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**Population Dynamics of Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) in
Canada's Four Mountain Parks**

by
Rod A. Lastra

A thesis presented to the University of Manitoba in partial fulfillment of the
requirements for the degree Master of Science in the Faculty of Graduate Studies

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**POPULATION DYNAMICS OF INTERIOR DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII*
VAR. *GLAUCA*) IN CANADA'S FOUR MOUNTAIN PARKS**

BY

ROD A. LASTRA

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
of
MASTER OF SCIENCE**

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Pseudotsuga menziesii var. *glauca*

ABSTRACT

Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) is endemic to western north America, reaching its eastern distributional limit in the Alberta Rockies. Douglas-fir is a long-lived species (>500 years) that is characterized by its relatively large stature and thick, furrowed outer bark. Interior Douglas-fir forests are considered one of the few montane communities in the Rocky Mountains that are able to attain 'old-growth status'. Within this region, scattered stands occur on south-facing montane slopes, but relict individuals trees may also occur in cooler-wetter forests of the montane and lower subalpine ecoregions. This study was prompted by growing concerns that past and current land-use practices within the Four Mountain Parks (Banff, Jasper, Kootenay and Yoho National Park) may be detrimental to the long-term ecological integrity of 'old-growth' Douglas-fir stands. Two hundred and twenty plots were enumerated within Banff, Jasper, Yoho and Kootenay National Park to assess the status of these forests. Stands were characterized by estimating percent cover of all vascular and nonvascular plants. In addition, tree size and age data were obtained, and environmental information collected, from each plot.

Species abundances were used to classify the data into three stand-types (I, II and III) and seven sub-types: Ia = very xeric ($n = 34$); Ib = xeric ($n = 61$); IIa = subxeric ($n = 32$); IIb = submesic ($n = 30$); IIc = mesic ($n = 18$); IIIa = subhygic ($n = 31$) and IIIb = hygic ($n = 14$). In addition, statistical analyses were performed to determine relationships between plots, species, and environmental variables. Stands were found to be distributed along a light-moisture gradient. Soil texture, soil nutrients, slope/aspect, and incident solar radiation, and fire history are strong determinants of stand structure and floristic composition.

The growth response of Douglas-fir saplings was examined across each stand-type. Growth of advance regeneration was limited by low soil moisture and high daily temperatures within dry open-canopied forests (stand-type I). Low-light levels and insufficient seedbed conditions in hygic stands (stand-type III) decrease the mean growth rate of seedlings. Spatially heterogeneous canopy conditions created areas of differential growth within mesic stands (stand-type II). Radial growth was favoured under canopy gaps (IIb & IIc) and underneath canopy cover in the drier sub-variant (IIa). Competitive interaction restricted the growth of Douglas-fir to more marginal growing conditions.

A regeneration of Douglas-fir was shown to be dependent on both available understory light, soil moisture, and seed source proximity. Probable successional vectors were created for each stand-type using static size class ordination, under the assumption that species composition/abundance in the subcanopy and regeneration layers are indicative of the future canopy composition. In the absence of fire, Douglas-fir forms self-perpetuating stands in xeric open-canopied forests and is replaced by white spruce in more hygic growing conditions.

Management of Interior Douglas-fir forests in the Four Mountain Parks should be contingent on an understanding of the 'natural states and processes' that have shaped these communities for the last 8,000 years as well as the inherent variability which exist in these forests. Given the changes in climatic condition over the last 1,000 years it seems erroneous to restore these forests to some arbitrary point in time. Instead, management considerations should attempt to recognize the dynamics and resilience of natural forests communities. Consideration should be given to the effects of natural fire, pest or pathogen attacks, herbivory/granivory and episodic stochastic events on stand development. The synergistic interaction of these factors has historically given rise to complex spatial and temporal vegetation patterns currently evident in forest structure and composition. Natural disturbance such as these increase landscape heterogeneity, promoting species diversity at the stand level, and increasing genetic diversity at the population level.

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CHAPTER 1

TAXONOMY & SPECIES BIOLOGY OF *Pseudotsuga menziesii*, AND OTHER MONTANE SPECIES

1.1 SYSTEMATICS & BIOGEOGRAPHY OF *Pseudotsuga*

The genus *Pseudotsuga* includes two species native to North America, and six native to eastern Asia:

North America: *P. menziesii* and *P. macrocarpa*.

Japan: *P. japonica*.

Republic of China (Taiwan): *P. wilsoniana*.

Republic of China (mainland): *P. sinensis*, *P. forestii*, *P. gaussenii* and *P. brevifolia*.

The phylogeny of *Pseudotsuga* suggests that it evolved in western North America and subsequently migrated into eastern Asia. Fossilized seed cones of *Pseudotsuga* from western North America have been dated to the mid-late Tertiary (about 40 million years BP), predating the arrival of the genus in Japan by 20 million years. Strauss et al. (1990) postulate that a common ancestor of *Pseudotsuga* split to produce the North American and Asian lineage's. Based on Alaskan microfossils, it is speculated that the dispersal route of *Pseudotsuga* crossed North America to Asia via the Bering land bridge (Gernandt and Liston 1999). However, the fossil record is "fragmentary and regionally biased", and it is possible that older, extinct lineage's in Asia left no fossil record (Gernandt and Liston 1999). A chromosomal mutation appears to have occurred in the North American lineage, giving rise to *P. macrocarpa* ($2n = 24$) and *P. menziesii* ($2n = 26$). The karyotype of *P. menziesii* is unusual, since most other members of the Pinaceae family are $2n = 24$. It is speculated that *P. menziesii* split from *P. macrocarpa*. *P. japonica* represents an intermediate species in the migration of *Pseudotsuga* into eastern Asia, as the other Asian species appeared much later. Immunological and morphological studies indicate that the North American *Pseudotsuga* species are most closely allied to the genus *Larix* (Price et al. 1987; Praeger et al. 1976). The two genera share a similar phylogeny, geologic timeline, continent of origin and dispersal of genera between continents (Gernandt and Liston 1999; LePage and Basinger 1990).

The general characteristics of the genus include (cf. Lipscomb 1993):

- Bark: initially smooth with resin blisters; develops a reddish brown, corky, furrowed bark around 30 years of age.
- Branches: Pendulous (hanging loosely), irregularly whorled short shoots absent; leaf scars transversely elliptic, slightly raised proximally but essentially flush with twig distally.
- Buds: Elongate, not resinous, apex acute.
- Leaves: Borne singly, persisting around 6-8 years, alternate, short stalked, flattened; resin canals 2, marginal.
- Cones: Borne on year old twigs. Pollen cones: Axillary. Seed cones: Maturing first season, shed whole, deflexed or pendent, ellipsoid, ovoid or cylindric, near sessile; scale persistent, lacking apophysis and umbo; apex rounded; bracts +/- exerted, apex 3-lobed with acute apices, central lobe narrow, longer than lateral lobes.
- Seeds: winged cotyledons 6-12.

1.1.1 Taxonomic history of Douglas-fir

The nomenclature of Douglas-fir has gone through at least 18 different revisions since the late 1700's when Archibald Menzies first described the species at Nootka Sound on Vancouver Island (Stringer 1966). The initial taxonomic characteristics of the species were based on collections sampled from the Pacific Northwest and stored in the Horticultural Society of London. Given confusion over needle morphology the species was initially thought to belong to the genus *Abies*. It was first recognized as *P. taxifolia* Lambert. in 1803 which was later changed to *A. menziesii* Mirb. in 1825. Around this time, the Horticultural Society of London commissioned the assistance of David Douglas, a pioneer British field botanist to collect voucher specimens of several plants species including *A. menziesii* near the Columbia river. His collection consisted of cones and seeds as well as other materials. It was based on his cone collection that botanists in 1867 were able to change *A. menziesii* to *Pseudotsuga mucronata* (Raf.) Sedw. (Krajina 1956). The specific epithet was later changed to *P. taxifolia* (Lambert.) Britton in the early 1900's. A revision proposed by J. Do. Aramal Franco stated that since *P. taxifolia* was a synonym of *A. menziesii* the two names should be combined, and in 1950 *Pseudotsuga menziesii* became the first available name at the rank of species.

Known synonyms of *Pseudotsuga menziesii*:

- *Pinus taxifolia* Lambert 1803 not Salisbury 1796.
- *Abies taxifolia* Poiret 1805 not Desfontaines 1804; *A. mucronata* Rafinesque; *A. menziesii* Mirbel 1825.
- *Pseudotsuga douglasii* (Lindely) Carrière; *P. mucronata* (Rafinesque) Sudworth; *P. taxifolia* (Lambert) Britton.

The following is a summary of the current taxonomic and biological information for the North American members of the genus *Pseudotsuga*: emphasis will be given to *P. menziesii*.

1.2 GEOGRAPHICAL DISTRIBUTION OF *PSEUDOTSUGA* IN NORTH AMERICA

1.2.1 Bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr, Wald. Nordamer)

Two species of *Pseudotsuga* occur in North America, *P. menziesii* and *P. macrocarpa* (Fig. 1.1). It's currently not known if the two species are monophyletic or paraphyletic (Gernandt and Liston 1999). The genus is confined to the western portion of North America, from southern California to central British Columbia. Bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr) is a long-lived species (up to 600 years) that has a very restricted distribution in southern California along the Traverse and Peninsular Ranges. It occurs on steep, sparsely vegetated slopes and forms persistent, open-canopy stands in association with canyon live oak (*Quercus chrysolepi* Liemb). These fragmented forest patches are thought to be remnants of an extensive forest community type that existed in the region millions of years ago (McDonald 1990).

1.2.2 Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco)

Of the six species in the genus *Pseudotsuga*, only *P. menziesii* is of significant economic importance. The species is widely planted as an exotic in both Europe and South America (Hermann 1987). Two distinct varieties of *P. menziesii* are recognized, coastal (var. *menziesii*) and interior (var. *glauca*). These two varieties overlap in central British Columbia and northern Washington, forming varietal intermediates that occur as far east as Jasper National Park (Hermann and Lavender 1968). The two recognized varieties and their intermediates are distinguished based on variation in leaf terpenoids (von Rudloff 1971). Morphological traits include (cf. Lipscomb 1993):

- *P. menziesii* var. *menziesii*. Bracts straight, appressed; seed cones 6-10 cm; leaves yellowish green.
- *P. menziesii* var. *glauca*. Bracts spreading, often reflexed; seed cones 4-7 cm; leaves bluish green to dark green or gray green.

A third varietal has also been described (grey Douglas-fir, var. *caesia*; Isaac 1949), but is poorly defined and has been rejected by most taxonomists. It has been postulated that different 'races' of coastal Douglas-fir exist along a topoclinal gradient (Hermann and Lavender 1968).

The following is a summary of the biology of both varieties of Douglas-fir, with emphasis on the interior variety. Since many of the physiological characteristics of these two varieties are shared, details are included in the interior Douglas-fir section.

1.2.3 Coastal Douglas-fir (*P. menziesii* (Mirb.) Franco. var. *menziesii*)

Coastal Douglas-fir occurs along the Pacific coast of North America, from northern California (34°N) to central British Columbia (54°N). It is a long-lived species, achieving over 1,000 years of age. The oldest tree (about 1,400 years) was found near Mount Vernon in Washington state. The growth rate of coastal Douglas-fir is dependent on site condition. In general, maximum growth rates are achieved between 20 to 30 years, although the species is able to maintain a relatively rapid growth rate for about 200 years. The maximum height of mature trees is around 90(-100) m; maximum diameter of 4.4 m (Lipscomb 1993). The largest recorded tree, found near Little Rock in Washington state, stood over 100 meters in height with a diameter of 1.82 m (Hermann and Lavender 1990).

Coastal Douglas-fir forests occur across a broad band of vegetation zones from sea level to the upper montane ecoregions of the Cascade range. In the Pacific Northwest, Coastal Douglas-fir forms a seral stand-type within the western redcedar (*Thuja plicata* Donn ex D.Don) Pacific silver fir (*Abies amabilis* Dougl. ex Forbes) and western hemlock (*Tsuga heterophylla* (Rafinesque) Sargent; Hermann and Lavender 1990).

The shade-tolerance of Coastal Douglas-fir increases with increasing aridity along the Pacific coast south into California. In the southern portion of its range, coastal Douglas-fir is codominant with Pacific ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa* Dougl.), sugar pine (*Pinus lambertiana* Dougl.) incense-cedar (*Libocedrus decurrens* Torr.), and white fir (*Abies concolor* (Gord. & Glend.) Lindl ex Hildebr.). At its southern limit, coastal Douglas-fir is considered to be a strong competitor, forming persistent stand-types with tanoak (*Lithocarpus densiflorus* (Hooker & Arnott) Rehder in L.H. Bailey), Pacific madrone (*Arbutus menziesii* Pursh.), canyon live oak, giant chinkapin (*Castanopsis chrysophylla* (Dougl-) A. DC.), sugar pine, Pacific ponderosa pine, and incense-cedar (Hermann and Lavender 1990).

The Cascade region of western Canada is characterized by a mild, wet climate. The frost-free period lasts from 195 to 260 days. The mean fire return interval (MFR) for this area ranges from 400 to 500 years, but drops to 100 to 150 years on drier sites. In these dry sites, coastal Douglas-fir often achieves 'climax' status (Hermann and Lavender 1990).

Coastal Douglas-fir is an economically important timber species in North America. In addition, old-growth Coastal Douglas-fir forest provides critical habitat for many wildlife species, including the endangered spotted owl (Hermann and Lavender 1990).

1.2.4 Interior Douglas-fir (*P. menziesii* (Mirbel) Franco var. *glauca* (Mayr) Franco)

Interior Douglas-fir occurs along the eastern slopes of the Cascade, Coastal, Sierra Nevada ranges, and along the eastern and western slopes of the Rocky mountains from central British Columbia (55°N) to northern New Mexico (Stringer 1966). Its range is continuous from central British Columbia to central Idaho and western Wyoming. In Utah, Nevada, Colorado, New Mexico, Arizona, western Texas, and northern Mexico, the species is restricted to mountainous terrain and thus has a discontinuous distribution (Hemstrom et al. 1987).

In the Canadian Rockies (from Waterton to Jasper National Park), interior Douglas-fir occurs primarily on south-facing montane slopes ranging from 550 to 2,400 m in elevation. Along the Rocky Mountain chain, the altitudinal distribution of bioclimatic zones increases from north to south as climatic conditions become warmer and drier (760 to 410 mm mean annual precipitation). In the southern Rockies, interior Douglas-fir stands occur on northern slopes ranging from 2,440 to 2,900 m in elevation. The highest recorded elevation is 3,260 m on Mount Graham in southeastern Arizona (Hermann and Lavender 1990).

Interior Douglas-fir has a wide ecological amplitude, occurring from bunchgrass community types to subalpine forests. In the Canadian Rockies, interior Douglas-fir is often associated with Rocky Mountain lodgepole pine. In cooler and moister sites, it is often associated with white spruce and trembling aspen. On rocky ridges or gravelly soils, interior Douglas-fir often grows in association with limber pine and whitebark pine. In the montane ecoregion east of the Continental Divide, interior Douglas-fir and Rocky Mountain ponderosa pine form two of the major climax forest communities. Interior Douglas-fir forms extensive stands at elevations above the ponderosa pine zone. It may also occur at lower elevations, but is generally restricted to less xeric sites (Stringer and La Roi 1970).

In the southern Rockies, interior Douglas-fir grows in association with Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.), southwestern white pine (*P. strobiformis* Engelm.) and blue spruce (*Picea pungens* Engelm.). The distribution of interior Douglas-fir becomes more restricted further south as the abundance of white fir increases.

Although white fir is a stronger competitor when grown with interior Douglas-fir, mixed 'climax' stands of the two species do occur.

In the inland Mountains of the Pacific Northwest (including the Columbia plateau), interior Douglas-fir is found in association with Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and Pacific ponderosa pine (Hermann and Lavender 1990). In British Columbia three 'biogeoclimatic zones' (Krajina 1969) containing Douglas-fir have been recognized:

Canadian Cordilleran Forest (CCF)

- Cariboo Aspen-Lodgepole pine-Douglas fir zone (CALPDF).
- Interior Douglas-fir zone (IDF): IDFa xeric zone, IDFb mesic zone.

Pacific Coastal Mesothermal Forests (PCMF)

- Coastal Douglas-fir zone (CDF)

In addition, four 'vegetation types' (Achuff et al. 1993) containing Douglas-fir are recognized in the Mountain Park region of the Rockies:

Open Forest Vegetation Type:

- O05: Douglas-fir/common juniper/bearberry.

Closed forest vegetation type:

- C01: Douglas-fir/hairy wildrye.
- C55: Douglas-fir, lodgepole pine/buffaloberry-Rocky Mountain maple/Pleurozium.
- C05: White spruce/Douglas-fir/Hylocomium.

Compared to the Coastal form, Interior Douglas-fir has adapted to growing in much colder, drier environments (Hermann and Lavender 1990). The frost-free period in the Canadian Rockies is short, ranging from 60 to 120 days. Mean annual precipitation ranges from 56 to 100 cm, most of which falls as snow (Hermann and Lavender 1990).

Reproductive Cycle of Douglas-Fir

The reproductive cycle of Douglas-fir extends over 17 months. With the onset of axillary growth in the spring, the newly formed buds differentiate into vegetative, pollen or ovulate cone buds (Allen and Owens 1972). Megaspore and pollen development begins the following year. This phenology is similar to *Picea*, *Abies*, and members of the Cupressaceae. Pollination, cone ripening, embryo-seed development and seed dispersal occur over seven months. The timing of these events varies according to weather, elevation and latitude. For example, seed fall is temporally variable and depends on temperature, humidity, and air circulation. Cone opening is a result of the drying of specialized mechanical tissue at the base

of each ovuliferous scale. It has been estimated that at least 50% of the wet weight of the cone must be lost before the ovulate cone scales fully open. Early cone scale opening may be triggered by dry, warm weather. In the Canadian Rockies, the phenologic period of interior Douglas-fir starts several weeks earlier for populations occurring on the eastern continental slopes (Allen and Owens 1972).

In general, minimum seed-bearing age of interior Douglas-fir is around 20 years. Staminate and ovulate strobili appear between April and mid-May, depending on elevation. Pollination occurs soon thereafter. Megagametophyte development begins after pollination. Fertilization leads to zygote development and enlargement of the ovulate cone, which takes on the appearance of a mature ovulate cone but remains green in colour. Cone enlargement, which is completed by mid-summer, is followed by cone tissue differentiation. Embryo development is completed by the end of August, at which time the cones turn brown and begin to dehisce. Seeds are generally mature by September and disperse in late September or early October. Ovulate cones are retained on the tree for several years following seed fall. About 75% of the seeds are released in the fall, with the remainder being dispersed from late fall to the spring of the following year. Seed quality varies during this period, and generally declines during the winter and spring since cone scales in the center of the cone, where the highest quality seeds are borne, open earlier. Douglas-fir is a prolific seed producer, with large to medium cone crops (masting years) occurring at least once every ten years. Each cone contains between 20 and 30 seeds on average. The prominent cone scale bracts of Douglas-fir promote seed dissemination by wind and gravity (passive dispersal). Depending on topography, the estimated radius of seed dispersal is 90 to 180 m from seed source. Small mammals such as red squirrels can distribute seeds further. Seeds remain viable in the soil for one to two years (Hermann and Lavender 1990; Stringer 1966).

Germination and Establishment

In the Canadian Rockies, interior Douglas-fir commonly occurs on sandy-loams to loams derived from rocky, glacial till or outwash parent material. Stands are usually situated on well-drained sites, such as ridge tops and south-facing basal slopes that are subjected to higher mean daily temperatures (Stringer 1966). Moisture and available soil nitrogen are considered the limiting factors for successful regeneration of interior Douglas-fir in this region (Stringer 1966). Regeneration is enhanced where nitrogen mineralization rates are higher, particularly in moist sites with high litter quality. Seeds germinate under a variety of edaphic conditions, from mineral to organic (less than 5 cm depth) seedbeds. Once established, seedlings require moderate to low light conditions. Young seedlings grow best on well aerated sandy loams (Stringer 1966). Soils of low albedo (e.g. blackened soils) are unfavourable for seedling development, as diurnal extremes in surface temperatures are high. Anaerobic substrates (e.g.

stagnant water in fine textured or compacted soils) are also detrimental to the long-term survival of seedlings (Stringer and La Roi 1970). Competition with herbaceous vegetation can also reduce Douglas-fir seedling survival (Rose et al. 1999). Growth rates of interior Douglas-fir seedlings are often slowed by water and nutrient deficiency. Seedling dormancy is initiated by midsummer if soil moisture levels are low. This dormant period can extend from midsummer until the following spring (Hermann and Lavender 1990).

Interior Douglas-fir is considered a late-successional, moderately shade-tolerant montane species that is able to regenerate beneath its own canopy. Sun leaves are distributed in whorls around branches, with shade leaves oriented on a nearly horizontal plane (Chen and Klinka 1997). Douglas-fir responds to low light conditions by maintaining a limited number of healthy branches in the live crown and allocating more resources to lateral growth. A conical growth-form is attained under full light conditions, but low light results in a more horizontal, umbrella-like form that is more efficient in intercepting sunflecks and capturing light that may otherwise go to competing vegetation (Williams et al. 1999).

Interior Douglas-fir is exceeded in shade tolerance by Engelmann spruce, white spruce, subalpine fir, western red cedar and western hemlock, but can endure more shade than western larch, ponderosa pine, lodgepole pine, juniper and aspen (Hermann and Lavender 1990). In the absence of frequent disturbance, interior Douglas-fir may be replaced by species that are able to regenerate under lower light conditions, such as white spruce and subalpine fir (Williams et al. 1999).

Douglas-fir seedlings and saplings respond well to canopy openings, as long as they have not been suppressed too severely and/or for too long. Slightly elevated light levels increase the leader-to-lateral ratio of established saplings. This increased allocation to terminal growth results in more light becoming available to the lower branches, thus increasing canopy depth (Kneeshaw et al. 1998). However, less-developed subordinates that have established under a very closed canopy respond poorly to dramatic and sudden increases in light. Such individuals are also highly susceptible to damage from snow compaction, windfall and ultraviolet light. Sudden release may cause a temporary reduction in height growth of subordinate trees as they adjust their root-to-shoot ratio (Hermann and Lavender 1990). Under low light conditions, small saplings have a better chance of surviving under a dense canopy than larger, pole-sized individuals, since maintenance costs increase significantly with size (Williams et al. 1999).

Rooting Habit and Mycorrhizal Associations

Douglas-fir is a deep-rooting species, which allows it to grow under more xeric conditions than either white spruce and aspen (Stringer 1966). Root morphology varies in response to soil depth, the presence of consolidated material, and water table depth. In the absence of obstructions, Douglas-fir forms a tap root and lateral supportive roots in the first few years of growth. In deep soils (greater than 70 cm), tap roots can grow up to half of their final depth in 3 to 5 years, and 90% of their final depth in 6 to 8 years. In shallow soils, Douglas-fir develops a horizontal rooting system (Hermann and Lavender 1990). Root mass decreases with age, with nearly 50% of the root mass being lost by 21 years and over 80% in trees greater than 100 years. Root grafting is common; an interconnected rooting system is characteristic of many old-growth Douglas-fir stands (Hermann and Lavender 1990; Stringer and La Roi 1970).

