A Study of Forest Understories in Two Parts: Community Structure of Forage Plants Consumed by Coastal Black Bears and Effects of Partial Cutting on Understory

by

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Abstract

Coastal British Columbia is the focus of conflict between timber extraction and protection of forest components such as forage plants consumed by black bears. To protect foraging habitat and to enhance forage plant abundance, researchers and managers must understand habitat requirements of these forage plants. Also, because forest managers increasingly use partial cutting as primary silvicultural treatment, forest managers must know how partial cutting affects the abundance of understory plants.

I assess the community structure of plants consumed by black bears in the Nimpkish Valley, British Columbia, with respect to environmental gradients. I also survey the literature for evidence about effects of pattern (spatial arrangement) and intensity (amount of timber removed) of partial cutting on understory species.

Non-metric multidimensional scaling (NMS) ordination revealed that variation in community structure of forage plants was related to soil nutrient and moisture content, elevation, and tree overstory dominance. Of these three factors, soil nutrient and moisture content were most strongly related to forage plant communities, while tree overstory dominance was the most weakly related factor. Species richness of forage plants and abundance of invasive forage plants generally increased with increasing soil nutrient and moisture content and with decreasing tree overstory dominance. Compared to invasive forage plants, residual forage plants did not respond consistently to any of the three factors revealed by the ordination. However, abundance of many residual forage plants was depressed where tree overstory dominance was high. To maintain the quality of foraging habitat, forest managers should: (1) prioritize for protection some forests with nutrient rich and moist soils; (2) ensure these forested sites are distributed across the biogeoclimatic variants occupied by black bears; (3) where harvesting occurs in these forested sites, avoid harvesting regimes resulting in large areas with a dense, structurally homogeneous tree cover.

The partial cutting literature revealed that short-term understory dynamics are a function of intensity and pattern of disturbance. Increasing the cutting intensity increases the short-term abundance of invasive species and decreases the abundance of forest-interior species. In the long-term, dispersed retention ameliorates the depauperate understory phase observed after crown closure in previous clearcuts.

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1. Introduction

The forests that occur along Canada's west coast are among the most productive conifer-growing sites in British Columbia, making them important areas for timber harvesting (Gagnon and Bradfield 1987, Hamilton et al. 1991, Meidinger and Pojar 1991, MacKinnon 2003). These coastal temperate rainforests have always been rare globally, and timber harvesting has further reduced their area (MacKinnon 2003). In addition to their economic value, coastal temperate rainforests support a myriad of species (Kohm and Franklin 1997). These species include a range of understory plants essential as forage for many wildlife species such as American black bears (*Ursus americanus*) (Hamilton 1987, Hamilton et al. 1991, Pojar et al. 1991).

Because of the potential conflict between timber management and wildlife habitat requirements (Bunnell et al. 1999), forest managers are challenged to increase the protection of foraging habitat and actively enhance the abundance of forage plants (e.g., Garcia 1985, Noyce and Coy 1990, Deal 2001, Stamp 2003). Many wildlife species, such as black bears, depend on a variety of herbs and shrubs to meet their dietary requirements (Noyce and Coy 1990, MacHutchon 1996, Bull et al. 2001). Conventional industrial forest management, such as clearcutting and subsequent management actions intended to establish the next tree harvest, often results in the short-term (e.g., Hamilton et al. 1991) and long-term decline of forest herbs and shrubs (Alaback 1982b, Deal 2001). Thus, managers are looking for ways to actively manage the abundance of herbs and shrubs consumed by wildlife species to maintain adequate amounts of foraging habitat.

To effectively manage foraging habitat, managers need baseline information on the patterns of abundance of forage plants across habitats (e.g., Stamp 2003). Patterns of abundance of all understory plants, including those important as forage for wildlife, are the result of complex multi-scale interactions of a range of biotic and environmental factors (Stewart 1988). It is not clear how these factors interact to shape abundance patterns of understory plants.

In the past, clearcutting has been the most common silvicultural system in coastal British Columbia (Beese et al. 2003). Recently, the inability of clearcutting to address a variety of ecological concerns, including the maintenance of wildlife forage, has led forest managers to increasingly propose silvicultural alternatives (Clayoquot Scientific Panel 1995, Franklin et al. 1997, Beaudry et al. 2001). I will refer to these alternative logging practices as partial cutting. Traditionally, partial cutting methods, such as the shelterwood and seed tree systems, focus primarily on the regeneration and growth of a new crop of trees (Franklin et al. 1997, Beese et al. 2003). Recent partial cutting strategies, not only consider timber objectives, but also accommodate a wide array of forest management goals, including the maintenance of non-timber resources such as wildlife forage (Arnott and Beese 1997, Kohm and Franklin 1997, Beese et al. 2003). Variable retention (Clayoquot Scientific Panel 1995, Mitchell and Beese 2002, Beese et al. 2003) is the most widely used partial cutting strategy used on the coast today (BC Ministry of Forests 2002).

Thus, to effectively maintain and enhance understory plants important as bear forage in managed forests on Canada's west coast, forest managers must understand both patterns of abundance of forage plants related to environmental gradients and the effects of partial cutting (and clearcutting) on the understory. The objective of my research project is to assess patterns of abundance of forage plants consumed by black bears in coastal temperate rainforests of the Nimpkish Valley, British Columbia. In addition, I survey the literature to examine the response of (all vascular) understory plants to partial cutting. In this literature review, I also emphasize the coastal temperate rainforests of British Columbia.

2. Ecological setting

Researchers classified the coastal temperate rainforests of western North America as the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991, Pojar et al. 1991, MacKinnon 2003). This zone occurs at low to middle elevations, mostly west of the Coast Mountains that extend north from Oregon, along the entire coast of Washington and British Columbia, and into Alaska (Meidinger and Pojar 1991, MacKinnon and Trofymow 1998). This zone has, on average, the greatest precipitation of the 14 biogeoclimatic zones in British Columbia (Pojar et al. 1991).

A characteristic feature of the vegetation in the CWH zone is an overwhelmingly coniferous tree overstory (Pojar et al. 1991, MacKinnon 2003). Characteristic of the tree overstory is the prominence of western hemlock (*Tsuga heterophylla*), which freely regenerates under mature stands on zonal sites and some azonal sites (Pojar et al. 1991). Other major tree species of the CWH are Douglas-fir (*Pseudotsuga menziesii*) on drier sites, Amabilis fir (*Abies amabilis*) at higher elevations, Sitka spruce (*Picea sitchensis*) on south-facing beaches and floodplains, and Western redcedar (*Thuja plicata*) south of 56° N latitude (Burns and Honkala 1990, Pojar et al. 1991, Pojar and MacKinnon 1994). Common deciduous species are red alder (*Alnus rubra*) on disturbed sites and black cottonwood (*Populus balsamifera*) on extensive riverine floodplains (Pojar et al. 1991).

3. Community structure of forage plants consumed by black bears in the Nimpkish Valley, British Columbia

Introduction

Influence of biotic and environmental factors on community structure of understory plants

A broad array of ecological factors interact at multiple scales to form the vegetation patterns in the forests of North America (Swanson et al. 1997, Wimberly and Spies 2001). Forested landscapes, at a scale of up to 20 000 hectares, contain communities of understory plants that are the result of complex interactions between deterministic and stochastic factors. These factors are related to characteristics of plant life history (Grime 1977, 1979, Noble and Slatyer 1980, Rabotnov 1986, Grime et al. 1988, Tilman 1988, McCook 1994, Noble and Habiba 1996, Grime 2001), site history, disturbance regime, and other biotic and environmental factors (Eis 1981, Haeussler and Coates 1986, Halpern 1988, Tilman 1988, Grace 1990, Karakatsoulis and Kimmins 1993). How do these multiple factors interact to shape the community structure of understory plants?

To extract dominant patterns from the complex multi-scale interactions that shape plant communities, researchers in British Columbia, Canada directed decades of effort into producing a Biogeoclimatic and Ecosystem Classification (BEC) system (e.g., Krajina 1965, 1969, Pojar et al. 1987, Meidinger and Pojar 1991, MacKinnon 1992, Green and Klinka 1994). Studies related to the BEC system emphasize 3 factors out of the numerous environmental factors affecting the community structure of understory plants. These 3 factors are climate, soil nutrient, and soil moisture content. Other studies in North America also emphasize 1 or more of these 3 environmental factors (e.g., Yarie

1980, Gagnon and Bradfield 1987, Spies 1991, Barton 1994, Arsenault and Bradfield 1995, Swanson et al. 1997, Brockway 1998, Ohmann and Spies 1998, Wimberly and Spies 2001, Ohmann and Gregory 2002, Chan et al. 2003). Unfortunately, the BEC system is limited by its inability to incorporate important dynamics affecting the community structure of understory plants such as temporal changes in species diversity after disturbance (i.e., forest succession).

In British Columbia and elsewhere, soil nutrients and moisture are often limiting to plant growth and productivity (Kozlowski 1972, Kramer and Kozlowski 1979, Haeussler and Coates 1986, Burns and Honkala 1990). Thus, species composition and abundance of plants in forested ecosystems often vary substantially along gradients of soil nutrient and moisture content (e.g., Haeussler and Coates 1986, Gagnon and Bradfield 1987, Klinka et al. 1989, Karakatsoulis and Kimmins 1993, Halpern and Spies 1995, Hutchinson et al. 1999). However, the complex interactions of biotic and environmental factors in forest ecosystems often confound relationships between community structure of understory plants and individual environmental gradients (e.g., see Ohmann and Spies 2001). Thus, relative to other biotic and environmental factors, it is not clear how important soil nutrient and moisture content are in determining the community structure of understory plants at the landscape scale.

At the landscape scale of up to 20 000 hectares, various environmental factors affect the micro- and meso- climates, which in turn affects the community structure of understory plants. In mountainous coastal areas, elevation and continental influence are often dominant factors that mediate the regional climate; thus, substantially affecting the community structure of understory plants (see Gagnon and Bradfield

1987, Klinka et al. 1989, Meidinger and Pojar 1991, Davis 1996). At the local scale, fine scale topographical characteristics, such as variations in slope and aspect, often further mediate the prevailing regional climate which further affects the plant community structure (Haeussler and Coates 1986, Klinka et al. 1989, Burns and Honkala 1990, Meidinger and Pojar 1991).

Disturbance and the resultant dynamics of forest succession add spatial and temporal variation to the community structure of understory plants. This variation is not accounted for in the BEC system at scales relevant to management of wildlife such as black bears. In this research project, I do not explicitly focus on the spatial dimension of forest succession. Abundant resources are provided for many herbs and shrubs in open, post-disturbance environments. However, after young forest stands reach canopy closure, the once abundant resources quickly diminish. This occurs because intermediate aged stands tend to have dense, fine-textured canopies which allow little light penetration (Wells 1996, Wells et al. 1998). Canopy closure during this intermediate period of stand development often temporarily results in depauperate understories with low overall abundance and species richness, especially on productive sites (Alaback 1982b, Oliver and Larson 1990, Halpern and Spies 1995, Wells 1996, Franklin et al. 2002). After forest stands reach maturity, various processes, such as the mortality of canopy dominants, initiate an increase in understory diversity and productivity in canopy gaps (Alaback 1982b, Alaback and Herman 1988, Franklin et al. 2002). Especially in coastal British Columbia, older stands usually have more canopy gaps than intermediate seral stages. These gaps allow more light to reach the forest floor and increase the diversity and abundance of understory species (Lertzman et al. 1996, Wells 1996, Franklin et al. 2002). Again, it is not clear how the dynamics associated with forest succession interact with other biotic and abiotic factors to shape the community structure of understory plants.

Life history strategies of understory plants

Many ecologists agree that complex successional pathways inherent to communities of understory plants can be conceptually simplified by grouping plant species according to similar life history strategies and autecological characteristics (Dyrness 1973, Connell and Slatyer 1977, Grime 1977, 1979, Noble and Slatyer 1980, Alaback 1982a, Pickett 1982, Rabotnov 1986, Grime et al. 1988, Tilman 1988, Grace 1990, see Wagner and Zasada 1991, Bazzaz 1996, Noble and Habiba 1996, Gitay and Noble 1997, Shugart 1997, Woodward and Kelly 1997, Platt and Connell 2003). One of the broadest classifications of life history strategies applicable to the forests of coastal British Columbia (Dyrness 1973) categorizes understory plants relative to their occurrence in undisturbed forests and disturbed areas. Invasive plant species (invasives) are either absent from the above-ground vegetation of undisturbed coniferous forests (but not necessarily from the below-ground seed bed) or restricted to strongly disturbed microsites, such as sites dominated by windthrow (Dyrness 1973, Schoonmaker and McKee 1988, Halpern 1989). Such disturbed microsites often contain a deciduous overstory (Dyrness 1973, Meidinger and Pojar 1991). Residual plant species (residuals) are present in undisturbed coniferous forests prior to disturbances, even if only in small quantities (Dyrness 1973, Halpern 1989). Invasives and residuals should be viewed as a continuum of diverse life history strategies, ranging from early-seral invasives, or ruderals, such as the annual *Senecio vulgaris* (see Grime 1977, Rabotnov 1986), to late-seral residuals, or forest-interior species, such as the perennial *Goodyera oblongifolia* (see Pojar and MacKinnon 1994, Halpern et al. 1999).

Ruderal invasives are predominantly adapted to conditions prevailing after intense, spatially-unpredictable disturbance (Grime 1977, 1979, Rabotnov 1986, Grime et al. 1988, Bazzaz 1996), as is often caused by harvesting systems with low (or no) dispersed and aggregated retention (Halpern and McKenzie 2001). Empirical evidence from clearcutting studies in the Oregon Cascades confirms that mature individuals of ruderal invasives mostly occur immediately after disturbance, rather than in undisturbed forests (Dyrness 1973, Schoonmaker and McKee 1988, Halpern 1989). Ruderals rarely depend upon vegetative propagation (Grime 1977, 1979); they usually either arrive after disturbance in the form of seeds capable of long distance dispersal, or else persist through the disturbance event as numerous long-lived seeds that would have occurred in the mature forest prior to disturbance (Grime 1977, Noble and Slatyer 1980, Bell 1991). Storing long-lived seeds in "soil banks" allows ruderals to rapidly exploit a site immediately after disturbance (see review in Oakley and Franklin 1998). Disturbance usually enhances germination of seeds from soil banks (Bazzaz 1996).

Ruderal invasives are particularly adapted to exploit the ephemeral period of low competition that immediately follows a disturbance event (Grime 1977, 1979, Noble and Slatyer 1980). These adaptations include fast growth rates, relatively small shoots, and rapid completion of the life cycle to allow quick and maximized seed production (Grime 1977, Rabotnov 1986, Campbell and Grime 1992). Early-successional plants such as ruderals are also able to drastically increase photosynthesis in response to increased light following intense disturbance (Bazzaz 1996).

However, adaptations to intense and frequent disturbance involves trade-offs. Many ruderal early-seral invasives do not compete well, do not tolerate shade-related stress, and rarely invest in vegetative propagation (Connell and Slatyer 1977, Grime 1977, Halpern 1989, Bell 1991, Bazzaz 1996). Vegetative propagation allows plants to compete in dense vegetation (Grime 1979). Consequently, ruderal invasives flourish immediately after disturbance when competition is low, but decrease in abundance after this initial period after disturbance (Grime 1979, Noble and Slatyer 1980, Halpern 1989). Following the initial period after disturbance, understory competition progressively intensifies (Noble and Slatyer 1980) until many understory species become (temporarily) suppressed by overstory crown closure (Franklin et al. 2002).

Late-seral, forest-interior residuals adopt life history strategies that contrast starkly to those of ruderal invasives. Late-seral residuals are especially adapted to forest-interior, late-successional environments (R species of Noble and Slatyer 1980, R5 species of Halpern 1989, Halpern et al. 1999), which are characterized by relatively low disturbance and limited light (patients of Ramenskii 1935, 1938 cited in Rabotnov 1986, stress tolerators of Grime 1977, Grime 1979, Bazzaz 1996). These adaptations include slow growth rates, evergreen habit, greater shade tolerance, and longer lived organs compared to ruderal invaders (Connell and Slatyer 1977, Grime 1977, 1979, Meier et al. 1995, Bazzaz 1996). Many forest-interior herbs also possess a higher proportion of below-ground biomass than early-seral species, indicating frequent below-ground vegetative propagation and nutrient storage capabilities (see citations in Lezberg et al. 1999).

Adaptations to late-seral environments also involve trade-offs. Late-seral, forest-interior residuals disperse propagules slowly, thereby requiring more time to grow to maturity than ruderals. These residual species are also typically unable to substantially increase photosynthesis in response to increased light (Grime 1977, 1979, Meier et al. 1995, Jules 1997, Jules 1999). Forest-interior species such as *Chimaphila umbellata* require the survival of (intact) individuals for vegetative propagation after disturbance (Halpern 1989). Thus, as empirical evidence in the Pacific Northwest and life history theory confirm, many late-seral forest interior species are not resilient to (logging) disturbance and require a long time to recover following disturbance (Connell and Slatyer 1977, Grime 1977, 1979, Schoonmaker and McKee 1988, Meier et al. 1995, Jules 1998, Halpern et al. 1999, Jules 1999).

The life history strategies of ruderal invasives and late-seral, forest interior residuals represent the extremes of a continuum of understory life history strategies (Grime 1977, see also Noble and Slatyer 1980, Rabotnov 1986). The life history strategies of most shrubs and herbs in coastal temperate rainforests of Canada's west coast occur somewhere between these two extremes (see for example the autecological descriptions in Haeussler and Coates 1986).

For example, the life history strategies of many invasive understory plants on Canada's west coast diverge substantially from the strategies described above for ruderal invasives. Although the competitive ability and shade tolerance of annual ruderals is often low (Grime 1977, 1979), the competitive ability and shade tolerance of many invasives often increases with increasing longevity (Grime 1977, Halpern 1989, Bell 1991, McCook 1994). As well, longer-lived perennial invasives often proliferate using vegetative regeneration in addition to seed-based regeneration (Grime 1979), in contrast to most annual ruderals. As described above, vegetative expansion enhances a species' ability to compete in dense vegetation (Grime 1979). Consequently, longer-lived invader species are often more abundant than annual ruderals (Grime 1979, Eis 1981, Schoonmaker and McKee 1988, Halpern 1989, Hannerz and Hanell 1993) during the increased competition following the initial period immediately after stand replacing disturbances such as clearcutting.

The life history strategies of many residuals diverge substantially from the "extreme" strategies described above for late-successional, forest-interior residuals. For example, residuals such as *Rubus ursinus* (a subordinate in the forest interior) and *Gaultheria shallon* (a forest understory dominant) are very tolerant to disturbance (Halpern 1989, Bunnell 1990, Coates et al. 1990, Tappeiner and Zasada 1993). Therefore, these "release herbs" often increase in abundance following clearcut harvesting (Haeussler and Coates 1986, Halpern 1989, Coates et al. 1990). Likewise, with greater light levels following complete canopy removal, many other residuals experience an initial decline, followed by an increase in abundance (Minore 1984, Haeussler and Coates 1986, Stewart 1988, Tappeiner and Alaback 1989, Bunnell 1990, Bell 1991, Lezberg et al. 1999).

The *mature* plants of invasives and residuals differ in their ability to integrate into the post-disturbance environment as biological legacies (Franklin et al. 2002). A characteristic of all invasives is that they usually only become established and reach maturity in the post-disturbance environments, not in undisturbed coniferous forests. In contrast, the *mature* plants of many residuals have the potential to integrate into the post-disturbance environment as biological legacies (Franklin et al. 2002), because mature residual plants are an integral component of the interior of forests prior to disturbance (some stress tolerators of Grime 1977, patience of Rabotnov 1986). As well, many residuals are relatively resilient to disturbance (see above).

Importance to management of black bear habitat

Ecosystems in coastal British Columbia, are amongst the most productive conifer-growing sites in British Columbia, making them important areas for timber harvesting (Gagnon and Bradfield 1987, Hamilton et al. 1991, Meidinger and Pojar 1991, MacKinnon 2003). In addition to their economic values, these forest ecosystems support understory plants essential as forage for American black bears (*Ursus americanus*) and grizzly bears (*Ursus arctos*) (Hamilton 1987, Hamilton et al. 1991, Nagy and MacHutchon 1991, Pojar et al. 1991).

Because of the potential conflict between timber management and wildlife habitat requirements (Bunnell et al. 1999), managers are challenged to increase protection of foraging habitat and actively enhance the abundance of forage plants (e.g., Garcia 1985, Noyce and Coy 1990, Deal 2001, Stamp 2003). There is an increasing need to understand habitat requirements of understory plant species consumed by wildlife species such as black bears. One question faced by managers is "should specific habitats be set aside to maintain the abundance of forage plants?" If the answer is yes, then we need to ask if different habitats are important for different groups of forage plants? Are there specific silvicultural prescriptions that aid to maintain or increase the long-term abundance of forage plants?

Studies concerned with the community structure of understory plants which focus on bear forage plants are rare. Thus, although in this study I focus on forage plants important to black bears, I use studies on forage plants important to grizzly bears as an additional source of information. In coastal British Columbia, many forage plants consumed by black bears are also consumed by grizzly bears (see MacHutchon 1996). Hence, researchers can make limited inferences for grizzly bear studies regarding patterns of abundance related to forage plants consumed by black bears.

In the past, researchers evaluated patterns of the abundance of black bear and grizzly bear forage plants in coastal British Columbia either by evaluating one plant species at a time (e.g., MacHutchon et al. 1993, see Noyce and Coy 1990 for a study outside of coastal British Columbia) or by simply evaluating the aggregated abundances of plant species (e.g. Stamp 2003). Although these approaches are appealing because they are simple, they are unlikely to resolve complex patterns among plant species across environmental gradients. Neither of these approaches permits evaluation of the integrated response of communities as a whole. Such an integrated analysis of community structure (species composition and abundance) is desirable because assessing one species at a time makes it difficult to evaluate the combined response of a group of forage species to several environmental factors (see McCune and Grace 2002). Furthermore, both of these univariate approaches do not reflect the interactions among plant species in responding to environmental factors. Consequently, these approaches sacrifice ecological insight and statistical power (see McCune and Grace 2002). I am not aware of a single study that directly quantified the relative strength and nature of the relationships between community structure of forage plants consumed by black bears (or grizzly bears) and various abiotic and biotic factors.

Objectives

In this research project, I use a multivariate approach to assess patterns of abundance of forage plants. My objective is to examine the species composition and abundance (community structure) of invasive and residual plant species consumed by black bears in the western variant of the very dry maritime Coastal Western Hemlock zone (CWHxm2), the submontane and montane variants of the very wet maritime Coastal Western Hemlock subzone (CWHvm1 and CWHvm2 respectively) (Pojar et al. 1987, Meidinger and Pojar 1991). Specifically, I will describe the nature and strength of the relationships between the community structure of these forage plants and various environmental gradients and environmental units (e.g., site series and structural stages). Results from my analyses are important because they will help managers to maintain and enhance the abundance of forage plants.

Methods

Origin of the data and sample design

I based my analysis on data collected in the Nimpkish Valley located approximately 40 km south of Port McNeill on northern Vancouver Island, British Columbia, Canada, 50°27′ latitude, 127° 06′ longitude (Figure 1). Davis (1996) collected the data to assess the array of forest stands available to black bears for denning. Her study area covered 20 000 ha, encompassing the home ranges of 21 radio-collared black bears including spring and breeding ranges. Over a period of 4 years, she collected all data based on random point sampling (Marcum and Loftsgaarden 1980). Davis (1996) classified 170 randomly located plots by site series and structural stage and measured a full range of vegetation and stand structural attributes in these plots. Of these 170 plots, I was able to include 133 in my analysis (see details below).

Davis (1996) performed vegetation inventories using 20 by 20 meter plots (Lutmerding et al. 1990). Within these plots, she collected abiotic data such as elevation as well as percentage cover data on plant species in all vegetation layers ranging from the moss layer to the dominant tree layer. To estimate stocking density of live and dead trees, she established prism cruise plots with a variable radius (Bull et al. 1990) at the centre of each vegetation plot. Within the prism cruise plots she measured the mean diameter at breast height, restricting her measurements to live and dead trees with a diameter at breast height greater than 17.5 cm. From these data, she estimated mean basal area of trees per hectare.

Plot location and terrain

In British Columbia, terrestrial ecosystems are classified using the hierarchical Biogeoclimatic Ecosystem Classification (BEC) systems (Pojar et al. 1987, Meidinger and Pojar 1991, MacKinnon 1992). Climate is an important determinant of the nature of terrestrial ecosystems (Meidinger and Pojar 1991). Thus, within the BEC system, ecosystems are classified at the biogeoclimatic zone level to reflect variation in regional climate. Zones are further divided into biogeoclimatic subzones to reflect climatic differences within a zone. Subzones can still contain considerable climatic variation and are often further subdivided into biogeoclimatic variants.

I limited my analysis to Davis' plots located in the Coastal Western Hemlock (CWH) biogeoclimatic zone representing three biogeoclimatic variants. Thus, I excluded 13 of the 170 random plots from my analysis, because these plots were not located in the CWH zone. After further data screening, I excluded 24 of the remaining 157 plots from the analysis (see details below). 86 of the remaining 133 plots used in the analysis were located in the western very dry maritime variant (CWHxm2). The CWHxm2 occurs in valley bottoms usually below 400 meters elevation. 26 plots were located in the very wet submontane variant (CWHvm1) and 21 plots in the montane variant (CWHvm2) of the CWH zone. The CWHvm1 variant occurs above the CWHxm2 variant to about 600 meters elevation, and the CWHvm2 variant occurs above the CWHvm1 variant to about 800 meters elevation (Green and Klinka 1994) (see Figure 1). The topography and land forms of the study area are typical of the Northern Island ecosection of the West Vancouver Island ecoregion (Demarchi 1995). The mean annual precipitation over a 15-year period at Woss (approximately 20 kilometers southeast of the study area) ranged from 180 to 295 cm (mean = 229 cm) (Rochele 1980). The precipitation between April and September accounted for only 23 % of the total annual precipitation (Rochele 1980).

The study area represents a range of disturbance histories and forest structural stages. The study area is located within Tree Farm License # 37 which, at the time of data collecting, contained second growth stands up to 70 years old (Davis 1996). Recent disturbances in the study area included prescribed burns, wildfires, windthrow, juvenile spacing, thinning, as well as planted regeneration.

I grouped plots into structural stages based on a seral classification system frequently used for describing ecosystems in British Columbia, Canada (BC Ministry of Environment Lands and Parks and Ministry of Forests 1998). This "provincial" classification of structural stages is comparable to other classifications but omits various distinct stages of stand development (see Table 1). At the time of sampling, 42 plots were located in the Shrub/Herb stage, 14 plots were located in the Pole/Sapling stage, 34 plots were located in the Young Forest stage, 25 plots were located in the Mature Forest stage, and 18 plots were located in the Old Forest structural stage.

