereichen dichten Koniferenaufwuchses, der allen Unterwuchs unterdrücken kann (Anderson 1967). In dieser Vegetationseinheit fehlte auch *A. circinatum*. Zum Zeitpunkt der Messung reichten die Lichtverhältnisse in dieser Vegetationseinheit für ein Überleben von *A. circinatum* aus. Die Abwesenheit von *A. circinatum* an Standorten dieser Vegetationseinheit wurde daher von einem historischen Faktor bedingt.

5 Mikrotopographie

An größeren Bachläufe trat *A. circinatum* signifikant gehäuft auf, wie es oft in der Literatur beschrieben wird (Haeussler et al. 1990, Parish und Thomson 1994, Lyons und Merilees 1995, Pojar und MacKinnon 1994, Anderson 1967, UBC Botanical Garden 1976). Bei einer Stratifikation der Daten nach Oberflächengeologie blieb die Signifikanz nur für Erdrutschmaterial erhalten. Dies mag allerdings an dem geringeren Stichprobenumfang auf den anderen Oberflächenmaterialien gelegen haben. Es bestand kein Zusammenhang zwischen dem Deckungsgrad von *A. circinatum* und der Nähe zu größeren Bächen.

Das gehäufte Auftreten von *A. circinatum* an größeren Bachläufen lässt sich nicht durch einen erhöhten Wasserbedarf von *A. circinatum*, erklären, da die Verbreitung von *A. circinatum* unabhängig von der Höhe des Grundwasserspiegels war. Statt dessen ist wahrscheinlich ein erhöhter Lichteinfall entlang der Bachläufe für das verstärkte Auftreten von *A. circinatum* verantwortlich. Die Hangneigung hatte keinen Einfluss auf die Verbreitung oder den Deckungsgrad von *A. circinatum*.

6 Beharrungsvermögen und Prioritätseffekte von *A. circinatum*

Die Verhinderung der Ansiedelung anderer Organismen durch die Besetzung eines freien Raumes durch einen Organismus wird als Prioritätseffekt bezeichnet (Robinson and Edgemon 1988). *A. circinatum* kann Bestandeslücken (gaps) für zumindest 80 Jahre durch Prioritätseffekte freihalten (McGhee 1996). Im über 700 Jahre alten Bestand des LSCR konnte auf allen Oberflächenmaterialien eine Verzögerung der Schließung von Bestandeslücken durch die Anwesenheit von *A. circinatum* festgestellt werden. *A. circinatum* fand sich daher in der Mehrzahl der untersuchten Bestandeslücken. Die wahrscheinliche Ursache der Verzögerung ist eine Unterdrückung des Koniferenjungwuchses durch Beschattung, wie es von anderen Unterwuchsarten bekannt ist (Huenneke 1987, Beckage et al. 2000, Lorimer et al. 1994, Klinka et al. 1996a, Spies and Franklin 1989, Wardman 1997). Eine Unterdrückung von Koniferenkeimlingen durch die Austrocknung der Humusschicht durch *A. circinatum* ließ sich nicht nachweisen.

Eine vollständige Verhinderung der Schließung von Bestandeslücken durch *A. circinatum* konnte auf Erdrutschmaterial nicht festgestellt werden. Auf Felssturz- und Mosaikmaterial konnte die Existenz von Bestandeslücken, die nur aufgrund von Prioritätseffekten von *A. circinatum* bestanden, nicht ausgeschlossen werden. Bei diese Bestandeslücken könnte es sich um Reste eines von *A. circinatum* dominierten Sukzessionsstadiums auf

Felssturzmaterial handeln. Durch die versuchsweise Bestimmung des Alters eines Wurzelballens konnte keine größere Klarheit über das Beharrungsvermögen von *A. circinatum* am Standort gewonnen werden.

7 Rametenbildung durch Bewurzelung von Stammabschnitten

In geschlossenen Wäldern verbreitet sich *A. circinatum* fast ausschließlich vegetativ (O'Dea 1992). Da Stämme von *A. circinatum* zum Licht neigen und Stammabschnitte häufig in Neigungsrichtung einwurzeln (Anderson 1967, O'Dea 1992), könnte ein Klon durch die Bewurzelung von oberen Stammabschnitten in durchschnittlich 170 Jahren 10 m in Richtung günstigere Lichtverhältnisse „wandern" (Tappeiner and Alaback 1989). Verglichen mit der relativ statischen Verteilung der bis zu maximal 400 oder sogar 1000 Jahre alten Nadelbäume der küstennahen Regenwälder BCs (Waring and Franklin 1979) könnte die Rametenbildung durch Bewurzelung von Stammabschnitten eine gute evolutionäre Adaptation an das sich langsam aber konstant ändernde Mosaik des Koniferenwaldes darstellen.