The role of soil biota in increasing the uptake efficiency of mineral nutrients and water in trees is well established (Kloepper et al. 1989; Schroth and Weinhold 1986; Dommergues and Krupa 1978). Nonpathogenic rhizosphere bacteria may stimulate or depress Douglas-fir seedling growth, depending on the genotypic match between plant and bacteria (Chanway et al. 1989). Over 2,000 fungal species have been identified as mycorrhizal associates of Douglas-fir, and both ectomycorrhizal and ectendomycorrhizal structures have been observed. The most common mycorrhizal associate is *Cenococcum graniform* (Chanway and Holl 1992; Stringer 1966).

Size and Age at Maturity

Mature individuals of interior Douglas-fir (200 to 300 years old) rarely exceed 40 m in height and 1.2 m in diameter (Lipscomb 1993). After 200 years, diameter growth decreases dramatically and height growth practically ceases. The longevity of Interior Douglas-fir averages 400 years, although trees exceeding 600 years of age occur in Banff National Park (Achuff 1994). The morphological characteristics of the external bark dramatically changes between the sapling and adult stages of interior Douglas-fir. Younger trees (<8 m in height) generally have a smooth, photosynthetically active, resin covered outer bark very similar to that of balsam fir and subalpine fir. The carbohydrate-rich resin blisters attract insects and ungulates, often resulting in the mortality of young trees. After 30 years, the bark thickens (to 2-5 cm) and develops deep fissures. The thickened bark acts as a thermal insulator, protecting the cork cambium (phellogen) from heat damage associated with low intensity groundfires (Hermann and Lavender 1990). This adaptation enables mature interior Douglas-fir trees to survive periodic low-intensity fires.

Vital Attributes : Fire Adaptation

Compared to other western conifer species, mature individuals of Douglas-fir are relatively resistant to low-intensity fires. However, saplings are vulnerable to surface fires, since they have a thin, photosynthetically active bark, resin blisters, and closely-spaced, flammable needles (Bradley et al. 1992). Resin flow resulting from bark beetle activity contributes to the enlargement of old fire scars during subsequent fires. Partial basal girdling and root damage may also affect the survival of fire-scarred individuals by increasing moisture stress and reducing resistance to pest or pathogen outbreaks (Ryan et al. 1988). In older trees (>40 years of age), the development of a relatively thick layer of insulative corky bark protects the cambium from heat damage. Bark thickness increases with diameter, with the result that larger trees are more resistant to crown and bole damage from fires (Ryan et al. 1988). Cambial temperatures exceeding 60°C are lethal to most tree species (Johnson 1992). Since the bark has poor thermal conductive properties, cambial damage is reduced by increasing bark thickness: the time required to raise the temperature of the cambium to lethal levels is proportional to the square of bark thickness (Gutsell and Johnson 1996; Vines 1968; Gill and Ashton 1968). In addition, the height of the crown base also decreases the probability of mortality (Gutsell and Johnson 1996). In moister sites, rapid tree growth ensures that some individuals reach fire-resistant size before the next fire. On drier sites, growth rates are lower and natural fire frequencies higher. Historically, groundfires maintained many of these drier sites as seral grasslands. Fire suppression policies through much of the interior region of British Columbia allowed Douglas-fir to invade these grasslands, resulting in open savannah-like stands. In moister sites, dense sapling 'thickets' have developed that may provide a continuous fuel ladder into the overstory (Hermann and Lavender 1990).

Pests and Pathogens

Fungal

Of the over 300 species of heart rot fungi that attack Douglas-fir, the most widespread and damaging is red ring rot (*Phellinus pini*). Both red ring rot and yellow ring rot (*Poria weirii*) are serious diseases of Coastal Douglas-fir. The only root rot fungi listed as a serious disease on the eastern slopes of the Canadian Rockies is Armillaria root rot (*Armillaria mellea*), which has infected lodgepole pine and Douglas-fir stands throughout Alberta. The first recorded outbreak in Banff National Park occurred in 1964 (Hermann and Lavender 1990; Stringer 1966). On the west coast of British Columbia, Armillaria root disease may play an important role in forest succession, causing mortality, reduction in growth, and predisposition to wind throw (Dettman and van der Kamp 2001). Canopy gaps are created when pioneer species such as Douglas-fir and lodgepole pine are killed. These gaps are invaded by western

hemlock and western red cedar, which are more tolerant of *Armillaria*. In addition, fungal pathogens such as *Armillaria* may predispose Douglas-fir trees to bark beetle infestations.

Needle cast fungus (*Rhabdocline pseudotsugae*) infections are most common on emerging needles of young saplings following prolonged periods of rain. This disease commonly affects young Douglas-fir growing in areas receiving higher precipitation levels, such as the western slopes of the Rockies (Stringer 1966).

Parasitic Plants

Douglas-fir Dwarf Mistletoe (*Arceuthobium douglasii*) is the smallest of the Mistletoe species native to western North America. Although both coastal and interior Douglas-fir are considered primary hosts, the interior variety is more commonly infected. Wildfires have played an important role in determining the distribution and abundance of dwarf mistletoe (Hawksworth and Weins 1996; Herman and Lavender 1990). Spot fires may increase the distribution of mistletoe by leaving live infected trees scattered on the landscape. Fire also promotes the regeneration of mistletoe-susceptible host species (Hawksworth and Weins 1996). Low fire frequency has resulted in the absence of Douglas-fir Dwarf Mistletoe from old-growth coastal forests. Most mistletoe seeds are dispersed by birds. The dense and abnormally branched 'witches brooms' caused by dwarf mistletoe are commonly utilized by birds as nesting sites or platforms (Hawksworth and Weins 1996).

Insects

Over 60 species of insect are endemic to Douglas-fir cones, but only a small number of these are damaging to the seed crop. Seed loss from insect infestations are only significant during low crop years. Insect damage to seedlings is rare, although some insect species are problem pests in commercial nurseries.

The principal insect pest of mature Douglas-fir trees is the Douglas-fir beetle (*Dendroctonus pseudotsugae*), a cambial borer that normally attacks dead, injured or weakened trees (Stringer 1966). However, epidemic populations are capable of killing apparently healthy trees in large numbers, and may adversely affect younger saplings (Hermann and Lavender 1990). Higher stand density and greater stand age increase the susceptibility to bark beetle infestation (Furniss et al. 1981). The probability of bark beetle outbreaks increase under various disturbances, including root disease, defoliation, windthrow, snowbreakage, fire, and logging (Wright et al. 1984; Berryman and Wright 1978; Rudinsky 1966; Furniss 1965; Lejeune et al. 1961; Wright and Lauterbach 1950). For example, insect defoliation results in a reduction in total sugars in the first year, and of stored starch in the second year (Wright et al. 1979). This is important, since starch is required for the synthesis of secondary defensive compounds such as monoterpenes (Webb 1980). A reduction in

monoterpenes increases the probability of bark beetle infestation. High stand density may also result in a reduction in the production of these secondary compounds (Mitchell et al. 1993). Mortality rates during Douglas-fir beetle outbreaks increase with increasing stand basal area ($> 57.4 \text{ m}^2 \text{ ha}^{-1}$), stand age (>120 years), and tree size (DBH > 25.4 cm; Negron 1998; Weatherby and Thier 1983). Signs of infection include:

- Reddish-orange frass, consisting of phloem expelled from bark crevice by the invading beetles.
- Clear resin flow (pitch streamer) exuded from entrance holes on the stems. Pitch flow is not always present on successfully attacked trees.
- After several months, the foliage becomes discoloured, first turning yellow, then sorrel, and finally reddish-brown (Schitz and Gibson 1996).

Other damaging insect species include:

- Douglas-fir seed chalcid, which develops and matures exclusively in Douglas-fir.
- Douglas-fir cone moth and fir cone moth larvae, both of which bore through the developing tissue of the seed-cone. The cone moth is a more serious threat in submesic-xeric sites, while the fire cone moth occurs more commonly in mesic-hydric sites.
- Douglas-fir cone gall and scale midge, which destroy seeds and inhibit the opening of cone scales.
- Douglas-fir Tussock moth (*Oygyia pseudotsugata*) and western spruce budworm (*Choristoneura fumifana*), which often affect multi-aged interior Douglas-fir stands. Infestation by insect larvae of these species can cause severe defoliation of Douglas-fir throughout its range (Stringer 1966; Hermann and Lavender 1990).

Many species of bark beetle may carry with them one or more species of blue-stain fungi. Two species of blue-stain fungi are commonly associated with the Douglas-fir beetle, *Ophiostoma pseudotsugae* and *Leptographium abietinum*. These fungi are transported within pits of the bark beetle exoskeleton. It has been suggested that the interaction between blue-stain fungi and the Douglas-fir beetle may help overcome the secondary metabolic defenses of mature Douglas-fir trees (Ross and Solheim 1997).

1.3 BIOLOGY OF OTHER MONTANE TREE SPECIES

Please refer to **Table 1.1** for a brief summary on the following species.

1.3.1 Lodgepole Pine (*Pinus contorta* Dougl. ex Loud.)

Lodgepole pine (*Pinus contorta*) is one of the most wide-ranging pine species in North America (Critchfield 1980). It has a wide ecological amplitude, occurring from sea level to high elevation mountain ecoregions. Its north-south range extends from the Yukon Territory (64°N) to Baja California (31°N). Its west-east range extends from the Pacific coast to the Black hills of South Dakota. Four varieties of lodgepole pine are recognized:

- Shore pine (*P. contorta* var. *contorta* = *P. contorta* var. *bolanderi*): west coast of North America..
- Sierra lodgepole pine (*P. contorta* var. *murrayana*): Sierra Nevada and Cascade Mts.
- Rocky Mountain lodgepole pine (*P. contorta* var. *latifolia*): Rocky Mts.

The following synopsis focuses exclusively on Rocky Mountain lodgepole pine.

The general climatic requirements for lodgepole pine are the widest for any coniferous tree (Krajina 1969), with minimum temperatures ranging from -7°C on the coast to -57°C in the northern Rocky Mountains (Lotan and Critchfield 1990). In some locations, seedlings are resistant to frost injury and often survive in 'frost-pockets' where other tree species cannot.

Lodgepole pine is highly shade-intolerant and grows best in full sunlight. It can regenerate beneath its own canopy (Krajina 1969), but lodgepole pine saplings grown under low light conditions are stunted and may reach only 2 to 4 m in height by age 60 (Williams et al. 1999). Once established, lodgepole pine grows on a wide variety of substrates, from nutrient rich to highly infertile (Lotan and Critchfield 1990). Growth is best on granite and shale parent materials. In Canada, extensive stands of lodgepole pine grow on calcareous glacial till that provides a balance of moisture and porosity. The species grows under various topographic regimes, from gentle slopes to steep rocky terrain. Northern and eastern slopes are favoured over southern and western aspects (Lotan and Critchfield 1990).

Lodgepole pine is considered to be moderately resistant to surface fires, but the thin bark renders it highly vulnerable to cambial heating (Bradley et al. 1992). The main pyric adaptation of lodgepole pine is cone serotiny. Stands may contain both serotinous and nonserotinous trees, with the ratio depending on historic fire frequency and stand age. Cone serotiny is not pronounced until 20 to 30 years of age (compared to 10 to 20 years in *Pinus banksiana*; Gauthier et al. 1993). Temperatures of about 60°C are required to break the resinous bonds; the cone scales are then free to open hygroscopically (Johnson and Gutsell

1993). Trees in the upper canopy (>20m in height) generally require fires of moderate to high intensity and low spread rates (<6m min⁻¹; high fuel consumption) to facilitate cone opening. At intensities > 2,000 kWm⁻¹ and spread rates > 2 m min⁻¹ cone ignition will occur (Johnson and Gutsell 1993). During prolonged fire-free periods, the vast majority of the seed rain is derived from nonserotinous cones. Lodgepole pine stands are eventually dominated by nonserotinous trees if fire frequency is low (Bradley et al. 1992). In the absence of fire, lodgepole pine is usually outcompeted by shade tolerant associates such as Douglas-fir, white spruce, Engelmann spruce and subalpine fir (Lotan and Critchfield 1990). However, it forms a pyric climax in areas where fire frequencies are high, or where fires are so widespread that potential seed sources of other species are locally extirpated (Daubenmire 1943). Other factors promoting lodgepole pine dominance include drought, summer frosts, and soil infertility (Lotan and Critchfield 1990).

Growth rates in lodgepole pine are density dependent, with tree sizes (bole diameter) declining with increasing stand density. Lodgepole pine is a relatively short-lived species, ranging from 140 to 200 years of age (Lotan and Critchfield 1990). However, older trees have been recorded from secondary drainages in the Rocky Mountains. The oldest recorded trees were found in the Yoho and Ottertail Valleys of Yoho National Park, where stand ranging in age from 393 to 461 years occur (Tymstra 1991).

Dissemination of seed from nonserotinous cones occurs in September and October. The winged seeds, which are dispersed by wind and gravity, generally fall within 60m of the parent tree (Lotan and Critchfield 1990). Seeds in serotinous cones remain viable for many years, but once released they remain viable for about one year. Seed viability is generally high, ranging from 65 to 90% under ideal conditions. Lodgepole pine seeds do not require stratification, but germination success depends largely on temperature. Seed germination is low when daylight soil temperature is less than 15°C, and is optimal between 21 and 27°C. At 2-4 weeks in age, seedlings can withstand soil temperatures in excess of 60°C. Germination and successful establishment requires full sunlight, adequate soil moisture, exposed mineral soil or disturbed duff, and low cover of competing vegetation (Johnson and Gutsel 1993; Lotan and Critchfield 1990). Drought is the most common cause of mortality in first-year seedlings.

1.3.2 White spruce (*Picea glauca* (Moench) Voss)

The taxonomy of white spruce is complicated. In the upper montane and lower subalpine ecoregion of the Canadian Rockies white spruce is known to hybridize with Engelmann spruce where the two sympatric giving rise to var. *albertiana*. The hybrid is recognized based on its "prominent leaf bases, cones nearly as broad as long, cone scales acute and broader than long, and an unusually narrow crown" (Talyor 1993). Currently var. *albertiana* is not

recognised (Taylor 1993). White spruce also hybridizes with Sitka spruce (*Picea sitchensis* (Bongard) Carriere) along the northern coast of British Columbia and coastal Alaska. The name *Picea x Lutzi* Little is applied to this hybrid. Hybrids of black spruce (*Picea mariana* (Miller) Britton) and white spruce have also been reported, but are apparently rare (Nienstaedt and Zasada 1990). In the Canadian Rockies the similarities between white spruce and Engelmann spruce are such that the two are often referred to as interior spruce. The only major differentiation is based on their elevational distribution: white spruce occurring at < 1,200 m and Engelmann spruce at > 1,825 m and hybrids occurring in between (La Roi and Dugle 1968). Allozyme research for both putative and natural hybrid populations of white spruce and Engelmann spruce in the Canadian Rockies suggests that Engelmann spruce should be recognized as a subspecies of white spruce (Rajora and Dancik 2000). The authors concur with Taylor's (1959) treatment which recognized interior spruce as two subspecies of white spruce (*P. glauca* ssp. *glauca* and *P. glauca* ssp. *engelmannii*). They postulate that a single species may be evolving along an elevational gradient in the Alberta Rockies (Rajora and Dancik 2000). For the purposes of this study white spruce shall include both *P. glauca* and *P. engelmannii*.

White spruce has a transcontinental distribution, occurring from Newfoundland and Labrador, west across Canada and north to Hudson Bay, Northwest Territories and Yukon. Its distribution extends south into the Rocky Mountains of Alberta, British Columbia and Montana, where it is found on the foothills and Montane ecoregions. The southern extent of white spruce occurs in the Black Hills of Wyoming and South Dakota (Nienstaedt and Zasada 1990). Throughout its range, white spruce grows from sea level to about 1,500 m.

White spruce has a wide ecological amplitude, and is capable of surviving under highly variable and extreme climatic and soil conditions. Conditions are most severe through the prairie provinces (Alberta, Saskatchewan and Manitoba), where mean annual precipitation ranges from 380 to 510 mm with July temperatures as high as 43°C (Nienstaedt and Zasada 1990). The range of sites supporting the species becomes limited in northern latitudes and at higher elevations, where climatic conditions are most severe. For example at its northern limit temperatures can reach -54°C in January (Nienstaedt and Zasada 1990). White spruce can grow on somewhat acidic and alkaline soils, but requires a dependable supply of well-aerated water. White spruce does poorly in sites with a high water table, and it is generally intolerant of permafrost (Nienstaedt and Zasada 1990).

White spruce is considered to be intermediately shade-tolerant. It is equally or less shade-tolerant than western hemlock, balsam fir and subalpine fir, but more tolerant than aspen, paper birch, lodgepole pine and interior Douglas-fir. White spruce is considered to be both a pioneer and 'climax' species (Dix and Swan 1971), since it can establish soon after a

disturbance but can also establish later and remain suppressed in the understory for many years (Leiffers et al. 1996). Initial flush in recruitment within post-fire stands is augmented by exposed mineral soils and seed source proximity (Leiffers et al. 1996). In cases where seedbed conditions are poor and seed supply low, white spruce recruitment is delayed and sporadic: often occurring on rotten logs within structurally old-growth stands (Leiffers et al. 1996). Like subalpine fir, white spruce responds well to canopy release (Nienstaedt and Zasada 1990).

White spruce can reproduce both sexually and asexually. Vegetative propagation from layering is more common in regions where climatic conditions limit sexual reproduction. Cone and seed production begin as early as 4 years of age, but maximum production does not occur until age 30. Cone production occurs primarily in dominant and codominant trees, with sporadic production from suppressed individuals in the lower subcanopy (Nienstaedt and Zasada 1990). Under optimal conditions, cone crop production occurs once every 2 to 6 years, but in many areas of its range heavy cone crops only occur once every 10 to 12 years. Seed dissemination begins in late August, with most of the seeds falling in September. Seeds are usually dispersed by prevailing winds, and most fall within 90 m of the parent tree. Long-distance dispersal of seeds usually occurs over snow cover, from updrafts, or by red squirrels (Greene and Johnson 1995).

The germinative capacity of white spruce is estimated to be 50 to 70% (Nienstaedt and Zasada 1990). Seedlings establish best on exposed mineral seed beds, but they may also establish on organic substrates. Adequate soil moisture and warm soil temperatures make ideal seedbeds. White spruce seedlings can grow under a wide variety of light conditions, but they prefer full light (Nienstaedt and Zasada 1990). Humidity conditions present at seedling establishment can significantly affect the morphological and physiological characteristics during the second growing season (Roberts and Zwiazek 2001). Seeds remain viable for 1 to 2 years.

White spruce is considered a long-lived species, maximum tree ages (1,000 years) having been documented near the treeline where climatic conditions are suboptimal. In areas where white spruce dominates, such as the boreal and montane ecoregions, trees commonly range in age from 100 to 300 years (Nienstaedt and Zasada 1990).

1.3.3 Rocky Mountain Subalpine Fir (*Abies bifolia* A. Murrat bis.)

Rocky Mountain subalpine fir (*Abies bifolia*) is often included in synonymy with Subalpine fir (*Abies lasiocarpa*). They differ in their wood chemistry, the presence/absence of ray parenchyma crystals, and terpene chemistry. Morphologically, *A. bifolia* has shorter and fewer prominently notched leaves than *A. lasiocarpa*: they can also be separated by periderm

colour (red in *A. lasiocarpa* and tan in *A. bifolia*) and basal bud scale shape (equilaterally triangular in *A. lasiocarpa* and isosceles triangular in *A. bifolia*). Rocky Mountain Subalpine fir is restricted to the interior regions of the North American Cordillera, whereas Subalpine fir occurs primarily along the Pacific Coast (Hunt 1992).

Rocky Mountain subalpine fir extends from the interior valleys of British Columbia west to the Continental Divide and south to New Mexico and Arizona (Alexander et al. 1990). It is a major component of the subalpine forests of the Rocky Mountains, growing from 600-3,600 m elevation (Hunt 1992). The species is restricted to cool, mesic forests and is intolerant of high temperatures. Within the species range, the mean annual temperature ranges from -3.9°C to 4.4°C, and the mean annual precipitation is about 600 mm (Hunt 1992).

Subalpine fir can establish on a wide variety of seedbeds, from mineral soils or litter to duff and decaying wood. It is able to establish under low light conditions, and can remain suppressed in the understory for many years. Under such conditions, suppressed saplings often takes on an umbrella-like appearance and may be well over 50 years old but less than 2 m in height (Williams et al. 1999). Depending on the type and severity of disturbance, elevation, and the presence/absence of a conspecific seed source, subalpine fir may or may not establish immediately following a disturbance. Subalpine fir re-establishes soon after disturbance if early-successional species such as aspen and lodgepole pine are scarce. However, aspen and lodgepole pine are common seral species in the upper and lower subalpine ecoregions and will normally form extensive even-aged stands following fire. These seral species grow rapidly and soon overtop the slower-growing, shade-tolerant conifers that have established contemporaneously. Subalpine fir may remain suppressed in the understory for many years, but responds well to canopy release and attains dominance once the aspen or pine canopy begins to break up. In more xeric habitats, subalpine fir rarely attains dominance since higher fire frequencies favour less shade tolerant species such as Douglas-fir and lodgepole pine (Alexander et al. 1990).

Subalpine fir can reproduce both sexually and vegetatively, but vegetative layering is largely restricted to trees growing near timberline. Cone production begins by about 20 years of age. Yearly seed production is erratic, with good seed crops being produced every 3 to 5 years. Seed dissemination begins in September and is usually completed by October. Most of the wind-dispersed seed fall within 30 m of the parent tree, but in mountainous terrain upslope winds can increase dispersal distances. Seeds remain dormant under the snow until the following spring, and cold stratification is required to trigger germination. Seed viability is often less than 30% (Alexander et al. 1990).

In closed canopy situations, subalpine fir can attain a diameter of 30 to 60 cm and a height of 14 to 30 m. It is a slow-growing tree, often achieving a diameter of only 25 cm after 150 years. The maximum age is estimated to be 250 years, but most trees succumb to heartrot at an earlier age (Alexander et al. 1990).

1.3.4 Western Redcedar (*Thuja plicata* Donn ex D.Don)

Western redcedar is one of two native North American species of the genus *Thuja* (Cupressaceae family). The genus displays a high degree of selfing with low gene diversity: outcrossing was considered one of the lowest of among western conifers (O'Connell et al. 2001). There are no known varieties or forms of the species (Chambers 1993). The species occurs in two distinct regions in western North America: along the Pacific coast, and along the interior ranges of the Cordillera. These two populations are geographically isolated from one another. The coastal range extends from northern California (40°30'N) to the southern part of the Alaskan panhandle (56°30'N). The interior range extends from Idaho and Montana (45°50'N) to the western slopes of Continental Divide in central British Columbia (54°30'N). The species is normally confined to mesic-hydric sites (Owens and Molder 1980). It occurs from sea level to about 900 m elevation along the Pacific coast, and from 320 to 1,190 m in the interior Cordilleran region (Minore 1990).

Western redcedar grows best in cool Pacific climates, characterized by mild summers and winters. The lack of an epidermal cutin or wax layer on the leaves renders the species highly susceptible to moisture stress. The species distribution is limited by cold temperatures; bottomland 'frost-pockets' are generally occupied by more frost-resistant species. In British Columbia, western red cedar will tolerate absolute minimum temperatures ranging between -10°C and -30°C (Minore 1990).

Western red cedar tolerates a wide range of edaphic conditions. Although it can tolerate low-nutrient soils, adequate levels of available nitrogen, calcium and soil water are required to ensure successful establishment (Minore 1990). The species is shade-tolerant and relatively slow-growing. Only Pacific silver fir, western hemlock, and Pacific yew (*Taxus brevifolia* Nuttall) are considered to be more shade-tolerant. In the drier regions of the interior, western red cedar is generally restricted to protected, moist depressions. It is usually overtopped by Douglas-fir (Minore 1990).