Construction of the data sets and outlier analysis

Plots-by-species matrix

I constructed a plots-by-species matrix containing percentage cover of plant species consumed by black bears in the CWH zone. This plot-by-species matrix contained 133 plots by 28 species. In collaboration with T. Hamilton (Species specialist, British Columbia Ministry of Water, Land and Air protection) and based on a comprehensive compilation of plants consumed by black bears in the CWH zone (MacHutchon 1996), I developed the list of forage plants included in this study. Because no information on *preferred* forage species was available, I did not distinguish preferred forage species in my analyses.

Various data manipulations, including transformation of the raw data into the Daubermire cover scale (Daubenmire 1959), substantially improved the data distribution. For the final plots-by-species matrix, I chose to log-transform the percentage cover data, because this transformation most effectively reduced the influence of multivariate outliers and reduced the coefficient of variation (see Tabachnik and Fidell 1989, Zar 1999, Tabachnik and Fidell 2001). Log-transformation also decreases the influence of the dominant species on the data analysis (see van der Maarel 1979).

After further data screening, I excluded 24 of the 157 plots located in the CWH zone from the analysis. To reduce the noise in the data set, I excluded the relatively few plots (19 out of 157) located in previously thinned and spaced stands. I also deleted 5 multivariate outlier plots with a compositional dissimilarity greater than 2.3 standard deviations from the average (McCune and Grace 2002). Such outliers have a disproportional large influence on multivariate analyses (Tabachnik and Fidell 2001, McCune and Grace 2002). The sample units with multivariate outliers all represented "high" elevation locations (above 800 meters) within the Old Forest structural stage, leaving only 2 high elevation sample units within this structural stage. Thus, the remaining 133 plots do not allow generalizations with respect to high elevation locations within the Old Forest structural stage.

"Environmental" matrix

I constructed an environmental matrix (plots-by-environmental variables) consisting of categorical and quantitative variables. These variables included environmental data and forest mensuration data. The environmental data consisted of data on elevation and soil nutrient and moisture conditions (Table 2). Forest mensuration data consisted of data on percentage canopy cover of trees, stocking density, diameter at breast height (1.3 m), and basal area of live and dead trees (Table 2).

To assess the variation in the summed abundances of forage species, I appended a plots-by-traits matrix to the environmental matrix.

In this plots-by-traits matrix, I summarized percentage cover values of forage plants by trait, season of consumption, functional group membership, and indicator status (Table 2). I tabulated data on the autecological characteristics of forage species from the literature (Table 3). I classified species as either residuals or invaders based on existing classifications (Dyrness 1973, Dyrness et al. 1974, Halpern 1988, Schoonmaker and McKee 1988, Halpern 1989, Halpern et al. 1992a) or based on autecological accounts (Grime 1977, 1979, Bierzychudek 1982, Grime et al. 1988, Klinka et al. 1989, Coates et al. 1990, Haeussler et al. 1990, Lieffers and Stadt 1994, Pojar and MacKinnon 1994, Willson and Hennon 1997, Haeussler et al. 1999). I constructed the plots-by-traits matrix as follows: I constructed a species-by-traits matrix consisting of grouping variables (1 = "trait membership", 0 = no "trait membership") (see McCune and Grace 2002). Then, I transposed this matrix of species-by-traits to multiply the transposed matrix with a plots-by-species matrix containing raw species cover values expressed as percentages.

To reduce the variation and skewness in the environmental matrix, I log-transformed all variables in this matrix with a skewness greater than 1.1 (see Maarel 1979, Zar 1999, Limpert et al. 2001, McCune and Grace 2002) This transformation also substantially reduced the number and influence of univariate outliers in the environmental matrix.

Species diversity measures

I calculated diversity measures for all plants, for all bear forage plants, and for bear forage plants across various environmental units. Unfortunately, I was not able to differentiate between individual species of the *Gramminae, Carex, Fragaria, Salix,* and *Equisetum* species groups. I calculated *Alpha* diversity as the average species richness per plot and *Beta* diversity, or the amount of species compositional change, as the total number of observed forage species divided by *Alpha* diversity (McCune et al. 2000, Deal 2001). Where possible I used parametric tests to determine differences in *Alpha* diversity of bear forage species in environmental units. However, where I observed high heteroscedasticity in variance among groups I used non-parametric tests. Whenever I used the Mann-Whitney U test for multiple comparisons, I checked for significance using the sequential Bonferroni correction (Rice 1989, Wells 1996).

Multivariate analyses

To analyze patterns of abundance and species composition (community structure) of forage plants consumed by black bears, I performed non-metric multidimensional scaling (NMS) ordination (Kruskal 1964, Mather 1976) on the plots-by-species matrix. NMS is especially suited for ecological data sets because the method is robust to large numbers of zero values and does not assume multivariate normality (Fasham 1977, Clarke 1993, Pitkanen 1997, McCune and Mefford 1999, Peterson and McCune 2001). Furthermore, the method works well with data on arbitrary or discontinuous scales as commonly observed in community ecology (McCune and Grace 2002). Unlike certain other ordination methods such as Canonical Correspondence Analysis (CCA), NMS is an unconstrained method in the sense that it does not attempt to maximize correlation with the environmental matrix. Thus, correlations with environmental factors are exclusively based on similarities in community structure of the forage plants.

NMS iteratively searches for a global stress minima. A stable solution is accepted if the same minimum stress configuration is achieved from several different starting configurations (Kruskal 1964, Anderson 1971, Kruskal and Wish 1978, Kenkel and Orloci 1986, Pitkanen 1997). Stress in this study is the derivation from the monotone relationship between the original dissimilarity matrix and the derived distance matrix (Kruskal 1964, Kruskal and Wish 1978). Distances in the original dissimilarity matrix are best measures as Sorenson's (Bray-Curtis) distances because this measure best deals with the peculiarities of ecological community data (Beals 1984, McCune and Mefford 1999). I performed the ordination using Sorenson's distance measure, a random starting configuration, 100 runs with the real data, a stability criterion of 0.0007 and 20 iterations with this criterion (see McCune and Mefford 1999, Peterson and McCune 2001, McCune and Grace 2002). To further ascertain that the ordination avoids local minima, I also ran the ordination once with initial configurations derived from Bray-Curtis ordination (see Deal 2001, Peterson and McCune 2001, McCune and Grace 2002).

I chose the 3 dimensional solution as the final solution because it represented the highest variability in the community data on the fewest number of axes. Fewer axes would have increased the stress between the original dissimilarity matrix and the derived distance matrix to unacceptable levels (see Clarke 1993). Additional axes would have spread the important variation in the data over too many axes to produce interpretable results and would have only resulted in small additional reductions in stress. I performed a Monte Carlo test with 50 randomized runs to ensure that the ordination extracted stronger axes than expected by chance (probability that equal or lower stress could have been obtained by chance < 0.05). I rigidly rotated the ordination maximizing the loading of strongest explanatory variable with axis 1. I evaluated the relationships of "environmental" variables with the ordination axis using Pearson's r^2 and scatter plots of species abundance in relation to ordination axis scores (see McCune and Grace 2002).

To test if plots in various environmental units (such as site series and structural stages) occupy different regions in species space (i.e., to test if these units contain different communities of forage plants), I used the non-parametric Multi Response Permutation Procedure (MRPP) (Mielke 1984, Zimmerman et al. 1985) on the rank-transformed Sorensen's distance matrix. MRPP is similar in purpose to the t-test and one way analysis of variance, but compared to these univariate methods, it is much more relaxed with respect to requirements on the data structure and is readily applied to multivariate problems (Zimmerman et al. 1985). I chose to rank-transform the Sorensen's distance matrix to enhance the correspondence of the MRPP results with the NMS results (see McCune and Grace 2002). The A statistic in this non-metric MRPP is a measure of the "chance-corrected within group agreement". If $A = 0$, community structure is no different from that expected by chance. When $A = 1$, sample units are completely homogeneous within each group. In community ecology, even groups that are significantly different often result in an $A < 0.1$; an $A > 0.3$ is high (McCune et al. 2000, McCune and Grace 2002).

Finally, I used Indicator Species Analysis (Dufrene and Legendre 1997) on a plots-by-species matrix containing raw species cover values to contrast performance of individual forage species across environmental units. I evaluated the significance of indicator values based on a Monte Carlo test with 10,000 runs. While MRPP tests for differences between various environmental units, indicator species analysis complements the MRPP results by showing *how* various environmental units are different (e.g., McCune et al. 2002). The indicator value (IV) of a species is the species' relative abundance multiplied by its relative frequency multiplied by 100. Relative abundance is a species' average abundance in plots within a given environmental unit divided by its average abundance in all plots. Relative frequency is the proportion of plots in which the species occurs within an environmental unit.

I used various software packages for the analyses. For error checking the raw data, I used Vpro97 (MacKenzie and Klassen 1999), for all univariate analyses I used SPSS version 10.0 (SPSS Inc. 1999), and for all multivariate analyses I used PC-ORD version 4 (McCune and Mefford 1999).

Results

Summary of autecological literature on bear forage plants

Based on a review of the autecological literature (Pojar et al. 1984, Klinka et al. 1989, Meidinger et al. 2002)), of the 28 bear forage plants found in the study area, 15 are often invasive and 13 are often residual plants (see Table 3). Most of these forage plants indicate specific soil nutrient and/or moisture conditions (see Table 3). Fourteen forage plants are known indicators of nutrient rich soils. Eight of these 14 indicator plants are often invasive. Five forage plants are indicative of nutrient medium sites. Three of these 5 plants are often invasive. Finally, 14 forage plants are indicative of fresh to wet soils and 5 of these 14 are often invasive (Klinka et al. 1989, Meidinger et al. 2002, see Table 3 for details).

The invasive forage plants found in the study area range from very shade intolerant to shade tolerant / intolerant, whereas residual forage plants are mostly shade tolerant and some are shade tolerant / intolerant (see Table 3). The measure of shade tolerance used here is based on five relative qualitative classes ranging from very shade tolerant to very shade intolerant (see Klinka et al. 1989). Four (out of the 15) invasive forage plants represent one extreme on the continuum of shade tolerance of bear forage plants because these 4 plants are very shade intolerant or shade intolerant. Five (out of 13) residual forage plants represent the other extreme on this continuum because these residuals are shade tolerant. Most other invasive and residual forage plants cluster in the middle of the continuum of shade tolerance because they are shade tolerant / intolerant.

Species diversity

The 133 plots sampled in the study area yielded a total of 136 plant species of which 28 species are consumed by black bears (see Table 4). *Alpha* diversity (average species richness per plot) of all bear forage plants was 4.8 (n = 133, sd=2.6). *Alpha* diversity of invasive forage plants was 2.0 (n=133, sd=2.0) and of residual plants was 2.8 (n=133, sd=1.3) (Table 4).

Alpha diversity of bear forage plants differed across various environmental units (Table 4). Variation in *Alpha* diversity was strongly related to nutrient class (Mann-Whitney U test, $p < 0.001$), moisture class (one-way ANOVA, df=2, 130; F=17.0; $p < 0.001$), and structural stage (Kruskal-Wallis test, df=4, 128; H=41.500; $p < 0.001$), but less to biogeoclimatic variant (Kruskal-Wallis test, $\alpha > 0.001$, df=2, 130; H=12.156; p=0.002). *Alpha* diversity was highest in the high nutrient and moisture class (Mann-Whitney U test for nutrient classes, $p<0.001$, Tukey's HSD for moisture classes, $p<0.001$).

Across structural stages, *Alpha* diversity was higher in the youngest structural stage than in the intermediate aged structural stages (Table 4, Figure 2). *Alpha* diversity in the Shrub/Herb structural stage was not significantly different from the Pole/Sapling structural stage (Mann-Whitney U test, $p=0.413$). In contrast, *Alpha* diversity in the Shrub/Herb structural stage was significantly different from the Young Forest and Mature Forest structural stages (Mann-Whitney U test, $p<0.001$). After the sequential Bonferroni correction (Rice 1989), *Alpha* diversity in the Shrub/Herb structural stages was still significantly different from the Old Forest structural stage at $\alpha > 0.05$ but not at $\alpha > 0.001$ (Mann-Whitney U test, $p=0.002$).

Beta diversity, or the amount of species compositional change, also differed across various environmental units (Table 4, Figure 2). *Beta* diversity of all bear forage species combined was 5.9 ($n = 133$). *Beta* diversity of forage species divided into various environmental units was consistently lower than the combined *Beta* diversity, except for the Young Forest and Mature Forest structural stages (Table 4). With respect to species richness, these two structural stages were more heterogeneous than all other environmental units.

Gradients extracted by the ordination

The ordination accounted for 84.8 % of the variation in the data set with 35.2%, 27.6%, and 22.0% of the variation loaded on axes 1, 2, and 3 respectively. The first axis expressed a gradient of increasing soil nutrient and moisture content. Plots in nutrient rich and moist sites mostly concentrated on the right side of axis 1, whereas nutrient poor and dry sites concentrated on the left side of axis 1 (Figure 3 A, B). My interpretation of axis 1 was strengthened by the positive correlation of the summed abundance (measured as percentage cover) of bear forage species that are indicators of nutrient rich and moist sites with axis 1 ($r^2 = 0.594$ and 0.658 respectively, both $p < 0.001$) (Figure 4 A, B). The weaker second axis was strongly related to an altitudinal gradient as shown by the correlation with plot elevation ($r^2 = 0.676$, $p < 0.001$) (Figure 4 A).

The third axis was weakest and was strongly related to increasing dominance and contiguity of the tree overstory as shown by the increase of various measures of overstory abundance such as total tree cover and basal area per ha of stems with a diameter greater than 17.5 cm (all $r^2 > 0.200$, all $p < 0.001$) (Figure 4 B, C). My interpretation of axis 3 was strengthened by the negative correlation of the summed abundance of shade intolerant forage species with the gradient of overstory dominance ($r^2 = 0.223$, $p < 0.001$).

Patterns of abundance of various forage plant groups in relation to environmental gradients

The summed abundance (measured as percentage cover) of bear forage plants in various assemblages and overall species diversity correlated with the ordination. The summed abundance of all bear forage plants increased with decreasing dominance and contiguity of the tree overstory, mostly independently of the other 2 ordination gradients (i.e., axis 2 and 3)($r^2 > 0.200$ and $p < 0.001$ for each) (Figure 5). Species richness increased with decreasing dominance and contiguity of the tree overstory and increasing soil nutrient and moisture content, mostly independently of the gradient related to elevation ($r^2 > 0.200$, $p < 0.001$). Nevertheless, although species richness did not strongly correlate with the gradient related to elevation (where $r^2 > 0.200$ and $p < 0.001$), species richness roughly followed a unimodal pattern on this gradient (Figure 6). Thus, species richness was slightly elevated in plots at medium elevations.

Invasive forage plants responded strongly to the gradient related to the tree overstory. The summed abundance of all invasive plants and invasive shrubs (particularly *Rubus* sp.) increased with decreasing dominance and contiguity of the tree overstory and increasing soil nutrient and moisture content, mostly independently of the gradient related to elevation ($r^2 > 0.200$, $p < 0.001$ for each) (Figure 5). The summed abundance of invasive forbs increased with decreasing dominance and contiguity of the tree overstory mostly independently of the other 2 ordination gradients (i.e., axis 2 and 3)($r^2 > 0.200$ and $p < 0.001$). The summed abundance of all graminoids increased with increasing soil nutrient and moisture content mostly independently of the other two ordination gradients ($r^2 > 0.200$, $p < 0.001$). Nevertheless, the summed abundance of all graminoids was also depressed in plots located on the right side of the gradient related to the tree overstory, where the tree overstory was very dominant (Figure 7). As well, the summed abundance of all invasive plants, invasive shrubs, and graminoids was depressed in plots located on the right side of the gradient related to elevation, where elevation was highest (Figure 6).

Contrary to the summed abundance of all invasive forage plants, the summed abundance of all residual forage plants did not correlate strongly with the ordination (Figure 5). However, the summed abundance of all residuals was depressed in plots falling on the right side of the gradient related to the tree overstory (Figure 8). To investigate if further patterns of abundance existed for all residual plants, I overlaid the proportional (summed) abundance of all residual plants on the ordination. The proportional (summed) abundance of all residuals is the (summed) abundance of all residual forage plants divided by the (summed) abundance of all forage plants (see Table 2). The proportional (summed) abundance of all residual forage plants increased with increasing overstory gradient and with decreasing soil nutrient/moisture content mostly independently of increasing elevation ($r^2 > 0.200$, $p < 0.001$, Figure 5 A, B). However, the number of plots with low proportional abundance of residuals decreased roughly with increasing elevation (Figure 9).

Some residual forage plants also correlated with the ordination as individuals or in sub-assemblages (i.e., assemblages of residuals less than the assemblage of all residuals). All *Vaccinium* forage species responded strongly to increasing elevation. *Vaccinium parvifolium* decreased with increasing elevation mostly independently of the other two ordination gradients ($r^2 > 0.200$, $p < 0.001$, Figure 5 A, C). In contrast, the summed abundance of all other *Vaccinium* species (excluding *Vaccinium parvifolium*) *increased* with increasing elevation mostly independently of the other two ordination gradients ($r^2 > 0.200$, $p < 0.001$, Figure 5 A, C). But, the summed abundance of all *Vaccinium* species (including *Vaccinium parvifolium*) roughly followed a unimodal pattern on the gradient related to the tree overstory (Figure 8). Thus the abundance of all *Vaccinium* species was depressed at the extremes of this gradient.

Other residual forage plants responded mostly to increasing soil nutrient and moisture content. The abundance of ferns and *Trautvetteria caroliniensis* increased with increasing soil nutrient and moisture content, mostly independently of the other 2 ordination gradients ($r^2 > 0.200$, $p < 0.001$, Figure 5 A). But, the abundance of the fern *Dryopteris expansa* was somewhat depressed in plots located on the left of the gradient related to elevation, where elevation was low (Figure 10). *Gaultheria shallon* increased in abundance with decreasing soil nutrient and moisture content mostly independently of the other 2 ordination gradients ($r^2 > 0.200$, $p < 0.001$, Figure 5). However, the abundance of *Gaultheria shallon* was depressed in plots located on the right of the gradient related to the tree overstory, where the tree overstory was very dominant (Figure 11). None of the other residual forage plants, either as individuals or in sub-assemblages, correlated strongly (i.e., $r^2 > 0.200$, $p < 0.001$) with the ordination.

Patterns of abundance of forage plants grouped by season of consumption in relation to environmental gradients

The summed abundance of forage plants grouped by season of consumption responded strongly to the three main environmental gradients (where strong is $r^2 > 0.200$ and $p < 0.001$; Figure 12). The abundance of forage plants with foliage important as spring forage increased with increasing soil nutrient and moisture content and elevation and decreasing overstory dominance and contiguity ($r^2 > 0.200$ and $p < 0.001$). The abundance of forage plants with foliage important as fall forage increased with both increasing soil nutrient and moisture content and increasing elevation ($r^2 > 0.200$ and $p < 0.001$). The abundance of both forage plants with foliage important as summer forage and forage plants with fruits important as summer forage increased with decreasing overstory dominance and contiguity ($r^2 > 0.200$ and $p < 0.001$ for each). The overlay of summed abundances of forage species on the ordination did not reveal any strong (i.e. $r^2 > 0.200$ and $p < 0.001$) patterns of abundance for any other forage groups.

Patterns of abundance of forage plants with respect to environmental units

I used Multi Response Permutation Procedure (MRPP) to test *if* various environmental units, such as site series, contained bear forage plants with different community structure (i.e. species composition and abundance). I complemented the MRPP results with results from the indicator species analysis to show *how* various environmental units were different (see McCune and Grace 2002). Furthermore, I used results from the MRPP and indicator species analysis to confirm and complement ordination results and results from the univariate analyses.

The ordination showed that plots roughly arranged according to the soil nutrient and moisture regime (Figure 3 A, B). Plots in various nutrient and moisture classes also differed in *Alpha* diversity (see results in the section on species diversity above). Of all environmental units included in my analyses, plots grouped by site series achieved the highest MRPP effect size or A statistic (i.e. the species composition and abundance of bear forage plants differed the most across site series) (Table 5). Site series indicates the soil nutrient and moisture regime at a given site (Meidinger and Pojar 1991). Indicator species analysis revealed that many bear forage plants were significantly associated with plots in nutrient rich and / or moist sites (Table 6). Only *Gaultheria shallon* was significantly associated with both nutrient poor and dry sites (Table 6). Those *Vaccinium* species that are of minor importance as bear forage were also significantly associated with dry sites (Table 6).

Along the altitudinal gradient represented by axis 2 of the ordination, plots roughly clustered together according to variants (see Figure 3 C). Although, *Alpha* diversity in the 3 variants did not differ (Kruskal-Wallis test, $\alpha > 0.001$, df=2, 130; H=12.156; p=0.002), MRPP results confirmed that the 3 variants in the study area have a distinctly different community structure with respect to bear forage species (MRPP, A = 0.208, $p \ll 0.001$). The performance (i.e. relative abundance multiplied by frequency) of *Gaultheria shallon, Vaccinium parvifolium,* and *Rubus ursinus* was best within the CWHxm2 variant (Table 6). Other *Rubus* sp., *Epilobium angustifolium, Trautvetteria caroliniensis,* and *Oplopanax horridus* performed best within the CWHvm1 variant (Table 3). *Vaccinium* species (excluding *Vaccinium parvifolium*) performed best in the "higher elevation" CWHvm2 variant (Table 6).

Along the gradient of increasing dominance and contiguity of the tree overstory (i.e., along axis 3 of the ordination), plots roughly separated by structural stage. Plots in the "youngest" structural stage (i.e. the Shrub/Herb structural stage) concentrated in the lower portion of axis 3 (Figure 4 C). Relative to plots of the Shrub/Herb structural stage, plots of the Young Forest and Mature Forest concentrated more in the upper portion and plots in the Old Forest structural stage more in the middle portion of this axis. Plots in various structural stages also differed in *Alpha* diversity (Kruskal-Wallis test, df=4, 128; H=41.500; p<0.001, Table 2). However, especially plots of the Young Forest and Mature Forest structural stage extended over a wide range of axis 3, which confirms that plots within these structural stages have a high species compositional change (Table 2). Thus, along axis 3 of the ordination, there was some overlap between various structural stages (see arrows in Figure 4 C).

MRPP results partially confirmed that plots in different structural stage contained different communities of bear forage plants. In the CWHxm2 and vm1 variants, plots grouped by structural stage differed in the species composition and abundance of bear forage plants (A = 0.136, 0.267 respectively, $p < 0.001$ each) (Table 5). However, in CWHvm2 variant, plots grouped by structural stage did not differ in species composition and abundance of bear forage plants ($\alpha > 0.05$, A = 0.015, p = 0.363).

Multiple MRPP comparison confirmed further differences between plots in various structural stages in the CWHxm2 and vm1 variants (Table 7). The species composition and abundance of bear forage plants did not differ significantly between plots in the Pole/Sapling structural stage and plots in the Shrub/Herb structural stage ($\alpha > 0.05$; A = 0.028, p = 0.066). In contrast, the species composition and abundance of bear forage plants in the Young forest and Mature forest structural stages increasingly and significantly differed from the Shrub/Herb structural stage (A = 0.112, 0.141 respectively, $p << 0.001$ for both) (Table 7). Compared to the Mature Forest structural stage, the species composition and abundance of bear forage plants in the Old Forest structural stage was more similar, but still significantly distinct from the Shrub/Herb structural stage (A = 0.128, $p < 0.001$). However, these MRPP results must be treated cautiously because the sampling design did not permit blocking for the effects of soil nutrient and moisture content and elevation.

Indicator species analysis revealed *how* plots in the CWHxm2 and CWHvm1 variant differed by structural stage. None of the forage species were significantly associated with the Young Forest and Mature Forest structural stages (Table 6). Except for the fern *Dryopteris expansa*, all forage species with a significant association for the Shrub/Herb or Pole/Sapling structural stage were invasive species. All forage species significantly associated with the Old Forest structural stage were residuals (Table 6).

Discussion

Overall trends derived from existing literature on bear forage plants

Variation in community structure of forest plants in the study area was largely (84.8%) related to 3 environmental gradients (Figures 2, 3). Of these 3 gradients, the gradient of soil nutrient and moisture content explained most (35.2%) of the variation in community structure of forage plants (see Figure 13 for a summary of selected results related to this gradient). The altitudinal gradient explained 27.6%, and the gradient of increasing dominance and contiguity of the tree overstory explained 22.0% of the variation in community structure of forage plants (see Figures 14, 15, and 16 for a summary of selected results related to these gradients). Species richness of forage plants and the abundance of invasive forage plants increased with increasing soil nutrient and moisture content and with decreasing dominance and contiguity of the tree overstory (see Figures 5, 13, 15). In contrast to the abundance of invasive forage plants, the abundance of residual forage plants did not respond consistently to any of the 3 environmental gradients (see Figure 5), but was depressed where the tree overstory was very dominant (Figures 8, 11). Invasive forage plants generally performed best early on in forest succession, whereas residual forage plants performed best much later on in forest succession (see Table 6, Figure 16). None of the forage plants performed well during intermediate stages of forest succession (i.e.

Young Forest and Mature Forest structural stages). Average species richness (*Alpha* diversity) of forage plants was also depressed during intermediate stages of forest succession (see Table 3).

My results confirm the little knowledge currently available on patterns of abundance of groups of forage plants important to black bears and grizzly bears. Researchers in British Columbia and elsewhere identified sites with high precipitation (Koehler and Pierce 2003), sites rich in soil nutrients, wetlands and other sites high in soil moisture (MacHutchon et al. 1993, Stamp 2003), and sites lacking a dense tree cover (Zager 1980, Martin 1983, Bratkovich 1985, MacHutchon et al. 1993, Hammer 1996) as habitats with a high abundance of bear forage plants. Confirming these results, my ordination analysis indicates that nutrient rich and moist sites and sites with an open tree canopy support habitats with a high abundance of understory plants important to black bears. I did not have a direct measure of precipitation in my study, but the high affinity of many forage plants for soil moisture (Table 4, 6) very roughly confirm a positive response of these forage plants to an increase in available water.