8 Ausblick

Es ist gängige Forstpraxis *A. circinatum* nach Kahlschlägen aus den Beständen zu entfernen (Tashe 1998, Haeussler et al. 1990), da es durch dichte Gebüschbildung in Konkurrenz zu Koniferenjungwuchs treten kann. Hohe Deckung von *A. circinatum* und damit auch ein erhöhtes Risiko der Gebüschbildung trat vorwiegend auf Felssturzmaterial auf. Bei Kahlschlägen auf diesem Material besteht eine erhöhte Erosionsgefahr. Femel- oder Plenterschläge sollten sowohl die unerwünschte Ausbreitung von *A. circinatum* als auch eine Verminderung der Bodenfruchtbarkeit durch Erosion verhindern.

Auf Erdrutsch- und limnischem Material fanden sich vorwiegend verstreute kleine Klone von *A. circinatum*. Von diesen ist auch nach Kahlschlägen bei geeigneten Forstmaßnamen keine Gebüschbildung zu erwarten (O'Dea 1992). Wird *A. circinatum* im Bestand belassen, wird dadurch die Erosionsgefahr verringert, die Bodenfruchtbarkeit gesteigert und die Biodiversität des Standortes auf vielfältige Weise erhöht (Wardman 1997, Ogden 1996, Tashe 1998, Slaymaker 2000, McGhee 1996, Bailey und Poulton 1968, Singleton 1976, Miller 1968, Haeussler et al. 1990, Harding und McCullum 1994). Zumindest bei Douglasien ist dabei keine verringerte Bestockung zu erwarten (Wardman 1997). Daher sollte *A. circinatum* als wertvolle Komponente in forstliche Bewirtschaftungspläne aufgenommen werden.

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APPENDIX

Description and interpretation of measured sections not presented in detail in Results 2.1.

Section 6, located within the LSCR site:

0 - 60 cm below surface: Massive, loose, unsorted diamict with all particle sizes present. Distinct lower contact. Typical debris flow sediment.

60 - 65 cm below surface: dark-gray cobbly pebble gravel, matrix supported. Very compact. Some vague lenses of wavy bedding visible. Debris flow sediment identical to bed one section three.

Section 7, located within the LSCR site:

0 - 130 cm below surface: Dark gray cobbly pebble gravel, supported by silty sand matrix. Poorly sorted, some wavy beds of sand and granules. Compact. Debris flow sediment identical to bed one section three.

Section 8, Coquitlam site:

Granodiorite bedrock visible to a height of 20 m to the east of the section. The bottom 2.5 m of the section were obscured by loose rubble.

2.5 - 3.2 m from the level of the road: Cobbly pebble gravel, matrix supported. Very poorly sorted with some horizontal lenses of sand or pebbles. Compact matrix of silty fine to coarse sand. Clasts show random orientation, clasts granite, granodiorite and some volcanic rocks, mainly angular. Debris flow sediment.

3.2 - 4.3 m: Loose bouldery (boulders < 50 cm) cobble gravel, matrix supported, in places clast supported. Mainly sandy matrix. Very poorly sorted, random orientation, mainly granodiorite. Clasts predominantly subrounded. Lower boundary distinct, deposit draped over bed one. Debris flow sediment.

Ich möchte mich bedanken bei

Prof. Dr. Dietrich Hagen und Prof. Dr. Wolfgang Eber für die Jahre guter Zusammenarbeit, ihr starkes inhaltliches Interesse und ihre gute Betreuung auch aus der Ferne,

Prof. Dr. Margaret G. Schmidt dafür, dass sie diese Arbeit durch meine Aufnahme in ihre Arbeitsgruppe ermöglicht hat, für das interessante Thema, für ihre weitreichende finanzielle und materielle Unterstützung und ihre gute Betreuung während meines Aufenthaltes in Kanada,

Prof. Dr. Marie-Jose Fortin und Dr. Hans-Peter Bäumer für ihre Hilfe bei der statistischen Auswertung,

der Verwaltung des Department of Geographie, SFU, insbesondere Marcia Crease, für ihre weitreichende unbürokratische Hilfe,

Forest Renewal British Columbia für die Finanzierung dieser Arbeit,

dem Greater Vancouver Watershed District für Zugang zu den Untersuchungsgebieten, Kartenmaterial und sonstige Unterstützung,

den Squamish, Chilliwack und Sunshine Coast Forest Districts für Kartenmaterial,

Tasha, die mit mir Bären und *A. circinatum* ins Auge geschaut hat, Craig, der Rat in allen Lebenslagen wusste, und Shirley, die mir alles über Geologie beigebracht hat,

meinen Feldassistenten Anoja, Jon, Matthias, Laura, Eva und Darin für all die Arbeit bei Regen, Sonnenschein und im fensterlosen Labor,

den TA’s Sylvia, Anke und Dorothea für ihre Hilfe,

Elke, Jens, Martina, Ann und Karin für das Korrekturlesen,

meinen Eltern und meinem Bruder Paul für ihre Hilfe und Unterstützung,

und natürlich bei Christian, ohne den diese Arbeit nie geschrieben worden wäre.

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Erklärung

Hiermit versichere ich, dass ich die vorliegende Dissertation selbstständig verfasst und nur die angegebenen Quellen und Hilfsmittel verwendet habe.

Oldenburg, den 1. April 2002