Western redcedar is known to reproduce both sexually and asexually. Three modes of vegetative propagation are known: layering, rooting of fallen branches, and branch development from fallen trees. Vegetative reproduction is more common in undisturbed forests, while sexual reproduction is favoured following disturbance (Minore 1990).

A prodigious seed producer, mature trees produce many few-seeded cones (Owens and Molder 1980). Seed production is related to temperature, with fewer cones being produced under colder conditions (Owens and Molder 1980). Seed production generally starts at 20 to 30 years of age, but may occur as early as 10 years in trees growing in open forests. Large seed crops occur once every 4 years. Seeds are wind-dispersal between October and November, usually within 100 m of the parent tree (Minore 1990). The seeds do not require cold stratification in order to germinate, and they remain viable for up to 8 years following release. Germination and establishment is optimal on mineral soils; moss and duff mats dry out too rapidly. Drought and high soil temperatures are detrimental to seedling survival, and deciduous tree litter can smother the seedlings. Seedlings are very shade-tolerant and respond well to canopy release. They are also tolerant of stagnant water (Minore 1990).

Western redcedar is a long-lived species; trees along the Pacific coast may exceed 1,000 years in age. At maturity, western red cedar can attain heights ranging from 21 to 60 m and diameters of 0.6 to 3 m (Minore 1990).

1.3.5 Trembling aspen (*Populus tremuloides* Michx.)

Trembling aspen is the most widely distributed tree species in North America, occurring from Newfoundland to Alaska south to Virginia and New Mexico (Peterson and Peterson 1992). In the Rocky Mountains, aspen is considered a seral species that is maintained by periodic fire (Kay et al. 1994; Shepperd 1993). Aspen groves are found scattered throughout Engelmann spruce-subalpine fir and montane Douglas-fir-white spruce forests. In the aspen parkland, aspen is considered a climax species, often occurring with bur oak (*Quercus macrocarpa* Michx.), Manitoba maple (*Acer negundo* L.), green ash (*Fraxinus pennsylvanica* Marsh.) and balsam poplar (*Populus balsamifera* L.; Bird 1961).

Aspen tolerates a wide range of edaphic conditions, occurring from dry mountain slopes to moist river flats and poorly to well-drained, nutrient rich soils (Moss 1955). In the Canadian Rockies, aspen attains its best growth on soils derived from neutral to calcareous shales and limestones. The species occurs from sea level to 3,500 m (in Colorado; Sheppard 1993). In western Canada, aspen grows best on south facing slopes. In the eastern prairie provinces, aspen stands are usually found on north and east facing slopes and in depressions (Perela 1990).

The species is highly shade-intolerant and does not usually reproduce beneath its own canopy (Peterson and Peterson 1992). In the absence of fire, most stands are eventually invaded by conifer species. In some stands aspen and conifers establish contemporaneously, but in others conifer invasion does not occur until canopy breakup (about 100 years following stand initiation). In central Utah, conifer succession takes less than 100 years on

sandstone soils but over 140 years on alluvial or calcareous soils. In drier regions of the west, decadent aspen stands may revert to dense shrublands (Perela 1990).

Although aspen reproduces both sexually and asexually, sexual reproduction is apparently uncommon and limited by soil moisture. Seedlings survive best on moist, well-drained mineral seedbeds. Moderate soil temperatures and low vegetation cover are also required. Aspen seedlings are flood-intolerant (Perela 1990).

Vegetative reproduction is the most common form of aspen regeneration (Barnes 1966). Sucker shoots, which are generated from the root cork meristem, can develop at any time during secondary development. The root system of aspen is wide-spreading and shallow. Root sprouts are produced in individuals as young as one year old. Sprouting is initiated by the loss of apical dominance, which may be caused by burying, defoliation, cutting or girdling of dominant stems (Perela 1990). Aspen usually sprouts vigorously following fire, and often dominates post-burned sites. The blackened soil resulting from fire further promotes aspen suckering by increasing soil surface temperatures (Hungerford 1988).

Aspen clones are potentially long-lived, and may survive for several centuries as new suckers replace dying stems (Bradley et al. 1992). However, individual stems rarely exceed 80 to 100 years in age. Trembling aspen is a small to medium sized tree that ranges from 15 to 36 m in height and 40 to 137 cm in diameter (Perela 1990).

1.3.6 Rocky Mountain Juniper (*Juniperus scopulorum* Sarg.)

Rocky mountain juniper (one of 13 junipers native to North America) is the most widely distributed tree-sized juniper in western North America. It occurs primarily in the interior and eastern regions of the Cordilleran, but has a scattered distribution throughout its range (31° - 55°N; Noble 1990). It is a dry subhumid species that occurs on open, exposed south-facing bluffs, ridges and ravines. A drought-enduring species, rocky mountain juniper is more hardy than western red cedar, but less so than other western juniper tree species (Noble 1990).

Rocky Mountain juniper is considered semi-shade tolerant at the seedling and sapling stages, but becomes increasingly shade-intolerant at maturity. In the Rockies, the species occurs on the drier montane and foothills ecoregion zones. It is considered an early pioneer of mesic habitats, but a climax tree species in xeric sagebrush-grassland communities (Noble 1990; Bradley et al. 1992). It occurs over a wide range of edaphic conditions, but is most commonly encountered on calcareous or alkaline soils. It occurs from sea level to 2740 m in elevation, depending on aspect and latitude (Noble 1990).

Reproduction is exclusively by seed. Seed production begins at about 10 years of age, with optimum production occurring from 50 to 200 years. Heavy seed crops are produced once

every 2 to 5 years. Seeds are dispersed primarily by birds, gravity and/or water; dispersal by mammals is thought to be insignificant (Noble 1990). Germination requires a period of warm stratification (20°C at night, 30°C during the day) for 45 to 90 days, followed by cold stratification. The passage of seeds through the digestive tracts of birds or mammals may improve germination (Noble 1990).

Rocky Mountain juniper is a slow-growing species. In Canada, Rocky Mountain juniper usually grows 30 cm in diameter and 3 to 4 m in height. It is considered a long-lived species, with most trees surviving from 250 to 300 years of age. However, an individual in Logan Canyon, Utah was estimated to be about 3,000 years old (Noble 1990).

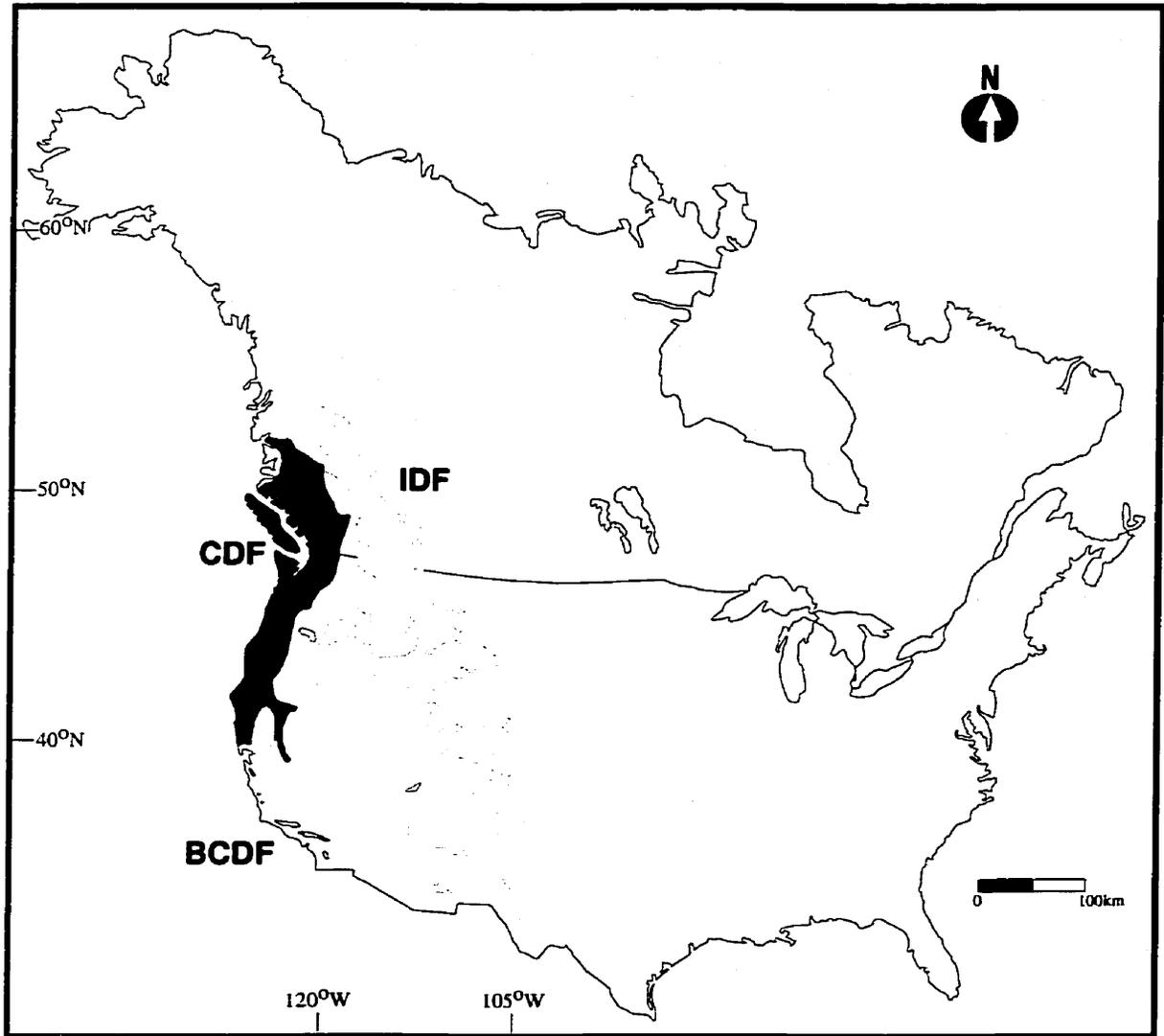


Figure 1.1. Native range of Interior Douglas-fir (IDF), Coastal Douglas-fir (CDF) and Bigcone Douglas-fir (BGDF).

Table 1.1. Life history characteristics of major montane tree species (Herman & Lanvender 1990; Lotan & Critchfield 1990; Nienstaedt & Zasada 1990; Minore 1990; Perela 1990; taken from McCune & Allen 1985)

| Species | Potential longevity (years) | Shade Tolerance | Growth rate | Fire resistance | Establishment in closed forest | Population controls |
|--|-----------------------------|-----------------|------------------------------------|---|---|--|
| Interior Douglas-fir <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | >500 | Moderate | Moderate | High in mature trees (>30years) Low in younger trees | Seedlings establish high Saplings have high mortality rate | Douglas-fir bark beetle Spruce bud worm dwarf mistle toe |
| Rocky Mountain Juniper <i>Juniperus scopularum</i> | >300 | Very Low | Low | Low | Rare | Soil erosion ungulate bark damage ungulate herbivory |
| Lodgepole pine <i>Pinus contorta</i> | >150 | Low | Fast | Low in young and mature trees Moderate at old age | Rare | Windthrow Mountain pine beetle dwarf mistletoe |
| Trembling aspen <i>Populus tremuloides</i> | >120 (stems) | Low | Fast (sprouts) Moderate (seeds) | Low | Rare | Ungulate herbivory ungulate bark damage |
| White spruce <i>Picea glauca</i> | >200 | Moderate | Moderate | Low | High in canopy gaps | Windthrow Granivory bark beetle |

| Species | Potential longevity (years) | Shade Tolerance | Growth rate | Fire resistance | Establishment in closed forest | Population controls |
|---|-----------------------------|-----------------|-------------|---|--|--|
| Rocky Mountain subalpine fir <i>Abies bifolia</i> | >150 | High | Moderate | Low | High in canopy gaps | Windthrow Western spruce bud worm Decay fungus |
| Western red cedar <i>Thuja plicata</i> | >500 | High | Moderate | Low in young tree Moderate in older tree | Layering Seedling est. high under canopy gaps | Windthrow (wet habitats) Decay fungus |

CHAPTER 2

VEGETATION DYNAMICS

2.1 THEORIES OF SUCCESSION

Vegetation change has been well documented in the paleoecological record. Climate change is recognized as a major influence on the expansion or extirpation of species or groups of species from a region. Such long-term trends in vegetation dynamics are generally undisputed by ecologists.

A new paradigm evolved in plant biology at the turn of the century: succession. Plant succession is defined as the change in vegetation assemblages, over time periods ranging from years to a few centuries (Cook 1996). The basis of this concept is centered around a few very contentious issues: (a) what drives succession? (b) is there a stable end point?; (c) if such an end point exists, can it be predicted?

2.1.1 Succession: an Evolving Paradigm

Clementsian Succession Theory: The concept of directional change and a stable end point

The concept of vegetation change was first developed by Henry Cowles (1899) in his classic study of sand dune succession at the south end of Lake Michigan (Cooper 1926). The idea was later refined by Fredrick E. Clements in his 1916 publication '*Plant Succession*'. In it he laid the foundation for the study of vegetation dynamics, by introducing the concepts of succession and climatic climax (Johnson 1979). The Clementsian 'community unit', as it later became known, was based on the following assumptions:

- Succession is directional and predictable.
- The 'community' has a modifying effect on the physical environment, which in turn drives succession (reaction).
- Vegetation change almost invariably converges to a self-perpetuating climax state that is under the control of the regional climate.

Clements stated that 'the climax community is an organic entity, with structure and function corresponding to those of an individual organism' (Cooper 1926). The concept of dealing with plant communities as evolving 'organic entities' became the foundation of 'ecosystem' research (Tansley 1935) with each 'evolving' state or sere characterized by a set of numerical properties (e.g., productivity, biomass, diversity). The notion of a predictable, unidirectional, community-oriented successional theory dominated academia for nearly 40 years (Cook

1996). Clement's theory revolutionized the field of ecology by introducing the concept of vegetation dynamics in a time when plant communities were seen as static entities (Miles 1979). Nevertheless the Clementsian theory of succession was criticized by some of his contemporaries (Tansley 1935; Cooper 1926; Gleason 1926), the most notable and influential of which was H.A. Gleason (Cook 1996). Gleason's theory of succession was a strong departure from the Clementsian view of communities as 'superorganisms'. Gleason emphasized the principles of vegetational continuity and species individuality. Furthermore, he stressed that vegetation change is unpredictable and strongly influenced by chance events (Anand 1997). Thus species replacements occur on a plant-by-plant basis, reflecting differences in life-history characteristics (Kenkel et al. 1997).

Natural Disturbance and Chance Events: An Argument against 'community climax'

Both Clements and Gleason, as well as their contemporaries, failed to explicitly acknowledge the role that natural disturbance plays in precluding the development of a climatic climax. Disturbance, which introduces heterogeneity and a lack of compositional stability, was viewed as 'the nemesis of classical succession' (Johnson 1979). Watt (1947) was the first to incorporate the mitigating effects of disturbance into successional theory, and to hypothesize the possibility of multiple successional pathways. While acknowledging that individual plants are the ultimate components of a community, Watt recognized that the study of community dynamics at the individual level is impractical. He therefore concentrated his efforts on 'aggregates of individuals' that together form a mosaic of patches on the landscape (Watt 1947). In this model, each patch is subject to cyclic rather than seral changes in floristic composition (Cook 1996).

Egler (1954) challenged the Clementsian notion that communities develop through the facilitative replacement of species, a mechanism known as 'relay floristics' (Egler 1954; Noble and Slayter 1980). His 'initial floristics' model of succession hypothesizes that all species that are part of a sere are present soon after disturbance (Egler 1954; Cook 1996). Changes in species composition during succession are thus primarily a function of seed and propagule availability, which are in turn determined by site history and episodic stochastic events.

Species Life-history: Explaining the mechanism of succession at the species level

The theories of Watt and Egler were important in modifying the classic Clementsian paradigm, and paved the way for the development of a modern theory of succession (Cook 1996). The next twenty years were noted as an era of 'confusion' in community ecology, as many of the founding principles of successional theory were brought into question (McCormick 1968; Dury and Nisbet 1973). Neo-Gleasonian theories, based on autecological

and physiological characteristic of species, soon took precedence over the Clementsian community-unit theory in explaining the mechanisms of succession (Drury and Nisbit 1973). A non-equilibrium successional paradigm was proposed by Horn (1975), who hypothesized that secondary succession is a result of stochastic processes rather than a series of linear and predictable events as advocated by Clements. Pickett (1976) expanded on these ideas, proposing the first theory of succession stressing the importance of species adaptive traits. He hypothesized that differences in species life-history strategies (such as shade tolerance and susceptibility to fire) may account for changes in species dominance along a successional sere. He also acknowledged that both biotic and physical disturbances are integral components of succession (Cook 1996).

Connell and Slatyer (1977) provided a valuable overview of various successional theories, and were the first to attempt a refinement and clarification of classical successional principles. They proposed that mechanisms of vegetation change be incorporated into three alternative models of succession: facilitation, tolerance and inhibition (Cook 1996; Pickett et al. 1987; Connell and Slatyer 1977):

- *Facilitation*: the Clementsian concept of relay floristics, whereby one species prepares the way for another (autogenic succession).
- *Inhibition*: competitive dominants regulate vegetation change by preventing later successional species (or species of any succession sere) from establishing. Succession only occurs when acute biotic and/or physical disturbances remove the initial cohort.
- *Tolerance*: two variants of this model are recognized. In the first, subordinate species remain suppressed until more resources are made available by the removal of an adjacent dominant individuals ('passive tolerance'). In the second, species turnover results from changes in resource partitioning, since later successional species are more efficient at exploiting limiting resources than earlier successional ones ('active tolerance').

Connell and Slatyer (1977) departed from classical Clementsian succession theory in two ways: (a) succession rarely results in a 'stable end point' or climax community; (b) multiple successional pathways are possible. They also acknowledged that disturbance is a frequent and pervasive force driving vegetation dynamics.

Building on Pickett's theory of plant life-history strategies, Grime (1977) recognized three fundamental species life-history traits: ruderal, stress tolerator and competitor. Ruderal species are best adapted to early successional stages, and to highly disturbed environments. They tend to have rapid growth rates and, distributing a large number of small seeds. Competitors

increase in dominance during the intermediate stages of succession, while stress-tolerators often dominate late-successional stages (Cook 1996). Stress-tolerators are characterized by slow growth and larger seed size. Site conditions also influence successional trajectories, such that any species with an appropriate life-history strategy can be present either at an early or late successional stage (Cook 1996).

The vital attribute model (Noble and Slatyer 1980) builds on earlier works, emphasizing the role of life-history characteristics in succession. It is essentially a 'refinement of the Gleason hypothesis' developed for fire-prone ecosystems, and was the first successional model to explicitly incorporate disturbance and to recognize that multiple successional trajectories are possible at a single site (Cook 1996). The vital attributes of a given species are defined as those life-history characteristics that enhance its ability to establish during later successional stages. Vital attributes are grouped according to:

- Method of arrival or persistence of a species following disturbance (e.g., seed or belowground tissue).
- Ability to establish and grow to maturity in a developing community (e.g. Shade-tolerance).
- Time taken for a species to reach critical stages in its life-history (e.g. reproduction).

Specific life-history attributes are selected for based on disturbance frequency, intensity and type (Kenkel et al. 1997). For example, cone serotiny in lodgepole pine is usually favoured on fire-prone sites, but such a trait becomes maladaptive when fire frequencies are low.

McCune and Allen (1985) reinforced the importance of disturbance and episodic stochastic events during vegetation development. Their research established that 'differences in climax vegetation can be unrelated to site differences'. They attributed changes in canopy composition and vegetation development to the 'vagaries of seed production, weather, insects and disease' (McCune and Allen 1985). The random nature of these factors would prove to be difficult to incorporate into quantitative models. Ecologists would have to either include them in abstract mathematical models or rely on a more reductionist approach, integrating species biology and resource utilization to explain the mechanism of succession.

Two prominent successional models that focus on resource utilization and competition between species have been proposed to explain the mechanisms of vegetation dynamics. The 'life history' model (Huston and Smith 1987) is an expansion of the vital attribute model, but is not restricted to frequently disturbed ecosystems. The model relies on asymmetric competition (for light) as the driving force in succession. A steady state dynamic equilibrium

is achieved once a balance is struck between prevailing disturbance regimes and local successional dynamics (Kenkel et al. 1997). The life history model is based on three premises:

- Competition for limiting resources occurs between all individuals.
- Species alter their environment by changing the availability of limiting resources (e.g. nutrient depletion zone), thus affecting the relative competitive abilities of other species.
- Physiological and energetic costs preclude any one species from completely dominating a site.

These ideas were taken a step further by David Tilman who introduced the resource-ratio hypothesis (Tilman 1985) emphasizing interspecific competition as the mechanism driving successional change. The model is based on the assumption that resource availability, and the ratio of light to belowground resources, change over time. Species turnover during succession is thus driven by changes in the relative efficiency of species at acquiring and utilizing two or more limiting resources (Cook 1996). As resource supply rates change, competitive exclusion occurs as subordinate species are eliminated, which in turn drives successional change. The model also predicts that greater heterogeneity in resource supply rates within an area will promote long-term coexistence and biodiversity.

In the dawn of a new millennium, a consensus over the succession paradigm has yet to be achieved. Complex disturbance regimes, multiple successional pathways, and the stochastic nature of community dynamics make it difficult if not impossible to develop a robust theory of succession. Despite these problems, agreement has been reached on several of the mechanisms underling vegetation pattern and processes (Cook 1996):

- Disturbance drives the spatial and temporal dynamics of most terrestrial ecosystems. Disturbance may preclude systems from reaching a Clementsian climax state. In addition, multiple pathways (non-equilibrium), retrogression and cessation of succession may occur at any seral stage.
- Stochastic events play as significant role in vegetation dynamics.
- Species life-history characteristics and vital attributes, and interspecific competition for limiting resources, are useful in explaining successional processes.
- Different mechanisms may drive succession on closely related sites.

Recently, there has been a move toward mathematical models that attempt to find 'order out of disorder', utilizing fractal and chaos theory to explain spatial and temporal processes in vegetation dynamics (Kenkel et al. 1997).

2.1.2 Modelling Vegetation Dynamics

Succession theory has shifted from the Clementsian (deterministic) paradigm toward a more mechanistic view of succession, the foundation of which is the Gleasonian disorder principal: 'succession is an extraordinary mobile phenomenon' (Gleason 1926). Mathematical ecologists attempting to model natural systems may be tempted by Clementsian determinism, as it provides predictability: modelling is much more difficult under the Gleasonian paradigm (Anand 1997). Despite this obstacle, ecologists have in recent years made significant contributions to the understanding of temporal vegetation dynamics. The following is a synopsis of methods commonly used to model forest stand dynamics.

Permanent Study Plots

The most effective way to monitor stand dynamics is to actually follow vegetation change in permanent plots. Numerous studies of this type have been undertaken using comparatively short-lived species (e.g. Bullock et al. 1996, Schlesinger and Gill 1978, Sarukhan and Harper 1973, and Antonovics 1972). Unfortunately, the time required for forest successional processes to be properly elucidated is often greater than 100 years, rendering the use of permanent plots unfeasible (Finegan 1984). Alternate theoretical methods are often thus required to infer succession processes (Johnson 1979).