Relationship between community structure of forage plants and dominance of the tree overstory

Dominance of tree overstory as surrogate for conditions in the understory

According to our present understanding of landscape dynamics in forested areas in coastal British Columbia, the prevailing disturbance regime substantially affects the structure of the tree overstory (Lertzman et al. 1996, Spies 1997, Lertzman et al. 2002, Gavin et al. 2003a, Gavin et al. 2003b). The coastal temperate rainforests of British Columbia are noted for the near-absence of recent fires and the dominance of a late seral forests in unmanaged landscapes (Gavin et al. 2003b). In these late seral forests, small gap-forming disturbances substantially affect the structure of the tree overstory (Lertzman et al. 1996). Changes in the structure of the tree overstory substantially affect the development of understory plants (e.g., Alaback 1982a, Klinka 1985, Halpern 1989, Huffman et al. 1994, Klinka et al. 1996, Hanley and Brady 1997, Franklin et al. 2002). My results confirm for the study area that the community structure of forage plants is responsive to changes in the structure of the tree overstory. Although the gradient related to the tree overstory was the weakest of the 3 main factors affecting community structure of forage plants, the total abundance of forage plants and particularly the abundance of invasive forage plants was consistently negatively correlated with this gradient (Figure 5). Species richness of forage plants was also negatively affected by this gradient (Figure 5).

Studies in coastal British Columbia and elsewhere demonstrate that the interception of light by the overstory canopy has a significant impact on the development of certain understory plants (Alaback 1982a, Stewart 1988, Haeussler et al. 1990, Lieffers and Stadt 1994, Klinka et al. 1996, Hanley and Brady 1997, McKenzie et al. 2000, Roburn 2003). Low levels of understory light are associated with minimal understory growth, whereas high levels of understory light are associated with increased understory growth, berry production, and sexual reproduction (Stewart 1988, Tappeiner and Alaback 1989, Bunnell 1990, Haeussler et al. 1990, Huffman et al. 1994, Klinka et al. 1996).

However, studies of succession in managed and unmanaged forests suggest that the degree of overstory dominance is not just a surrogate for the level of understory light. For example, in some mature forests in western Washington, various measures related to the degree of overstory dominance were surrogates of understory dynamics directly dependent on time (McKenzie et al. 2000). Studies of succession after partial removal of the tree canopy in coastal British Columbia and elsewhere suggest, that during initial stages of stand development, the degree of overstory dominance is a surrogate for the degree of understory light (Drever and Lertzman 2003) as well as ground disturbance (Halpern and McKenzie 2001, Vanha-Majamaa and Jalonen 2001). The degree of ground disturbance in turn substantially effects the understory development (Halpern and McKenzie 2001, Roberts and Zhu 2002). Life-history theory emphasizes the substantial effect of disturbance on understory development. For example, many invasives depend on the period of minimal competition for resources immediately after disturbance to be able to establish and mature (Grime 1977, 1979, Noble and Slatyer 1980, Platt and Connell 2003). Nevertheless, it is not clear if these overstory-understory relationships related to partial cutting apply to unmanaged forests.

Differences in response of invasives and residuals to increasing dominance of tree overstory

Few studies have explicitly examined the differential responses of invasives and residuals to increasing dominance of the tree overstory. Thus, I used papers from studies of succession in managed forests as the main sources of information about the response of invasives and residuals to increasing dominance of the tree overstory. In my study, invasive forage plants responded positively to increasing canopy openness and decreasing dominance of the overstory. These findings are consistent with research on understory plant succession after complete removal of the tree canopy in mature and old-growth western hemlock and Douglas-fir forests in western Washington and Oregon (Dyrness 1973, Halpern 1988, Schoonmaker and McKee 1988, Halpern 1989, Halpern and Spies 1995). In these studies, invasives became established and increased in abundance within several growing seasons after complete removal of the tree canopy. Short-lived invasive herbs, then invasive shrubs, and finally residual shrubs dominated throughout the initial period after the disturbance (Schoonmaker and McKee 1988). Relative to residuals, invasive herbs and shrubs are more adapted to early seral conditions (Grime 1979). Thus, invasives will likely profit the most from disturbances that open up the tree canopy if such disturbances also substantially reduce the competition for resources in the understory (Noble and Slatyer 1980, Grime et al. 1988, Halpern 1989).

My results on the response of invasives to increasing dominance of the tree overstory are comparable to findings from partial cutting studies. Research on forest succession after partial cutting in Douglas-fir dominated forests in Oregon and Washington predicted that the abundance and diversity of invasives would decrease with increased levels of retained tree cover (Halpern et al. 1999). Empirical support for this hypothesis comes from a partial cutting study in Sweden. The study in Sweden found that shelterwood treatments (reduction from 650 trees/ha to 200 and 140 trees/ha) in mature spruce stands exhibited less increase in invasives than in clearcuts (Hannerz and Hanell 1993, see also section 4). As noted above, the level of retention of the tree overstory affects both the level of ground disturbance and understory light. Again, it is not clear how much these findings from partial cutting studies apply to unmanaged forests.

Except for *Vaccinium* species, residuals in my study area did not respond negatively to increasing canopy openness and contiguity (see Figures 5, 8). Also, the abundance of residuals was depressed were the tree overstory was very dominant (Figures 8, 11). The lack of a pronounced negative response of residuals to a very open tree canopy indicates that many of the residuals in my study area are located in the middle of the continuum of life history strategies ranging from early-seral invasives to late-seral residuals. Accordingly, none of the residual forage plants observed in the Nimpkish Valley are dependent on the forest-interior and / or late-successional conditions. Autecological descriptions show that many of these residuals benefit from increased light associated with decreased dominance of the tree overstory and some are relatively resistant to various disturbances (see Alaback 1982b, Minore 1984, Klinka et al. 1989, Coates et al. 1990, Pojar and MacKinnon 1994, also see introduction). After complete removal of the tree overstory in mature and old-growth forests in western Washington and Oregon, the abundance of many residuals also recovered to pre-disturbance levels prior to tree canopy closure, indicating that many residuals in these forests are also relatively resistant to disturbance (Schoonmaker and McKee 1988, Halpern and Spies 1995). However, intensive disturbance during canopy removal delayed the recovery of some of these residuals (Halpern and Spies 1995, see also Minore 1984).

There is some indication that *Vaccinium* forage species in the Nimpkish Valley are relatively sensitive to disturbance. Relative to the summed abundance of all residual forage species, the abundance of *Vaccinium* forage species was depressed at very low levels of dominance and contiguity of the tree overstory, presumably where ground disturbance is high (see Figure 8). As well, although the autecological literature indicates that most residuals experience an initial (temporary) decline *immediately* after disturbance (see introduction), I was not able to detect such a decline for most residuals because my data did not include plots in the Sparse/Bryoid and Herb structural stages. These two structural stages are the initial structural stages after disturbance.

I expected the abundance of most residual forage plants (when measured as a proportion of the total abundance of forage plants) to increase with increasing tree overstory dominance and contiguity. Compared to residuals, invasive plants do not grow well in undisturbed forests (Dyrness 1973, Halpern 1989). Thus, increasing tree overstory dominance and contiguity should represent more of a competitive exclusion gradient for invasive rather than residual forage plants. Ordination results and indicator species analysis confirmed this expectation: the summed proportional abundance of residual forage plants increased with increasing tree overstory dominance and contiguity (Figure 5). Invasive species performed the best in the Shrub/Herb structural stage (Table 6), which presumably provided much less competition from the overstory than did the older stages.

Relationship between community structure of forage plants and distinct structural stages

Many ecologists agree that patterns of change in forest structure can be associated with recognizable stages of forest development (e.g., Franklin 1982, Spies and Franklin 1988, Oliver and Larson 1990, Wells 1996, Franklin et al. 2002). My results partially confirmed that the community structure of forage plants differs across structural stages. The Shrub/Herb structural stage had a higher species richness than most other structural stages (Table 3). In the CWHxm2 and CWHvm1 variant, the community structure of forage plants in the Shrub/Herb structural stage differed distinctly from most other structural stages but differed the most from the intermediate aged structural stages (Table 7, Figure 4C). None of the forage plants had an affinity for structural stages of intermediate age (i.e. the Young Forest and Mature Forest structural stages).

A gradient analysis in the CWH zone in the Fraser Valley and on southern Vancouver Island also reported significant differences in the species composition of understory plants between young structural stages without dominant tree cover and all other structural stages (Klinka et al. 1985). Although Klinka et al. (1985) did not explicitly distinguish between invasives and residuals, I noted that their results showed that invasives such as *Epilobium angustifolium* had a higher affinity for the two youngest structural stages when compared to all other structural stages. None of the residual vascular plants had a higher affinity for the two youngest structural stages when compared to all other structural stages. According to Klinka et al. (1985), a species has a relative affinity for a structural stage if such a species is diagnostic of one or more structural stages according to classification system proposed by Mueller-Dombois and Ellenberg (1974). Confirming the results of Klinka et al. (1985) for forage plants, my results show that except for one residual, invasive forage plants performed best in the structural stages with the least dominant tree overstory (i.e. Shrub/Herb and Pole/Sapling structural stage) (Table 6). Indicator species analysis also confirmed the suggestion of Klinka et al. (1985) that the abundance of understory species generally was suppressed during intermediate stages of forest succession (see Table 6). Klinka et al. (1985) also noted that individual structural stages did often not contain distinct communities of understory plants.

There are several explanations why plots in different structural stages were often not distinct with respect to community structure of forage plants. First, life history theory dictates that multiple successional pathways are possible (Noble and Slatyer 1980) for sites in the same structural stage (Klinka 1985, Hamilton 1988). Deterministic and stochastic factors related to timing and intensity of ground disturbance, availability of propagules, and other biotic and environmental factors affect the successional pathway at a given site (Noble and Slatyer 1980, Pickett et al. 1987, Schoonmaker and McKee 1988). Although plots in my study often originated from different disturbances, I was not able to account for differences related to disturbance history. Differences in disturbance history likely caused communities of forage plants in different plots of the same structural stage to follow somewhat different successional trajectories.

Second, the model of structural stages used in my analysis does not reflect certain distinct stages of forest development. For my analysis I adopted a model of structural stages developed by the British Columbia Ministry of Environment, Lands and Parks and the Ministry of Forests (1998) which is partially based on a model proposed by Oliver and Larson (1990) (Table 1). Except for the initiating disturbance, canopy closure is the most dramatic developmental stage in rate and degree of change in stand condition and thus causes significant shifts in composition and function of forest ecosystems (Franklin et al. 2002). These significant shifts cause major environmental changes in the understory (Franklin et al. 2002). Neither the Provincial model (BC Ministry of Environment Lands and Parks and Ministry of Forests 1998) nor Oliver and Larson (1990) explicitly account for canopy closure. There are other distinct developmental stages not accounted for in the Provincial model (see Table

1). Therefore, it is not surprising that structural stages did often not clearly separate along the axis of increasing dominance of the tree overstory (see overlap of arrows in Figure 4 C).

Finally, the legacy effect (Franklin et al. 1997, Franklin et al. 2002) likely blurs otherwise apparent differences in the community structure of forage plants expected along the continuum related to the tree overstory. To explain this "blurring" phenomenon, I first explain why, without the legacy effect, I expect certain differences in the community structure of forage plants in different structural stages. The continuum related to the tree overstory represents more of a competitive exclusion gradient for invasive than for residual forage plants (see discussion above, see also Figure 4). In addition, the total abundance of forage plants is inversely related to increasing dominance and contiguity of the tree overstory (Figure 5). Thus, it is likely that the community structure of forage plants is fundamentally different at the extremes of this continuum. With respect to dominance of the tree overstory, young and intermediate aged structural stages represent extremes. From an understory plant's perspective, young structural stages have the least - and intermediate aged structural stages have the most dominant tree overstory (see the introduction). Simply based on the continuum related to overstory structure I would thus expect the community structure of forage plants in intermediate aged structural stages to be the most dissimilar from the youngest structural stages.

However, arranged along a temporal axis, young and intermediate aged structural stages are not separated but are adjacent (Table 1). We can thus expect a legacy effect related to understory development during the young structural stage to be present in the intermediate structural stage

(Franklin et al. 2002). Although most invasives do not survive as the tree canopy closes in a forest, some invasives in such a forest may survive on disturbed microsites (Dyrness 1973). As well, as noted above, various residual forage plants are at an intermediate position on the continuum of life history strategies. These residuals often establish themselves before closure of the tree canopy and also often survive this phase of forest development, even if only in a suppressed state (e.g., Bunnell 1990, Halpern et al. 1999). Researchers in Douglas-fir dominated forests in Oregon and Washington also observed that although understory species changed significantly in their abundance in various structural stages, many understory species occurred in all structural stages (Halpern and Spies 1995). The legacy effect likely blurs otherwise apparent differences in communities of forage plants in various structural stages.

Relationship between community structure of forage plants and soil nutrient and moisture content

In the study area, the soil nutrient/ moisture content is the most important determinant of the community structure of forage plants. Accordingly, the strongest variation in community structure of forage plants occurred along a gradient of increasing soil nutrient and moisture content. More forage species occurred on richer and moister sites, and most species performed best (i.e. had a significant and maximum indicator value) at sites with elevated nutrient and moisture content (Figure 5, Table 6). In particular, invasive species consistently increased in abundance with increasing soil nutrient and moisture content (Figure 5). These results are consistent with the autecological literature on these species. Again, of the 28 forage plants occurring within the home ranges of black bears in the Nimpkish Valley, 14 are known indicators of nutrient rich soils, 5 of nutrient medium sites, and 14 of fresh to wet soils (Klinka et al. 1989, Meidinger et al. 2002, see Table 1 for details).

Although my results do not clearly reveal whether the forage plants in the study area responded more to changes in soil nutrients or soil moisture, the autecological literature indicates that most forage plants respond positively to both of these environmental factors (Taylor and MacBryde 1977, Haeussler and Coates 1986, Klinka et al. 1989, Haeussler et al. 1990, Meidinger et al. 2002). Of the 20 plants indicative of fresh to wet soils and of nutrient medium or rich soils, only 5 plants are *not* known indicators of both increased soil nutrient and moisture content (Table 4). Furthermore, except for the *Vaccinium* forage species, forage plants that are known indicators of fresh soils or soils with higher moisture content are also known indicators of nutrient medium or rich soils. The literature further suggests that most of those forage plants that do not have a recorded indicator status with respect to soil nutrient or moisture content often perform better on richer and moister sites (see Taylor and MacBryde 1977, Coates et al. 1990, Pojar and MacKinnon 1994).

However, compared to the group of invasive forage plants, the residual forage plants as a group did not respond as homogeneously to the soil nutrient and moisture gradient or any of the other main gradients (Figure 5). A more heterogeneous response of these residuals agrees with the autecological literature. The affinities of these species for nutrients and moisture are more heterogeneous than those of the invasive forage plants. Accordingly, the group of residual forage plants includes plants with affinities for nutrient rich and moist sites as well as several plants with affinities for nutrient poor and / or dryer sites (Table 4).

The fundamental differences in life history strategy between invasives and residuals also explain why invasives responded more consistently to the gradient of increasing soil nutrient and moisture content than residuals. Residual forage plants are contrary to invasive forage plants not restricted to forests with an open tree canopy (Dyrness et al. 1974, Halpern 1989). For the proportion of the residuals on sites with a dominant tree overstory, light is probably more limiting than soil nutrient/ moisture content. Hence, those residuals in environments with low light levels do likely not express a strong response to the gradient of increasing soil nutrient and moisture content.

Relationship between community structure of forage plants and elevation

Effects related to elevation were the sources of the second most variation in community structure of forage plants. Elevation is a complex gradient that covaries with various factors (Ohmann and Spies 1998). For example, due to orthographic uplifting, precipitation in form of rain and snow often increases with elevation (Lavender et al. 1990). Temperature often decreases with elevation (Lavender et al. 1990). Both, temperature and precipitation substantially affect the community of understory plants (e.g., Klinka et al. 1989). In addition to climatic factors, other historical and environmental factors such as soil chemistry also change with changes in elevation (Ohmann and Spies 1998).

Forage plants differed in their response to the altitudinal gradient. *Dryopteris expansa* was less abundant at lower elevations (Figure 10). *Vaccinium* species important as bear forage responded strongly to elevation, and, except for *Vaccinium parvifolium,* all *Vaccinium* species performed best in the higher elevation CWHvm2 variant (Figure 5, Table 6). In contrast, all other forage species (with a significant indicator value) performed best in the CWHxm2 or CWHvm1 variant (Table 6). Also, many invasives were less abundant at higher elevations (Figure 6, see also Figure 9). These results confirm knowledge about the autecology of these species in that many bear forage plants do not have a great affinity for "high" elevations (Klinka et al. 1989, Pojar and MacKinnon 1994, see details in Table 1).

Relationship between community structure of forage plants and various environmental units

Researchers and managers often divide the landscape into smaller environmental units, such as site series and structural stages, to capture groups of (bear forage) plants distinct in abundance and species composition. Thus, it is important to know which dividing criteria are best suited to produce distinct environmental units. The ordination revealed 3 environmental gradients that largely (84. 8% of the variation in the data set) determine the patterns of species composition and abundance of bear forage plants (Figures 3, 4, 5). Thus, I expect that partitioning the landscape across these three environmental gradients likely results in environmental units with more distinct plant communities than if the landscape is not portioned across these gradients.

Unfortunately, the sampling effort in my study was too low to partition the landscape across these three environmental gradients (i.e. the soil moisture / nutrient gradient, altitudinal gradient, and gradient of increasing tree overstory dominance and contiguity). Nevertheless, my results showed that, of the units evaluated in my study, those units that reflected the variance associated with the two strongest ordination gradients produced the most distinct groups of forage plants (see Table 5). These units - site series - likely capture distinct communities of bear forage plants because these units account for the effects of changes in soil nutrient and moisture content and elevation (i.e. the strongest ordination gradients).

Davis (1996) combined site series into Black Bear Habitat Types (BBHTs) to reduce the number of categories. These BBHTs were site series combined across and within variants based on similarities in moisture and nutrient regimes (see Davis 1996). My results revealed that BBHTs produced less distinct groups of forage plants than site series, probably in part because not all BBHTs distinguish between variants (i.e. between differences in elevation, the second strongest ordination gradient) (Table 5).

Both site series and various structural stages in the CWHxm2 and CWHvm1 variants contained distinct units of forage plants (see Table 5) and together reflect each of the ordination gradients. Thus, I suspect that, at least in lower elevation variants, further differentiating site series into structural stages captures even more distinct units with respect to bear forage plants. Unfortunately the sampling effort was too low to evaluate this idea.

Management implications

My results indicate that active management and / or protection of appropriate areas could maintain or increase the abundance of forage plants in landscapes similar to the home ranges of black bears in the CWH zone of the Nimpkish Valley. If achieved with minor soil disturbance, harvesting regimes ranging from clearcutting with much of the harvested area near the surrounding forest, to low to medium levels of retention (Arnott and Beese 1997, Beese and Bryant 1999, Mitchell and Beese 2002) are likely to increase the short-term abundance of invasive forage plants (before tree crown closure). There would be an initial decline immediately after harvest, but then many residual forage plants would increase to or surpass their pre-disturbance levels of abundance. As mentioned above none of the residual forage plants are forest-interior species dependent on forest-interior or late-successional conditions. However, this benefit from timber harvesting is lost with canopy closure (e.g., Alaback 1982a, Franklin et al. 2002). Thus, to the extent that black bear habitat is a management priority, tree canopy closure should be delayed as long as possible, in addition to avoiding vegetation management treatments intended to establish and manage the next tree harvest.

After harvesting, residuals will likely recover faster in "clearcuts" and retention systems if much of the harvested area close to the surrounding forest or retained patches of forest. Residuals use the surrounding forest as a source of propagules for re-colonizing the harvested areas. An underlying premise of variable retention is that retained forest patches provide habitat islands and a source of propagules for dispersing organisms (Franklin et al. 1997). I am not aware that this premise has been tested for residual forage plants, but presumably, forest aggregates would serve as "stepping-stones" for residual forage plants re-colonizing the harvested area.

To improve quality of foraging habitat in the long-term, forest managers should avoid harvesting regimes resulting in large areas with a dense, structurally homogeneous tree cover, such as typically develops 15-

45 years after clearcutting. In the absence of other management actions intended to establish and manage the next tree harvest, in the short-term, clearcutting and harvesting at short rotations convert forest stands to an early structural stage which is productive with respect to bear forage. However, in the medium-term, this increases the proportion of forest stands with a homogeneous, contiguous overstory (Deal 2001, Franklin et al. 2002). Such forest stands of intermediate age and development often contain a depauperate understory (Alaback 1982a, Wells 1996). Under normal industrial forest management practice, these stands would dominate the landscape (Lertzman et al. 1997). Alternative harvesting regimes likely improve the long-term quality of foraging habitat because they provide a more heterogeneous overstory and thus more heterogeneous understory light levels (see section 4, Franklin et al. 1997, Drever and Lertzman 2003). Such alternative harvesting regimes are not limited to lengthening the rotation interval, but include retaining variable quantities of various stand components as biological legacies (Franklin et al. 2002).

Most importantly, to improve the quality of foraging habitat in the long-term, forest managers should avoid or minimize harvesting in both nutrient rich and moist areas. Where harvesting in such nutrient rich and moist areas is unavoidable, managers should avoid harvesting regimes that result in large areas with a dense, structurally homogeneous tree cover. To prevent the development of such a dense tree overstory after harvesting, managers should retain some of these areas in forest patches. When it is desirable to maintain the abundance of certain residual forage plants such as *Vaccinium* species and *Gaultheria shallon*, managers should also set aside and actively manage areas with less soil nutrient and moisture content (see Figure 5, Table 4 for plants with affinities for low soil nutrient and moisture content).

Forest managers should set aside and actively manage foraging habitat throughout the range of elevations and variants in the CWH zone. Higher elevation areas, particularly in the CWHvm2 variant represent important habitat for many forage plants with foliage consumed in the fall (see Figure 12). However, lower elevation areas are important for most other forage plants (see Table 3, 6).

Forest managers should vary the intensity of protection and active management efforts over time and space. For example, in areas where bear foods are not limiting, management prescriptions aimed to increase the abundance of bear foods can be relaxed. In areas where bear foods are limiting, management prescriptions aimed to preserve existing feeding sites and to increase the abundance of bear foods should be emphasized.

For areas similar to my study area, I established a set of guidelines aimed to maintain or increase the short-term (prior to tree crown closure) and long-term (after tree crown closure) seasonal availability of forage plants (see Table 8). In general, forest managers best maintain and increase the seasonal availability of forage by focusing their active management and protection efforts on three criteria: the soil nutrient/ moisture regime, elevation, and harvesting regime.

Table 8 should be used as follows. First, choose one or more management objective(s). Second, choose one or more forage plant group(s) on which to apply the objectives. Third, as described in italics next to each management objective, identify the correct guidelines for the chosen objective(s). Finally, identify the correct yes / no sequence appropriate for the chosen combination of forage plant group(s) and management objective(s). For example, assume the manager desires protection of foraging habitat consisting of forage plants with foliage that is important for consumption in the fall. The correct yes / no sequence for the desired objective for this forage plant group would be yes, yes[c]. The first yes in this sequence signifies that sites with higher soil nutrient and moisture content are more important for protection than sites with lower soil nutrient and moisture content. The second yes signifies that sites for protection should be chosen so that all elevations / variants are represented, but the protection of higher elevation sites (especially those in the CWHvm2 variant) should be emphasized. Because the management guidelines described in Table 8 are, in part, based on findings that are the least likely to extend to a broad spectrum of forests, these prescriptions only apply to areas similar to the study area. However, similar approaches could be devised for other regions if local knowledge of the ecosystem is used to assess sites based on community structure of forage plants.

Limitations of study

The study area boundaries encompassed the home ranges of black bears in the Nimpkish Valley (see Davis 1996). Thus, inferences beyond the home ranges of these bears must be made cautiously. To extend these conclusions to these three variants over their entire distribution in the CWH zone requires more geographically extensive data collection.

I was unable to include plots located in the Sparse/Bryoid and Herb structural stages or within other non-forested areas in my analysis.

Thus, the gradients extracted in this study do not reflect the variation represented in such potentially very important foraging areas.

Future work

When managing the availability of bear forage plants, managers have little guidance for choosing an adequate spatial resolution. For example, it is often not clear if it is ecologically sensible to manage for a forage plant group at very fine resolution such as at the level of site series modifier or to manage at a much coarser resolution such as at the level of the BBHT. Dufrene and Legendre's (1997) indicator species analysis can aid managers in finding such an appropriate resolution.

Accordingly, indicator species analysis can be used to find the environmental unit most congruent with the ecological amplitude of a group of species. If the sum of indicator values of a given group of forage plants is plotted for successive levels of hierarchical management units (e.g., variant, BBHT, site series, site modifier), then, the most appropriate resolution can be determined. For a given forage group, this resolution is where the summed indicator value for the forage group is at a maximum (see Dufrene and Legendre 1997 for details on this method, see also McCune and Grace 2002). Of course, ecological considerations other than those related to the ecological amplitude of a species may cause a manager to still use a resolution different from the one suggested by this method.

As part of adaptive management, researchers and managers should establish long-term monitoring plots to confirm and complement my findings. Forest development after disturbance has long-term effects on understory plant communities (e.g., Deal 2001, Franklin et al. 2002). This long-term monitoring is needed to confirm the relationship between forest seral dynamics and community structure of forage plants. In particular, the long-term effects of conventional and alternative harvesting regimes on forest seral dynamics and thus on the community structure of forage plants need to be examined further.

Researchers and managers should sample the full range of variation of forage plant communities within the CWH zone in the Nimpkish Valley and elsewhere including wetlands, non-forested areas, and very young structural stages. Such a sampling effort enables researchers and managers to determine whether my findings can be generalized beyond the study area and extrapolated to the rest of the CWH zone. To be effective, sampling must be based on a stratified, balanced, and random design.

In future analyses, researchers and managers should integrate information on differences in the forage value of forage plants. Although the dietary value of forage plants often differs among individual plants and seasons, I was unable to include information on these differences. Once an importance rating for forage plants is established, it can be easily integrated into future analyses and management recommendation by adding a weighting factor to abundance values of forage plants.

4. Effects of partial cutting on community structure of understory plants (emphasizing the Coastal Western Hemlock Biogeoclimatic zone)

Introduction

Ecosystems within the Coastal Western Hemlock (CWH) biogeoclimatic zone (Meidinger and Pojar 1991, Green and Klinka 1994) are among the most productive conifer-growing sites in British Columbia, and thus, they are important areas for timber harvest (Hamilton et al. 1991, MacKinnon 2003). As well, these forest ecosystems support understory plants essential as forage for grizzly (*Ursus arctos*) and black bears (*Ursus americanus*) (Hamilton 1987, Hamilton et al. 1991, Nagy and MacHutchon 1991, Pojar et al. 1991). Because of the potential conflict between timber harvest and wildlife habitat requirements, management and research must predict the future availability of forage plants as a function of particular silvicultural systems.

To address a variety of ecological concerns about non-timber forest resources, forest managers increasingly propose silvicultural alternatives to clearcutting (Clayoquot Scientific Panel 1995, Franklin et al. 1997, Beaudry et al. 2001, Mitchell and Beese 2002, Beese et al. 2003) hereafter referred to as partial cutting. "Natural" forests of the CWH zone are characterized by complex, multi-layered, uneven-aged stands (Arsenault and Bradfield 1995, Lertzman et al. 1996). Equally complex are the dynamics among various forest components and understory herbs and shrubs (Franklin et al. 2002). Partially removing the forest canopy affects stand structure and stand dynamics and thus affects the distribution, composition, and abundance of understory plants (Franklin et al. 1997, Franklin et al. 2002).