Static Age Models

Chronosequencing

Chronosequencing attempts to elucidate vegetation dynamics by sequentially 'linking' together various age classes of a particular forest stand-type. The observed changes in stand structure and composition are then used to infer successional dynamics: younger stands represent earlier stages of succession, while older ones represent later stages. In chronosequencing, it is assumed that the stands enumerated share similar site histories and environmental characteristics. Unfortunately, older age classes are usually underrepresented (especially in fire-prone sites), and when present may be atypical (Heinselman 1973; Johnson et al. 1994). Chronosequencing is therefore seldom used on its own, but may be useful when used in conjunction with size and/or age class distribution analysis (Kenkel and Watson 1998).

Size and Age Class Distributions (Canopy-Subcanopy Relationships)

Successional trajectories are inferred based on the size and/or age class distributions of tree species within a stand (Horn 1976). Large and small diameter classes are assumed to represent the past and future successional stages of the stand respectively (Bergeron and Dubuc 1989). For example, a stand dominated by lodgepole pine in the upper canopy and Douglas-fir in the subcanopy suggests a probable successional pathway of gradual (or possibly rapid) canopy replacement of lodgepole pine by Douglas-fir. This method explicitly assumes that life-history traits and demographic parameters (mortality, natality and growth rates) are similar both within and between species. There are several problems with these assumptions:

- The existing upper canopy may suppress the regenerating (subcanopy and sapling) trees, greatly slowing their growth and preventing them from reaching the canopy (e.g. Williams et al. 1999).
- Selective biotic disturbance, such as browsing of the regeneration layer by large ungulates, may offset the inferred successional trend.

Size-Class Ordination

Size-class ordination uses a series of 'pseudo-stands', each representing a different size (diameter) class in a given stand. An ordination is performed on the pseudo-stands, based on the relative abundance of species in each. On the ordination diagram, points representing each size class of a given stand are then linked in their order of presumed establishment, e.g. canopy, upper subcanopy, lower subcanopy, sapling (Watson and Kenkel 1998). The vector produced represents the potential successional trajectory for the stand. As in size and/or age distribution analysis, it is assumed that the smaller diameter individuals represent later stages of succession (Gutsell and Johnson 1999). 'Directional' models such as this one assume that the vegetation will reach an equilibrium state (climax). Since most systems are in a constant state of flux, the equilibrium assumption can be problematic. Other potential problems with this method include:

- Mortality rates of younger age/size classes may differ as a result of selective browsing, fire kill, and/or pest-pathogen infestations.
- Differential growth rates may 'mask successional change' (Watson and Kenkel 1998).
- The approach is aspatial: natural spatial variability is not accounted for.

McCune and Allen (1985) examined forest dynamics in the Bitterroot canyons of Montana using size-class ordination. Successional trends were inferred based on vertical (canopy) differences in tree species composition (seedlings, saplings and mature trees). Bergeron and Dubuc (1989) used a similar approach to model boreal forest vegetation dynamics in northwestern Québec. They enumerated several post-fire communities in order to assess the

effects of fire suppression on forest succession. They determined that all stands will eventually converge towards a late-successional sere dominated by shade-tolerant species. To minimize the problem of differential mortality of younger trees in the regeneration layer, they excluded the sapling and seedling layers from their analysis.

Stand Reconstruction

Stand dynamics can also be examined by reconstructing site histories based on the birth and death of individuals. Instead of inferring successional processes, stand reconstruction methods produce a temporal profile of stand dynamics based on demographic information obtained from dead (standing and fallen) and live individuals. Using dendrochronological techniques to account for missing rings, stand histories can be accurately reconstructed. Tree ages are obtained from root-collar cross sections of all individuals in a stand. This method is very laborious, but is considered more accurate than the traditional method of aging live trees at breast height. Since suppressed trees may take 15 to 20 years to reach coring height, aging trees at points above the root collar may underestimate actual establishment dates (Gutsell and Johnson 1999; DesRochers and Gagnon 1997). Using stand reconstruction methods, Johnson et al. (1994) demonstrated that lodgepole pine and Engelmann spruce establish contemporaneously following fire in forest stands of the Kananaskis valley, Alberta. Dendrochronology demonstrated that differential growth rates, rather than noncontemporaneous establishment, account for the vertical stratification observed in these stands. Mortality rates were low for initial post-fire cohorts. Continuous recruitment was apparent in most stands, but later-recruited individuals remained very suppressed and rarely reached the canopy. A static age/size profile analysis of these stands may have led to an erroneous interpretation of successional dynamics in these stands (Johnson et al. 1994).

Given the relatively short fire interval in this region, succession through canopy replacement seem unlikely: the maximum tree age in the Kananaskis was 222 years. As a result of recurrent fires, less than 5% of the Kananaskis watershed consists stands older than 200 years (Johnson and Larsen 1991). In regions where fire return intervals are longer, gap dynamics may result in canopy replacement as individual trees of the initial canopy cohort die.

The stand reconstruction approach also has its limitations. In particular, advanced decomposition may result in some snags and fallen trees not being included in the analysis. Since decomposition rates are faster for smaller individuals, a bias towards larger snags may exist (Gutsell and Johnson 1999). The greatest limitation of the stand reconstruction approach is that it is very laborious and destructive, with the result that such studies are confined to very small areas. The method is therefore difficult if not impossible to apply to large-scale landscape studies.

2.2 DISTURBANCE

Disturbance is regarded as the major driving force in boreal forest dynamics (Bergeron et al. 1998). Ecological disturbance has been defined as 'any relatively discrete event in time that disrupts ecosystem, community or population structure and changes resources, substrate availability or the physical environment' (Pickett and White 1985). Plant communities exist as a mosaic of discrete patches on the landscape, with each patch initiated by disturbance and/or the presence of a strong spatial gradient (Dearden and Rollin 1993; De Grandpré 1993).

2.2.1 Synchronous Stand Dynamics:

Fire ecology concepts and definitions

Fire is the principal large-scale disturbance driving forest dynamics in most regions of the world (Keane et al. 1996; Habeck and Mutch 1973). The mosaic of forest ages in the Boreal and Montane forests of Western Canada is the result of large, lightning-caused fires that generally reoccur within the lifespan of most tree species (Johnson and Larsen 1991). Fire acts as the primary regenerating mechanism in pyric ecosystems, by releasing nutrients and reducing competitive interactions (MacLean et al. 1983; Heinselman 1973). Given the importance that fires play in determining the age, composition and structure of northern temperate forests: an understanding of the basic mechanisms which control the timing, areal extent and severity of fires is critical.

Two distinct characteristics of fire are recognized: fire behavior, and fire effects. The behavior of a fire is determined by the fire frequency, frontal-fire intensity (includes flame length and scorch height), duff consumption and area burned. Fire behavior is dependent on factors such as weather, topography and fuel (Keane et al. 1996; Johnson and Miyanishi 1995; Fryer and Johnson 1988; Tande 1979). Fuel moisture content, which is of prime importance in determining fire behavior, is closely related to weather and climatic patterns (Johnson and Miyanishi 1995). Two types of fire behavior have been recognized, wind driven and convectively driven fires, both of which are dependent on wind and topography. Wind-driven fires are characterized by high rates of spread and low fuel consumption. Convectively driven fires are characterized by low rates of spread and high fuel consumption (Johnson 1995).

Fire effects ('ecological effects') are defined as the direct or indirect consequences of fire on vegetation. Direct fire effects include fuel consumption, tree mortality, and smoke generation. Indirect effects include soil erosion, soil fertility, vegetation patchiness and plant succession (Keane et al. 1996). Fuel consumption occurs as two sequential steps: flaming combustion (which dominates the flame front), followed by glowing (smoldering)

combustion. Flaming combustion involves the oxidation of highly combustible compounds and the ignition of volatile gases (Johnson 1995). The rapidly dried fine fuels consumed by flaming combustion contribute to the propagation of the fire and its intensity. The remaining carbon is consumed by glowing combustion, which is defined as the 'surface oxidation of char' (Johnson 1995). Glowing combustion consumes the duff layer, facilitating the redistribution of carbon and nutrient cycling (Johnson and Miyanishi 1995; Keane et al. 1996). The ecological effects of flaming and glowing combustion differ. Flaming combustion results in plant mortality, while glowing combustion results in mineral soil exposure. This is closely related to the concept of radiant heat flux. Upward heat flux (flame length) is largely responsible for aboveground plant mortality, while downward heat flux leads to litter and duff consumption and often results in seedbed preparation and root damage (Bradley et al. 1992).

Fire intensity, defined as the rate of heat transfer from a flame front ('intensity per length of fire front', Johnson 1995), is expressed as kilowatts per meter (kWm^{-1}). Convection and radiation are the primary modes of heat transfer. Empirical evidence suggests that fire intensity, flame length and scorch height are correlated, particularly when the buoyancy generated by the fire is greater than the downward inertial force exerted by the boundary layer above the forest floor (Johnson 1995). Fire intensity is often used to empirically predict fire mortality, based on either flame duration, flame length or scorch height. Low intensity surface fires often result in differential tree mortality rates within a stand. Cambial death (girdling of the stem) occurs when the inner bark is heated to above 60°C . The time required to raise the temperature of the cambium to a lethal level is proportionally related to bark thickness and stem diameter. Thus tall trees with thick bark, such as Ponderosa pine and Douglas-fir, have a greater probability of surviving a low intensity surface fire than do white spruce or subalpine fir. Intense frontal-fires ($>7,000 \text{ kWm}^{-1}$) result in complete tree mortality within a stand, regardless of bark thickness or stem diameter. Scorch height and crown base height are the two most important parameters in determining crown kill (bud and foliage kill; Johnson 1995). Fire intensity should not be confused with fire 'severity', which is a qualitative term often used to describe the impact of fire on vegetation or the removal of organic soil (Y. Bergeron 1999, pers. comm.). While observations about 'fire severity' can be used to infer 'fire intensity' (K. Lertzman 1999, pers. comm.), confusion exists over the use of the term 'fire severity'. The Canadian Forest Service (CFS) defines fire severity in terms of duff removal, while the USDA defines it in terms of fire effects (E. Johnson 1999, pers. comm.). In this report, fire 'severity' will be used to refer to effects on vegetation.

Other terms commonly used in fire studies include fire 'frequency', 'cycle' and 'return interval'. Fire frequency (FF) is defined as the 'probability of a stand (element) burning per

unit time' (Johnson and Gutsell 1994). The inverse of this is the fire cycle (FC), which is the time required to burn an area equal in size to the study area. The fire return interval (FRI) is the expected return time per stand. Annual percent burn (APB) is defined as the proportion of the study region that burns per annum.

Fire frequency can also be expressed as a 'probability distribution of survival or mortality from a fire' (Johnson and Gutsell 1994), which can be estimated from stand-origin maps. The areas of each forest age-class are used to estimate the time-since-fire distribution, which can normally be described using a negative exponential model (Masters 1990): the regression coefficient (slope) of the age-distribution plot is an estimate of the fire cycle (Tymstra 1991). Abrupt changes in the slope are indicative of alterations in the fire cycle (Johnson and Lassen 1991). The negative exponential model only considers stand replacing fires (total canopy mortality), and assumes spatial homogeneity within the study area. Area specific fire chronologies can be extrapolated from fire scar dates and age-class information to determine the mean fire return interval for low to moderate intensity fires (i.e. non-stand replacing fires). The mean fire return interval (MFRI) is defined as the 'average number of years between consecutive fires' (Tande 1979).

Fires are controlled primarily by climatic conditions. The hot, dry weather associated with a high-pressure system facilitates the rapid drying of fine, medium and heavy fuels. In western Alberta, large fire years are associated with mid-tropospheric anomalies (surface-blocking high pressure systems). These systems, which can last from several days to many weeks, occur at regional rather than local scales (100 to 1,000 km²; Johnson and Wowchuck 1993). They are characterized by low windspeeds, above average temperatures, and below average precipitation. These high pressure systems block the normal flow of moist Pacific air, resulting in extensive fuel drying (Johnson et al. 1990). High pressure systems lasting less than ten days typically have 'little influence on area burned' (Johnson and Wowchuk 1993): while fine fuels (<2 cm in diameter) dry within 24 hours, drying of soil organic matter takes a few weeks (Johnson 1992).

The mixing of low and high pressure systems (i.e. weakening of the high pressure system) produces convective storms characterized by high lightning density, localized precipitation, and high and variable winds (Nash and Johnson 1996). The initial spread rate of a lightning fire is slow, but spread rate increases dramatically at the frontal boundary between low and high pressure cells. High spread rates ($\geq 20\text{m min}^{-1}$) and intensities are characteristic of fires that are oriented by wind direction, wind speed and topography. Strong winds and dry fuels favour the development of high frontal-fire intensities ($>10,000\text{ kWm}^{-1}$; Weir et al. 1995). Such 'catastrophic' stand-replacing fires may occur in any forest type regardless of stand

age, composition (fuel type), aspect or elevation (Weir et al. 1995; Bessie and Johnson 1995; Johnson and Larsen 1991; Fryer and Johnson 1988).

While the interaction of stagnant high pressure systems, dry fuels and lightning ignition occurs infrequently (about 3% of fires), the resulting 'catastrophic' fires may account for 95% or more of the total area burned (Weir et al. 1995). The remaining lightning fires, which occur when low-pressure systems predominate, are small in areal extent: in Alberta and Saskatchewan, 98% of lightning-fires burn less than 1% of the total land area. The behavior of these small fires is strongly influenced by topographic features (e.g., slope, aspect) and fuel characteristics (Wier et al. 1995).

The climatic conditions preceding a burn influence fire behavior and effects, with high-intensity fires occurring during extended dry periods (Heinselman 1973). Prolonged dry periods can decrease the time and energy required to ignite live fuels, and extreme drought conditions can further increase total fuel loads by drying out the leaves of deciduous shrubs and trees (Heinselman 1996). Drought years account for 70% of northern forest fires, and 92% of the total area burned (Tande 1979). Nash and Johnson (1996) found a 'striking resemblance' between the number of 'drying-days' and the total area burned. Seasonality is also important: spring fires tend to be less severe than summer fires (Heinselman 1996; White 1985). Spring fires seldom burn deep into the organic layer (which is still cool and wet), but they can nonetheless result in 'crowning' (Heinselman 1981). Soil moisture reserves are generally much lower in summer, resulting in greater consumption of the organic layer.

Summer fires are common, since lightning activity is greatest in the mid-summer months (Heinselman 1981). In western Canada, a 'lightning-shadow' along the eastern and western slopes of the Continental Divide results in variable strike intensities: for example, lightning strikes are much most common in western portions of Yoho and Kootenay National Parks than in eastern portions (Tymstra 1991). Low lightning ignition intensities in the Rockies are offset by more conducive fire conditions when strikes do occur. Lightning strikes are more common in the foothills and boreal forest regions, but most (about 98%) do not start fires since they are accompanied by heavy precipitation (Johnson 1992).

Fire Regime

Factors affecting fire behavior have been used to develop the concept of 'fire regimes' (Heinselman 1973). The term fire regime is defined as the 'ecologically significant kinds of fire activity that characterize a specific region' and so does not include the effects of smaller fires (Heinselman 1996). The fire regime for a region is usually defined within a specific reference period (Lertzman 1998): variation at temporal scales shorter than the reference period is interpreted as 'noise', while time scales longer than the reference period are

interpreted as changes in fire regime. Sources of variation include both temporal and spatial heterogeneity. Temporal heterogeneity includes long-term climatic trends and weather patterns (e.g. mid-tropospheric anomalies), while spatial heterogeneity incorporates topographic variation within a study area (e.g. aspect, slope). It therefore becomes difficult to objectively define the fire regime for a region, since the inferences drawn from a fire history study depend on the temporal and spatial scales chosen. This makes comparisons between studies difficult (Lertzman 1998).

Three major fire regimes have been identified in western North America, based on fire frequency, intensity and areal extent (Agee 1996):

- *High Severity*: infrequent, stand replacing fires (>100 years).
- *Moderate or Mixed Severity*: a complex combination of high, moderate and low fire intensity regimes (25-100 years).
- *Low Severity*: frequent, low intensity fires (< 25 years).

The Montane ecoregion is described as having a low to moderate severity fire regime. In Jasper National Park, Douglas-fir forests have a mean fire return interval (MFRI) of 17.6 years, open grasslands 20.6 years, and lodgepole pine forest 26.8 years (Tande 1979). MFRI values in Banff National Park are estimated to be longer: about 42 years for Douglas-fir, lodgepole pine and whitebark pine stands. Mesic Douglas-fir, white spruce and lodgepole pine stands have a MFRI of 56 years. At 26 years, aspen stands have the shortest MFRI (White 1985). MFRI values in Yoho and Kootenay National Park range from 80 to >250 years for large, moderate to high intensity fires, and from 15 to 150 years for small to large, low to moderate intensity fires (Tymstra 1991; Masters 1990). Fires in the montane ecoregion either occur early in the spring or fall (whereas subalpine stands generally burn in summer). Most fires occur in the spring following snow melt, and usually spread through 'cured' vegetation (White 1985).

Vegetation Effects and Adaptations

In mountainous terrain, weather patterns, fuel availability and topography vary considerably (Tymstra 1991), with the result that fires rarely consume all the forest (Rowe and Scotter 1973). Variation in physiography, fuels, winds and fire intensities results in a 'peppered landscape' of unburned forest patches within the boundaries of a large burn (Tande 1979; Romme and Knight 1981). These patches are important in providing the seed and propagule sources necessary for the eventual re-establishment of stands following fire. Initial vegetational heterogeneity following fire has been attributed to the spatial heterogeneity of fire intensity, particularly when unburned patches of vegetation are left behind (Shafi and Yarranton 1973).

Physiographic complexity affects the behavior of fire, and is reflected in the mosaic patchiness of vegetation on the landscape (Walker and Kenkel 1999). Research in the Medicine Bow Mountains of southeastern Wyoming suggests that topographic complexity creates 'natural' fire breaks. As a result, spruce-fir forest are restricted to 'protected' areas such as ravines and valley bottoms, whereas upland slopes and ridges are dominated by mono-dominant stands of lodgepole pine (Romme and Knight 1981). Similar patterns are seen in southern Alaska, where centuries-old western cedar stands occur along streams and 200 year old white spruce forests along ravines (Romme and Knight 1981). In the boreal forest, old-growth stands are usually found on hygic sites where local topography affords some protection from fire (Heinselman 1973).

High frequency, low intensity fire regimes favour species whose vital attributes are suited to pyric environments. In the montane and lower subalpine ecoregions, periodic fires favour cone serotiny in lodgepole pine. In the absence of competition, trembling aspen regenerates by root suckering following fire. Mature Douglas-fir trees can withstand low intensity fires, since the species develops a thick corky outer bark and has a moderately high branching habit. In the understory, both bearberry and twinflower are considered fire susceptible but can survive low severity fires if the duff layer is not fully consumed. Pine grass is considered moderately resistant to fire, since it can endure low intensity fires by resprouting from surviving rhizomes (Bradley et al. 1992).

Fire Regime Dynamics in the Canadian Rockies

A large percentage of the intact natural forest of Canada exist under the guidance of the National Parks system, where active fire management policy has been enforced since its inception in the early 1900's. The future viability of fire dependent forest such as interior Douglas-fir stands is dependent on the clear understanding of the factors and conditions controlling the fire regime of an area.

The historic fire regime of the Boreal and Cordilleran ecoregions in western North America have changed since the early 1900's. Historical fire records in the four Mountain National Parks indicate that the mean annual number of fires has declined. This decrease has been attributed to fire suppression policies implemented in the early 20th century (White 1985). However, others have argued that decreased fire frequency is the result of changing climatic conditions, not anthropogenic influences. For example, Johnson et al. (1998) note that the areal extent of burns has been increasing over the past 20 years, irrespective of fuel conditions.

Aboriginal-Mediated Fire Regimes

Based on archaeological data, human occupation of the major valleys in the Canadian Rockies may extend as far back as 12,000 years BP, with intensive human occupation occurring between 1,700 and 500 year BP (White 1985). During this period, nomadic human populations occupied the montane valleys in winter and the subalpine-alpine regions in summer. It is believed that periodic fires were set to maintain optimal forage land for large game herds. These fires may have been significant ignition sources, especially on the eastern slopes where lightning strikes were less common (Larsen 1997; Kay et al. 1994). Ethno-historical research in northern Alberta indicates that aboriginal burning practices may have caused a temporary change in fire frequency. Prior to introduction of the 'trapping economy' in 1790, aboriginal peoples may have relied on fires to increase browse for large game animals.

Kay (1997) suggests that the decrease in fire frequency in the Canadian Rockies is attributable to 'modern fire suppression and the elimination of native burning, not climatic factors'. However, changes in fire frequency have also been documented in areas with no historical record of extensive human activity, including the Kicking Horse Valley and Glacier National Park (Tymstra 1991; Johnson et al. 1990). Evidence for aboriginal burning cannot be determined empirically, nor can it be dismissed. Burning practices of the Cree in Northern Alberta were documented by Lewis (1982). Fires were systematically set in the spring and fall to maintain open rangeland, but most were small and of low intensity. Assuming that such practices also occurred in the Rockies, it seems unlikely that such fires could have had a significant influence on the regional fire cycle.

Climate-Induced Changes in Fire Regime

The decrease in fire frequency throughout much of the northern hemisphere has been attributed to climate change. Since the 1890's, global temperatures have increased at a rate of 1.7°C per century (Flannigan et al. 1998). In some regions north of the 35th parallel, increases in temperatures have also been associated with increased precipitation (Larsen 1997). Since 1980, mean annual precipitation in the four Mountain parks has increased relative to historical records (Luckman 1999).

Increases in fire activity near the turn of the century have been attributed to road and railway construction. This argument has been rebutted by some researchers, who argue that most of the larger burn years (1885 to 1890) were strongly correlated with hot, dry weather. Most human-caused fires originated in close proximity to trails, roads and railway right-of-ways (Tymstra 1991), but these fires do not account for the extensive burns that originated in remote regions. Severe forest fires occurred throughout north-central North America during

the late 1800's. Parks records from Manitoba, Minnesota, Wyoming, Alberta and British Columbia all document the occurrence of large fires between 1885 and 1900 (Johnson and Miyaniski 1991; Masters 1990; Tande 1979; Heinselman 1973; Rowe 1955).

Based on tree ring analysis and pollen data, climatic conditions and fire frequencies have been reconstructed for several regions in the Canadian Rockies. The period between 1500 and 1700 was warm and dry. Large high pressure systems that blocked the flow of moist Pacific westerlies into the region were probably common during this period (Larsen 1997; Johnson and Larsen 1991). In Jasper National Park, sections taken from large Douglas-fir trees indicate that extensive fires occurred between 1727 and 1758 (Tande 1979). In Yellowstone National Park, forest fires between 1740 and 1855 produced over 70% of the pre-1988 lodgepole pine stands (Barrett 1994). In Kootenay National Park, extensive fires occurred in 1708 (5,768 ha), 1748 (5,576 ha) and 1768 (9,694 ha; Masters 1990).

Reduced fire frequency between 1780 and 1830 was likely attributable to a return to cooler, wetter conditions, the result of intrusions of strong low-pressure weather systems. Anthropogenic influences were minimal during this period, since an outbreak of smallpox decimated the Kootenay Indian population (Johnson and Larsen 1991).