Based on a survey of the existing literature, this study summarizes the effects of partial cutting on the shrubs and herbs in the CWH forest understory. Specifically, my objectives in this review are to:

1. Describe understory successional pathways after *clearcutting* and after *partial cutting*.
2. Describe differences in understory development following *alternative configurations* of partial cutting (aggregated versus dispersed retention).
3. Describe *short-term* (after logging but prior to crown closure) and *long-term* (after crown closure) shrub and herbaceous development. (However, I did not find any literature discussing long-term development after *aggregated* retention.)
4. Identify gaps in the understanding of understory development over time.

A thorough understanding of these successional patterns will help to improve management of non-timber resources through partial cutting treatments.

Most partial cutting literature focuses on traditional silviculture systems, such as the even-aged shelterwood. Because traditional silviculture systems emphasize timber objectives, they represent only a small subset of the spectrum of partial cutting systems that are possible when considering a broader range of management objectives (Franklin et al. 1997, Mitchell and Beese 2002). Consequently, the results of this review apply most directly to the subset of partial cutting systems addressed in traditional silviculture systems. More recent alternative approaches such as "variable retention" are not adequately addressed by the literature available for this review.

In the next subsection, I describe the understory successional pathways after clearcutting. Following that, I describe short-term and long-term understory responses to dispersed retention and then provide a review of short-term understory responses to aggregated retention. This review on aggregated retention consists of two parts: understory processes in the interior of the forest aggregate and in the harvested area of aggregated retention treatments. Next, I relate understory development to coniferous regeneration after partial cutting. Finally, I summarize gaps in the understanding of understory development over time, and finish with concluding remarks.

Understory successional pathways after clearcutting

Forest development after clearcutting is distinctly different from the historic gap-phase dynamics common in the CWH zone (Lertzman et al. 1996, Deal 2001). Clearcutting does not resemble the complexity of historic, natural large-scale or small-scale disturbances characteristic of the CWH zone (Franklin et al. 1995). Large scale clearcutting in these forests represents a substantial departure from the frequency and severity of disturbances common over the past several thousand years (Clayoquot Scientific Panel 1995, Lertzman et al. 2002, Gavin et al. 2003a, Gavin et al. 2003b). Short-term stand development after clearcutting follows a typical pattern: after substantial initial losses of understory, shrubs, and herbaceous plants are rapidly established while conifers regenerate (Halpern 1988, Halpern 1989, Karakatsoulis and Kimmins 1993, Deal 2001). Although (at least in the Pacific Northwest) these newly established stands initially provide equal or greater species richness and heterogeneity than old-growth stands (Halpern et al. 1992b, Halpern and Spies 1995), understory composition after clearcutting is distinctly different from old-growth. Immediately after logging, native late-seral residual species (or forest-interior species, see section 3 on life history strategies of understory plants) temporally decline and native invasive species, as well as exotic species, rapidly increase (Dyrness 1973, Franklin and Dyrness 1988, Halpern 1988, Schoonmaker and McKee 1988, Halpern and Spies 1995).

Over the long-term, clearcutting often creates young forests that provide poor habitat for many (shade intolerant) shrub and herbaceous plant species (see section 3, Alaback 1982a, Franklin et al. 2002). Even-aged tree cohort development after clearcutting is often characterized by extremely dense stands (see review in Deal 2001) and by the absence of a conspicuous understory, especially excluding shade-intolerant colonists (Halpern et al. 1992b). As well, during this period of a depauperate understory, plant communities typically have very low abundance of forage plants for wildlife (Bratkovich 1985, MacHutchon et al. 1993).

The understory is at its most depauperate during canopy closure, which occurs earliest on nutrient-rich sites (Wells 1996, Franklin et al. 2002) and may never be achieved on the lowest-productivity sites (Franklin et al. 2002). The depauperate understory can persist to the maturation/understory re-initiation phase (Oliver and Larson 1990, Franklin et al. 2002).

A study in Southeast Alaska suggests that deciduous riparian stands do not undergo the depauperate understory phase observed in coniferous stands. Forty years after clearcut logging (presumably after crown closure), riparian red alder stands sustained understories with high species richness and biomass (Hanley and Hoel 1996). Accordingly, the understory of the 40-year old riparian red alder forest was as productive as an old-growth riparian floodplain and old-growth upland forests. These understories contrast sharply with the depauperate understories of 40-year old coniferous forests in Southeast Alaska uplands (see review in Hanley and Hoel 1996).

Short-term understory responses to dispersed retention

There are many complex relationships between forest understory and overstory (Franklin et al. 2002), making it difficult to use indirect measures of partial cutting configuration such as tree basal area and canopy cover as surrogates for understory growth (Alaback 1982a). Nevertheless, for partially cut stands there is evidence that the pattern and intensity of disturbance can be used to predict short-term understory development. Pattern and intensity of the initial cut strongly influence the degree of ground disturbance and the amounts of residual slash (e.g. coarse woody debris), which in turn are expected to affect short-term vegetation responses (Dyrness 1973, Alaback 1982a, Halpern 1988, Halpern and McKenzie 2001, Vanha-Majamaa and Jalonen 2001, Roberts and Zhu 2002). A retrospective study of partially cut stands in hemlock–spruce forests of Southeast Alaska confirmed the influence of initial disturbance intensity on short-term understory development: both short-term (12–38 years) and long-term (53–96 years) understory developments depended on the initial cutting level (also, see review in Deal 1999, Deal 2001).

There is *indirect* evidence that understory response to the initial cut is in part due to change in light levels. Not surprisingly, partial cutting changes the light levels available to the understory (see citations in Beaudry et al. 2001, Drever and Lertzman 2003). In the very dry maritime

Coastal Western Hemlock subzone (CWHxm) (Green and Klinka 1994), 1–6 years after harvesting including contrasting levels of dispersed retention, structural attributes of the retained stands were strong predictors of understory light levels (Drever 1999, Drever and Lertzman 2003). Changes in light due to partial cutting likely affect understory development, because many studies suggest that understory development is very responsive to available light (Alaback 1982a, Stewart 1988, Haeussler et al. 1990, Lieffers and Stadt 1994). More specifically, low light levels are often correlated with minimal understory growth, whereas higher light levels are correlated with increased understory growth (Stewart 1988, Haeussler et al. 1990). However, relative to other disturbance-induced changes to forest stands such as initial ground disturbance, it is not clear how important understory light level is in predicting short-term understory development after dispersed (and aggregated) retention.

In general, disturbance after dispersed retention is characterized by a uniform distribution of target conditions such as microclimate modifications (Franklin et al. 1997). In contrast with aggregated retention, the entire harvested area is subject to mechanical damage and edge effects (Vanha-Majamaa and Jalonen 2001).

Studies of forest types within and outside of the CWH biogeoclimatic zone mostly confirm an inverse relationship between the level of dispersed retention and short-term (several months to 38 years post-harvest) herb (Beese and Bryant 1999), shrub (Foliott and Clary 1972, Irwin and Peek 1979, Hannerz and Hanell 1993), and fleshy fruit production (Perry et al. 1999). However, 3 years after harvesting, the "clumped" shelterwood treatment of the Montane Alternative Silviculture

System study (MASS), implemented in the moist maritime Coastal Western Hemlock subzone (CWHmm), supported a greater increase in shrub abundance than seed-tree, clearcut, and patch-cut treatments (Beese and Bryant 1999). Also, four years after harvesting in the Interior Douglas-fir (IDF) and Montane Spruce (MS) biogeoclimatic zones, abundance (and species richness) of understory vegetation were similar for cutting intensities ranging from clearcut to uncut forests (Sullivan et al. 2001).

To estimate the abundance of plants after logging, we must know how short-term understory composition responds to various levels of tree retention. In Oregon and Washington, the Demonstration of Ecosystem Management Options (DEMO) study examines the effects of alternative levels and patterns of retention in Douglas-fir-dominated forests (Aubry et al. 1999, Halpern et al. 1999, McKenzie et al. 2000). DEMO researchers predicted that the abundance and diversity of early-seral, open-canopy species (invasive species) would decrease with increased levels of retention, while the abundance and diversity of forest-interior species (late-seral residual species) would increase with increased retention (Halpern et al 1999). This makes intuitive sense, because, as noted above, short-term understory development after partial cutting depends on the level of disturbance. Higher levels of disturbance favour exotic species, invasive species, and limit species dependent on forest-interior conditions (Grime 1977, Halpern 1989). Also, at higher levels of retention, scarcity of several resources such as light increases the competitive advantage of forest-interior species (see review of literature on life history theory in Halpern et al. 1999).

Support for the DEMO hypotheses comes from a variety of other studies. Researchers in Finland report that, three months after disturbance, higher levels of retention (70% of stand volume) in mature spruce (*Picea* sp.) forests, not surprisingly, produce more late-successional understory species than clearcutting (Vanha-Majamaa and Jalonen 2001). A study in Sweden found a similar understory trend 5 years after harvest at much lower levels of retention: shelterwood treatments (reduction from 650 trees/ha to 200 and 140 trees/ha) in mature spruce resulted in less increase in invasive (early seral) species than in clearcuts and species present before cutting decreased less in the shelterwoods than in the clearcuts (Hannerz and Hanell 1993).

Results of a retrospective study in Southeast Alaska (Deal 1999, 2001) reveal a possible threshold associated with retention levels (16–96% basal area removal) in hemlock-spruce forests. Recent lightly to moderately cut stands (up to 50% basal area removal, 12–38 years previous), which were not yet in the canopy closure/stem exclusion phase (as well as older stands), did not significantly differ from uncut stands in plant species composition and abundance. In contrast, cutting intensities above 50% resulted in significantly different understory plant composition and abundance (Deal 2001).

Sullivan et al. (2001) obtained results for mixed Douglas-fir–lodgepole pine (*Pinus contorta*) forests that are inconsistent with the general trend reported for other forest types. Species richness and abundance in this dry forest type remained constant over a range of retention levels (0.1 to 2.5 m^2/ha basal area for clearcuts, single tree, and group tree retention, 23.4 m^2/ha basal area for patch cuts, and 39 m^2/ha basal area for uncut forest). These observations are contrary to Halpern et al.'s (1999) prediction because, except for two species, forest-interior species did not decrease with a decreased levels of retention.

A variety of studies covering various smaller sections of the possible range of retention levels are too dissimilar in treatments and ecological conditions for meaningful comparison. The results of these studies (e.g., North et al. 1996, Reader and Bricker 1992) should not be indiscriminately quantitatively or qualitatively compiled to characterize changes in understory composition and abundance over the entire range of cutting intensities. However, when clearcutting and partial cutting are compared at the gross level, most of these studies confirm profound differences between the effects of clearcutting and dispersed retention. Dispersed retention in the CWH biogeoclimatic zone in BC and in the Cascade Mountains in Washington produces many of the shade-intolerant invasive species found in clearcuts (North et al. 1996, Arnott and Beese 1997, Beese and Bryant 1999). On the other hand, dispersed retention also produces a higher proportion of shade-tolerant species and higher species heterogeneity than clearcutting (North et al. 1996, Beese and Bryant 1999, Halpern et al. 1999). Removal of 66% and 33% tree basal area in deciduous forests in Ontario also resulted in the preservation of "forest herb" communities similar to uncut stands (Reader and Bricker 1992). Greater heterogeneity after dispersed retention relative to clearcuts may be a result of greater microsite variability due to higher diversity in light levels and moisture conditions (North et al. 1996).

Long-term understory response to dispersed retention treatments

Successional trajectories after dispersed retention cuts contrast with those following clearcutting. Dispersed tree retention provides higher levels of structural heterogeneity than clearcutting (Franklin et al. 1997, Franklin et al. 2002). This heterogeneity more closely resembles "natural stands" in that there are a broad range of regeneration environments provided by diverse microclimatic conditions (Franklin et al. 1997, Deal 2001, Franklin et al. 2002). A 240-year simulation of forest succession confirmed that the structure of stands with remnant trees resembled untreated natural forests more than stands developing after clearcutting (Hansen et al. 1995). Furthermore, mature forest habitat develops sooner where trees are retained than in even-aged stands typically produced by clearcutting (Franklin et al. 1997, Sullivan et al. 2001). Zenner (2000) obtained results in a retrospective study in Oregon's western central Cascade Range that only partially confirmed these findings. The researcher compared natural two-tiered stands (55 – 110 years old) with natural stands without a remnant tree layer. At low densities (up to 40 trees/ha), remnant trees increased the horizontal structural complexity of forest stands (Zenner 2000). However, remnant trees decreased the vertical structural complexity due to their negative effect on the growth of Douglas-fir in the young cohort (Zenner 2000). Zenner (2002) implied that intermediate levels of retention (approximately 40 trees/ha) maximize structural complexity in managed forests.

There is only limited empirical evidence of long-term effects of dispersed retention on understory development. The few existing studies suggest that the depauperate understory phase observed in mature, even-aged stands after clearcutting is less severe in the more heterogeneous stands produced by partial cutting. Deal's (1999, 2001) retrospective study in western hemlock–Sitka spruce stands in Southeast Alaska is one of the few studies that provides insight into the "long-term" effects of partial cutting (12-96 years after 16-96% basal area removal) on understory development. As mentioned above, for older stands (53-96 years) past the normal onset of canopy closure (as well as for younger stands), there may be a threshold at about 50% of basal area retention, below which plant community composition and abundance is significantly different from uncut stands (Deal 2001). Surprisingly, the dominant factor in this study was the intensity of the cut and not time since the cut. Thus, moderate to high retention in partial cutting systems appears to ameliorate the depauperate understory phase.

Deal's (1999, 2001) results on long-term understory dynamics have not been confirmed by results from other long-term studies. Work completed in Douglas-fir-western hemlock forests of the CWH zone compared natural two-tiered stands (21 trees/ha, > 300 yr. overstory and 65-125 yr. regeneration) with natural stands lacking an older remnant layer (Traut and Muir 2000). Species richness and shrub and herb cover (including late successional shrubs and herbs) did not differ systematically between the two stand types. However, the understory was indirectly affected by remnant density: herb and shrub communities varied with the relative composition (percent basal area/ha) of Douglas-fir and western hemlock in the regeneration layer, which in turn varied with remnant density. Traut and Muir (2002) suggested that variable levels of green-tree retention in managed forests provide for a diversity of undergrowth communities.

A quantitative comparison of Traut and Muir's (2000) study with Deal's (1999, 2000) is difficult, because the ecological conditions that govern these two forest types are very different. I must especially emphasize that Traut and Muir (2000) studied stands originating after fire, whereas Deal (1999, 2000) studied stands originating after timber harvesting. In addition, retrospective studies must be treated cautiously; causal mechanisms and direct effects cannot be distinguished (Halpern *et al.* 1999). Thus, I can only speculate that the apparent lack of more distinct understory differences in Traut and Muir's (2000) study may in part be explained by the low level of retention in their stands with remnant trees. Retention of only 21 trees/ha is almost certainly below Deal's 50% threshold. This speculation is consistent with Traut and Muir's (2000) observation of increased western hemlock regeneration in stands with remnant trees, because Deal (1999, 2000) also observed an increase in hemlock regeneration for stands below 50% retention (see also Deal and Tappeiner 2002).

Short-term understory response to aggregated retention treatments

Interior of the forest aggregate

The short-term ecological consequences of aggregated retention differ from those of dispersed retention. Aggregated retention is more appropriate for "lifeboating" late successional/old-growth understory characteristics, because forest aggregates retain a broader array of structures and conditions resembling old-growth (Franklin et al. 1997, Vanha-Majamaa and Jalonen 2001). The interiors of forest aggregates provide refugia for residual understory plants (Halpern and Spies 1995, Vanha-Majamaa and Jalonen 2001) and other plants adversely affected by the environmental and climatic conditions in early seral stands (Hartley 2002).

One of the obvious reasons for the short-term lifeboating effect is that the interiors of uncut patches provide undisturbed areas of forest floor (Halpern and McKenzie 2001, Sullivan et al. 2001). Retaining trees in undisturbed patches results in smaller initial impacts or faster understory recovery, depending on the autecological characteristics of individual understory species (Vanha-Majamaa and Jalonen 2001). Three years after harvesting, the "clumped" shelterwood treatment of the Montane Alternative Silviculture System study retained greater diversity of pre-harvest understory shrubs and trees than seed-tree, clearcut, and patch-cut treatments. Beese and Bryant (1999) suggest that the observed diversity of pre-harvest plants in the shelterwood may be caused by protection of vegetation in undisturbed groups of trees.

Little of the literature directly addresses understory development as a function of retention levels in aggregated patches. Halpern and colleagues (1999) hypothesized that, similar to results for dispersed retention, abundance and diversity of invasive species would decrease and the abundance and diversity of forest-interior species would increase with increased aggregated green tree retention. The researchers draw this prediction from causal assumptions that reduced disturbance levels and greater shading from retained trees will enhance survival of forest-interior species. In contrast, abundance and diversity of invasive species respond positively to disturbance intensity and negatively to crown closure (see review in Halpern et al. 1999).

The conditions favouring forest-interior herbs and shrubs in forest aggregates are influenced by aggregate size and shape. Reducing aggregate size increases the influence of the forest edge (Chen et al. 1992, Franklin and Spies 1992, Chen et al. 1993, 1995, Franklin et al. 1997, Vanha-Majamaa and Jalonen 2001). Accordingly in Finland immediately after harvest, smaller patches of lower-level retention (0.01-0.02 ha, 15 –20 trees per patch) yielded understory characteristics that did not differ significantly from those in clearcuts (Vanha-Majamaa and Jalonen 2001). On the other hand, edge effect, which dominates small aggregates, appears to favour "forest dominants", which are residual understory species common in late seral ecosystems yet tolerant to disturbance (Halpern 1989, 1999). In addition to the influence of total patch area, patch shape determines the influence of edge effects: irregularly shaped forest patches provide more edge and less forest-interior area than circular patches (Forman 1995, Bannerman 1998). Such patches with a high perimeter-to-area ratio should also produce abundant forest dominants.

Increasing patch size decreases the proportion of the forest-interior area affected by the forest edge (Chen et al. 1992, Chen et al. 1993, 1995, Bannerman 1998), thus increasing conditions suitable for late-seral/forest-interior understory species. Empirical evidence from Finland indicates that understory vegetation in larger undisturbed patches remains relatively unchanged after harvesting (Vanha-Majamaa and Jalonen 2001, see also Franklin et al. 1997). In contrast, "average-sized" forest aggregates (< 1 ha) do not achieve true forest-interior conditions (Franklin et al. 1997), and thus conditions are most suitable for functional groups other than forest-interior species. Forest-interior species are expected to decrease with proximity to the edge, whereas the reverse is expected for invasive species. As the effects of disturbance lessen with time, these gradients in seral species distribution are expected to become less apparent (Halpern et al. 1999). Unfortunately, no direct empirical evidence of this sort exists for the CWH biogeoclimatic zone.

Harvested areas of aggregated retention treatments

Short-term "understory" development in harvested areas of aggregated retention systems is somewhat comparable to clearcuts in that overstory removal favors establishment of invasive species. Levels and pattern of disturbance due to harvest activities in these cleared patches resemble traditional clearcuts more than dispersed retention (Vanha-Majamaa and Jalonen 2001). This difference across alternate spatial patterns in partial cutting reflects a trade-off inherent to aggregated retention systems: the intensity of disturbance is higher than in dispersed treatments, but it is also limited to the cut areas alone (Halpern and McKenzie 2001). Consequently, Halpern and colleagues (1999) hypothesize that survival of forest-interior species, which are all sensitive to disturbance, should be low in the cut areas of aggregated systems. In contrast, abundance of invasive species should increase in the same areas.

However, there is *indirect* evidence that clearcut-like conditions in the harvested area of aggregated treatments are moderated by proximity to forest aggregates. In variable retention systems, retained forest aggregates are intended to fulfill important functions in both undisturbed *and* harvested areas (Franklin et al. 1997), thus extending the biophysical "forest influence" beyond the physical boundaries of the aggregates (Mitchell and Beese 2002). Limited evidence suggests that small harvested areas experience a significant forest influence from retained patches. For example, in the MASS study, nutrient loss immediately after logging was less in small patch cuts than in traditional clearcuts (Arnott and Beese 1997, Prescott 1997). Thus, at least in the long-term, after the effects of disturbance diminish with time, the harvested areas of aggregated retention treatments should support understory communities different from those that exist after clearcutting. However, no direct empirical evidence exists for this prediction.

For aggregated retention systems, I have not found any *direct* empirical evidence for the extension of the forest influence from retained forest aggregates into adjacent harvested areas. I hypothesize that with increasing distance from the forest aggregate edge, the influence of the forest on the cut area should decrease, thus creating conditions more closely resembling clearcuts. As discussed above, such clearcut-like conditions increase the short-term abundance of invasive species. Thus, in the harvested areas of aggregated retention patterns, abundance of invasive species should increase with increasing distance from the forest edge. Quantitative research is needed in the CWH zone to determine light levels, edge effects, nutrient release and leeching, and microclimate modifications as a function of distance on both sides of the aggregate's edge. The objective of this research should be to establish detailed predictions of understory dynamics in the harvested area of aggregated retention treatments.

Researchers have shown that gap dynamics studies can be used to estimate the effects of partial cutting on ecosystem processes (Coates and Burton 1997). Gap dynamics studies provide some limited support for the hypothesis that the forest influence in the harvested area decreases with increase in distance to the forest edge. A study investigating the effects of forest gaps (0.016 – 2.0 ha in size) in deciduous forests of the southern Appalachian showed that two years after harvesting, solar radiation, soil temperature, and air temperature was higher in the centre of the gap than at the edge (Phillips and Shure 1990). As well, an empirical study of natural and harvested forest gaps (5m to 150 m diameter) in the moist cold

Interior Cedar Hemlock subzone (ICHmc) showed that light levels in the gaps decrease with decreasing gap size (Coates and Burton 1997).

In the short-term, both invasive and forest-interior species are hypothesized to be more abundant in aggregated retention treatments than in dispersed retention treatments (Halpern et al. 1999). Researchers support this prediction with theories about the causal effects of disturbance level, which is uniformly moderate in dispersed patterns and thus causes uniformly distributed but moderate microclimatic stress. The hypothesized result is a loss of forest-interior species, which are sensitive to disturbance, and widespread establishment of invasive species (Halpern et al. 1999). As discussed above, cut areas of aggregated retention treatments provide conditions more favourable for early-seral species than those in dispersed treatments. In contrast, retained forest patches provide conditions more favourable for forest-interior species than those in dispersed retention.

Effects of coniferous regeneration on understory development

Coniferous regeneration strongly affects shrub and herb development (Alaback 1982a, Haeussler et al. 1990). Thus, to understand the effects of partial cutting on herb and shrub species, we must understand how such treatments affect tree regeneration composition and density.

In the past, partial cutting treatments occasionally resulted in overstocking of certain species of conifers. Partial cutting often resulted in stands with successful coniferous regeneration of (mostly) western hemlock (Harris and Farr 1971), especially at 1 – 50% basal area retention (Deal and Tappeiner 2002) and particularly in hemlock-dominated shelterwoods. The result has occasionally been overstocking of hemlock (Williamson and Ruth 1976, see also review in Deal 1999, and in Beese et al. 2000 unpublished report).

Regeneration studies in Douglas-fir dominated partially cut stands in the CWH zone also report greater amounts of natural hemlock regeneration than in clearcuts. In a study in the dry maritime Coastal Western Hemlock subzone (CWHdm), western hemlock dominated natural regeneration after dispersed retention (6 years after retaining 57 trees/ha) (D'Anjou 2001b). In addition, hemlock regeneration was greater in a dispersed retention treatment (3 years after retaining 95 trees/ha) than in a neighbouring clearcut, even though all western hemlock were felled to avoid such an outcome (D'Anjou 2001a). Finally, 7 years after harvesting, group tree selection (25% and 50% of basal area removed in rectangles < 0.3 ha) and single tree selection (25% basal area removed) in the central very wet hypermaritime variant (CWHvh2) of the CWH zone produced greater regeneration density of mostly hemlock than a clearcut, but did not cause a change in species mixture relative to the pre-harvest forest (D'Anjou 2000).

These results support previous empirical studies, affirming that tree retention both moderates microclimatic conditions for the establishment of natural regeneration (Hoyer 1990, Koppenaal and Mitchell 1992, see also Beese et al. 2000 unpublished report), especially for shade tolerant coniferous species (Lavender et al. 1990), and determines seed availability that can limit coniferous regeneration (see review in Beese et al. 2000 unpublished report, Beach and Halpern 2001). However, trees with light, wind-dispersed seeds depend less on proximity to the seed source (Lavender et al. 1990). Thus, the evidence suggests that partial cutting holds a greater potential than clearcutting for overstocking of only some species of conifers.

To correctly predict conifer establishment, one must consider a host of additional factors (Lavender et al. 1990). Factors that predict natural seedling establishment in the CWH zone are species-specific responses to light conditions created by the overstory, prevailing microclimate, intra- and inter-species competition, soil moisture and nutrients, seed production, seed dispersal, and disturbance size, timing and intensity (Oliver 1981, Alaback 1982a, Haeussler and Coates 1986, Lavender et al. 1990, Mitchell and Arnott 1995, Mailly et al. 2000, Drever and Lertzman 2001, Drever and Lertzman 2003). For example, western hemlock is extremely shade-tolerant and prefers cool, moist, undisturbed mor humus forms for germination (Koppenaal and Mitchell 1992).

Within the range of light environments created by various partial cutting configurations, a particular species will regenerate more densely under some conditions than under others (Mitchell 2001, Drever and Lertzman 2003). The level of solar radiation favouring seedling growth is also a function of prevailing edaphic conditions (Carter and Klinka 1992, Drever and Lertzman 2001). That is, the shade tolerance of many tree species increases with a decrease in soil moisture (Carter and Klinka 1991, 1992).

Several thinning studies report that dense shade-tolerant tree regeneration can suppress shrub and herb abundance (Alaback and Herman 1988, Deal and Farr 1994, see also Deal 2001). Although certain partial cutting conditions evidently facilitate outcompetition of shrub and herbaceous species by coniferous regeneration, an exact causal mechanism for these competitive dynamics cannot be derived from the literature.

Especially where partial retention of overstory trees creates conditions that favour western hemlock regeneration, the long-term effect of this regeneration on understory plants can be profound. Western hemlock canopies are denser than Douglas-fir (see review in Traut and Muir 2000), and therefore light levels under mature hemlock canopies are usually lower than for Douglas-fir (Stewart 1988, Spies et al. 1990, Canham and Burbank 1994). Consequently, cover and richness of several herb and shrub species is generally lower under hemlock regeneration (Alaback 1982a, Stewart 1988, Traut and Muir 2000).