Precipitation levels in the central Canadian Rockies have fluctuated since the 1890's (Larsen 1997). During this time, periods of very warm, dry weather were associated with extensive fire activity (Johnson and Miyaniski 1991). In Banff National Park, three of the driest periods occurred between 1885-1890, 1906-1908, and 1920-1940 (White 1985). These dry periods were associated with outbreaks of large fires throughout the Park. For example, in the spring of 1889 an estimated 12,150 ha burned in the lower Bow and Cascade River valleys. In the summer of 1908, a possible dry lightning fire burned over 5,000 ha near Castle Junction, and in 1936 a human-caused fire burned about 5,200 ha near Flint Park (White 1995). Fire history studies conducted in Jasper National Park indicate that medium to high intensity fires in 1889 consumed about 33,839 ha of valley and subalpine forest (Tande 1979). In the Kananaskis, most of the valley bottom burned during four major fires in 1891, 1904, 1920 and 1936 (Johnson and Fryer 1987). In Kootenay National Park, over 19,939 ha of forest burned in 1908 (Masters 1990). In Yoho National Park, a majority of the forest cover in the Kicking Horse corridor originated from fires occurring between 1883 and 1915 (Tymstra 1991). Regardless of their origin (human or lightning caused), the intensity of the late-1800's fires were influenced by the prevailing dry climatic conditions.

Impacts of Fire Suppression

The reduction in fire frequency which began in the early 20th-century has been attributed to 'climate change rather than the influence of European man' (Masters 1990). It has been

argued that fire prevention and suppression were largely ineffective until the advent of more sophisticated initial response programs of the 1980's, as well as the use of lightning strike detection equipment (Achuff et al. 1996; Masters 1980). In Kootenay National Park, the reduction in fire activity between 1928 to 1988 was attributed to fire suppression. However, large lightning-caused burns did occur in 1926 (13,000 ha) and 1968 (1,700 ha), indicating 'little success in suppressing these fires' (Masters 1990).

Suppression has not eliminated fire, but it has altered local fire regimes to include less frequent but more intense burns (Parsons and Botti 1996). Johnson and Larsen (1991) state that 'fires are controlled by climate ... and thus will be difficult if not impossible to suppress'. In fact, similar fire frequency reductions have occurred in areas without full or modified fire suppression zones (Flannigan et al. 1998). It should be noted that the extent of fire behaviour controlled by climate is dependent on vegetation type. Hely et al. (2001) found that differences in deciduous and coniferous dominance may explain differences in fire behavior between western Canada and eastern Canada. The conifer dominated forests of Alberta create a homogeneous land cover class where prolonged high pressure systems often result in wide spread fire activity. Conversely the spatially variable boreal-mixedwood region of Québec in combination with infrequent prolonged drying events creates heterogeneous burn areas (Hely et al. 2001).

On the other hand, fire suppression has been 'effective' in areas where public safety and park infra-structure are priorities. Fire exclusion has resulted in a shift towards closed 'decadent' forests. The once open, mixed forests of the lower montane ecoregion are now dominated by 'over-mature' lodgepole pine (Rogean 1996). In these communities, light surface fires once consumed understory woody fuel and killed most of tree saplings in the regeneration layer. Tree recruitment was confined to patches where canopy litter was reduced by previous fires. These 'litter-free zones' reduced the effects of subsequent fires and allowed saplings of Douglas-fir and other tree species to achieve a fire-resistant size. Unfortunately, fire suppression in these areas has resulted in extensive regeneration of conifers, resulting in a closed canopy (Bradley et al. 1992). Dramatic changes in stand composition are expected under fire suppression. The disturbance regime of boreal and montane ecoregions has favoured the evolution of species life-history characteristics such as cone serotiny, which may prove maladaptive under a fire suppression regime (Kenkel et al. 1997).

2.2.2 Asynchronous Stand Dynamics

In the absence of fire, stand structure becomes more entropic (complex) resulting in a patch mosaic.

Gap Dynamics

In the absence of large fires, boreal forest dynamics is dependent on the frequency of small-scale disturbances that create canopy gaps (Frelich and Reich 1995). Gaps created by windthrow, snow, ice storms, herbivory, insect damage and fungal pathogens may account for the high degree of forest canopy heterogeneity in older stands. Small-scale disturbances break up the 'spatial legacy' left behind by larger disturbances, thus increasing landscape heterogeneity (Walker and Kenkel 1999). Older 'decadent' stands that have not experienced large-scale fire disturbances are prime candidates for gap dynamics (Yong et al. 1998). In Québec, canopy gaps were found to increase from 7% in younger stands, to 40% in 'old-growth' boreal forest (Kneeshaw and Bergeron 1998). Canopy deterioration creates opportunities for cyclical successional processes to occur at the patch level (*sensu* Watt 1947). Gap openings are usually colonized by later successional species, resulting in the break-up of homogeneous early-successional stands of pine or trembling aspen. At large scales, this results in a complex heterogeneous forest at the landscape level (Frelich and Reich 1995).

The creation of gaps through the death of single trees (or small group of trees) alters understory growing conditions by changing resource availability (Kuuluvainen and Pauli 1998). Changes in light, temperature and soil moisture influence the growth rates and regenerative capacity of understory species (Yong et al. 1998). Latitude, slope, aspect, gap size, gap orientation and canopy height all affect the quality and quantity of light reaching the forest floor (Poulson and Platt 1989). The growth rates of many understory species are altered as light conditions change. In shaded environments, the apical control of shade-tolerant species is often reduced, producing a sympodial or umbrella-like growth form (Kneeshaw et al. 1998). Once a gap opening is created, saplings allocate more resources to terminal growth, thus increasing vertical growth rates (Williams et al. 1999). However, suppressed individuals that are close in age to canopy trees may not respond well to canopy release (Weir and Johnson 1998).

The formation of favourable regeneration microsites facilitates seedling germination and growth. Decomposed logs and exposed uprooted regions created by windthrow provide favourable regeneration sites for many shade-tolerant tree species. In addition, changes in understory community composition can also affect seedling establishment and growth (Kuuluvainen and Juntunen 1998). For example, increased cover of beaked hazelnut

resulting from canopy openings may limit white spruce regeneration in Riding Mountain National Park (Caners and Kenkel 1998).

Herbivory

Herbivory can have a direct impact on plant-plant interactions by removing the competitive influence of dominant species. In 'inhibition' succession models (Connell and Slatyer 1977), vegetation change occurs when a cohort is removed as a result of acute biotic or physical disturbance. Herbivory can potentially alter successional trajectories by altering competitive interactions, and by changing soil characteristics (compaction) and nutrient availability (Hobbs 1996). For example, in Sweden preferential browsing by reindeer has hampered the regeneration of birch (*Betula pubescens*) in post-fire conifer communities (Engelmark 1993).

2.2.3 Ungulate Population History in the Four Mountain Parks

The ungulate population of the Central Canadian Rockies includes moose (*Alces alces*), white-tail deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), woodland caribou (*Rangifer tarandus*), bighorn sheep (*Ovis canadensis*), and mountain goat (*Oreamnos americanus*). Elk are the most plentiful ungulate in Jasper and Banff National Park. There are an estimated 2500 elk in Banff National Park, including 570 in the Bow Valley and about 460 in the vicinity of the Banff townsite (Parks Canada 1998). Plans to relocate numerous elk which reside near the Banff townsite including 'active deterrence' is expected to dramatically reduce resident elk numbers as well as elk-human conflicts. Elk population records have been kept for several decades in Kootenay National Park, with a majority based on road side surveys. In Kootenay elk populations have declined since the 1950's; populations were estimated at 200-300 elk by the 1970's and 80's. The 90's saw a dramatic decline in populations, with less than 30 resident elk being surveyed in 1998. Attempts to replenish the population commenced that year and continued till 1999 with 25 animals imported annually from Banff (plus several habituated elk relocated from Banff). Many of the Banff elk migrated to the south end of the park while others didn't make it past their first year (Alan Dibb 2001 pers. comm.). Current estimates put the population at less than 50 resident elk (Alan Dibb 2001 pers. comm.; Van Egmond 1990). The situation in Yoho is similar with current estimates at around 30 resident animals (Alan Dibbs 2001 pers. comm.). There are currently an estimated 1000 to 1200 elk in Jasper National Park (Wes Bradford, 2001 pers. comm.).

Elk Habitat Requirements

Elk habitat is dependent on topography, weather, forage quality and vegetation cover. In summer, elk occupy a variety of habitat types from alpine meadows to montane valleys. Browse consists primarily of graminoids, shrubs and tree saplings within aspen-wild rye and shrub-meadow communities. In winter, elk migrate to lower montane and valley ecoregions where snow depths are lower (Van Egmond 1990). Depending on snow loads, elk winter range may include Douglas-fir and/or aspen stands. It has been demonstrated that browse selection is a function of population density. At low elk densities (<1 individual km⁻²), deciduous species such as willow and aspen experience very little browsing. At moderate densities (1-3 individuals km⁻²), browsing intensity on aspen, willow and other selected deciduous shrubs increases. At high elk densities (4-10 individuals km⁻²), aspen and willow are severely browsed. High elk densities also result in selective browsing of more palatable conifers, including Douglas-fir (White et al. 1998). Woody browse, such as aspen and willow, constitute only about 5% of the elk diet: the bulk of their diet is herbaceous vegetation. Elk abundance is primarily controlled by herbaceous plants and 'largely decoupled from woody browse' (Coughenour and Singer 1996).

In addition to ungulates, bears also preferentially browse on the fruits, roots and leaves of selected understory species (Hamer et al. 1979). Grizzly (*Ursus arctos*) and black bears (*U. americanus*) are known to consume hedsarum roots, graminoids, horsetails, fruits from Buffaloberry (*Shepherdia canadensis*), blueberry (*Vaccinium* sp.) and bearberry (*Arctostaphylos uva-ursi*), tree needles tree bark and bryophytes (Raine and Kansas 1987).

Parks Elk Management Policy

Current Parks policy on wildlife and vegetation management is based on the principles of the Leopold report (1963), and on Cole's 'natural regulation' hypothesis (1971). The Leopold report 'framed the modern conservation ethic in national parks' (Boyce 1998). It stressed the importance of protecting representative samples of ecosystems, and recognized the importance of fire and other disturbances in maintaining the ecological integrity of an area. Ironically, the Leopold report stated that ungulate populations within national parks should be actively managed to prevent overuse of rangeland (Leopold 1963). In 1968, the park biologist for Yellowstone National Park, G.F. Cole, proposed the natural regulation hypothesis for wildlife and vegetation management. It stated that ungulate populations are regulated by food-limited or density dependent mortality (bottom-up hypothesis) and not by predator-prey interactions (top-down hypothesis). This hypothesis was based on Lack's (1954) food-limiting theory, which states that winter range conditions determine ungulate population levels. In support of this theory, recruitment rates in elk appear to be inversely

related to population density and winter severity (Richards 1997; Singer et al. 1997). Houston (1982) concluded that elk mortality rates were significantly influenced by severe winters.

The mechanism of ungulate population control has been thoroughly debated in the recent literature (Ehrlich et al. 1972; Coughenour and Singer 1996; Boyce 1998; Sinclair 1998; White et al. 1998; Kay 1998). Advocates for the natural regulation hypothesis cite numerous examples, from the Serengeti-Mara to Yellowstone National Park, in which natural regulation of large ungulate populations has occurred (Sinclair 1998). In the Rocky Mountain Parks, the overriding factor affecting population fluctuation is winter mortality, while depredation appears to have little impact in regulating ungulate populations. Sinclair (1998) notes that wolves in Algonquin Provincial Park (Ontario) only kill deer in 'poor condition' and thus have very little effect on population regulation. However, preliminary results from the wolf-prey study in Banff National Park indicate an inverse relationship in the spatial distribution of gray wolves and elk. This result suggests that wolves are having an effect on elk numbers, especially where the two populations are sympatric (Hebblewhite 1998). In Yellowstone National Park, a 5-30% reduction in elk numbers is expected once wolves are reintroduced.

Parks Elk Management History

The abundance of elk in the Rocky Mountain Parks was undocumented prior to 1880. Based on historical accounts Mule deer, moose and bighorn sheep were more common than elk, at the time Banff was established (Stringer 1966). With the exception of Jasper National Park, elk disappeared from the Alberta Rockies in the 1880's, probably a result of severe winter conditions (Stringer 1966). A population of elk from Yellowstone National Park was relocated to Banff National Park between 1918 and 1920. The large fires of the late 1800's increased the extent of ungulate habitat, resulting in a population explosion of elk that lasted until the 1940's. By this time 'the range condition became critical', particularly in aspen and Douglas-fir stands within Banff (Stringer 1966). Elk were also considered widespread and problematic in Kootenay National Park (Van Egmond 1990). In an attempt to alleviate further range damage, Parks Canada adopted an 'artificial regulation' policy which lasted from the 1940's to 1969. Initially, between 400 and 700 elk were culled from Jasper and Banff National Park (Singer 1966). In 1968, the policy of 'natural regulation' was enacted in Yellowstone National Park in response to public pressure against the culling of wild animals (Coughenour and Singer 1996). Banff and the other Canadian Rocky Mountain Parks adopted a similar 'natural regulation' policy soon thereafter. The theory behind this policy stated that 'ungulate populations may be regulated without human interference through food limitation' (Coughenour and Singer 1996).

Elk populations in Banff and Jasper Parks have increased since 1969, especially in areas close to town sites (White et al. 1998). The prime feeding ranges of elk, such as grasslands,

aspen stands, and shrubfields, have diminished in extent as a result of fire suppression (Kay et al. 1994). Concern over willow and aspen over-browsing are being investigated in Banff. Similar studies in Yellowstone have created some dissension amongst researchers. Kay (1990) postulates that elk densities are greater than they have ever been in the past, and that the lack of aboriginal hunting practices, coupled with the current 'natural regulation' policy, has resulted in the degradation of aspen and willow communities. In pre-Columbian times, the human population in the western hemisphere has been estimated at about 8 million (Huff and Varley 1999; but see Kay 1995; Wagner 1995). It is argued that the population was too low to have had a significant influence on animal abundance and ecological processes.

In the 1800's both willow and aspen communities 'thrived' despite high ungulate numbers (Schullery 1997), but since the 1960's the development of these communities has been dramatically hindered (Huff and Varley 1999). If successful regeneration occurred during the late 1800's, why are these same communities not responding in the same manner today? Further research is required, but it has been speculated that synergistic interactions between herbivory and environmental effects could account for the decline in aspen and willow communities in Yellowstone National Park (Huff and Varley 1999).

Construction of ungulate-proof fencing and wildlife underpasses along major highways in Banff National Park has decreased density-independent elk mortality in recent years. In addition, the 'prey-refuge' zone around Banff townsite has significantly reduced predator-driven population regulation in the area. Together, these factors may explain the large population increases of elk within the Bow valley. Conversely, the reduction in the elk populations of Yoho and Kootenay National Parks has been attributed to a reduction of forage land. The forage range of elk is now limited to roadsides and railway right-of-ways, but grazing in these areas has increased density independent mortality (Van Egmond 1990). The lack of a 'prey-refuge' zone, and hunting in the winter range outside the Parks, may also be contributing to population declines (Van Egmond 1990).

CHAPTER 3

STUDY AREA

3.1 BACKGROUND

The synergistic interaction of climate, fire history, predator-prey interactions, as well as episodic stochastic events play an important role in shaping the structure of forest stands in Canada's four mountain parks. Growing concerns over the interference of 'natural process' created by 20th century development within National Parks has sparked debate over what role Parks should play in the future (e.g., passive vs active management paradigm). In the process past landuse practices and management philosophies have been brought into question in light of growing scientific information. The current study aims to elucidate the factors and conditions affecting the growth, regeneration, and succession of interior Douglas-fir stands in Canada's four mountain parks. Although much is already known about the biology of the species the majority of the peer-reviewed research has been done on the more economically important coastal variety. Stringer and La Roi's (1970) paper on Douglas-fir in Banff and Jasper was the only study done on the species within the Canadian Rockies, but failed to address the long-term status of the stands. The ecological land classification created for the parks was done at a coarser scale and tended to focus on mainly the description of forest stands. This study is the first to describe the structure and composition as well as use multivariate techniques to model the regeneration and successional trajectories of interior Douglas-fir within Banff, Jasper, Yoho and Kootenay National park. The study is partitioned into three chapters, the first (**chap. 4**) looks at the classification and environmental relationships of stands. The second (**chap. 5**) examines the growth of regenerating Douglas-fir in each 'stand-type'. Finally the third (**chap. 6**) examines the regeneration and succession of interior Douglas-fir. Study objectives are outlined in each chapter.

3.2 THE FOUR MOUNTAIN PARKS

The interior Douglas-fir stands enumerated in this study were located in Canada's four 'mountain parks' (Banff, Jasper, Kootenay, and Yoho National Parks), which together form a contiguous land area of 20,339 km². Of the total contiguous land area contained within the parks only 8% (1,671 km²) is occupied by montane vegetation. The four mountain parks occur on the eastern and western slopes of the Rocky Mountains in the provinces of Alberta and British Columbia (**Fig. 3.1**).

The main valleys of the four parks are U-shaped from previous glaciation events, with a majority of the Douglas-fir forests situated in the upland portions of the valley bottoms and basal slopes. The valley floors excluding the floodplains are composed of till and glacio-

fluvial deposits made up of mainly limestone, dolomite, shale, and quartz sandstone. The undulating valley topography within the parks is attributed to varying thicknesses of glacial outwash deposits overtop exposed bedrock (Stringer 1966). A majority of the soils encountered in the montane and lower subalpine ecoregions of parks are young Brunisols. Organic, Greyolic, and Regosols are common where soil development has either been inhibited by stagnant water or setback by active geomorphic activity (Achuff et al. 1993; Holland and Coen 1982).

3.2.1 Banff National Park

Banff National Park (est. 1885) covers an area of 6,833 km² that includes the main and front ranges of the Alberta Rockies east of the Continental Divide. The eastern boundary of the park borders on the Alberta foothills ecoregion. Around 83% of Banff National Park is vegetated. The subalpine zones occupy 53.3% (3442 km²) of the total land area, followed by the alpine ecoregion at 24% (13,44.3 km²) and finally the montane ecoregion which is the smallest of the four mountain parks, occupies around 3% (201.58 km²) of the total land area in the park.

Soils of the montane ecoregion of Banff range from well drained Regosols, Orthic Eutric Brunosols in subxeric stands to very poorly drained Gleysols with hydric stands. (Holland and Coen 1982). Stringer (1966) found that most of the humus encountered in Jasper and Banff was of the Mor type. This is important since interior Douglas-fir was found to grow better where the humus was Moder rather than the more nutrient poor Mor (Krajina 1969). All enumerated stands were located in the southern half of the Bow River Valley watershed, from the east gate to the Sawback range (115°28'W, 51°08'N to 115°50'W, 51°15'N). A total of sixty-three plots were established in Banff National Park (Fig. 3.2).

3.2.2 Jasper National Park

Jasper National Park (est. 1907) covers an area of 10,787 km² immediately north of Banff. Around 80% of Jasper National park is vegetated. The subalpine ecoregion makes up the largest forested zone in the park covering 66.9% (5,491 km²) of the total land area, followed by the montane ecoregion which covers 7.1% (800 km²) and the alpine which covers only 5.6% (628 km²): interestingly enough water bodies only occupy around 1.1% of the total land area (Parks Canada 1997). Like Banff, Jasper is located on the main and front ranges of the Alberta Rockies east of the Continental Divide, and its eastern boundary borders on the Alberta foothills ecoregion. All enumerated stands were located within the Athabasca River Valley watershed, from Mount Fryatt to Esplanade Mountain (117°45'W, 52°30'N to 118°05'W, 53°10'N). A total of fifty-nine plots were established in Jasper National Park (Fig. 3.3).

3.2.3 Yoho National Park

Yoho National Park (est. 1886) covers an area of 1,313 km². Around 97% of Yoho National Park is vegetated. The subalpine zones make up the largest ecoregion occupying 46% (601.8 km²) of the total land area, followed by the alpine ecoregion at 33% (437.9 km²) and the montane at 18% (240.9 km²). Yoho is situated within the southern extent of the Rocky Mountain Thrust belt which is located on the main and western ranges of the British Columbia Rockies west of the Continental Divide, and its western boundary borders the Columbia trench.

The soils of Yoho National Park are complex and considered young in origin with Brunisols and Podzols representing the most common developmental stages encountered (Achuff et al. 1992). Regardless of the diverse array of soils present on the region, there is a 'fundamental simplicity' which characterizes them, with only six out of the nine orders of the Canadian System of soil classification represented (e.g., Brunisol, Podzol Luvisol, Gleysolic, Organic and Reosolic; Achuff et al. 1993). Soils of the montane ecoregion of the park are classified as either Brunisolic or Regosolic. Soil parent material is mainly calcareous and includes glacial, fluvial, glacialfluvial, glaciolacustrine, and colluvium genetic material (Achuff et al. 1993). The montane ecoregion is mainly characterized by Eutric Brunisols soils. Both Orthic and Eluviated Eutric Brunisols are common in hygric white spruce – Douglas-fir dominated forests (Achuff et al. 1993). Subxeric Douglas-fir dominated stands in the park are characterized by well drained Eutric Brunisols and Regosols on colluvial and morainal landforms (Achuff et al. 1993). The study area is located along the watersheds of the Upper and Lower Kicking Horse Valleys (116°20'W, 51°29'N to 116°38'W, 51°05'N). A total of twenty-nine plots (0.29 ha) were established in Yoho National Park (Fig. 3.4).

3.2.4 Kootenay National Park

Kootenay National Park (est. 1920) covers an area of 1,406 km² along the main and western ranges of the British Columbia Rockies, west of the Continental Divide. Approximately, 97% of the Park is vegetated. The subalpine ecoregion takes up 48.9% (687.6 km²) of the total land area, followed by the montane at 30% (429.3 km²), and the alpine at 18% (257.5 km²). Soils and landform are similar to those encountered in Yoho National Park, with well drained Eutric Brunisol and Regosols characterizing xeric montane forests.

The western boundary of the park borders the Columbia trench. The enumerated stands were located along the southern end of the Vermilion Range, from the Kootenay River to Sinclair Creek (115°50'W, 50°55'N to 116°05'W, 50°35'N). A total of sixty-nine plots (0.69 Ha) were established in Kootenay National Park (Fig. 3.5).

3.3 CLIMATE

Climatic records for the four mountain parks have been maintained since the late 1800's. However, non-synchronous establishment of weather stations, historic data sequestered or lost on out dated storage media, interpretation of measurements, and the general logistic difficulties in maintaining remote weather sensors under harsh field conditions has resulted in incomplete climate data. Furthermore, the accuracy of long-term weather must also be taken into consideration. Janz and Storr (1977) indicate that one of the common problems encountered with winter precipitation records results from the non-uniform distribution and re-distribution of snow, within a canopy.

Given the dramatic effects that topography plays on mesoclimate in the parks it is often difficult to extrapolate conditions from weather stations situated in near townsites to the field, even when weather data is complete. Nonetheless, the overriding influence that latitude, mountain range orientation, proximity to large water bodies, and topography play on climate increases the confidence in the results obtained from incomplete weather records.

Vegetation zones in mountain environments are the product of geoclimatic heterogeneity and mountain topography. In the Canadian Rockies, biogeoclimatic zones (reflective of macroclimatic conditions) are determined by latitude and elevation (Daubenmire 1943). The Continental Divide (>3,000 m) acts as a physical barrier to Pacific and Continental air masses, thus modifying the regional climate of both the eastern and western continent ranges (Achuff et al. 1993). The eastward movement of Pacific air across the montane Cordillera has been cited as the causal factor in extending the distribution of coastal species to the western slopes of the Rockies (Heusser 1956). The amount of precipitation changes with proximity to the Continental Divide. As Pacific air masses rise, they cool and drop most of their precipitation on the western slopes. It has been estimated that over 75% of precipitation falls west of the Continental Divide (Kershaw et al. 1998; **Fig. 3.5**). The summer months are warm at lower elevations, but cooler and wetter at higher elevations. Winters are generally mild and characterized by heavy snowfall. Mean annual precipitation is lowest in valleys that are far from the Continental Divide (Tymstra 1990). The high mountain peaks of the Continental Divide block moisture-laden Pacific air masses from reaching the eastern slopes. As a result, the major valleys of the eastern slopes are drier than those west of the Divide. On the eastern slopes, the summer months are warm and dry at lower elevations, but cooler and wetter at higher elevation. Winters on the eastern slopes are colder, with snow accumulation ranging from light in the valleys to heavy at higher elevations (**Fig. 3.6**). The upper subalpine and alpine ecoregions can experience below-zero temperatures year round, severely limiting tree growth (Ecological Stratification Working Group 1995). Temperature extremes east of the

continental divide are reported to be around 83°C, west of the divide the range is less than 72°C at Radium Hot springs (Janz and Storr 1977). Minimum winter temperature are noteworthy since the main valleys of Banff and Jasper have all experienced temperatures around -50°C. In contrast Janz and Storr (1977) reported that the lowest record temperatures in Kootenay and Yoho were around -43°C, in the southwestern portions of Kootenay extreme minima are around -35 to -40°C (Janz and Storr 1977).

3.3.1 Western Parks (Yoho & Kootenay National Park)

The climate of the western parks is influenced by cold Arctic air masses originating in the Yukon and Alaska, and by warm intrusions of Pacific air (Janz and Storr 1977). Warm, moist Pacific air masses (westerlies) release most of their precipitation as they move east across the Coastal, Selkirk, and Columbia Mountains. By the time these air masses cross the Rocky Mountain Trench, most of their precipitation has been lost. As a result, lower-elevation western slopes of western Kootenay and Yoho National Park are generally classified as arid. But as these Pacific air masses rise in elevation they cool and become saturated, releasing precipitation on the upper slopes of the western Rockies before crossing the Continental Divide. The western valleys and higher mountain slopes of Kootenay and Yoho National Park thus receive much more precipitation than the lower slopes adjacent to the Rocky Mountain Trench (Janz and Storr 1977).

Intrusions of warm and moist Pacific air render the montane climate of the eastern British Columbian parks more moderate than that of the western Albertan parks. Temperatures are generally milder in both summer and winter, although periodic cold spells occur when Arctic air masses from Alberta cross the Kicking Horse and Vermilion River Passes. Mean monthly temperatures are highest in July, ranging from 22.1°C in the Kicking Horse Valley near Field (1,219 m asl) to 24°C near Radium (1,088 m asl) and 23.4°C near Kootenay Crossing (1,170 m asl). Mean monthly minimum temperatures occur in January, ranging from -14°C in the Kicking Horse valley near Field to -14.1°C near Radium and -18.1°C near Kootenay Crossing. Mean annual precipitation ranges from 623 mm (250 cm annual snow fall) in the Kicking Horse Valley near Field to 547 mm (190 cm annual snow fall) near Radium and 505 mm (193 cm annual snow fall) near Kootenay crossing. Field has 149 frost-free days, compared to 208 at Radium; corresponding data for Kootenay Crossing are not available (Gadd 1995).

3.3.2 Eastern Parks (Banff & Jasper National Park)

The climate of the eastern parks is influenced by Arctic, Continental, and Pacific air masses. During the winter months, valley bottoms are subject to intrusions of cold air ('cold-air drainages') that can persist for several weeks. The resulting temperature inversion creates a

'pool' of cold air in the valleys that may be up to 7°C colder than that of adjacent mountain slopes (Johnson and Larsen 1991). Warm westerlies from the Pacific flow over these cold, stagnant air mass while moderating temperatures on south-facing slopes (Henson 1969). The cold Arctic/Continental conditions of winter are occasionally interrupted by blasts of warm Pacific air (known as 'chinooks') that result in snow ablation in winter and rapid snow melt and runoff in spring (Stringer and La Roi 1970). The winter chinook winds, which can gust to over 50 km/h, are rarely associated with precipitation (summer chinooks also occur, but are more difficult to detect). These episodic warming periods result in south-west facing slopes having less snow accumulation, creating ideal winter range conditions for ungulates (Gadd 1995). Injury to conifer foliage may occur during the rapid transition from cold and warm air fronts, resulting in what is commonly referred to as 'red belt damage'. Foliar damage generally occurs on west-facing, sun-lit slopes; in Banff, such damage is often noticeable in areas opposite major mountain passes (Henson 1969).

The montane climate of Jasper and Banff National Park is classified as warm and dry in summer, and cold and snowy in winter. Mean monthly temperature is greatest in July, ranging from 22.5°C at Banff (1,397 m asl) to 23.1°C at Jasper (1,061 m asl). Mean monthly temperatures in January are -14.9°C at Banff and -15.6°C at Jasper. Mean annual precipitation is 508 mm (244 cm annual snow fall) at Banff and 445 mm (144 cm annual snow fall) at Jasper (Fig. 3.7). Potential evapotranspiration is greatest in Jasper National Park, resulting in early summer depletion of soil moisture reserves in most years. Within the montane ecoregion, drought-like conditions persist in Jasper National Park for about three months, compared to only two months in Banff (Stringer 1966). The total number of frost-free days averages 158 in Banff and 164 in Jasper.

3.4 GLACIAL HISTORY: LATE WISCONSIN ICE COMPLEX OF NORTH AMERICA

Most of the Pacific Maritime, montane Cordillera, Boreal, and mixed-temperate forests of Canada were glaciated during the Pleistocene epoch (1.5 million to 10,000 years before present (BP)). The Wisconsin Ice Sheet, which reached its maximum limit about 18,000 years ago, was the last major glacial advance of the Pleistocene epoch. This massive glacial complex was composed of two major ice sheets, the Laurentide and Cordilleran. The Laurentide Ice Sheet, which covered most of northern North America from the Atlantic east coast to the foothills of the Rockies, has been further subdivided into the Keewatin and Labradorian sectors (Heusser 1956). The much smaller Cordilleran Ice Sheet formed a continuous ice mass from the eastern slopes of the Rocky Mountains to the Pacific coast, extending from northern Washington to the Aleutian Islands. Further south, glaciation was relegated to the high elevations of the Sierra Nevada and Rocky Mountains. The Cordilleran and Laurentide Ice Sheets converged east of the Rocky Mountains to form a continuous ice mass across northern North America. Retreat of the Cordilleran and Laurentide Ice Sheets began 14,000-10,000 BP, initiated by a warming trend at the start of the Holocene epoch (Ritchie 1987).

3.4.1 Post-Glacial Climate of the Canadian Rockies

The Holocene epoch, which began about 10,000 BP, marked the end of the last major ice age and the beginning of organic matter sedimentation in the major montane valleys of the Rockies (Fig. 3.8). Throughout much of the Rockies, deglaciation occurred first at mid to higher elevations (Ritchie 1987). The early and mid Holocene were characterized by two climatic phases, the 'xerothermic' and 'mesothermic' (Davis 1984; Hebda 1995). Collectively, these two phases comprised the warmer, drier climate of the Hypsithermal or Altithermal period (Antens 1948). Mean temperatures of the Hypsithermal were 2-4°C warmer than during the rest of the Holocene. Temperatures were highest during the 'xerothermic' phase of the early Hypsithermal. This period, which extended from 10,000-7,000 BP, was characterized by warm and dry climatic conditions (Hallet 1996). Conversely, the 'mesothermic' phase of the late Hypsithermal was characterized by an increase in moisture and a gradual reduction in temperatures. This time-transgressive end of the Hypsithermal extended from 7,000-4,500 BP (Hallet 1996).

The neoglacial cooling trend that began at the end of the Hypsithermal lasted from 4500-150 years BP. This period was characterized by several glacial advances, the most significant of which was the 'Little Ice Age' (from the mid 1700's to 1860). In the Canadian Rockies, three glacial advances have been documented during this period. The first, which occurred about 4,000 years ago, is known the Boundary Advance. This was followed by the Peyto Advance (2,500 years BP), and the Cavell Advance during the Little Ice Age (250 years BP; Heusser 1956). A return to warmer climatic conditions followed each cooling period or

advance, the most significant of which was the Medieval Optimum that occurred about 1,000 years ago. Since the end of the Little Ice Age (about 1860), climatologists have noted that the global mean temperature has risen. In Canada, temperatures are estimated to have increased by 1.7°C since the 1890's (Flanningan et al. 1998; Luckman and Osborn 1979).

3.4.2 Post-Glacial Revegetation of the Canadian Rockies

The Younger Dryas: ≈10-12,000 yrs BP

The early post-glacial vegetation of the Canadian Rockies was characterized by grassland and shrubland communities dominated by juniper, alder, birch, and wormwood (*Artemisia* sp.). As substrate conditions improved, forest communities began to dominate the landscape (Ritchie 1987). Cold-tolerant taxa such as spruce and pine dominated the early post-glacial forests of the Canadian Rockies. The pollen records indicates that white spruce arrived in central Alberta about 11,000 years ago and reached the Rockies about 9,000 years ago. Seed dispersal by wind and water along the south-western edge of the retreating Laurentide Ice Sheet may have resulted in rapid post-glacial expansion of white spruce into western Canada (Ritchie and MacDonald 1986). These authors postulated that white spruce migrated north from a glacial refugia in southeastern North America. Others have speculated the existence of an 'ice-free corridor' between the Cordilleran and Laurentide Ice Sheets in southern Alberta. Moss (1955) postulated that this ice-free corridor may have facilitated the 'explosive surge' of spruce in western Canada from refugial populations south of the limit of glaciation. Ritchie (1987) disputes this hypothesis, citing problems with pollen-based carbon dating in the region. Regardless of their mode of arrival, the abundance of spruce and pine forests increased during the early half of the Hypsithermal (about 8,600-8,000 years BP; Hallet 1996).

The Hypsithermal: ≈4,800-10,000 yrs BP

Interior Douglas-fir first appeared in the pollen record of Kootenay National Park about 8,600 years ago, and constituted a dominant forest type in the area for the next 2,600 years (Fig. 3.1). The pollen record for this species on the western slopes of the Rockies predates its arrival east of the Continental Divide (MacDonald 1982; Hallet 1996). The warmer Hypsithermal period increased the tree line elevation by over 100 m, thus facilitating the migration of fire-adapted montane species such as Douglas-fir across the Continental Divide (Luckman and Kearney 1986; Hallet 1996).

As conditions became warmer and drier during the Hypsithermal, fire regimes appear to have shifted (Ritchie 1986). Evidence from lake cores (sediment charcoal accumulation rates, and pollen accumulation rates of fire-adapted taxa) taken throughout the Canadian Rockies

indicate that fire frequency increased during this period. A high sedimentation rate during the xerothermal period (8,000-6,000 years BP) has been attributed to extensive slope failure caused by a sparsely vegetated landscape, the result of frequent fires (Hallet 1996). During this period, closed stands of montane spruce were largely replaced by open-canopy stands of lodgepole pine and interior Douglas-fir (Hallet 1996; Ritchie 1986).

Rocky mountain maple (*Acer glabrum*), birch, and alder appeared in the pollen record between 8,000-6,700 years ago, marking the beginning of the mesothermal period. The warm, moist conditions characteristic of this period resulted in the development of decadent old-growth forests. It has been suggested that the increase of dwarf mistletoe (*Arceuthobium* sp.) in the pollen record by 6,700 years BP corresponds to the development of mature multistoried pine forests (Hallet 1996).

The Neoglacial: ≈100-4,8000 yrs BP

Sudden climate change during the neoglacial cooling period (beginning about 4,500 years ago) reduced fire intervals in the region, resulting in the loss of Douglas-fir and pine stands while favouring spruce-fir forests. The abundance of shade-tolerant species of spruce and fir increased between 4,000-2,600 years BP. The cooler and wetter neoglacial climate also favoured the eastward expansion of western redcedar as far as the western slopes of the Rockies by 2,300 years BP. This cooling trend also shifted the Cordilleran ecoregions and lowered the tree line (Hallet 1996).

Pine and Douglas-fir re-entered the pollen record between 1,200-700 years BP, indicating a return of warmer, drier climatic conditions and a probable increase in fire frequency (Fig. 3.1). Further increases of fire-adapted taxa in the pollen record occurred during the warmer and drier 'Medieval Optimum' or often called the Medieval Warming Period (600-1,100 years BP, variation in exact dates vary between regions). The warmer climate during this period increased tree line elevation in the Canadian Rockies, and resulted in increased forest fire activity throughout North America (Swetnam et al. 1990; Ritchie 1986). The Medieval Optimum was followed by a return to cooler, moister conditions characteristic of the Little Ice Age (Lamb 1995). The Little Ice Age refers to the cooler climatic conditions which occurred between the Middle ages (around 1450) and the warming period of the late 1800's (Hendon et al. 2001)

The mid-19th century, saw the maximum extent of glaciers in four mountain parks (Luckman 2000). The abundance of mesic forest species such as spruce and western redcedar increased during this period (Hallet 1996).

Warming trend of the 20th century

Climate records from the central Canadian Rockies indicate that the mean annual temperature has risen by 1.7°C since the 1890's. The greatest increase has occurred in winter (3.2°C per century), with smaller increases in spring and summer (1.3°C per century). This increase should be interpreted with caution since average temperatures during the latter half of the 19th century were below average (St. George and Luckman 2001). Nevertheless, evidence suggests that the areal extent of montane glaciers has decreased over the past 3,000 years. In addition, the upper ecotonal boundaries of the subalpine ecoregion have shifted in response to climatic trends during the 20th century. An upslope migration of the tree line has been documented at several sites in the central Canadian Rockies (Luckman 1999). Regeneration of subalpine fir and Engelmann spruce above tree line has been recorded since the 1940's, with a major regenerative pulse occurring in the early 1970's. Most of the increase in tree line has occurred on south-facing slopes. Many of the recent climatic trends documented for this region match global or hemispheric records over the same period (Flannigan et al. 1998; Luckman 1998).

3.5 VEGETATION ZONES: THE MONTANE CORDILLERA

When describing the vegetation zones of the Rockies it is important to keep in mind that these systems are in a constant state of change. Fluctuations in climatic conditions over the past 12,000 yrs have significantly altered species population distributions and ecotonal boundaries. Nonetheless the dramatic topographic relief of mountain environments has an overriding affect on macroclimatic conditions. The vertical banding of vegetation zones is attributed to changes in local climate associated with increasing elevation, aspect as well as underlying parent material (**Fig. 3.9**). The age-class distribution of species in the mountain parks is affected by the frequency and intensity of natural disturbances (e.g., geomorphic activity and forests fire) which change as a function of elevational. The vertical shifts in the biophysical characteristics of vegetation zones is similar to changes in composition resulting from increasing latitude. For example, alpine ecoregions have biophysical characteristics similar to Arctic as well as early post-glacial environments. The following is a summary of the current biophysical characteristics of the mountain parks.

The Cordillera forms part of a vast orogenic belt of mountains that includes the Coastal, Cascade, Selkirk, Columbia, and Rocky Mountain ranges. The Cordilleran region has been divided into three terrestrial ecozones: the Boreal, Pacific, and the montane Cordillera. The interior mountains, which include the Selkirk, Columbia, and Rocky Mountain ranges, are contained within the montane Cordillera ecozone. The Rocky Mountains, which form the eastern limit of the Cordillera, extend over 4,500 km (35°N to 59°N) from north to south and about 500 km (105°W to 125°W) from east to west. In Canada, the Rockies have been subdivided into three geographic provinces: the southern (48°N to 49°N), central (49°N to 55°N), and northern Rockies (55°N to 59°N). Within the central Rockies, four terrestrial sub-units are recognized: the central Canadian Rocky Mountains, the Western Continental Range, the Eastern Continental Range, and the northern Continental Divide (Ecological Stratification Working Group 1995; Clayton et al. 1977).

3.5.1 Ecoregions of the Canadian Rockies

In mountainous environments, elevation plays an important role in modifying the regional macroclimate. As a general rule, air temperature drops by approximately 1°C for every 100 m increase in elevation (the dry lapse rate), but this is an overestimate if condensation occurs (Gadd 1995). Four major climatic units or ecoregions have been delineated based on physiography and species composition (Achuff et al. 1986): (1) alpine; (2) upper subalpine; (3) lower subalpine; and (4) montane. The following is a synopsis of the ecoregions encountered in the central Canadian Rockies (Heusser 1956; Krajina 1969; Peinado et al. 1997).

Alpine Ecoregion (Alpine Tundra)

The alpine ecoregion is located above the tree line, including shrub-meadow communities and areas of exposed bedrock and ice. The tree line fluctuates both spatially and temporally: near the equator, the tree line occurs at about 4,000 m elevation, but it occurs at sea level north of the Arctic Circle. In the central Canadian Rockies, the tree line occurs at about 2,300 m, but has fluctuated significantly since the Holocene epoch ca. 10,000 year ago (Ecological Stratification Working Group 1995).

The vegetational composition of the alpine ecoregion is similar to that of the arctic tundra. Both environments are characterized by a short growing season and the presence of cryosolic soils (permafrost). The main difference between the alpine and tundra is the amount of incident solar radiation received. Except for steep north-facing slopes, alpine ecoregions experience a greater amount of solar radiation, particularly in the winter months (Ecological Stratification Working Group 1995).

The alpine ecoregion is a fragmented landscape composed of rock outcrops and drainage channels. Soil formation is slow since the cold climate retards natural chemical weathering processes. Mechanical processes such as frost heaving result in rock degradation and ultimately initial soil formation. The vegetation consists primarily of crustose lichens and crevice plants that range in growth form from dense cushions to mats. The lack of a recurrent natural disturbance regime in alpine ecoregions may result in dominance of a few species. For example, alpine meadow communities are usually characterized by sedge mats (*Carex* spp.), which competitively exclude other species and form a stable and persistent community type (Ecological Stratification Working Group 1995; Daubenmire 1943).

The Upper and Lower Subalpine Ecoregion (Spruce-Fir Forest)

The subalpine occurs as a band of vegetation between the montane and alpine ecoregions (about 1,800 to 2,300 m in elevation). A conifer dominated ecoregion, the subalpine occupies 20,7120 km² of mountain highlands in the Canadian Cordillera (Clayton et al. 1977). Morainal materials dominate the lower elevational regions, while colluvial and bedrock materials are more common at higher elevations. While edaphic conditions vary considerably, most soils are classified as Brunisols and Luvisols. Regosolic and Podzolic soils may also occur, particularly on active fluvial landforms or colluvial slopes where high elevation spruce-fir forests occur (Ecological Stratification Working Group 1995). Cryosolic soils form on steep north-facing slopes, while Chernozolic soils are limited to warmer south-facing slopes. Soil parent material ranges from non-calcareous to highly calcareous (Achuff et al. 1986). Throughout much of the central Canadian Rockies, the underlying parent material consists of middle Cambrian to Permian carbonate rock ranging from limestone-dolomite to shale.

Paleoproterozoic (2.9 billion years old) bedrock composed of gneiss and granite is deeply buried (about 10 km), and is only exposed along the eastern edge of the Rocky Mountain trench (Gadd 1995).

The subalpine ecoregion is divided into upper and lower elevational subregions. The upper subalpine is characterized by the absence of lodgepole pine, and the dominance of Engelmann spruce and Rocky Mountain subalpine fir (Johnson and Miyanishi 1991). Subalpine fir and Engelmann spruce form long-lived (250 and 1,000 years, respectively) stands throughout much of this subregion. These species are considered shade-tolerant, and both are susceptible to windthrow and fire damage (Alexander and Shepperd 1990). The shrub layer is dominated by buffaloberry (*Shepherdia canadensis* L. (Nut)), grouseberry (*Vaccinium scoparium* Leiberg), and low-bush cranberry (*Viburnum edule* (Michx.) Raf.; Kershaw et al. 1998). High elevation grassland communities also occur in the subalpine ecoregion, but are generally limited to steep south-western aspects. These communities are dominated by hairy wild rye (*Elymus innovatus* Beal), June grass (*Koeleria cristata* (L.) Pers.), and common bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.; Ecological Stratification Working Group 1995; Arno 1980).

The transition zone between the alpine and upper subalpine includes the forest (timber) line, the tree line, and the scrub line (Moss 1955). The transition between the spruce-fir forests and tree line is characterized by an open forest dominated by whitebark pine (*Pinus albicaulis* Engelm.), alpine larch (*Larix lyalli* Parl.), Engelmann spruce, and/or subalpine fir. Exposed trees often take on a crooked wind-blown appearance (krummholz) as a result of the harsh environmental conditions characteristic of higher elevations (Moss 1955).

The lower subalpine is characterized by the presence of multi-aged stands of lodgepole pine, Engelmann spruce, subalpine fir, and trembling aspen. Forest stand composition is dependent in part on edaphic conditions (Daubenmire 1943). Lodgepole pine often dominates well-drained xeric sites, while aspen is more characteristic of mesic areas along ravines or drainages. Secondary succession towards spruce and fir dominance occurs more rapidly along drainages, where fire frequencies are reduced (Romme and Knight 1981). Variation in disturbance regime and landform results in a mosaic of forest patches of varying ages and composition.

The transition zone between the lower subalpine and upper montane ecoregions is characterized by the presence of white spruce. Within this transitional zone, Engelmann spruce and white spruce hybridize freely to form 'interior' spruce (*P.glauca x engelmannii*). Relic stands of mature Douglas-fir are occasionally encountered on dry south-facing ridges.

The Montane Ecoregion (Douglas-Fir Forest)

The montane ecoregion lies between the foothills and the lower limit of the subalpine (around 1020-1550 m asl in Yoho; ~1050-1600 m asl in Kootenay; ~ 914-1300m asl in Jasper; ~ 1000-1400m asl in Banff). Although it occupies only around 8% of the land area, it is the most biologically diverse of the three ecoregions. It is contained within vast U-shaped valleys carved by glacial activity. These valleys are characterized by glaciofluvial and fluvial terraces and fans, with smaller areas of fluvio-lacustrine, glacio-lacustrine, eolian (loess), and morainal deposits. Edaphic conditions vary according to topography and climate. Brunisolic and Luvisolic soils dominate in forested regions, while Chernozemic, Brunisolic, and Regosolic soils characterize open grasslands (Ecological Stratification Working Group 1995). With a few localized exceptions, calcareous soils are characteristic (Achuff et al. 1993).

The montane ecoregion is characterized by forest, grassland, and wetland communities. The dominant tree species include Douglas-fir, white spruce, lodgepole pine, trembling aspen, and balsam poplar (*Populus balsamifera* L.). Tree species of more limited distribution include western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western redcedar, black spruce (*Picea mariana* (Mill.) B.S.P.), ponderosa pine, and limber pine (*Pinus flexilis* James). Open grasslands are dominated by blue bunchgrass (*Agropyron spicatum* (Pursh) Scribm. and Smith), fescues (*Festuca* spp.), oatgrass (*Danthonia* sp.), and a large diversity of forbs. Douglas-fir forests are dominated by juniper species, snowberry (*Symphoricarpos albus* (L.) Blake), common bearberry, northwestern sedge (*Carex concinnoides* Mack.), pine grass (*Calamagrostis rubescens* Buckl.), and hairy wild rye (*Elymus innovatus* Beal.). Lodgepole pine forests are dominated by buffaloberry, pinegrass, and hairy wildrye (Daubenmire 1943; Ecological Stratification Working Group 1995).