Over the long-term, increased retention usually reduces the productivity of the regenerating cohort. Observations of cohort development (to 70-100 years of age) under remnant trees in the *Tsuga heterophylla* zone have found a decrease in tree growth with increased remnant densities (Rose 1994, Hansen et al. 1995, Zenner 1995, Rose and Muir 1997, Acker et al. 1998, Traut and Muir 2000). The *Tsuga heterophylla* zone corresponds roughly with stands classified as the very wet, wet, dry, and very dry maritime and dry submaritime CWH biogeoclimatic zones in British Columbia (MacKinnon and Trofymow 1998).

Conclusions about the long-term effects of various retention levels on the species composition of the regenerating cohort differed among forests of different dominant tree species. Deal and Tappeiner (2002) did not find differences in tree species composition as a function of cutting intensity 12-96 years after harvest (16-96% basal area removal) in hemlock-spruce forests of southeast Alaska (see also Deal 1999). In contrast, several studies investigating long-term effects (> 65 years) of partial cutting agree that shade-tolerant species such as western hemlock (Rose 1994) and Western redcedar displace Douglas-fir at low to intermediate levels of dispersed retention (Hansen et al. 1995 (rotations > 120 years), see also Traut and Muir 2000).

Gaps in the understanding of understory development over time

The existing body of literature that discusses the effects of partial cutting on understory species leaves a great amount of uncertainty, especially regarding effects of partial cutting patterns and partial cutting intensities on understory composition and abundance over the *long-term*. Little direct quantitative evidence exists on how effects related to the tree canopy (such as understory light levels and microclimate) and (ground) disturbance interact to shape the response of the understory, particularly with respect to short and long-term succession after aggregated retention. The existing literature is also unclear on how these effects shape the understory response as a function of distance on both sides of the aggregate edge. Thus, with respect to detailed response patterns of various understory functional groups to partial cutting, aggregated retention treatments represent the greatest amount of uncertainty. In addition, the reviewed literature focuses exclusively on stand-level dynamics and neglects landscape-level impacts or landscape context of alternative harvest systems. Partial cutting studies within the CWH zone are rare and focus on a small portion of the variation related to the understory that exists in that zone. Thus, it is not clear to what extent findings from these studies can be extrapolated to the entire CWH zone. Furthermore, many studies investigated only traditional silviculture treatments that take timber production as the main management objective. Such studies cover only a small subset of the entire spectrum of possible retention options (Franklin et al. 1997).

As part of a silvicultural prescription, forest managers must decide which elements of the forest stand (for example coarse wood debris, trees with decay features) should be retained (Beese et al. 2003). The specific mixture of stand elements chosen for retention very likely affects understory composition and abundance. Unfortunately, no empirical evidence of that sort is yet available.

Section conclusion

Despite the great amount of uncertainty, existing studies show that forest managers are able to influence understory species composition and abundance by varying the level and pattern of tree retention. Results show that short-term understory dynamics are a function of intensity and pattern of disturbance. *Ceteris paribus,* increasing the cutting intensity increases the short-term abundance of invasive species and decreases the abundance of forest-interior species. Size and shape of forest aggregates also affects the short-term abundance of forest dominants and forest-interior species. In the long-term, dispersed retention ameliorates the depauperate understory phase observed after crown closure in previously clearcut areas.

For future work, additional to that implied above, I recommend that researchers should combine the results of this literature review with data about shrub and herb species autecology. This approach would help identify major causal mechanisms that determine overstory-understory composition and abundance particularly of forage plants used by bears. In this way, uncertainty may be reduced in predictions of species-specific responses to alternative silviculture treatments.

5. Conclusion

Forest managers are increasingly challenged to actively manage non-timber forest resources, such as understory plants, that are important as wildlife forage (e.g., Kohm and Franklin 1997). Thus, researchers and managers must understand how biotic and environmental gradients shape the community structure of forage species. I assessed the community structure of plants consumed by black bears in the Nimpkish Valley, British Columbia, with respect to environmental gradients. Also, because forest managers increasingly use partial cutting as the primary silvicultural treatment, I surveyed the literature for evidence about the effects of pattern and intensity of partial cutting on understory species.

At the gross level, findings from my analyses of community structure of forage plants and the review of my partial cutting literature complement and confirm each other. The analyses of community structure of forage plants showed that in the Nimpkish Valley, soil nutrient and moisture content, elevation, and tree overstory dominance and contiguity mostly determine the variation associated with community structure of forage plants. Literature on understory succession after partial cutting in managed forests of coastal British Columbia and elsewhere confirms that the abundance of invasive and residual understory species is very responsive to the degree of tree overstory dominance (i.e., the amount of tree retention). In addition, my review of literature on partial cutting revealed that the pattern (spatial arrangement) of tree overstory removal is a crucial determinant of the abundance and composition of understory species in managed forests. This further complements my results from the Nimpkish Valley because, in my statistical analyses, I was not able to explicitly investigate understory dynamics linked to the spatial arrangement of forest trees.

Partial cutting is an effective tool for managing a wide range of non-timber forest values such as the quality of foraging habitat. But, both conventional and alternative timber management can only be ecologically sustainable if founded on a sound understanding of ecosystems, including patterns of understory abundance and composition. Building an integrated understanding of coastal ecosystems and alternative silviculture will be a powerful tool to ensure that tomorrow's coastal temperate rainforests remain commercially *and* ecologically valuable.

Reference List

Acker, S. A., E. K. Zenner, and W. H. Emmingham. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: Implications for green tree retention. Canadian Journal of Forest Research **28**:749-758.

Alaback, P. B. 1982a. Dynamics of understory biomass in Sitka spruce-Western hemlock forests of southeast Alaska. Ecology **63**:1932-1948.

Alaback, P. B. 1982b. Forest community structural change during secondary succession in southeast Alaska. Pages 70-79 *in* J. E. Means, editor. Proceedings of the symposium: Forest succession and stand development research in the Northwest, 26 Mar. 1981, Corvallis Oregon. Oregon State University, Forestry Research Laboratory, Corvallis, Oregon.

Alaback, P. B., and F. R. Herman. 1988. Long-term response of understory vegetation to stand density in Picea-Tsuga forests. Canadian Journal of Forest Research **18**:1522-1530.

Anderson, A. J. B. 1971. Ordination methods in ecology. Journal of Ecology **59**:713-726.

Arnott, J. T., and W. J. Beese. 1997. Alternatives to clearcutting in BC coastal montane forests. Forestry Chronicle **73**:670-678.

Arsenault, A., and G. E. Bradfield. 1995. Structural-compositional variation in 3 age-classes of temperate rain-forests in southern coastal British-Columbia. Canadian Journal of Botany **73**:54-64.

Aubry, K. B., M. P. Amaranthus, C. B. Halpern, J. D. White, B. L. Woodard, C. E. Peterson, C. A. Lagoudakis, and A. J. Horton. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Science **73**:12-26.

Bannerman, S. 1998. Biodiversity and interior habitats: the need to minimize edge effects. Extension Note 21. British Columbia Ministry of Forests, Victoria.

Barton, A. M. 1994. Gradient analysis of relationships among fire, environment, and vegetation in a southwestern USA mountain-range. Bulletin of the Torrey Botanical Club **121**:251-265.

Bazzaz, F. A. 1996. Plants in changing environments : linking physiological, population, and community ecology. Cambridge University Press, Cambridge ; New York.

BC Ministry of Environment Lands and Parks and Ministry of Forests. 1998. Field manual for describing terrestrial ecosystems. Province of British Columbia, Victoria, BC.

BC Ministry of Forests. 2002. 2001/2002 Annual report. BC Ministry of Forests, Victoria, BC.

BC Resources Inventory Committee. 1998. Standard for terrestrial ecosystem mapping in British Columbia. Province of British Columbia, Resources Inventory Committee, Ecosystems Working Group, Victoria, BC.

Beach, E. W., and C. B. Halpern. 2001. Controls on conifer regeneration in managed riparian forests: effects of seed source, substrate, and vegetation. Canadian Journal of Forest Research **31**:471-482.

Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research **14**:1-55.

Beaudry, L., M. Martin, and J. Paczkowski. 2001. Using silviculture to maintain and enhance grizzly bear habitat in six variants of the Prince George forest region. Habitat Branch Ministry of Environment, Lands and Parks, Prince George, B.C.

Beese, W. J., and A. A. Bryant. 1999. Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. Forest Ecology and Management **115**:231-242.

Beese, W. J., B. G. Dunsworth, Z. K., and B. Bancroft. 2003. Maintaining attributes of old-growth forests in coastal B.C. through variable retention. Forestry Chronicle **79**:570-578.

Beese, W. J., J. S. Sandford, T. G. Andersen, and N. J. Martin. 2000 unpublished report. Natural Regeneration and Vegetation Dynamics in Coastal

Montane Forests at MASS. Montane Alternative Silviculture Project, Nanaimo, B.C.

Bell, F. W. 1991. Critical sivics of conifer crop species and selected competitive vegetation in northwestern Ontario. COFRDA 3310, Ministry of Natural Resources, Thunder Bay, Ontario.

Bierzychudek, P. 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytologist **90**:757-776.

Bratkovich, A. A. 1985. Grizzly bear habitat components associated with past logging practices on the Libby ranger district, Kootenai National forest. *in* Grizzly bear habitat symposium, Missoula, MT, April 30 - May 2, 1985.

Brockway, D. G. 1998. Forest plant diversity at local and landscape scales in the Cascade Mountains of southwestern Washington. Forest Ecology and Management **109**:323-341.

Bull, E. L., R. S. Holthausen, and D. B. Marx. 1990. How to determine snag density. Western Journal of Applied Forestry **5**:56-58.

Bull, E. L., T. R. Torgersen, and T. L. Wertz. 2001. The importance of vegetation, insects, and neonate ungulates in black bear diet in northeastern Oregon. Northwest Science **75**:244-253.

Bunnell, F. L. 1990. Reproduction of salal (*Gaultheria shallon*) under the forest canopy. Canadian Journal of Forest Research **20**:91-100.

Bunnell, F. L., L. L. Kremsater, and E. Wind. 1999. Managing to sustain vertebrate richness in forests of the Pacific Northwest: relationships within stands. Environmental Review **7**:97–146.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America Volume 1, Conifers. Agriculture Handbook 654, USDA Forest Service, Washington, DC.

Campbell, B. D., and J. P. Grime. 1992. An experimental test of plant strategy theory. Ecology **73**:15-29.

Canham, C. D., and D. H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research **24**:337-349.

Carter, R. E., and K. Klinka. 1991. A stand level guide to the selection of reproduction methods for regenerating forest stands in the Vancouver

Forest Region. Contract Report B.C. Min. For., Vancouver Forest Region, Burnaby, B.C.

Carter, R. E., and K. Klinka. 1992. Variation in shade tolerance of Douglas-fir, western hemlock, and western red cedar in coastal British Columbia. Forest Ecology and Management. **55**:87-105.

Chan, S. S., S. R. Radosevich, and A. T. Grotta. 2003. Effects of contrasting light and soil moisture availability on the growth and biomass allocation of Douglas-fir and red alder. Canadian Journal of Forest Research **33**:106-117.

Chen, J., J. Franklin, and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas-Fir forests. Ecological Applications **2**:387-396.

Chen, J., J. F. Franklin, and T. Spies. 1993. Contrasting microclimates among clearcut, edge and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology **63**:219-237.

Chen, J., J. F. Franklin, and T. Spies. 1995. Growing-season microclimate gradients from clearcut edges into old-growth Douglas-fir forests. Ecological Applications **5**:74-86.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117-143.

Clayoquot Scientific Panel. 1995. Scientific Panel for Sustainable Forest Practices in Clayoquot Sound Report 5, Sustainable ecosystem management in Clayoquot Sound : planning and practices. Victoria.

Coates, D., S. Haeussler, and J. Mather. 1990. A guide to the response of common plants in British Columbia to management treatments. FRDA Handbook No. 008 B.C. Min. For. and For. Can., Victoria, B.C.

Coates, K. D., and P. J. Burton. 1997. A gap-based approach for development of silvicultural systems to address ecosystem management objectives. Forest Ecology and Management. **99**:337-354.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist **111**:1119-1144.

D'Anjou, B. 2000. Alternative silvicultural systems on steep-sloped old-growth forests on the Queen Charlotte Islands– project overview and regeneration development. Final Report Project 13.3 EP 862.34, B.C. Ministry of Forests Research Section Vancouver Forest Region.

D'Anjou, B. 2001a. Effects of alternative silvicultural systems on windthrow and conifer regeneration in a coastal, Douglas-Fir-dominated forest: Summary of year 3 results. Technical Report 007, Research Section, Vancouver Forest Region, BCMOF, Nanimo, BC.

D'Anjou, B. 2001b. Effects of dispersed retention harvesting on stand structure and regeneration in a coastal mixed-conifer forest: Summary of year 6 results. Technical Report 006, Research Section, Vancouver Forest Region, BCMOF, Nanimo, BC.

Daubenmire, R. F. 1959. A canopy coverage method of vegetation science. Northwest Science **33**:43-64.

Davis, H. 1996. Characteristics and selection of winter dens by black bears in coastal British Columbia. Master of Science. Simon Fraser University, Burnaby.

Deal, R. L. 1999. The effects of partial cutting on stand structure and growth, and forest plant communities of western hemlock - Sitka spruce stands in southeast Alaska. Ph.D. dissertation. Oregon State University, Corvallis.

Deal, R. L. 2001. The effects of partial cutting on forest plant communities of western hemlock - Sitka spruce stands in southeast Alaska. Canadian Journal of Forest Research **31**:2067-2079.

Deal, R. L., and W. A. Farr. 1994. Composition and development of conifer regeneration in thinned and unthinned natural stands of western hemlock and Sitka spruce in southeast Alaska. Canadian Journal of Forest Research **24**:976-984.

Deal, R. L., and J. C. Tappeiner. 2002. The effects of partial cutting on stand structure and growth of western hemlock-Sitka spruce stands in southeast Alaska. Forest Ecology and Management **159**:173-186.

Demarchi, D. A. 1995. Ecoregions of British Columbia (fourth edition). 1:2,000,000 map. Ministry of Environment, Lands and Parks, Victoria, BC.

Drever, C. R. 1999. Made in the shade: regenerating coastal Douglas-Fir and Western redcedar under partial cutting treatments. Master of Resource Management. Simon Fraser University, Burnaby, BC.

Drever, C. R., and K. P. Lertzman. 2001. Light-growth responses of coastal Douglas-fir and Western redcedar saplings under different regimes of soil moisture and nutrients. Canadian Journal of Forest Research **31**:2124-2133.

Drever, C. R., and K. P. Lertzman. 2003. Effects of a wide gradient of retained tree structure on understory light in coastal Douglas-fir forests. Canadian Journal of Forest Research **33**:137-146.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Dyrness, C. T. 1973. Early stages of plant succession following logging and slash burning in the western Cascades of Oregon. Ecology **54**:57-58.

Dyrness, C. T., J. F. Franklin, and W. H. Moir. 1974. A preliminary classification of forest communities in the central portion of the western Cascades of Oregon. U.S.I.B.P. (Int. Biol. Prog.) Conif. For. Biome Bull. 4, University of Washington, Seattle.

Eis, S. 1981. Effect of vegetative competition on regeneration of white spruce Picea-glauca. Canadian Journal of Forest Research **11**:1-8.

Fasham, M. J. R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines and coenoplanes. Ecology **58**:551-561.

Foliott, P. F., and W. P. Clary. 1972. A selected and annotated bibliography of understory-overstory vegetation relationships. Technical Bulletin 198, University of Arizona Agricultural Experimentation Station.

Forman, R. T. 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge, U.K.

Franklin, J. F. 1982. Old-growth forests in the Pacific Northwest: an ecological view. Pages 5-27 *in* Old-growth forests: a balanced perspective. University of Oregon, Bureau of Governmental Research and Service, Eugene, Oregon.

Franklin, J. F., D. R. Berg, D. A. Thornburgh, and J. C. Tappeiner. 1997. Alternative Silvicultural Approaches to Timber Harvesting: Variable Retention Systems. Pages 11-30 *in* K.A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century. Island Press, Washington.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, OR.

Franklin, J. F., P. M. Frenzen, and F. J. Swanson, editors. 1995. Recreation of ecosystems at Mount St Helens: contrast in artificial and natural approaches., 2 nd edition. Lewis Publishers, Boca Raton, FL.

Franklin, J. F., and T. A. Spies. 1992. Vegetation responses to edge environments in old-growth Douglas fir forests. Ecological Applications **2**:387-396.

Franklin, J. F., T. A. Spies, R. Van Pelt, A. B. Carey, D. A. Thornburgh, D. R. Berg, D. B. Lindenmayer, M. E. Harmon, W. S. Keeton, D. C. Shaw, K. Bible, and J. Q. Chen. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management **155**:399-423.

Gagnon, D., and G. E. Bradfield. 1987. Gradient analysis of west central Vancouver Island forests. Canadian Journal of Botany **65**:822-833.

Garcia, E. R. 1985. Grizzly bear direct habitat improvement on the Kootenai National Forest. *in* Grizzly bear habitat symposium, April 30 - May 2, Missoula, MT.

Gavin, D. G., L. B. Brubaker, and K. P. Lertzman. 2003a. An 1800-year record of the spatial and temporal distribution of fire from the west coast of Vancouver Island, Canada. Canadian Journal of Forest Research **33**:573-586.

Gavin, D. G., L. B. Brubaker, and K. P. Lertzman. 2003b. Holocene fire history of a coastal temperate rain forest based on soil charcoal radiocarbon dates. Ecology **84**:186-201.

Gitay, H., and I. R. Noble. 1997. What are functional types and how should we seek them. Pages 3-19 *in* Plant functional types their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, New York.

Grace, J. B. 1990. On the relationships between plant trades and competitive ability. Pages 51-65 *in* D. Tilman, editor. Perspectives on plant competition. Academic Press, San Diego.

Green, R. N., and K. Klinka. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. Land Management Handbook 28, Province of British Columbia, Victoria, BC.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist **111**:1169-1194.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons.

Grime, J. P. 2001. Plant strategies, vegetation processes, and ecosystem properties. 2nd edition. Wiley, New York.

Grime, J. P., J. G. Hodgson, and R. Hunt. 1988. Comparative plant ecology. Unwin, London.

Haeussler, S., L. Bedford, J. O. Boateng, and A. MacKinnon. 1999. Plant community responses to mechanical site preparation in northern interior British Columbia. Canadian Journal of Forest Research **29**:1084-1100.

Haeussler, S., and D. Coates. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. FRDA Report 018, Victoria, BC.

Haeussler, S., D. Coates, and J. Mather. 1990. Autecology of common plants in British Columbia: A literature review. FRDA Report 158, Province of B.C. and Forestry Canada.

Halpern, C. B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology **69**:1703-1715.

Halpern, C. B. 1989. Early successional patterns of forest species - interactions of life-history traits and disturbance. Ecology **70**:704-720.

Halpern, C. B., J. A. Antos, K. Cromack, and A. M. Olson. 1992a. Species interactions and plant diversity during secondary succession. Northwest Environmental Journal **8**:203-205.

Halpern, C. B., S. A. Evans, C. R. Nelson, D. McKenzie, D. A. Liguori, D. E. Hibbs, and M. G. Halaj. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: An overview of a long-term experiment. Northwest Science **73**:27-44.

Halpern, C. B., J. F. Franklin, and A. McKee. 1992b. Changes in plant-species diversity after harvest of Douglas-fir forests. Northwest Environmental Journal **8**:205-207.

Halpern, C. B., and D. McKenzie. 2001. Disturbance and post-harvest ground conditions in a structural retention experiment. Forest Ecology and Management **154**:215-225.

Halpern, C. B., and T. A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications **5**:913-934.

Hamilton, A. N. 1987. Classification of coastal grizzly bear habitat for forestry interpretations and the role of food in habitat use by coastal grizzly bears. Master of Science. University of British Columbia, Vancouver, B.C.

Hamilton, A. N., C. A. Bryden, and J. C. Clement. 1991. Impacts of Glyphosate application on grizzly bear forage production in the Coastal Western Hemlock Zone. FRDA Report 165 Wildlife Branch, B.C. Ministry of Environment, Victoria, B.C.

Hamilton, E. 1988. A system for the classification of seral ecosystems within the biogeoclimatic ecosystem classification system: first approximation. Lands Research Report RR87004-HQ, Research Branch, Ministry of Forests and Lands, Victoria, BC.

Hammer, D. 1996. Buffaloberry (*Shepherdia canadensis* (L.) Nutt.) fruit production in fire successional bear feeding sites. Journal of Range Management **49**:520-529.

Hanley, T. A., and W. W. Brady. 1997. Understory species composition and production on old-growth western hemlock - Sitka spruce forests of southeast Alaska. Canadian Journal of Botany **75**:574-580.

Hanley, T. A., and T. Hoel. 1996. Species composition of old-growth and riparian Sitka spruce - western hemlock forests in southeastern Alaska. Canadian Journal of Forest Research. **26**:1703-1708.

Hannerz, M., and B. Hanell. 1993. Changes in the vascular plant vegetation after different cutting regimes on a productive peatland site in central Sweden. Scandinavian Journal of Forest Research. **8**:193-203.

Hansen, A. J., S. L. Garman, J. F. Weigand, D. L. Urban, W. C. McComb, and M. G. Raphael. 1995. Alternative silvicultural regimes in the Pacific Northwest simulations of ecological and economic effects. Ecological Applications **5**:535-554.

Harris, A. S., and W. A. Farr. 1971. Partial cutting of western hemlock and Sitka spruce in southeast Alaska. Research paper PNW 124, Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Hoyer, G. E. 1990. Shelterwood regeneration opportunities in Washington State, defined by forest habitats. Dept. of Natural Resources, Washington.

Huffman, D. W., J. C. Tappeiner, and J. C. Zasada. 1994. Regeneration of salal (*Gaultheria shallon*) in the central xoast range forests of Oregon. Canadian Journal of Botany **72**:39-51.

Hutchinson, T. F., R. E. J. Boerner, L. R. Iverson, S. Sutherland, and E. K. Sutherland. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (USA) *Quercus* forests. Plant Ecology **144**:177-189.

Irwin, L. L., and J. M. Peek. 1979. Shrub production and biomass trends following five logging treatments within the cedar-hemlock zone of northern Idaho. Forest Science **21**:415-426.

Jules, E. K. 1997. Consequences of forest fragmentation for the understory plant, *Trillium ovatum* (*Liliaceae*). Pages 201-206 *in* M. V. Wilson, editor. Conservation and management of native plants and fungi. Native Plant Society of Oregon, Corvallis.

Jules, E. S. 1999. Mechanisms of reduced trillium recruitment along edges of old-growth forest fragments. Conservation Biology **13**:784-793 .

Karakatsoulis, J., and J. P. Kimmins. 1993. Vegetation development and Douglas-fir growth following clearcut harvesting in the CWHdm subzone: 10-year results from the Blaney chronosequence. Land Management Report 81, Ministry of Forests Research Program, Victoria, BC.

Kenkel, N. C., and L. Orloci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology **67**:919-928.

Klinka, K. 1985. Vegetation relationships among some seral ecosystems in southwestern British Columbia. Canadian Journal of Forest Research **15**:561-569.

Klinka, K., H. Y. H. Chen, Q. L. Wang, and L. deMontigny. 1996. Forest canopies and their influence on understory vegetation in early-seral stands on west Vancouver Island. Northwest Science **70**:193-200.

Klinka, K., V. J. Krajina, A. Ceska, and A. M. Scagel. 1989. Indicator plants of coastal British Columbia. University of British Columbia Press, Vancouver, BC.

Klinka, K., A. M. Scagel, and P. J. Courtin. 1985. Vegetation relationships among some seral ecosystems in southwestern British-Columbia. Canadian Journal of Forest Research **15**:561-569.

Koehler, G. M., and D. J. Pierce. 2003. Black bear home-range sizes in Washington: Climatic, vegetative, and social influences. Journal of Mammalogy **84**:81-91.

Kohm, K. A., and J. F. Franklin. 1997. Creating a forestry for the 21st century. Island Press, Washington.

Koppenaal, R., and A. K. Mitchell. 1992. Regeneration of montane forests in the Coastal Western Hemlock zone of British Columbia: A literature review. FRDA Report 192, Forestry Canada, Pacific Forestry Centre, BC Ministry of Forests, Victoria BC.

Kozlowski, T. T. 1972. Physiology of water stress. Pages 229-244 *in* J. R. Goodin, editor. Wildland shrubs- their biology and utilization. U.S. Department of Agriculture.

Krajina, V. J. 1965. Biogeoclimatic zones and classification of British Columbia. Ecology of Western North America **1**:1-17.

Krajina, V. J. 1969. Ecology of forest trees in British Columbia. Ecology of Western North America **2**:1-146.

Kramer, P. J., and T. T. Kozlowski. 1979. Physiology of woody plants. Academic Press,, New York, N.Y.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika **29**:1-27.

Kruskal, J. B., and M. Wish. 1978. Multidimensional scaling. Sage Publications, Beverly Hills, California.

Lavender, D. P., C. M. Parish, C. M. Johnson, G. Montgomery, A. Vyse, R. A. Willis, and D. Winston, editors. 1990. Regenerating British Columbia's forests. University of British Columbia Press, Vancouver, B.C.

Lertzman, K., D. , D. Gavin, L. Hallett, L. D. Brubaker, D. Lepofsky, and R. Mathewes. 2002. Long-term fire regime estimated from soil charcoal in coastal temperate rainforests. Conservation Ecology **6**:5.

Lertzman, K., T. Spies, and F. Swanson. 1997. From ecosystem dynamics to ecosystem management. Pages 361-382 *in* E. Wolf, editor. The rainforests of home: Profile of a North American Bioregion. Island Press, Washington, D.C.

Lertzman, K. P., G. D. Sutherland, A. Inselberg, and S. C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology **77**:1254-1274.

Lezberg, A. L., J. A. Antos, and C. B. Halpern. 1999. Belowground traits of herbaceous species in young coniferous forests of the Olympic Peninsula, Washington. Canadian Journal of Botany **77**:936-943.

Lieffers, V. J., and K. J. Stadt. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis*, and *Epilobium angustifolium* in relation to overstory light transmission. Canadian Journal of Forest Research **24**:1193-1198.

Limpert, E., W. A. Stahel, and M. Abbt. 2001. Log-normal distributions across the sciences: keys and clues. BioScience **51**:341-352.

Lutmerding, H. A., D. A. Demarchi, D. V. Lea, D. V. Meidinger, and T. Vold. 1990. Describing ecosystems in the field. Manual 11, BC Ministry of Environment, Victoria, BC.