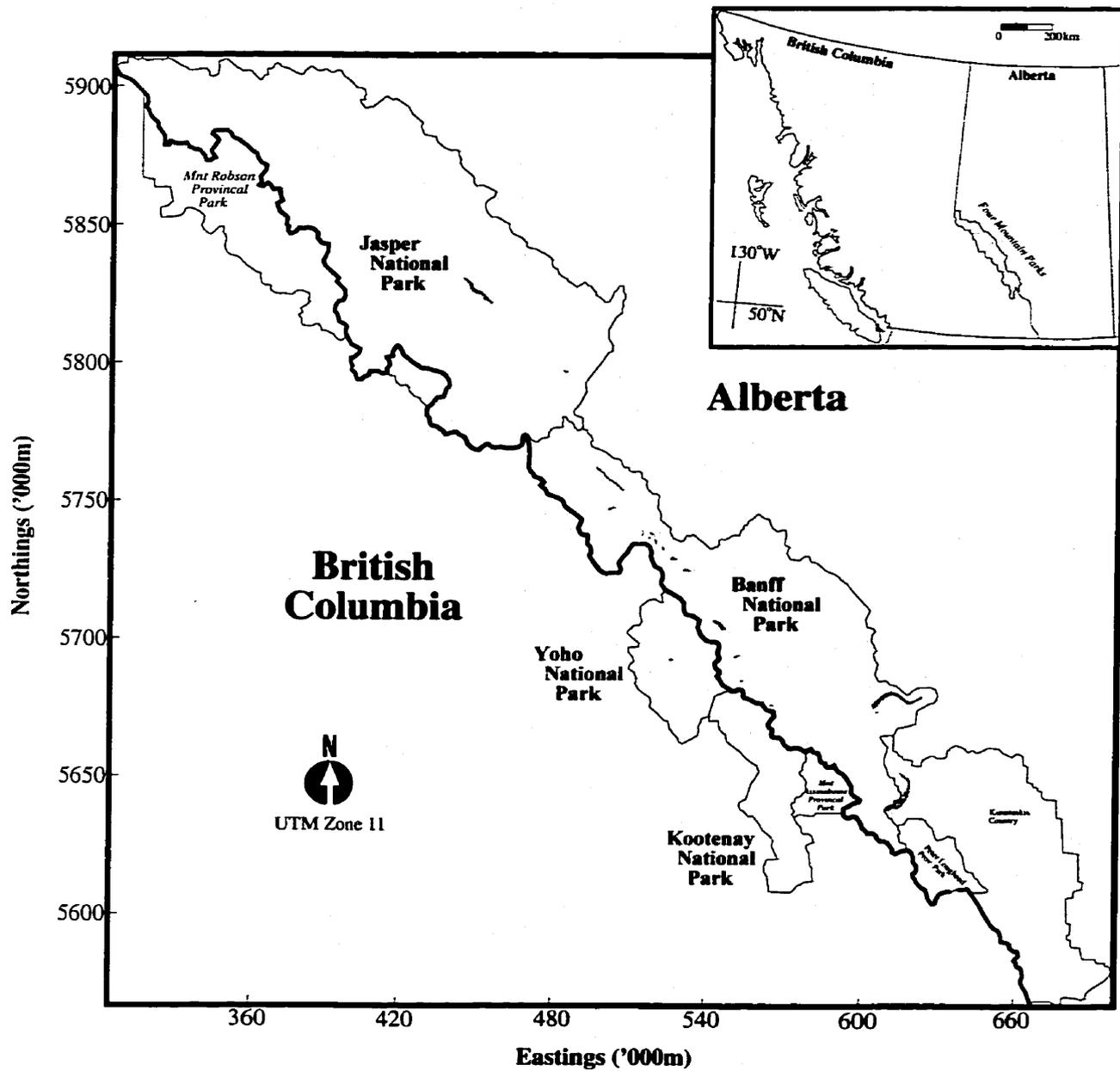


Figure 3.1 Map of the study area, showing the four mountain parks (Banff, Jasper, Yoho and Kootenay National Park; Total area ca. 20,339 km²).

BANFF NATIONAL PARK

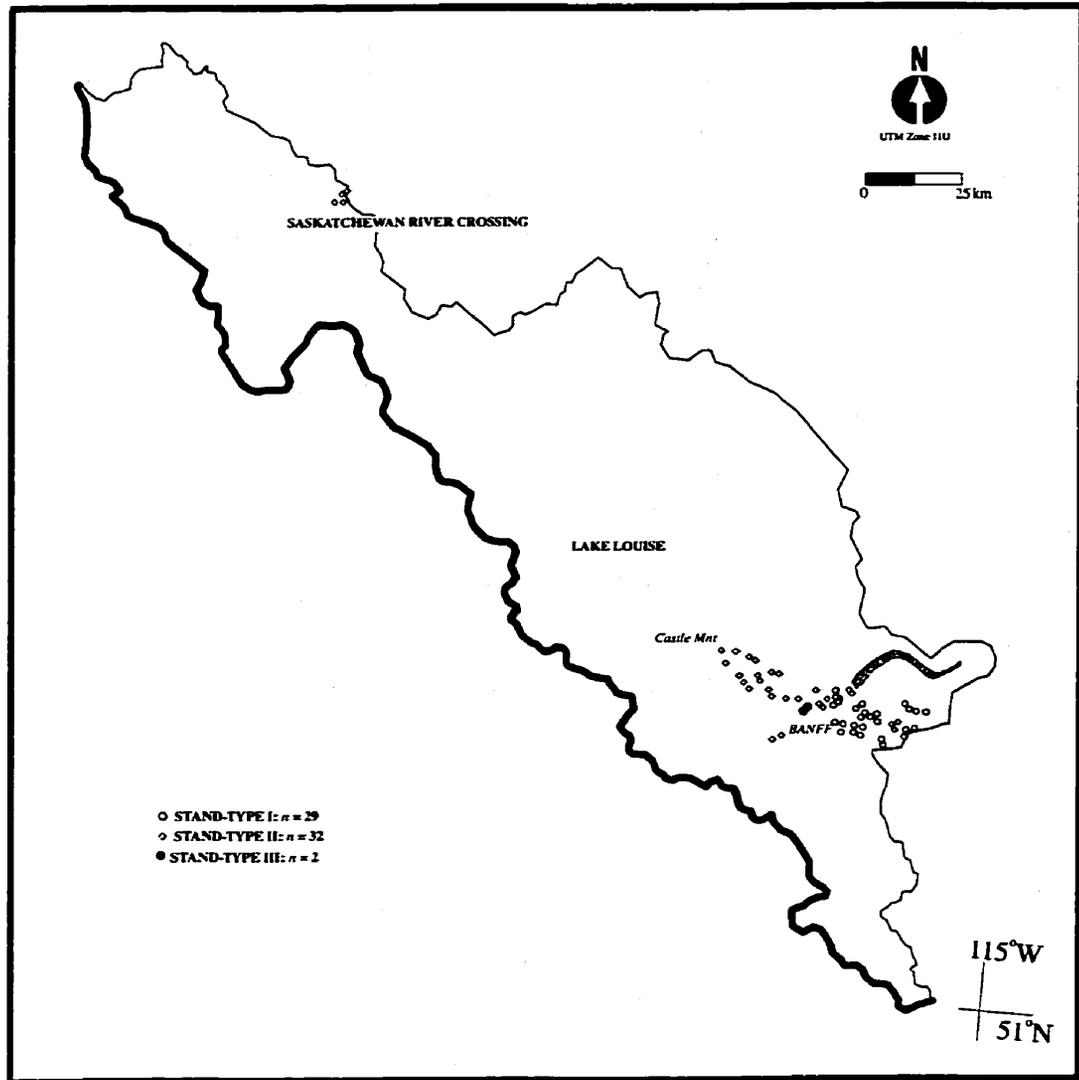


Figure 3.2 Plot locations within Banff National Park, delineated by stand-type.

JASPER NATIONAL PARK

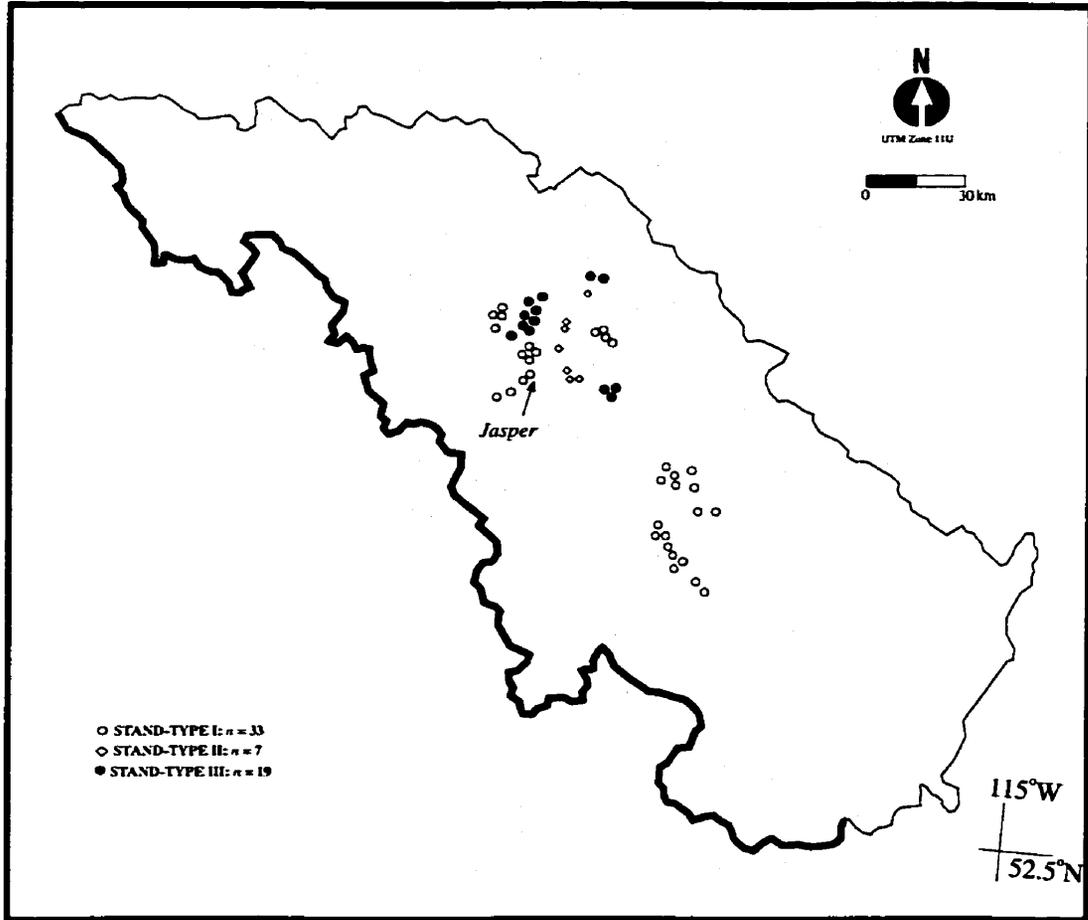


Figure 3.3 Plot locations within Jasper National Park, delineated by stand-type.

YOHO NATIONAL PARK

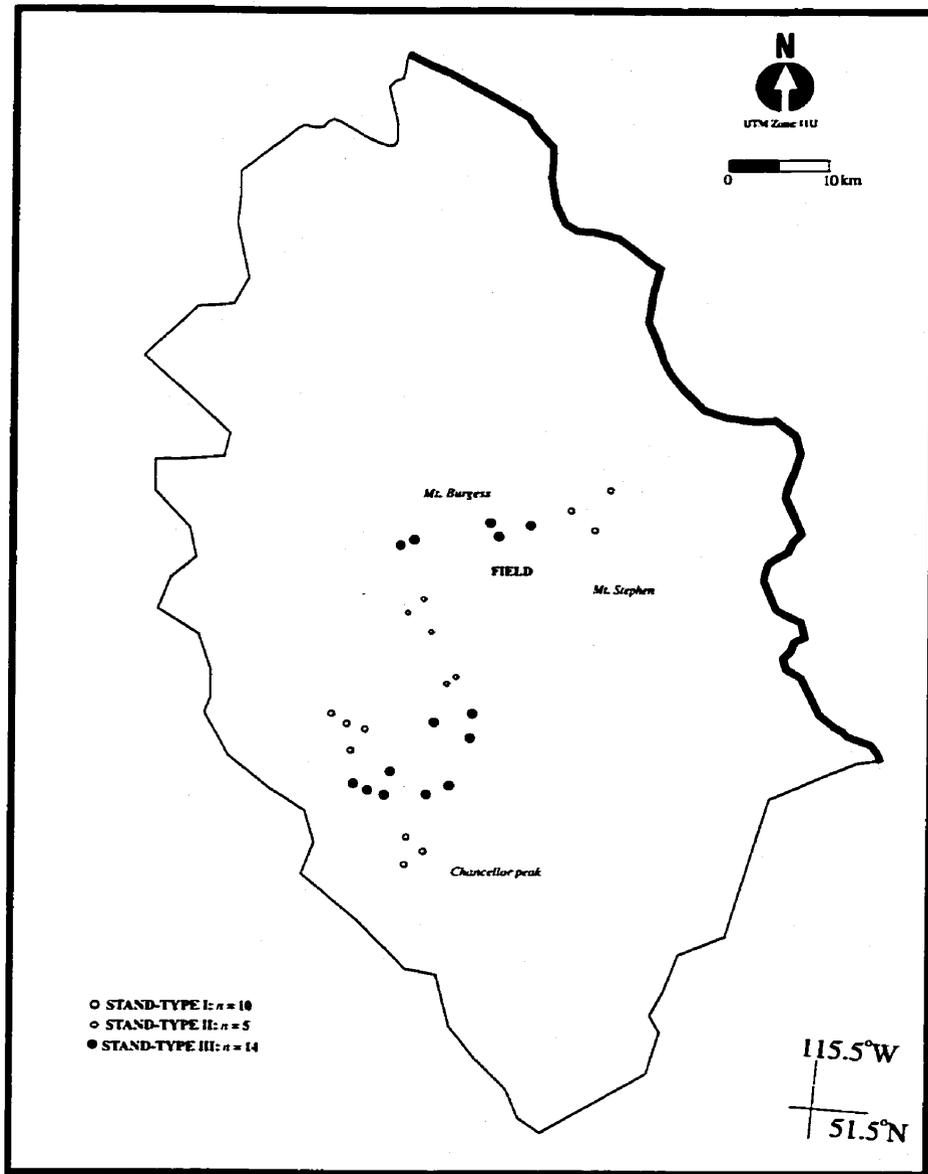


Figure 3.4 Plot locations within Yoho National Park, delineated by stand-type.

KOOTENAY NATIONAL PARK

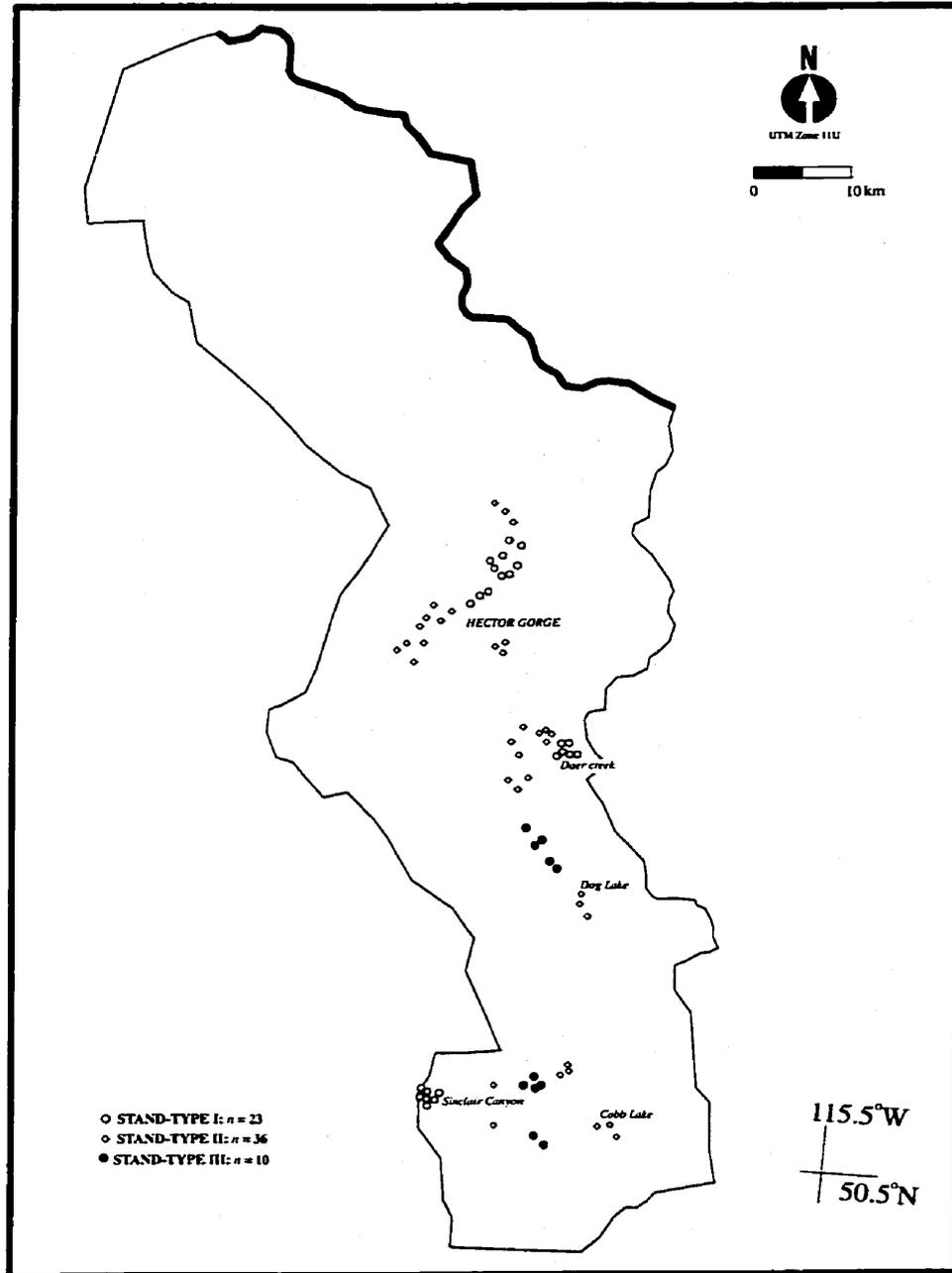


Figure 3.5 Plot locations within Kootenay National Park, delineated by stand-type.

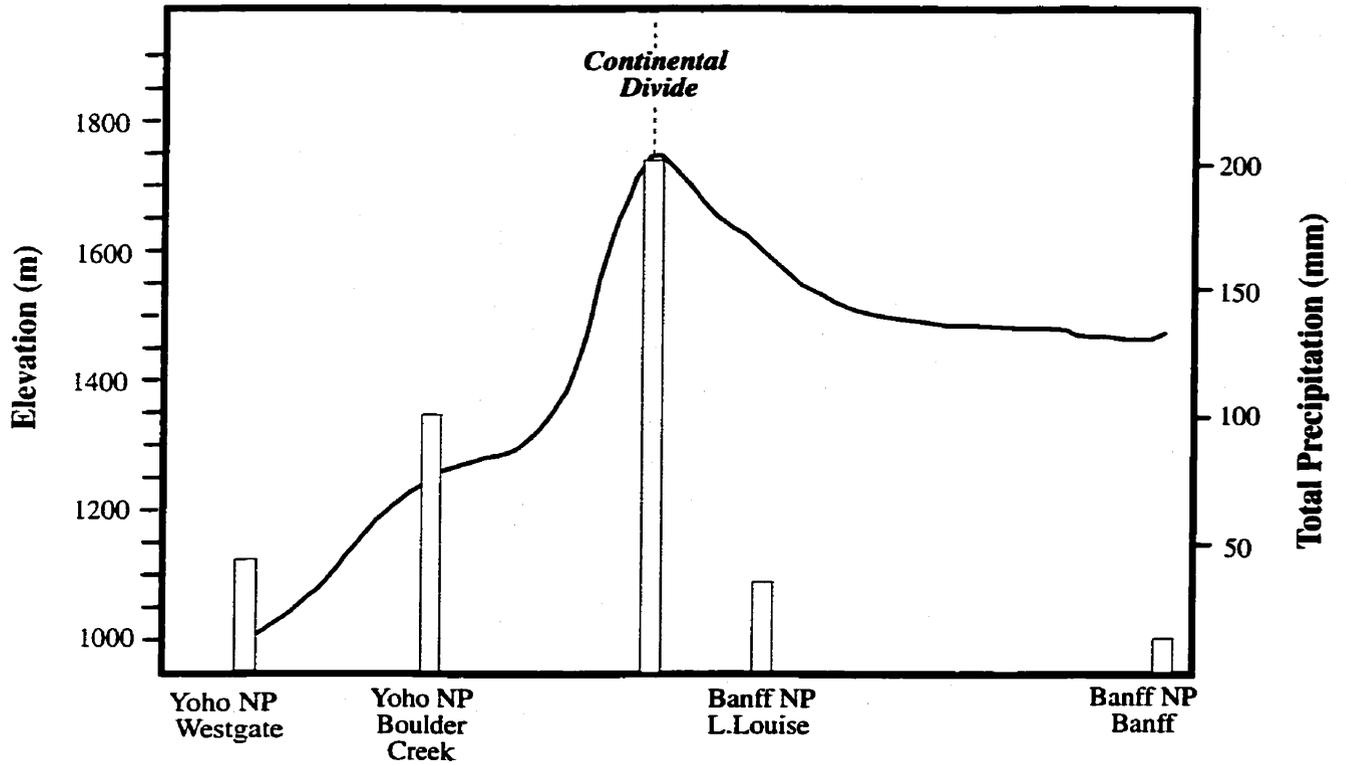


Figure 3.6. Elevation (solid line) and total precipitation (bars) profiles from the westgate of Yoho National Park to the Banff townsite. Precipitation records were measured between December 1, 1975 to March 31, 1976 (modified from Janz and Starr 1977).