MacHutchon, G. 1996. Grizzly bear and black bear foods described for the Coastal Western Hemlock and northern Interior Cedar Hemlock biogeoclimatic zones of British Columbia. unpublished report - acquired from T. Hamilton, B.C. Ministry of Water, Land, and Air Protection, Victoria, BC.

MacHutchon, G., S. Himmer, and C. Bryden. 1993. Khutzeymateen Valley grizzly bear study: final report. Habitat Research Report 31, B.C. Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria, B.C.

MacKenzie, W., and R. Klassen. 1999. VPro97 Version 2 for Access 8. Ministry of Forests.

MacKinnon, A. 1992. Use of the biogeoclimatic ecosystem classification system in British Columbia. The Forestry Chronicle **68**:100-120.

MacKinnon, A. 2003. West coast, temperate, old-growth forests. The Forestry Chronicle **79**:475-784.

MacKinnon, A., and J. A. Trofymow. 1998. Structure, processes, and diversity in successional forests of coastal British Columbia. Northwest Science **72**:1-3.

Mailly, D., J. P. Kimmins, and R. T. Busing. 2000. Disturbance and succession in a coniferous forest of northwestern North America: simulations with DRYADES, spatial gap model. Ecological Modelling **127**:183-205.

Marcum, C. L., and D. O. Loftsgaarden. 1980. A nonmapping technique for studying habitat preferences. Journal of Wildlife Management **44**:963-968.

Martin, P. 1983. Factors influencing globe huckleberry fruit production in Northwestern Montana. International Conference of Bear Research and Management **5**:159-165.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. Wiley and Sons, London.

McCook, L. J. 1994. Understanding ecological community succession. Causal models and theories, a review. Vegetatio **110**:115-147.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Sofware Design, Gleneden Beach, OR.

McCune, B., J. Hutchinson, and S. Berryman. 2002. Concentration of rare epiphytic lichens along large streams in a mountainous watershed in Oregon, U.S.A. The Bryologist **105**:439-450.

McCune, B., and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, version 4. MjM Software Design, Gleneden Beach, OR.

McCune, B., R. Rosentreter, J. M. Ponzetti, and D. C. Shaw. 2000. Epiphyte habitats in an old conifer forest in Western Washington, USA. The Bryologist **103**:417-427.

McKenzie, D., C. B. Halpern, and C. R. Nelson. 2000. Overstory influences on herb and shrub communities in mature forests of western Washington, USA. Canadian Journal of Forest Research **30**:1655-1666.

Meidinger, D., T. Lee, G. W. Douglas, G. Britton, W. MacKenzie, and H. Qian. 2002. British Columbia plant species codes and selected attributes. Version 4 Database. Research Branch. B.C. Ministry of Forests.

Meidinger, D., and J. Pojar. 1991. Ecosystems of British Columbia. Special Report Series 6, Research Branch, Ministry of Forests, Victoria.

Meier, A. J., S. P. Bratton, and D. C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecological Applications **5**:935-946.

Mielke, P. W., Jr. 1984. Meteorological applications of permutation techniques based on distance functions. *in* Handbook of Statistics. Elsevier Science Publishers.

Minore, D. 1984. *Vaccinium membranaceum* berry production seven years after treatment to reduce overstory tree canopies. Northwest Science **58**:208-212.

Mitchell, A. K. 2001. Growth limitations for conifer regeneration under alternative silvicultural systems in a coastal montane forest in British Columbia, Canada. Forest Ecology and Management **145**:129-136.

Mitchell, A. K., and J. T. Arnott. 1995. Effects of shade on the morphology and physiology of amabilis fir and western hemlock seedlings. New Forests **10**:79-98.

Mitchell, S. J., and W. J. Beese. 2002. The retention system: reconciling variable retention with the principles of silvicultural systems. Forestry Chronicle **78**:397-403.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and methods of vegetation Ecology. Wiley, Toronto.

Nagy, J. A., and A. G. MacHutchon. 1991. Annual progress report - year 1 (1989/90), annual working plan - year 2 (1990/91) Khutzeymateen Valley grizzly bear study. Wildlife Working Report WR-48, Ministry of Environment, Victoria, B.C.

Noble, I. R., and G. Habiba. 1996. A functional classification for predicting the dynamics of landscapes. Journal of Vegetation Science **7**:329-336.

Noble, I. R., and R. O. Slatyer. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio **43**:5-21.

North, R., J. Q. Chen, G. Smith, L. Krakowiak, and J. Franklin. 1996. Initial response of understory plant diversity and overstory tree diameter growth to a green tree retention harvest. Northwest Science **70**:24-35.

Noyce, K. V., and P. L. Coy. 1990. Abundance and productivity of bear food species in different forest types of northcentral Minnesota. International Conference of Bear Research and Management **8**:169-181.

Oakley, B. B., and J. F. Franklin. 1998. Bitter cherry (*Prunus emarginata*) distribution, successional dynamics, and implications for the role of the seed bank. Canadian Journal of Botany **76**:1725-1732.

Ohmann, J. L., and M. J. Gregory. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, USA. Canadian Journal of Forest Research **32**:725-741.

Ohmann, J. L., and T. A. Spies. 1998. Regional gradient analysis and spatial pattern of woody plant communities of Oregon forests. Ecological Monographs **68**:151-182.

Oliver, C. D. 1981. Forest development in North America following major disturbances. Forest Ecology and Management **3**:153-168.

Oliver, C. D., and B. C. Larson. 1990. Forest stand dynamics. McGraw-Hill, New York.

Perry, R. W., R. E. Thill, D. G. Peitz, and P. A. Tappe. 1999. Effects of different silvicultural systems on initial soft mast production. Wildlife Society Bulletin **27**:915-923.

Peterson, E. B., and B. McCune. 2001. Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in Western Oregon. Journal of Vegetation Science **12**:511-524.

Phillips, D. L., and D. J. Shure. 1990. Patch-size effects on early succession in southern Appalachian Forests. Ecology **71**:204-212.

Pickett, S. T. A. 1982. Population patterns through twenty years of oldfield succession. Vegetatio **49**:45-59.

Pickett, S. T. A., S. L. Collins, and J. J. Armesto. 1987. Models, mechanisms and pathways of succession. The Botanical Review **53**:335-371.

Pitkanen, S. 1997. Correlation between stand structure and ground vegetation: an analytical approach. Plant Ecology **131**:109-126.

Platt, W. J., and J. H. Connell. 2003. Natural disturbances and directional replacement of species. Ecological Monographs **73**:507-522.

Pojar, J., K. Klinka, and D. Demarchi. 1991. Coastal Western hemlock Zone. Pages 95-112 *in* J. Pojar, editor. Ecosystems of British Columbia. Research Branch, Ministry of Forests, Victoria.

Pojar, J., K. Klinka, and D. V. Meidinger. 1987. Biogeoclimatic ecosystem classification in British Columbia. Forest Ecology and Management **22**:119-154.

Pojar, J., and A. MacKinnon. 1994. Plants of Coastal British Columbia. Lone Pine Publishing, Edmonton, Alberta.

Pojar, J., R. Trowbridge, and D. Coates. 1984. Ecosystem classification and interpretation of the Sub-Boreal Spruces zone, Prince Rupert Forest Region, British Columbia BC. Land Management Report 17, Ministry of Forests, BC.

Prescott, C. E. 1997. Effects of clearcutting and alternative silvicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. Forest Ecology and Management **95**:253-260.

Rabotnov, T. A. 1986. Types of plant strategies. Soviet Journal of Ecology **16**:123-130.

Ramenskii, L. G. 1935. Principal apparatus, major concepts, and terms in the production typology of lands, geobotany, and ecology. Soviet Botany **4**:25-42.

Ramenskii, L. G. 1938. Introduction to comprehensive soil - geobotanical study of lands (in Russian), Sel'khozgiz, Moscos.

Reader, R. J., and B. D. Bricker. 1992. Value of selectively cut deciduous forest for understory herb conservation - an experimental assessment. Forest Ecology and Management **51**:317-327.

Rice, W. 1989. Analyzing tables of statistical tests. Evolution **43**:223-225.

Roberts, M. R., and L. X. Zhu. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. Forest Ecology and Management **155**:17-31.

Roburn, A. E. 2003. Light transmission and understory vegetation in two old-growth riparian stands: A study in spatial pattern. Master of Resource Management. Simon Fraser University, Burnaby, BC.

Rochele, J. A. 1980. Mature forests, literfall and patterns of forage quality as factors in the nutrition o black-tailed deer on Northern Vancouver Island. Ph.D. thesis. University of British Columbia, Vancouver, BC.

Rose, C. R. 1994. Relationship of green-tree retention following timber harvest to forest growth and species composition in the western Cascade Mountains. Master of Science. Oregon State University, Corvallis.

Rose, C. R., and P. S. Muir. 1997. Green-tree retention: Consequences for timber production in forests of the western Cascades, Oregon. Ecological Applications **7**:209-217.

Schoonmaker, P., and A. McKee. 1988. Species composition and diversity during secondary succession of coniferous forests in western Cascade Mountains of Oregon. Forest Science. **34**:960-979.

Shugart, H. H. 1997. Plant and ecosystem functional types. Pages 20-43 *in* Plant functional types their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, New York.

Spies, T. A. 1991. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington. Pages 91-109 *in* M. H. Huff, editor. Wildlife and vegetation of unmanaged Douglas-fir forests. PNW General Technical Report 285, USDA Forest Service.

Spies, T. A. 1997. Forest stand structure, composition, and function. *in* K.A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, DC.

Spies, T. A., and J. F. Franklin. 1988. Old growth and forests dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal **8**:190-201.

Spies, T. A., J. F. Franklin, and M. Klopsch. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. Canadian Journal of Forest Research **20**:649-658.

SPSS Inc. 1999. SPSS Base 10.0 Users Guide. SPSS Inc., Chicago, IL.

Stamp, J. P. 2003. Abundance of Forage Plants and Seasonal Habitat Value for Grizzly Bears in the North Cascades, British Columbia. Master of Resource Management. Simon Fraser University, Burnaby, B.C.

Stewart, G. H. 1988. The influence of canopy cover on understory development in forests of the western Cascade Range, Oregon. Vegetatio **76**:79-88.

Sullivan, T. P., D. S. Sullivan, and P. M. F. Lindgren. 2001. Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. Journal of Applied Ecology **38**:1221-1233.

Swanson, F. J., J. A. Jones, and G. E. Grant. 1997. The physical environment as a basis for managing ecosystems. *in* K.A. Kohm and J. F. Franklin, editors. Creating a forestry for the 21st century: the science of ecosystem management. Island Press, Washington, DC.

Tabachnik, B. G., and L. S. Fidell. 1989. Using Multivariate Statistics, 2 nd edition. Harper and Row, New York.

Tabachnik, B. G., and L. S. Fidell. 2001. Using Multivariate Statistics, 3 rd edition. Allyn and Bacon, Boston.

Tappeiner, J. C., and P. B. Alaback. 1989. Early establishment and vegetative growth of understory species in the western hemlock - Sitka spruce forests in southeast Alaska. Canadian Journal of Botany. **67**:318-326.

Tappeiner, J. C., and J. C. Zasada. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. Canadian Journal of Forest Research **23**:1775-1780.

Taylor, R. L., and B. MacBryde. 1977. Vascular plants of British Columbia: a descriptive resource inventory. Technical Bulletin 4, University of British Columbia Botanical Garden, Vancouver, BC.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton.

Traut, B. H., and P. S. Muir. 2000. Relationships of remnant trees to vascular undergrowth communities in the Western Cascades: a retrospective approach. Northwest Science **74**:212-223.

van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. Vegetatio **39**:97-114.

Vanha-Majamaa, I., and J. Jalonen. 2001. Green tree retention in Fennoscandian forestry. Scandinavian Journal of Forest Research Suppl. **3**:79-90.

Wagner, R. G., and J. C. Zasada. 1991. Integrating plant autecology and silvicultural activities to prevent forest vegetation management problems. Forestry Chronicle **67**:506-513.

Wells, R. W. 1996. Developmental trends of stand structure and tree mortality in coastal western hemlock forests. Master of Resource Management. Simon Fraser University, Burnaby, BC.

Wells, R. W., K.P. Lertzman, and S.C. Saunders. 1998. Old-growth definitions for the forests of British Columbia, Canada. Natural Areas Journal **18**:279-292.

Williamson, R. L., and R. H. Ruth. 1976. Results of shelterwood cutting in western hemlock. U.S. Forest Service Research Paper. PNW-201.

Willson, M. F., and P. E. Hennon. 1997. The natural history of western skunk cabbage (*Lysichiton americanum*) in southeast Alaska. Canadian Journal of Botany **75**:1022-1025.

Wimberly, M. C., and T. A. Spies. 2001. Influences of environment and disturbance on forest patterns in coastal Oregon watersheds. Ecology **82**:1443-1459.

Woodward, F. I., and C. K. Kelly. 1997. Plant functional types: towards a definition by environmental constraints. Pages p. 47-65. *in* Plant functional types their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge; New York.

Yarie, J. 1980. The role of understory vegetation in the nutrient cycle of forested ecosystems in the mountain hemlock biogeoclimatic zone. Ecology **61**:1498-1514.

Zager, P. 1980. The influence of logging and wildfire on grizzly bear habitat in northwestern Montana. Ph.D. dissertation. University of Montana, Missoula, MT.

Zar, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ.

Zenner, E. 1995. Effects of residual trees on growth of young to mature Douglas-fir and western hemlock in the western central Oregon Cascades. Master of Science Thesis. Oregon State University, Corvallis, Oregon.

Zenner, E. K. 2000. Do residual trees increase structural complexity in pacific northwest coniferous forests? Ecological Applications **10**:800-810.

Zimmerman, G. M., H. Goetz, and P. W. Mielke. 1985. Use of an improved statistical method for group comparisons to study effects of prairie fire. Ecology **66**:601-611.

Table 1. Comparison of different models of distinct stages of forest development. I excluded "early" structural stages from this table because my data did not contain plots in those structural stages. I adapted this table in part from Franklin et al. (2002).

Typical stand age[1] (BC Ministry of Environment Lands and Parks and Ministry of Forests 1998, Franklin et al. 2002)	BC Ministry of Environment, Lands and Parks and Ministry of Forests (1998) (*used in this analysis*)	Oliver and Larson (1990)	Franklin et al. (2002)
20	(3) Shrub/Herb	Stand initiation	Cohort establishment
			Canopy closure
30	(4) Pole/Sapling	Stem exclusion	
	(5) Young Forest		Biomass accumulation/ Competitive exclusion
80-250	(6) Mature Forest	Understory reinitiation	Maturation
150->250	(7) Old Forest	Old-growth	
			Vertical diversification Horizontal diversification
800			
			Pioneer cohort loss

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[1] Provincial data (BC Ministry of Environment Lands and Parks and Ministry of Forests 1998) is limited to values for the CWH zone. Data from Franklin et al. (2002) is based on Douglas-fir (*Pseudotsuga menziesii*) – western hemlock (*Tsuga heterophylla*) forests in the Pacific Northwest.

Table 2 List of variables related to environmental factors and assemblages of forage plants.

Variable name	Character	Units or symbol description	Variable type[a]
Variables related to terrain, soil, and climatic conditions			
ELEV	elevation	meters	Q
n/a	soil nutrient class	L = low, H = high, ? = unknown (see Table 6 for details)	C
n/a	soil moisture class	L = low, M = medium, H = high (see Table 6 for details)	C
n/a	biogeoclimatic variant	xm2, vm1, vm2	C
Variables related to the tree overstory			
TREET	crown cover of all trees > 2 meters tall	percentage cover per plot	Q
A1 – A3	crown cover of trees > 10 meters tall	percentage cover per plot	Q
BASAL	basal area of trees and snags with a diameter at breast height > 17.5 cm	m^2 per hectare	Q
MEAND	Mean diameter at breast height of trees and snags with a diameter at breast height > 17.5 cm	centimeters	Q
DBH3	live trees with an average diameter of 57 – 76 cm	centimeters	Q
GREEN	all live stems	stems per hectare	Q
n/a	structural stage	(3) = Shrub/Herb, (4) = Pole/Sapling, (5) = Young Forest, (6) = Mature Forest, (7) = Old Forest structural stage	C

Table 2 continued

Variable name	Character	Units or symbol description	Variable type^a
Variables related to assemblages of forage plants			
Alpha	richness of forage plants	number of species per plot	Q
TOTAL	abundance of all forage plants	percentage cover per plot	Q
SHADE	abundance of forage species that are shade intolerant (see Table 3)	percentage cover per plot	Q
MOIST	abundance of forage species indicative of very moist to very wet soils (see Table 3)	percentage cover per plot	Q
Nhigh	abundance of forage species indicative of nutrient rich soils (see Table 3)	percentage cover per plot	Q
% RESID	abundance of all residuals divided by TOTAL	percentage cover per plot	Q
INVA	abundance of all invasive forage plants	percentage cover per plot	Q
InSh	abundance of all invasive forage shrubs	percentage cover per plot	Q
InFo	abundance of all invasive forage forbs	percentage cover per plot	Q
GRAM	abundance of all forage graminoids	percentage cover per plot	Q
Rubus	abundance of all forage *Rubus* species	percentage cover per plot	Q
VACCT	abundance of all forage *Vaccinium* species excluding *Vaccinium parvifolium*	percentage cover per plot	Q
VACCPAR	abundance of *Vaccinium parvifolium*	percentage cover per plot	Q
GAULSHA	abundance of *Gaultheria shallon*	percentage cover per plot	Q
DRYOEXP	abundance of *Dryopteris expansa*	percentage cover per plot	Q

Table 2 continued

Variable name	Character	Units or symbol description	Variable type[a]
Variables related to assemblages of forage plants (continued)			
ATHYFIL	abundance of *Athyrium filix-femina*	percentage cover per plot	Q
TRAU	abundance of *Trautvetteria caroliniensis*	percentage cover per plot	Q
Variables related to forage plants grouped by season of consumption[b]			
Fol S	foliage important as spring forage	percentage cover per plot	Q
Fol Su	foliage important as summer forage	percentage cover per plot	Q
Fol F	foliage important as fall forage	percentage cover per plot	Q
Fr Su	fruit important as summer forage	percentage cover per plot	Q

[a] Q = quantitative, C = categorical

[b] list of forage plants grouped by season of consumption adopted from MacHutchon (1996)

Table 3. Important autecological characteristics of black bear forage plants occurring in the Nimpkish Valley, B.C.
I adapted all information from Klinka et. al. (1989), Pojar and MacKinnon (1994), and Meidinger et. al. (2002).

Residual Species	Soil Nutrient Regime	Soil Moisture Regime	Occurrence with elevation	Shade tolerance	Wetland indicator
Trautvetteria caroliniensis	rich	fresh to very moist	decreases with increasing elevation[a]	shade tolerant to intolerant	?
Cornus stolonifera	rich	very moist to wet	decreases with increasing elevation[a]	shade tolerant / intolerant	indicative
Athyrium filix-femina	rich	very moist to wet	all	shade tolerant	facultative
Lonicera involucrata	rich	very moist to wet	low to subalpine	shade tolerant / intolerant	facultative
Oplopanax horridus	rich	very moist to wet	low to middle	shade tolerant	?
Lysichiton americanum	rich	wet to very wet	low to middle	shade tolerant / intolerant	indicative
Rosa gymnocarpa	medium	very dry to moderately dry	decreases with increasing elevation[a]	shade tolerant / intolerant	?
Dryopteris expansa	medium	fresh to very moist	low to subalpine	shade tolerant	facultative
Gaultheria shallon	poor	?	decreases with increasing elevation[a]	shade tolerant	facultative
Vaccinium parvifolium	poor	?	decreases with increasing elevation[a]	shade tolerant	?
Vaccinium alaskaense	poor	fresh to very moist	low to subalpine	shade tolerant	facultative
Vaccinium ovalifolium	poor	fresh to very moist	low to subalpine	shade tolerant	facultative
Vaccinium sp. of minor importance	variable	variable	variable	variable	variable

Table 3 continued

Invasive Species	Soil Nutrient Regime	Soil Moisture Regime	Occurrence and elevation	Shade tolerance	Wetland indicator
(*Populus balsamifera ssp trichocarpa)*	rich	fresh to very moist	decreases with increasing elevation[a]	Shade intolerant	facultative
Epilobium angustifolium	rich	?	decreases with increasing elevation[a]	very shade intolerant	indicative
Ribes bracteosum	rich	very moist to wet	decreases with increasing elevation[a]	shade tolerant / intolerant	facultative
Rubus spectabilis	rich	very moist to wet	decreases with increasing elevation[a]	shade tolerant / intolerant	facultative
Sambucus racemosa	rich	fresh to very moist	decreases with increasing elevation[a]	shade tolerant to shade tolerant / intolerant	facultative
Rubus parviflorus	rich	?	decreases with increasing elevation[a]	shade tolerant / intolerant	facultative
Cirsium arvense	rich	?	low to middle	no info.	?
Lactuca muralis	rich	fresh to very moist	low to middle	shade tolerant / intolerant	?
Rubus ursinus	medium	moderately dry to fresh	decreases with increasing elevation[a]	shade tolerant / intolerant	?
Equisetum sp. (values are for *Equisetum arvense)*	medium	(water receiving sites)	low to alpine	shade tolerant / intolerant	facultative
Fragaria sp.	none - medium	none – moderately dry and fresh	decreases with increasing elevation[a]	mostly shade intolerant	?
Carex sp.	variable	variable	variable	mostly shade intolerant	variable
Grantminae	variable	variable	variable	variable	variable
Hypochaeris radicata	?	?	decreases with increasing elevation[a]	shade tolerant / intolerant	?
Prunus emarginata	?	(moist forests and along streams)	low to middle	no info.	?

[a] elevation description after Klinka et. al. (1989), all other elevation descriptions after Pojar and MacKinnon (1994). ? the plant was either not evaluated or the plant's indicator status is unknown or variable.

Table 4. Measures of species diversity for all plants and for various groups of bear forage plants.
Alpha diversity is the average species richness per plot. *Beta* diversity is the total number of species divided by the *Alpha* diversity.

Group	*Alpha* diversity	Standard deviation	Coefficient of variation (%)	*Beta* diversity	Total number of species	N
All plant species	15.2	5.5	36	9.0	136	133
All shrub species	3.5	1.7	49	8.3	29	133
All herb species	6.0	4.1	68	9.8	59	133
All bear forage species	4.8	2.6	54	5.8	28	133
Bear forage species per functional group						
Invasives	2.0	2.0	100	7.5	15	133
Residuals	2.8	1.3	46	4.6	13	133
Bear forage species per variant						
CWHxm2	4.4	2.5	57	5.7	25	86
CWHvm1	6.4	2.6	41	3.3	21	26
CWHvm2	4.5	2.0	44	3.1	14	21
Bear forage species per structural stage						
Shrub/Herb	6.5	2.4	37	3.7	24	42
Pole/Sapling	5.9	2.7	46	3.6	21	14
Young Forest	3.5	2.2	63	6.0	21	34
Mature Forest	2.8	1.6	57	6.4	18	25
Old Forest	4.4	1.8	41	3.9	17	18
Bear forage species per nutrient class[a]						
Low	3.9	2.0	51	5.4	21	75
High	6.0	2.8	47	4.3	26	54
Low	3.6	1.9	53	5.3	19	27
Medium	4.2	2.5	60	5.0	21	62
High	6.4	2.3	36	4.1	26	44

[a]Low soil nutrient class corresponds to very poor to medium and high soil nutrient class corresponds to rich to very rich soil nutrient regime(see Green and Klinka 1994 for details). [b]Low soil moisture class corresponds to very dry to medium dry, medium soil moisture class corresponds to slightly dry to fresh, and high soil moisture class corresponds to very moist to wet soil moisture regime (see Green and Klinka 1994 for details).

Table 5. MRPP comparison of community structure of forage plants consumed by black bears in the Nimpkish Valley, BC.
P is the probability of Type 1 error for the H_0 of no differences between groups.

Grouping variable:	Number of groups	Chance corrected within-group agreement (A)	P
Variant	3	0.221	<<0.001
Bear Habitat Type[a] (BBHT)	7	0.402	<<0.001
Site series[b] (per variant)	17	0.511	<<0.001
Soil moisture class (high nutrient class only)	3	0.100	< 0.001
Soil nutrient class (high moisture class only)	2	0.117	< 0.001
Structural stage (xm2)	5	0.136	<<0.001
Structural stage (vm1)	4	0.267	< 0.001
Structural stage (vm2)	5	0.015	0.363

See Table 1, 2 and 4 for details on soil nutrient and moisture classes and structural stages.

[a] Black Bear Habitat Types (BBHTs) are site series combined across and within variants based on similarities in moisture and nutrient regimes (Davis 1996).

[b] Site series indicate a site's soil nutrient and moisture regime, usually for a given variant (see Meidinger and Pojar 1991, Green and Klinka 1994 for further details).

Table 6. Maximum Indicator Values (IV_{max}) for forage plants consumed by black bears in the Nimpkish Valley, British Columbia.
I only reported IV_{max} values significant at least at the $\alpha = 0.05$ level.

Species	Frequency of occurrence (% of all plots)	IV_{max} per grouping variable			
		Soil Nutrient class^{b} (low or high)	Soil Moisture class^{a} (low, medium, or high)	Variant (xm2, vm1, or vm2)	Structural stage^{c}, xm2 and vm1 only (3,4,5,6, or 7)
RESIDUALS					
Athyrium filix-femina	36	67.2 (high)	71.0 (high)		
Dryopteris expansa	32	43.4 (high)	27.6 (high)		25.3* (4)
Trautvetteria caroliniensis	13	29.3 (high)	30.0 (high)	19.8* (vm1)	20.2* (7)
Oplopanax horridus	5	11.1 (high)	13.6 (high)	23.1 (vm1)	
Cornus stolonifera	8	8.9* (high)	13.0 (high)		
Gaultheria shallon	55	72.8 (low)	58.3 (low)	46.4 (xm2)	
Vaccinium ovalifolium	29		23.5* (high)	70.9 (vm2)	24.1* (7)
Lysichiton americanum	5		13.6 (high)		
Vaccinium sp.	2		7.0* (low)	9.5* (vm2)	
Vaccinium alaskaense	16			50.9 (vm2)	
Vaccinium parvifolium	77			41.1* (xm2)	
Rosa gymnocarpa	5				13.0* (7)
Lonicera involucrata	2				
INVASIVES					
Rubus spectabilis	52	78.2 (high)	74.0 (high)	44.3 (vm1)	
Sambucus racemosa	17	33.1 (high)	32.4 (high)	19.9* (vm1)	
Rubus parviflorus	21	25.8 (high)		25.2 (vm1)	28.7 (4)
Graminae.	14	22.4 (high)	20.2 (high)		
Carex sp.	7	11.1 (high)	20.5 (high)		
Equisetum sp.	2				
Rubus ursinus	20			29.4 (xm2)	
Epilobium angustifolium	29			26.7* (vm1)	77.6 (3)
Lactuca muralis	20				24.6 (3)
Hypochaeris radicata	6				20.8* (3)
Cirsium arvense	<1				
Fragaria sp.	2				
Prunus emarginata	5				12.5* (4)
Ribes bracteosum	2				
Populus balsamifera	2				

Note: Species with very low occurrence can not be statistically significant.
* Significant at the $\alpha = 0.05$ level. All other values are significant at the $\alpha = 0.01$ level.
[a] Low soil moisture class corresponds to very dry to medium dry, medium soil moisture class corresponds to slightly dry to fresh, and high soil moisture class corresponds to very moist to wet soil moisture regime (see Green and Klinka 1994 for details).
[b] Low soil nutrient class corresponds to very poor to medium and high soil nutrient class corresponds to rich to very rich soil nutrient regime (see Green and Klinka 1994 for details).
[c](3) corresponds to the Shrub/Herb, (4) to Pole/Sapling, (5) to Young Forest, (6) to Mature Forest, and (7) to Old Forest structural stage (for details see BC Resources Inventory Committee 1998).

Table 7. Multiple MRPP comparison of community structure of forage plants between structural stages in the CWHxm2 and vm1 variant.
P is the probability of Type 1 error for the H_0 of no differences between groups.
(Caution: I was not able to block for effects of soil nutrient/ moisture and elevation).

Structural stage (*n*)	Chance corrected within-group agreement (A)	P
3 (33) vs. 4 (10)	0.028	0.066
3 (33) vs. 5 (34)	0.112	<<0.001
3 (33) vs. 6 (22)	0.141	<<0.001
3 (33) vs. 7 (13)	0.128	<<0.001

Note: the sequential Bonferroni correction (Rice 1989) does not change the significance of the within-group agreement at $\alpha = 0.001$. See Table 1 and 4 for details on structural stages.

Table 8. Management guidelines for choosing forested sites for protection and active management of foraging habitat.
These guidelines are tailored to maintain the short and long-term abundance of forage plants grouped by season of consumption. Guidelines are based on findings from my data analyses as well as on my review of autecological literature (see Table 3).

	Management objectives		
	• Protection of foraging habitat (*If desired, consider guidelines 1 and 2 only*)		• Increase of short and long-term abundance of forage (only applicable when very low forage abundance due to a dense tree overstory) (*If desired, consider guidelines 1, 2, and 3*) • Timber harvesting (when unavoidable) (*If desired, consider guidelines 1, 2, and 3*)
	Guidelines		
	1. Sites with higher soil nutrient and moisture content are more important than sites with lower soil nutrient and moisture content (yes / no[b])	2. Sites identified in 1. that occur at "higher" elevation are more important than lower elevation sites (yes[c]/ no[d])	3. On sites identified in 1. and 2., use "alternative"[e] harvesting regimes
Forage group[a]			
Foliage Spring	yes	yes[c]	yes
Foliage Summer	no[b]	no[d]	yes
Foliage Fall	yes	yes[c]	yes (but increase in forage likely minimal)
Fruit Spring	*	*	yes
Fruit Summer	no[b]	no[d]	yes
Fruit Fall	*	*	yes

[a] the name of a forage group describes the part of the plant important for consumption and the season of consumption. Foliage forage groups include graminoids and *Equisetum* species. *Lysichitum americanum* is the only member of the forage group with

roots or corms important for consumption in the study area and should thus be managed individually.

[b] choose sites so all nutrient/moisture regimes are represented

[c] choose sites so all elevations / variants are represented but emphasize higher elevation sites including the vm2 variant.

[d] choose sites so all elevations / variants are represented but emphasize lower elevation sites including the xm2 and vm1 variant.

[e] i.e. low to medium levels of variable retention. As well, canopy closure should be delayed as long as possible, in addition to avoiding vegetation management treatments

*heterogeneous species ecologies or low abundance of forage plants in study area, manage individual species (see Table 2 for information on how to select the appropriate soil nutrient/moisture regime and elevation).

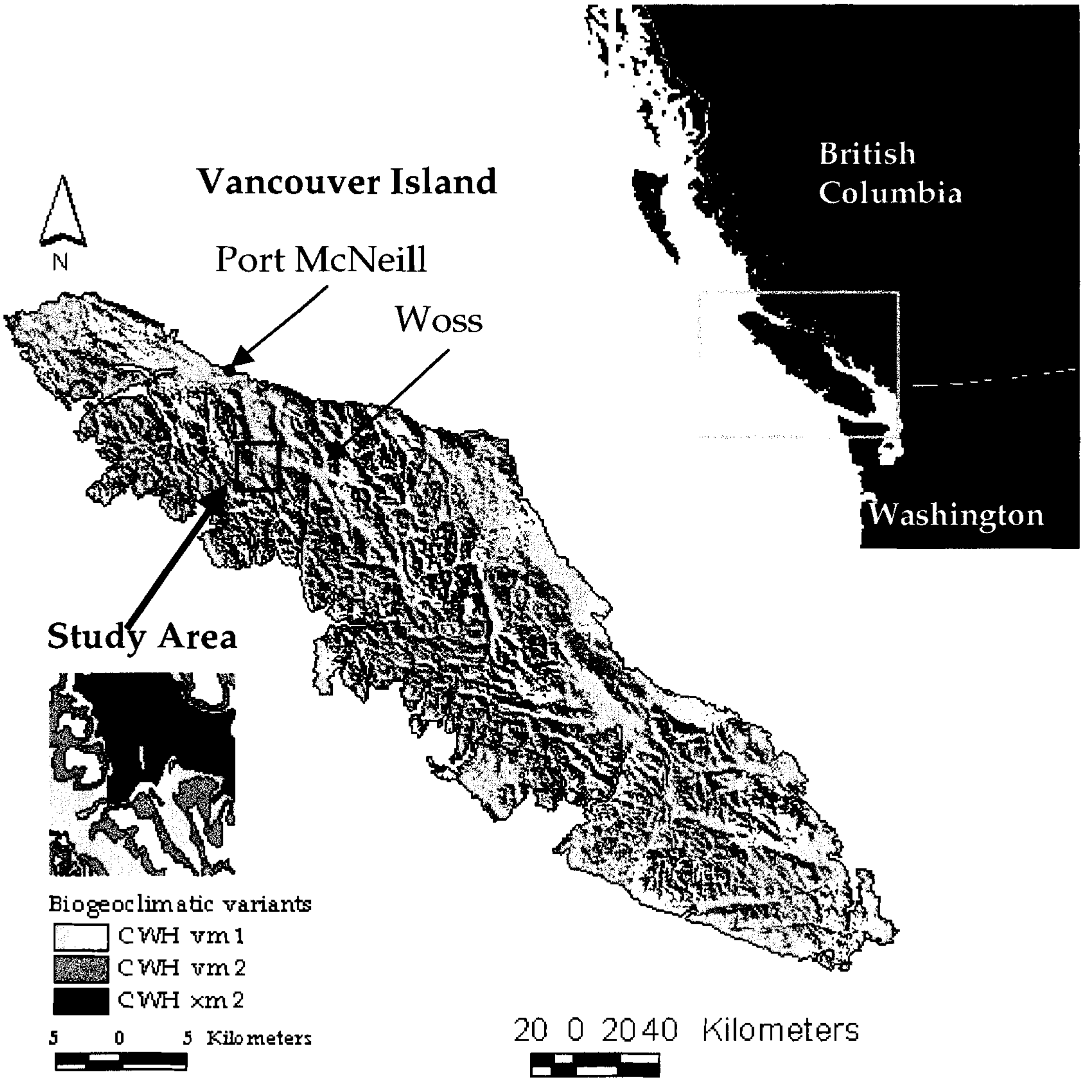

Figure 1. Location of the study area in the Nimpkish Valley on Vancouver Island, British Columbia.
Sources of the GIS data: hillshade coverage from the Ministry of Forests (1999), biogeoclimatic coverage from the Ministry of Sustainable Resource Management (2003). Biogeoclimatic variants are as follows: western variant of the very dry maritime CWH zone (CWHxm2), submontane variant of the very wet maritime CWH subzone (CWHvm1), and montane variant of the very wet maritime CWH subzone (CWHvm2).

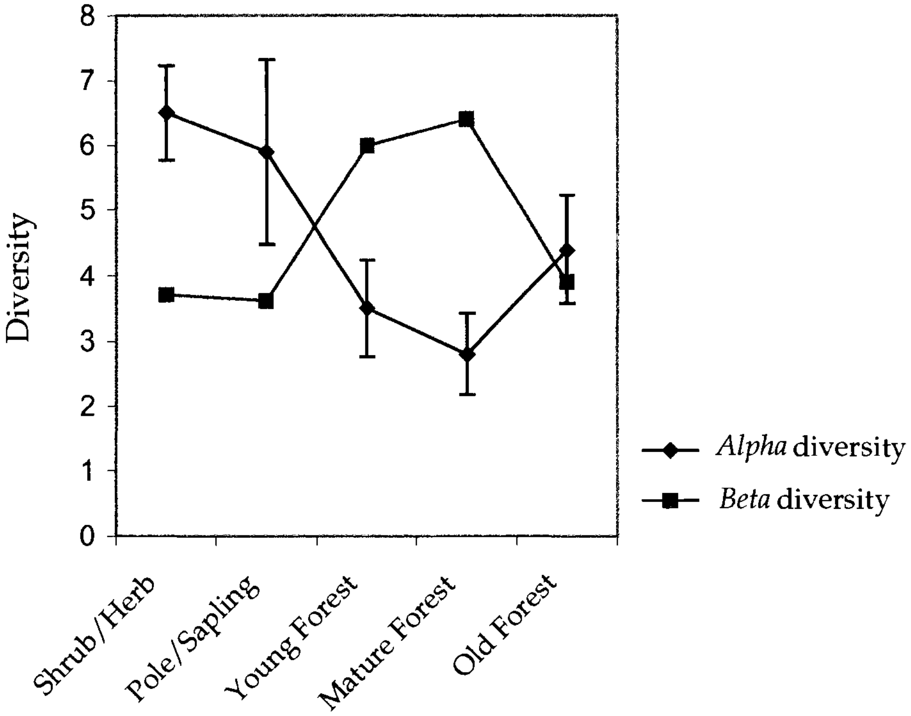

Figure 2 Relationship between *Alpha* diversity and *Beta* diversity of forage plants and structural stage.

Alpha diversity is the average species richness of forage plants per plot. *Beta* diversity is the total number of observed forage species divided by *Alpha* diversity. Error bars are 95 % confidence intervals.

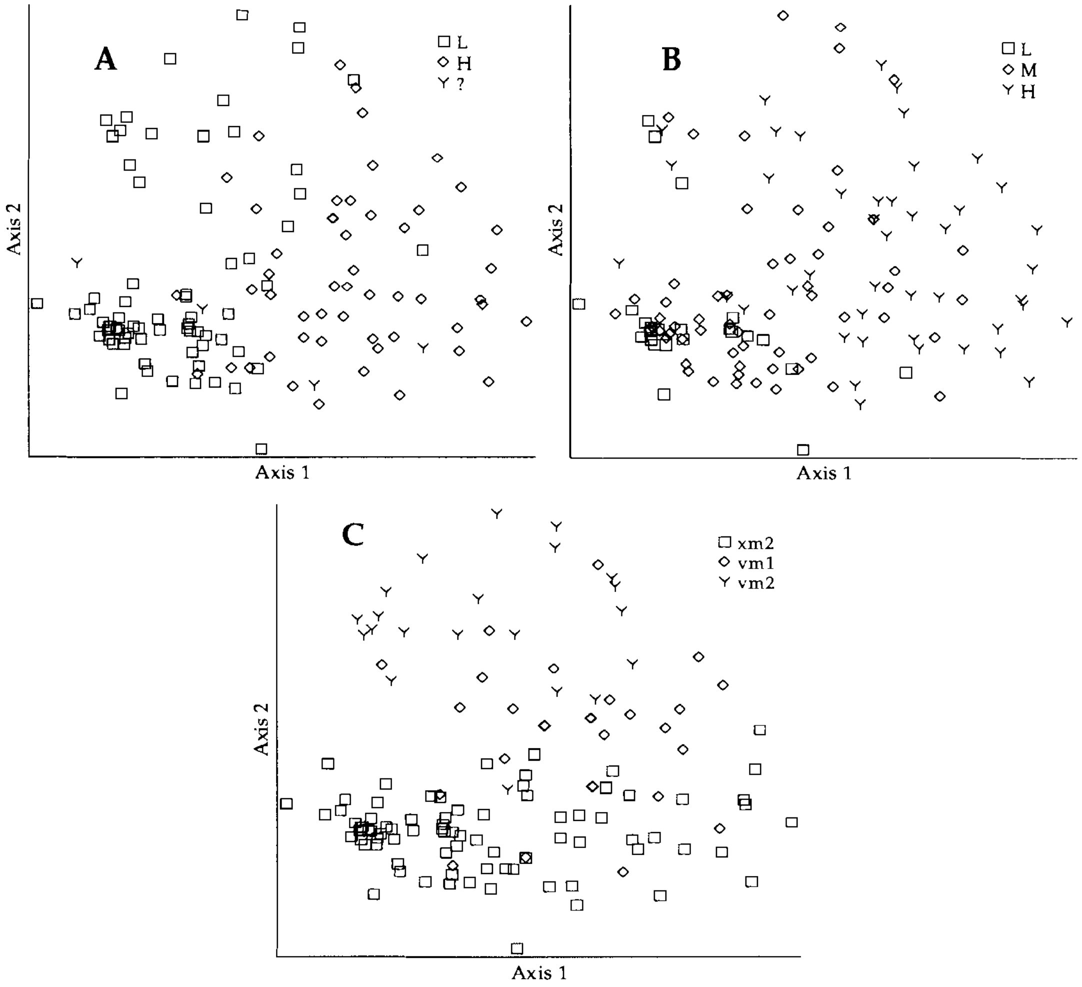

Figure 3. Ordination (NMS) of 133 plots in (forage) species space.
Axis 1 is related to soil nutrient and moisture content. Axis 2 is related to elevation. (**A**): Symbols code for soil nutrient classes (L = low, H = high, ? = unknown). Low soil nutrient class corresponds to very poor to medium and high soil nutrient class corresponds to rich to very rich soil nutrient regime (see Green and Klinka 1994 for details). (**B**): Symbols code for soil moisture classes (L = low, M = medium, H = high). Low soil moisture class corresponds to very dry to medium dry, medium soil moisture class corresponds to slightly dry to fresh, and high soil moisture class corresponds to very moist to wet soil moisture regime (see Green and Klinka 1994 for details). (**C**): Symbols code for biogeoclimatic variants of the CWH zone.

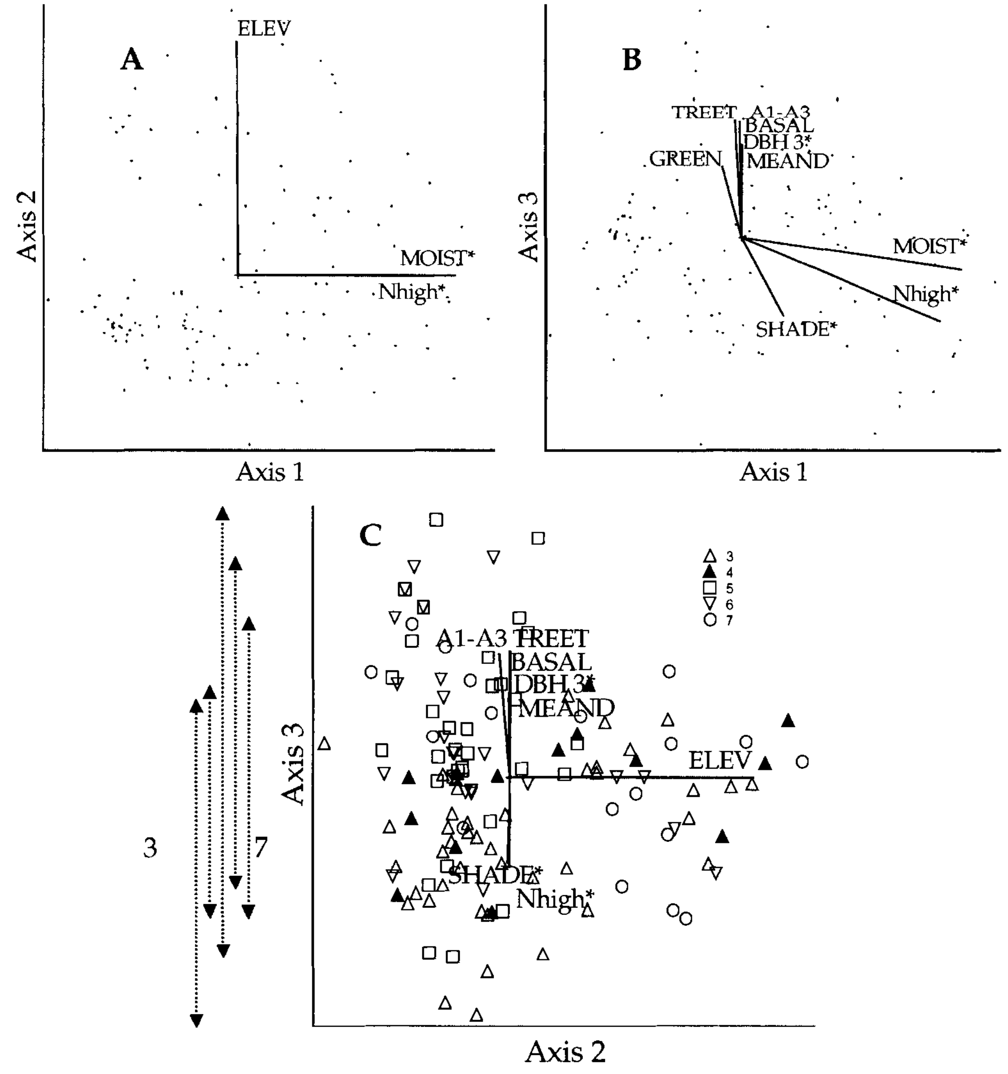

Figure 4. Ordination (NMS) of 133 plots in (forage) species space with correlation vectors of mostly "environmental variables".

Axis 1 is related to soil nutrient and moisture content. Axis 2 is related to elevation, and axis 3 is related to overstory dominance / contiguity. All correlation vectors have a $r^2 > 0.200$, and a r with a $p < 0.001$. Vectors represent the strength and direction of correlations between variables and axis scores (for visual clarity, I scaled vectors to 150 %). All variables coded with an * are log-transformed. (**A**): Variables are as follows: elevation (ELEV), forage species indicative of very moist to very wet soils (MOIST*) and nutrient rich soils (Nhigh*) (see Table 3 for details on these species). (**B** and **C**): Variables are as follows: total % cover of all trees (TREET), % cover of trees taller than 10 meters (A1 – A3), basal area and mean diameter of life trees and snags per ha including only trees that have a diameter > 17.5 cm (BASAL and MEAND respectively), live trees with an average diameter of 57 – 76 cm (DBH3*), the number of live stems per ha (GREEN), and forage species that are shade intolerant (SHADE*). (**C**): Symbols code for structural stages 3 to 7. For clarity, the lines to the left of the graph show the extent of the distribution of structural stages 3 to 7 along axis 3. Structural stage 3 = Shrub/Herb, 4 = Pole/Sapling, 5 = Young Forest, 6 = Mature Forest, 7 = Old Forest structural stage.

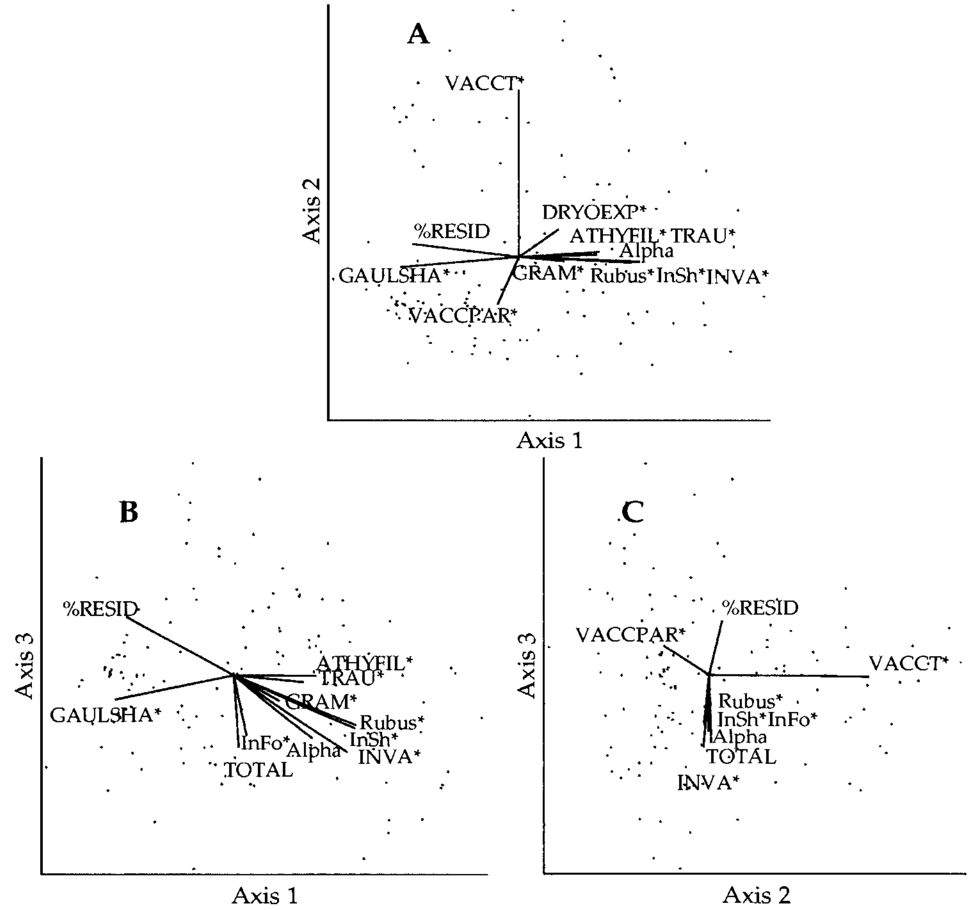

Figure 5. Ordination (NMS) of 133 plots in (forage) species space showing correlation vectors of both species diversity and abundance values of various groups of forage plants.

Axis 1 is related to soil nutrient and moisture content. Axis 2 is related to elevation, and axis 3 is related to overstory dominance / contiguity. Vectors represent the strength and direction of correlations between variables and axis scores. All correlation vectors have a $r^2 > 0.200$, and a r with a $p < 0.001$. Variables with an * are log-transformed. The variable relate to species diversity is forage plant richness (*Alpha*). All other variables are as follows: *abundance* of all forage plants (TOTAL*), all residual forage plants as % of the total abundance of all forage plants (% RESID), all invasive forage plants (INVA*), all invasive forage shrubs (InSh*), all invasive forage forbs (InFo*), all forage graminoids (GRAM*), all forage *Rubus* species (Rubus*), all forage *Vaccinium* species excluding *Vaccinium parvifolium* (VACCT*), *Vaccinium parvifolium* (VACCPAR*), *Gaultheria shallon* (GAULSHA*), *Dryopteris expansa* (DRYOEXP*), *Athyrium filix-femina* (ATHYFIL*), and *Trautvetteria caroliniensis* (TRAU*). See Table 3 for a list of various invasive and residual forage plants.

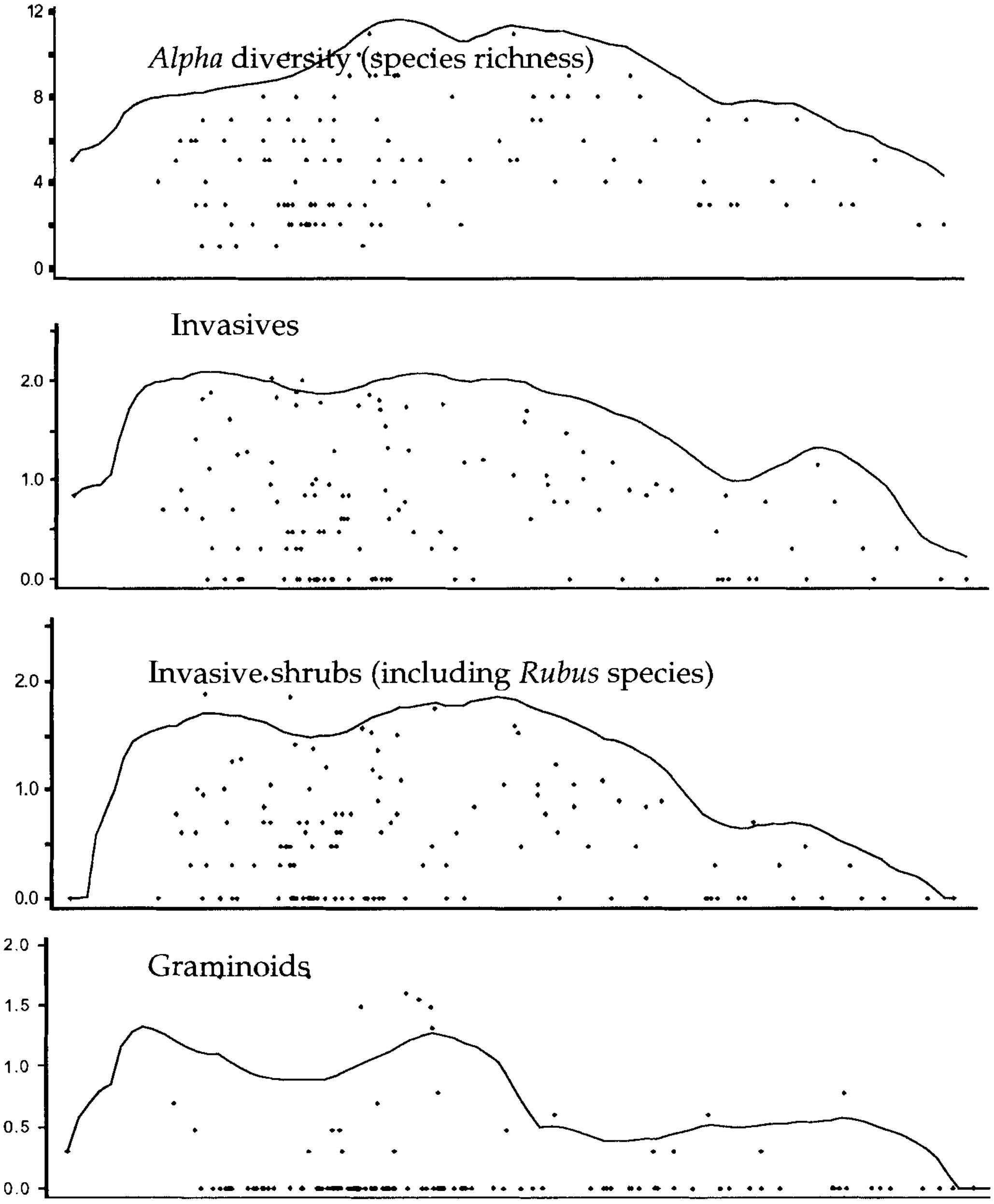

Figure 6. Scatter plots of *Alpha* diversity and the (log) abundance of various groups of invasive forage species in relation to ordination axis 2 (i.e., the gradient of increasing elevation).

Neither *Alpha* diversity nor any of the depicted forage species groups correlated strongly (where strong is $r^2>0.200$, $p<0.001$) with axis 2. Elevation increases from left to right. Points represent plots. The envelop line includes plots falling within 2 standard deviations of the running mean of *Alpha* diversity and the (log) abundance of species along the ordination axis.

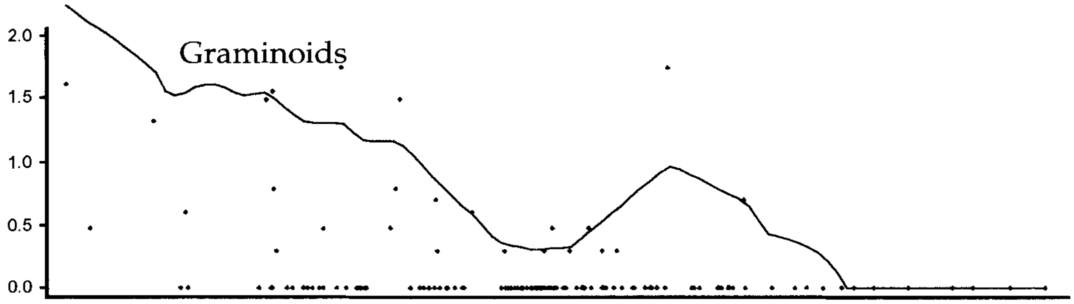

Figure 7. Scatter plot of the (log) abundance of graminoids in relation to ordination axis 3 (i.e., the gradient of increasing dominance and contiguity of the tree overstory). The abundance of graminoids did not correlate strongly ($r^2 > 0.200$, $p < 0.001$) with axis 3. Dominance and contiguity of the tree overstory increases from left to right. Points represent plots. The envelop line includes plots falling within 2 standard deviations of the (log) abundance of graminoids.

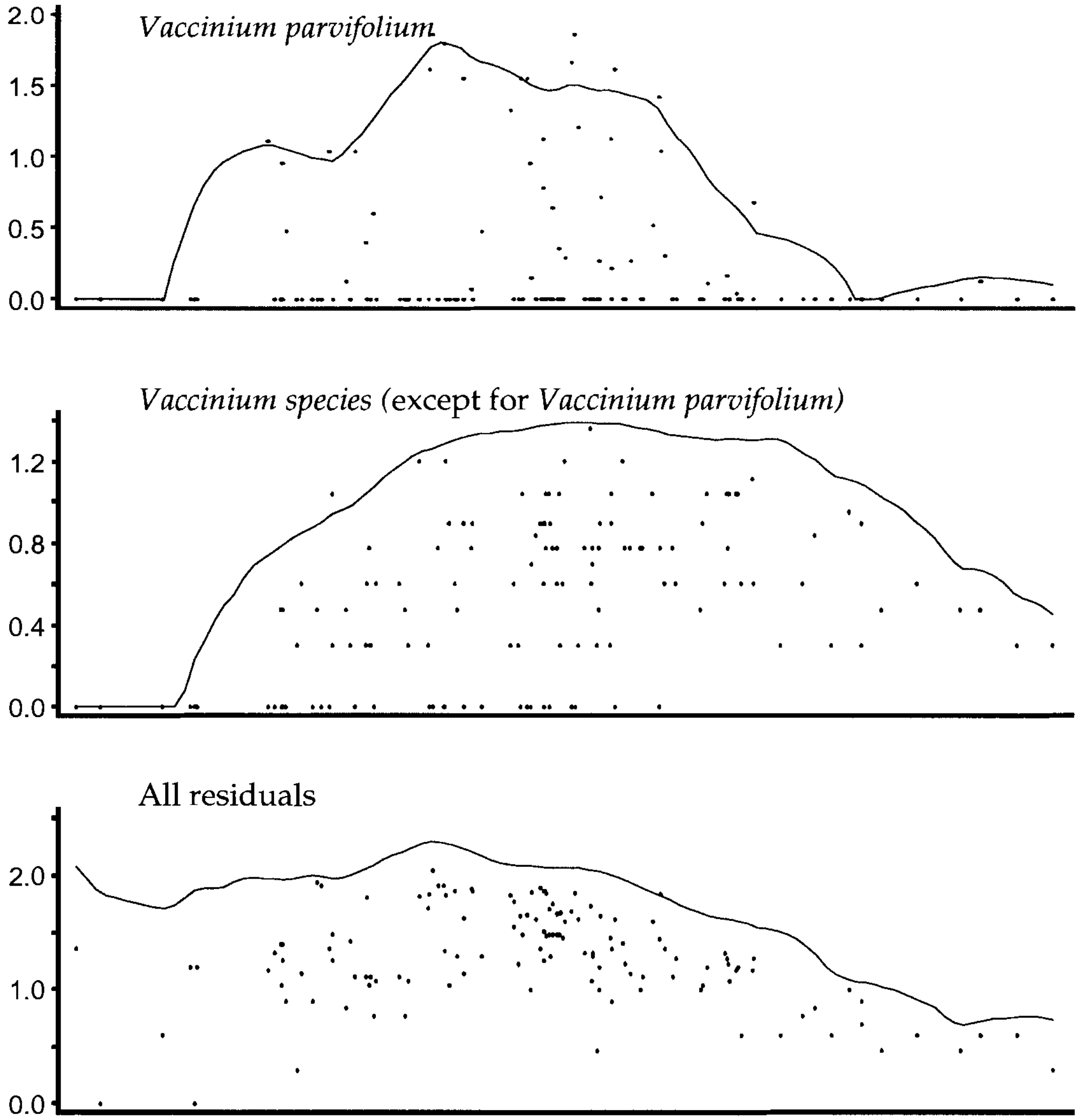

Figure 8. Scatter plot of the (log) abundance of *Vaccinium* forage species and all residual forage species in relation to ordination axis 3 (i.e., the gradient of increasing dominance and contiguity of the tree overstory).
None of these forage species groups correlated strongly (where strong is $r^2 > 0.200$, $p < 0.001$) with axis 3. Dominance and contiguity of the tree overstory increases from left to right. Points represent plots. The envelop line includes plots falling within 2 standard deviations of the running mean of the (log) abundance of species along the ordination axis.

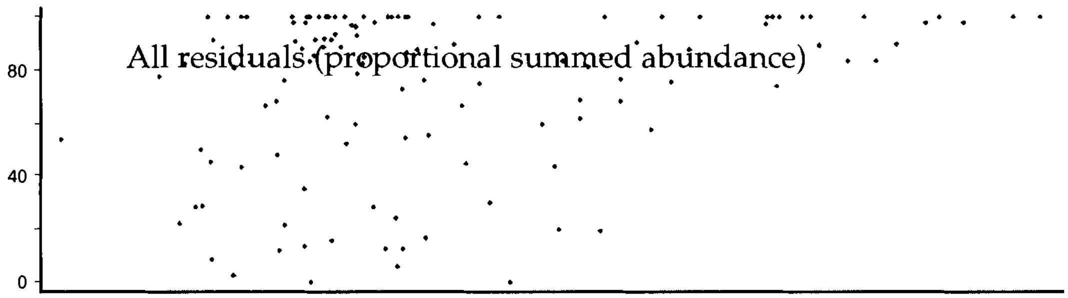

Figure 9. Scatter plot of the proportional summed abundance of all residual forage species in relation to ordination axis 2 (i.e., the gradient of increasing elevation). The summed proportional abundance of all residual forage plants did not correlate strongly (where strong is $r^2>0.200$, $p<0.001$) with axis 2. Elevation increases from left to right. Points represent plots.

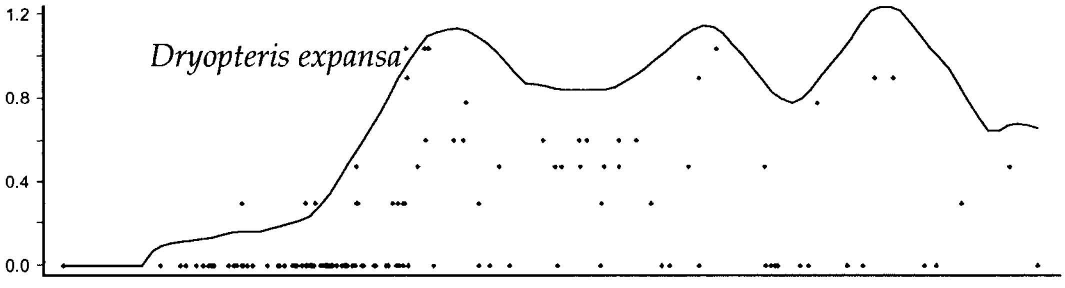

Figure 10. Scatter plot of the (log) abundance of *Dryopteris expansa* in relation to ordination axis 2 (i.e., the gradient related to elevation).
Dryopteris expansa did not correlate strongly (where strong is $r^2 > 0.200$, $p < 0.001$) with axis 2. Points represent plots. The envelop line includes plots falling within 2 standard deviations of the running mean of (log) abundance along the ordination axis.

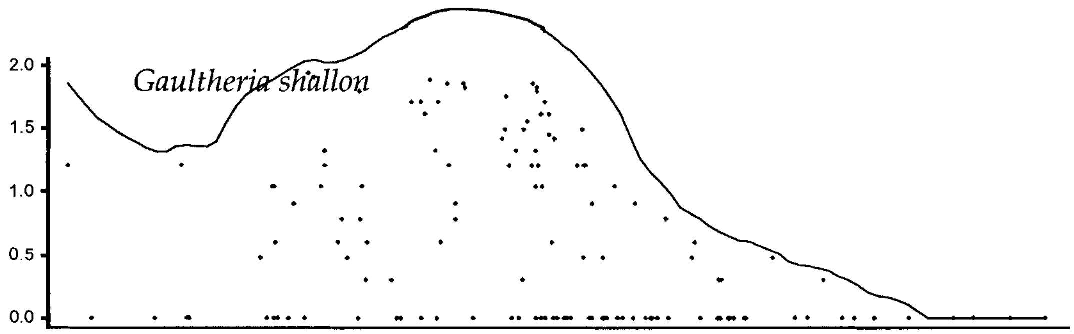

Figure 11. Scatter plot of the (log) abundance of *Gaultheria shallon* in relation to ordination axis 3 (i.e., the gradient of increasing dominance and contiguity of the tree overstory).
Gaultheria shallon did not correlate strongly (where strong is $r^2>0.200$, $p<0.001$) with axis 3. Dominance and contiguity of the tree overstory increases from left to right. Points represent plots. The envelop line includes plots falling within 2 standard deviations of the running mean of the (log) abundance along the ordination axis.

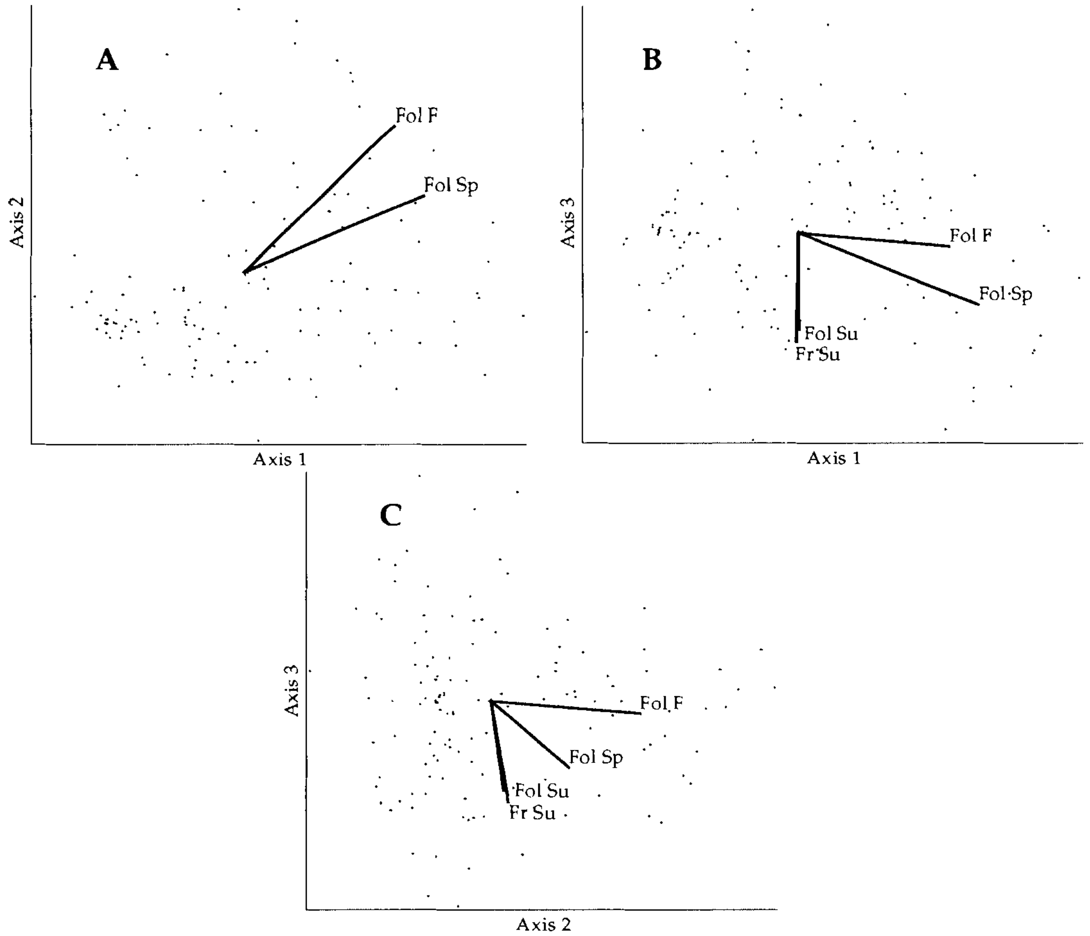

Figure 12. Ordination (NMS) of 133 plots in (forage) species space showing correlation vectors of forage plants grouped by seasonal importance.

Axis 1 is related to soil nutrient and moisture content. Axis 2 is related to elevation, and axis 3 is related to overstory dominance / contiguity. All correlation vectors have a $r^2 > 0.200$, and a r with a $p < 0.001$. Vectors represent the strength and direction of correlations between variables and axis scores. Except for Fol Su, all variables are log-transformed. Variables are as follows: forage plants with foliage important as spring forage (Fol S), summer forage (Fol Su), and fall forage (Fol F); forage plants with fruits important as summer forage (Fr Su). See MacHutchon (1993) for a list of forage plants grouped by season of consumption.

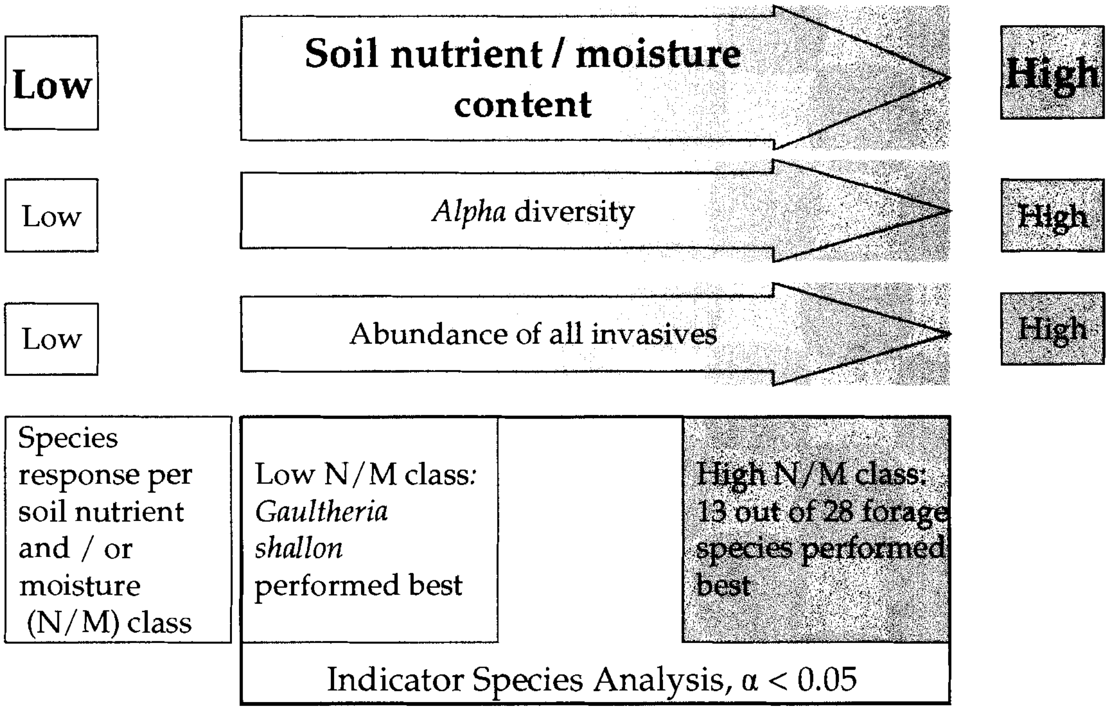

Figure 13. Summary of selected patterns of abundance of forage species and results from the indicator species analysis related to the gradient of increasing soil nutrient and moisture content (ordination axis 1).

Species response patterns represented by arrows have an $r^2>0.200$ and a r with a $p<0.001$. Soil nutrient classes are low and high, and soil moisture classes are low, medium, and high. None of the forage species performed best in medium moisture classes. See Table 6 for a definition of soil nutrient and moisture classes. For detailed results on species responses to the gradient related to soil nutrient and moisture content consult Table 4, 5, and 6 and Figure 5.

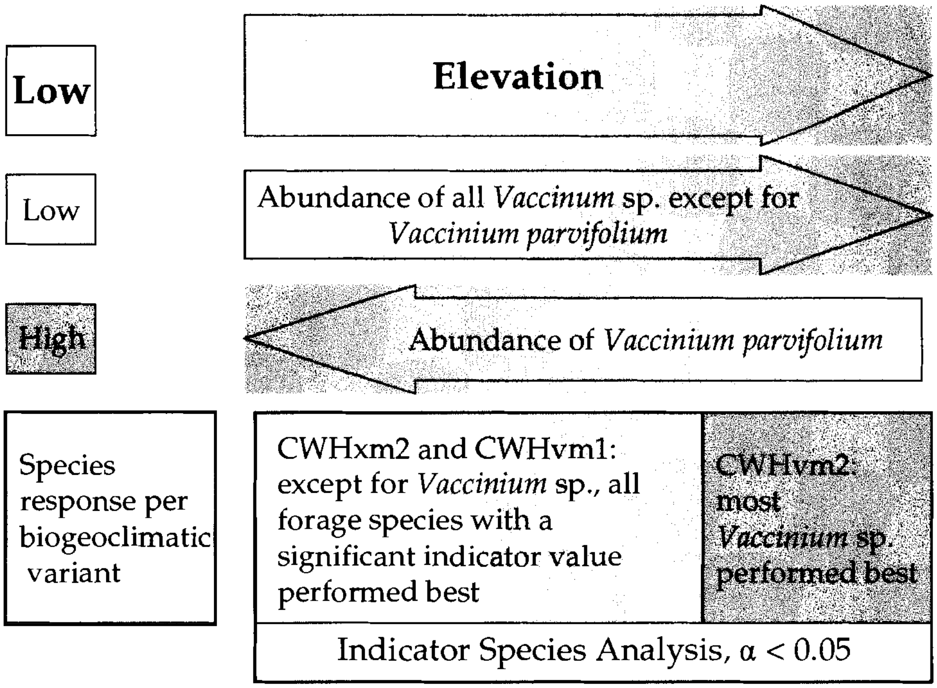

Figure 14. Summary of patterns of abundance of forage species and results from the indicator species analysis related to the gradient of increasing elevation (ordination axis 2).

All patterns of abundance represented with arrows have an $r^2>0.200$ and a r with a $p<0.001$. Along the altitudinal gradient, plots clustered together according to biogeoclimatic variants (see Figure 4). Thus, for the indicator species analysis, I grouped plots by biogeoclimatic variants. For detailed response patterns related to the gradient of increasing elevation consult Table 4, 5, and 6 and Figures 5, 6, 9, and 10.

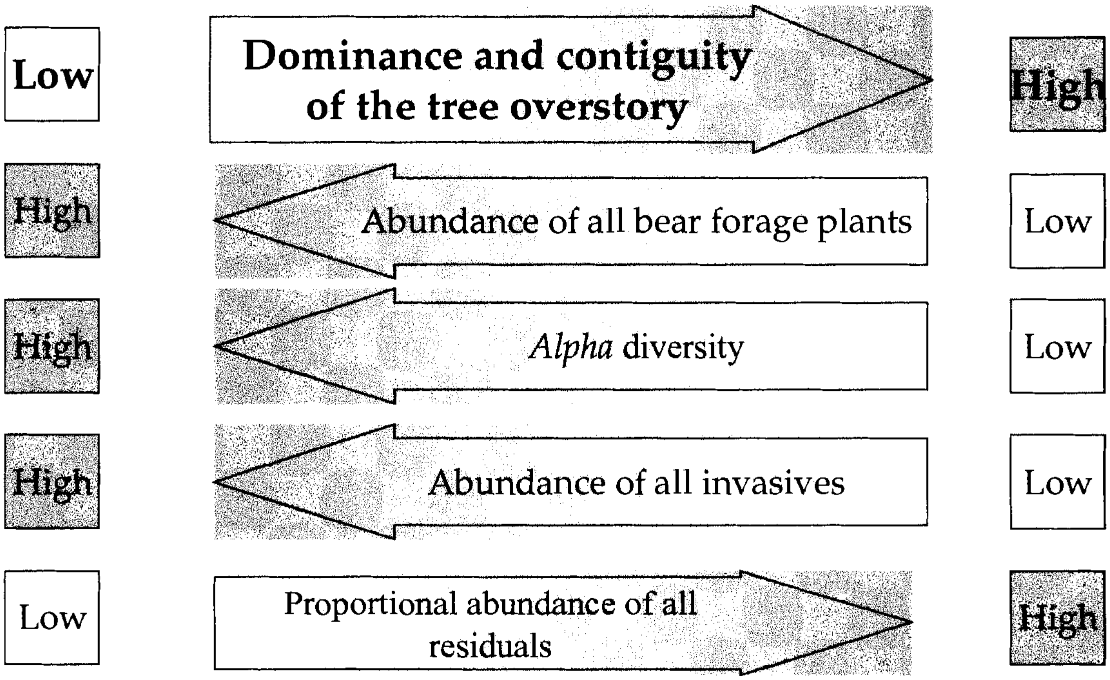

Figure 15. Summary of selected patterns of abundance of forage species related to the gradient of increasing dominance and contiguity of the tree overstory (ordination axis 3).

All species responses have an $r^2>0.200$ and a r with a $p<0.001$. For detailed results on species responses related to the gradient of increasing dominance and contiguity of the tree overstory consult Table 4, 6, and 6 and Figures 4, 5, 7, 8, and 10.

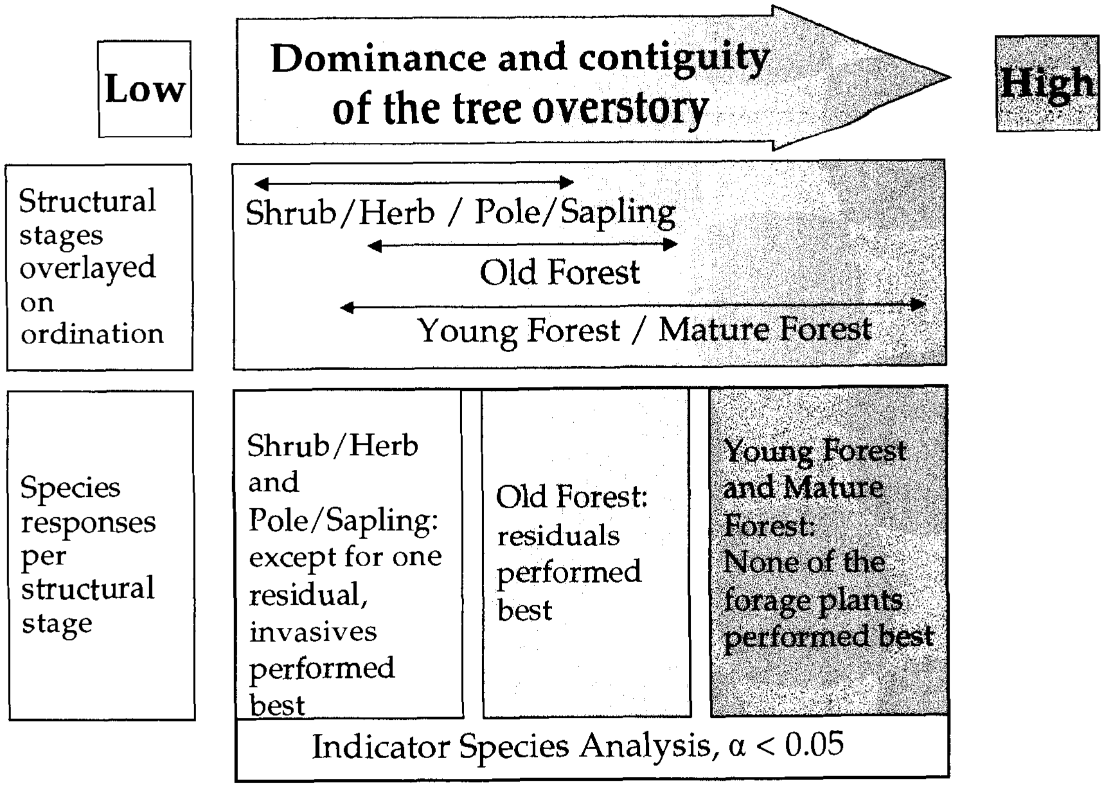

Figure 16. Summary of selected results from the ordination overlay and indicator species analysis related to the gradient of increasing dominance and contiguity of the tree overstory (ordination axis 3).
The thin black arrows roughly indicate the extent of the distribution of plots grouped by structural stages along the gradient related to the tree overstory. For detailed results related to plots grouped by structural stages consult Table 4, 5, 6, and 7 and Figure 4.