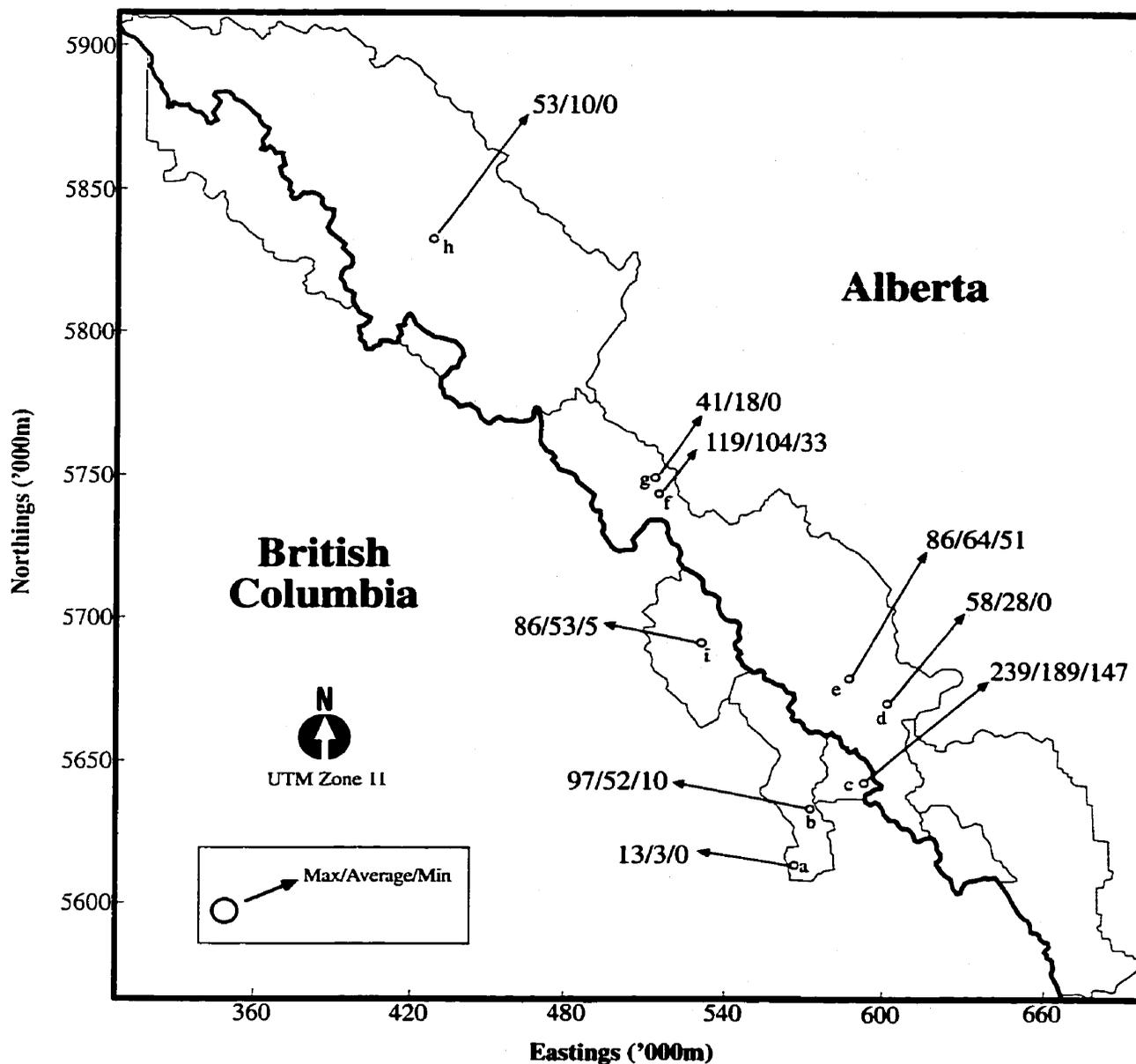


Figure 3.7 Mean April 1 (1935-75) snow depth (cm) for selected meteorological stations in the Four Mountains. Where a = Kootenay westgate, b = Sinclair pass, c = Mnt Assinabione, d = Banff townsite, e = Castle Mnt, f = upper Sarbach, g = Saskatchewan crossing, h = Jasper townsite, i = Field (Taken from Janz and Starr 1977).

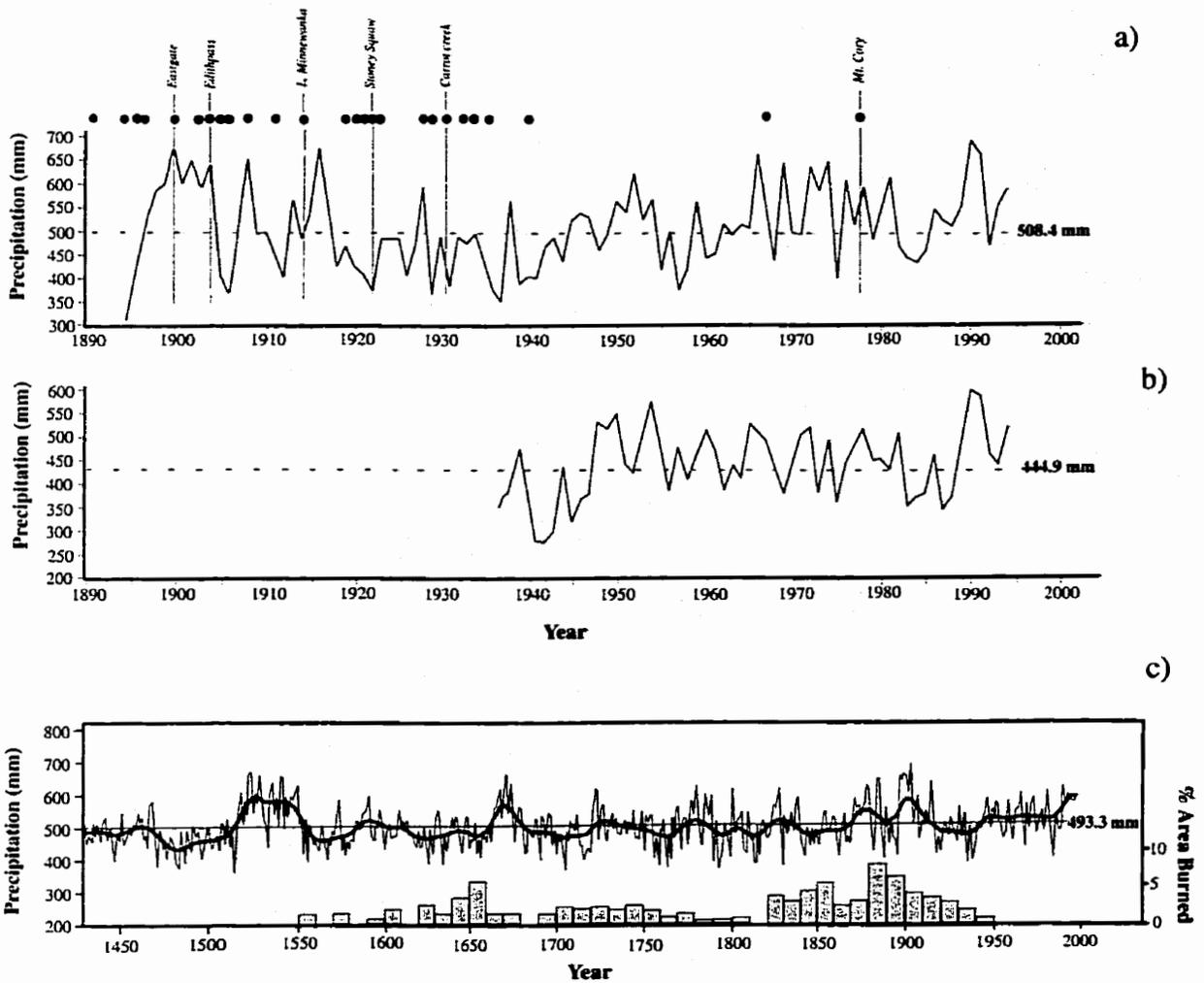


Figure 3.8. Instrument precipitation records for Banff (1896-1994, a) and Jasper (1937-1994, b) National Park. Mean annual precipitation for Banff and Jasper are 508.39mm and 444.93mm respectively. Points superimposed on the Banff data depict the occurrence of fire > 40ha in size (including specific site locations which correspond to known Douglas-fir stands (White 1980)). c) Reconstructed precipitation records for Banff based on 11 chronologies taken from open-grown moisture sensitive stands of interior Douglals-fir. The mean annual precipitation for the 1430-1994 period in Banff is 493.3 mm slightly lower than the instrumental observations, suggesting that annual precipitation has slightly increased during the 20th century. % forest area burned in Banff has tended to correspond to dry periods, data extend back to 1550 (Based on Watson & Luckman 2001; Luckman 1998).

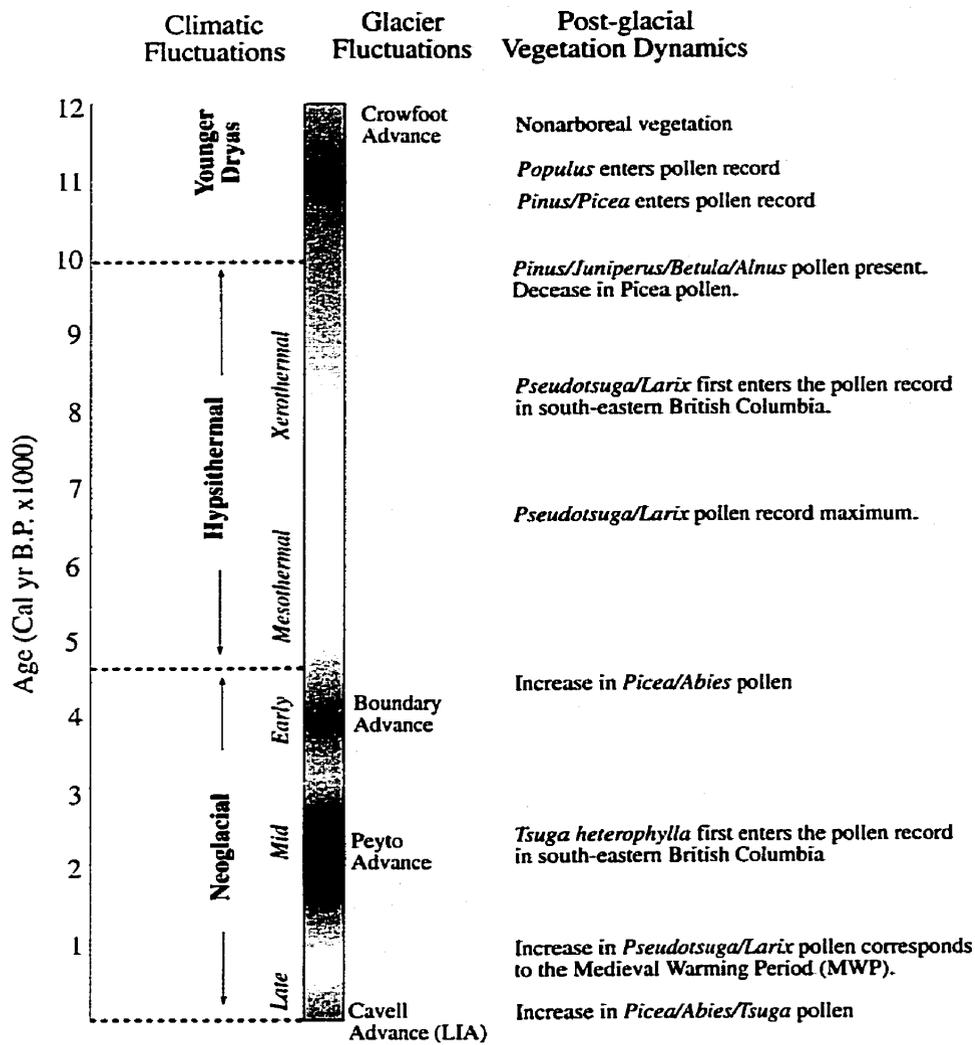


Figure 3.9. Synopsis of post-glacial Holocene vegetation dynamics in the Canadian Rockies. Gradients infer climatic changes (e.g., dark regions signify cooler, moister conditions). Modified from Hallet (1996) and Gadd (1994).

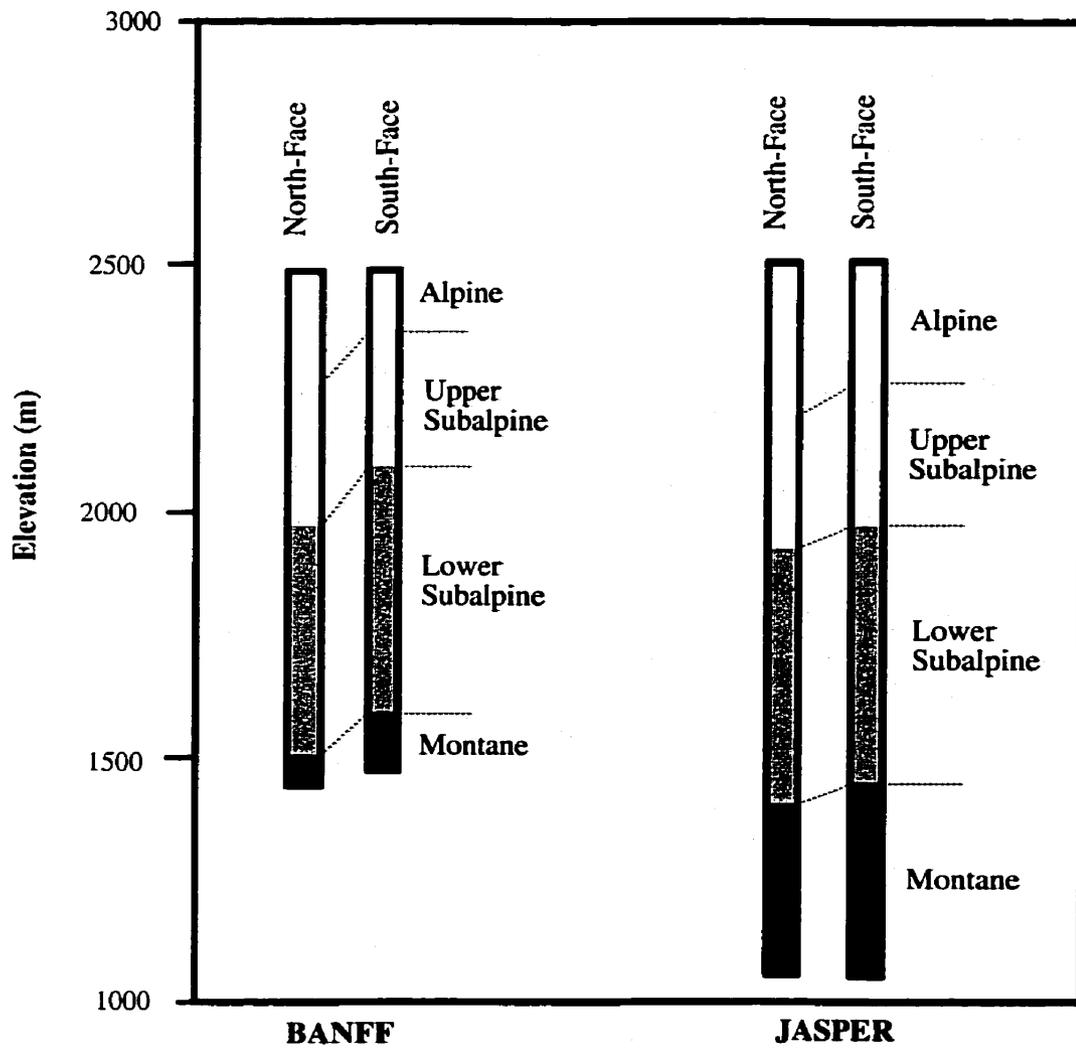


Figure 3.10 Changes in ecoregion boundary as a function of aspect in Banff and Jasper National Park (Modifies from Hollend and Coen 1982).

CHAPTER 4

DESCRIPTION & CLASSIFICATION OF DOUGLAS-FIR FORESTS IN CANADA'S FOUR MOUNTAIN PARKS

4.1 INTRODUCTION

4.1.1 Environmental gradients and species associations

The geographic distributions of tree species in nature seldom abide to random chance occurrences. Instead, they tend to be constrained by physiography, seed source proximity, disturbance history, and competitive interactions (LePage et al. 2000; Brown et al. 1999; Walker and Kenkel 1999; Wright et al 1998; Urban 1994; Oliver and Larson 1990). Strong underlying resource gradients such as soil moisture and nutrients are considered the organizing principals behind tree species distribution and composition on the landscape (Smith and Houston 1989; Chabot and Mooney 1985; Romme and Knight 1981). Local differences in the establishment and growth of tree species can result from the spatial heterogeneity of below ground resources and understory light conditions resulting from a multitude of factors such as complex topography, slope/aspect, surficial deposits, canopy height, and competition (Simpson 2000).

Ecologists often strive to find species associations which can be used to infer underlying environmental information based on commonly shared ecological requirements (Legendre and Legendre 1998; e.g., Allen and Peet 1990, MacNaughton and Wolf 1970). This is initially accomplished by partitioning a vegetation continuum into types using cluster analysis (e.g., Non-hierarchical and hierarchical): each type can be used to characterize the structure of the data (Legendre and Legendre 1998). Vegetation associations within each group are described where the concept of 'species associations corresponds to some fundamental properties of the interaction between species and their environment' (Legendre and Legendre 1998). This does not mean that the presence of species *a* can be used to predict species *b* but rather that species *a* and *b* are responding to a similar set of environmental conditions. Canonical methods are used to examine relationships between and among sites and species. Most importantly, ordination techniques such as these examine the variability of the association matrix thus deciphering general environmental gradients (Legendre and Legendre 1998). Environmental gradients are elucidated using 'indirect' techniques such as correspondence analysis or 'direct gradient analysis' using canonical correspondence analysis, where species and sites are constrained by a finite set of environmental parameters (ter Braak 1986). Discussion of species-environmental relationships would be incomplete without taking into account the synergistic effects of species interactions (e.g., competition),

stand history (e.g., fire), and stochastic events. In this study vegetation and environmental information will be used to describe the compositions and structure of interior Douglas-fir stands. These results will later be used to characterize the growth, regeneration, and stand dynamics of Douglas-fir in Canada's four mountain parks.

4.2 OBJECTIVES

The objectives of this study are:

- To describe and summarize the floristic composition and structure of interior Douglas-fir stands in Canada's four Mountain Parks.
- To examine the relationships between the vegetation and measured environmental variables using canonical ordination techniques.

4.3 METHODS

4.3.1 Field Sampling

Attempts to locate stands of interior Douglas-fir in the four mountain parks were initially conducted using existing Ecological Land Classification (ELC) maps and personal communication with park wardens. For the most part, the ELC maps proved to be a hindrance since many of the areas classified as pure Douglas-fir forest were dominated by lodgepole pine or white spruce. Furthermore, ELC maps for Jasper National Park were not available: previous copies were taken out of circulation and were in the process of being updated. A majority of the stands within the four parks were located in the first field season using extensive field reconnaissance. Potential sites were denoted as polygons on topographic maps (site maps).

The distribution of interior Douglas-fir is primarily restricted to less than 8% of the total land area in the four contiguous parks. The majority of the stands located within the montane ecoregion: for example, a majority of sites were located in the Bow valley watershed, within a 25km radius of the townsite (with the exception of sites near Saskatchewan crossing). Unlike the wide spatial distribution of lodgepole pine, Douglas-fir forests have a clumped and sporadic distribution (Stringer and La Roi 1970). To avoid spatial autocorrelation problems, sampled sites were selected in order to maximize the spatial dispersion within these localized regions. This was based on subjective stand selection derived from site maps.

The selection of sites was based primarily on subjective field observations regarding stand structure and forest aerial extent. The following basic criteria were used in the selection of suitable sites:

- The presence of mature Douglas-fir within at least a one hectare area (10,000 m²). Exceptions were made in xeric open stands where the distribution of mature trees were usually banded along narrow linear regions (<20m wide). Forest sites with only one or two large trees were not sampled.
- Forest stands with little to no evidence of anthropogenic disturbance. Surprisingly this was difficult to accomplish since many of the sites were situated along basal montane slopes often dissected by hiking trails, roads or high use backcountry sites.

This sampling protocol was used to enumerate a total of 220 sample 10 x 10m plots (sampled area totaled 2.2 ha) of during 1997 and 1998.

For enumeration purposes, the vegetation was stratified into six vertical height classes: (1) tree canopy, > 10 m; (2) tree upper subcanopy, 5-10 m; (3) tree lower subcanopy, 2-5 m; (4) tree sapling and shrub, 0.5-2 m; (5) herbs and graminoids; (6) cryptogams (Fig. 4.1).

The following data were collected from each 10 x 10 m plot:

- Species percent cover estimates were obtained from each of the six vegetation strata. Cover estimates of litter and bare ground were also taken. Cover was estimated to the nearest 5% (low cover values were recorded as < 5%, 1%, or < 1%). Epiphytic species cover was not estimated, but the presence of epiphytic species was noted. Species not present within the plot but occurring immediately outside the plot were also recorded. Voucher specimens were collected and deposited in the University of Manitoba Herbarium (WIN).
- Diameter at breast height (DBH) was measured for all trees and tall shrubs. Tree and tall shrub canopy heights were determined using a clinometer.
- A tree core was taken from at least three representative mature trees per site, using an increment borer. Cores were taken at breast height (1.3 m).
- Stem counts were made for all seedlings, saplings, and mature trees.
- Browsing intensity was estimated using a 5-point ordinal scale (1 = no browsing, to 5 = severe browsing).
- A soil core was taken from the center of each plot in order to determine soil pH, conductivity, and texture classes. Soil organic depth was also determined in the field.
- Physical environmental factors were recorded, including slope, aspect, topographic position, elevation, and UTM coordinates. GPS waypoints were logged for each site using a 12-channel Eagle receiver. Coordinate positions were obtained using the UTM

NAD 27 projection (zone 11). Elevations were also recorded; these were latter verified using topographic maps.

- Detailed field notes were made at each site, including information on the surrounding vegetation, the number of fallen and standing dead trees ('snags'), evidence of fire scars and other disturbances, granivory, and evidence of pests-pathogens.

Species Nomenclature

A complete species list was compiled for the 1997 and 1998 field seasons (**Appendix 1**). Species nomenclature for vascular plants follows Moss (1983) and Scoggan (1979), with the following exceptions:

- In the four mountain parks, *Abies lasiocarpa* is recognized as *A. bifolia* (Hunt 1993).
- No distinction was made between white spruce, Englemann spruce, and hybrid 'interior spruce'. Most of the stands enumerated occurred at lower elevations, making it very unlikely that Englemann spruce was encountered.
- *Pyrola secunda* is now recognized as *Orthilia secunda*.

Some grasses, notably members of the genera *Agropyron* and *Poa*, proved difficult to identify to species as they lacked flowering parts. In addition, some members of these genera freely hybridize, making their identification difficult (Moss 1983). *Elymus innovatus* was identified to species, but it is known to hybridize with closely related taxa (Moss 1983).

Nomenclature for bryophytes and lichens follows Schofield (1992) and Vitt et al. (1988), with one exception:

- *Drepanocladis uncinata* is now recognized as *Sanionia uncinata*.

All bryophytes were identified in the lab using a 40x stereoscope examining leaf and cell structures. A subset of the identified sampled were sent to UBC for verification. Lichen identification was large based on macromorphological characters and as such most were only identified to genus.

Minimum Stand Age

Minimum stand age was determined for each of the 220 plots, by increment coring (at 1.3 m height or DBH) of the largest trees. In some stands, a complete core could not be obtained from the largest tree since its diameter exceeded the length of the increment corer. In such cases, the minimum stand age was estimated from the oldest complete core (generally, the second largest tree in the stand). Tree cores were mounted onto wooden dowels and sanded using medium and fine-grained sand paper. Tree rings were then counted using a 40x dissecting microscope. The counts obtained are referred to as 'minimum' ages since:

- Cores were taken at 1.3 m (breast) height, thus underestimating actual tree ages.
- Complete cores were not always obtained from the largest (presumably oldest) tree. As the increment core was unable to reach the center of trees with a radius exceeding 50cm.

It should be noted that 'minimum' stand age is not necessarily a measure of time since last fire, since large individuals of Douglas-fir are known to survive fire events.

Fire History and Stand Origin

For all stands, the year of the last catastrophic fire was determined from fire history maps produced for the four mountain parks:

| <u>National Park</u> | <u>Reference</u> |
|----------------------|------------------|
| Banff | Rogean (1996) |
| Jasper | Tande (1979) |
| Kootenay | Tymstra (1991) |
| Yoho | Masters (1990) |

In these maps, the areal extent of past fires were determined from tree age data. In addition, fire scars on surviving trees (often relict individuals of Douglas-fir) were used to establish fire chronologies and verify stand origin dates. Refer to the specific references given above for more details.

For each enumerated plot, the estimated 'minimum' stand age was compared to its 'stand origin' age (based on fire history maps), to determine the proportion of stands that were entirely post-fire in origin (i.e., those stands in which the minimum stand age was less than the stand origin age). In plots where the 'minimum' stand age exceeds the 'stand origin' age, at least some of the trees (mainly Douglas-fir) survived the last catastrophic fire.

Environmental Data

Soils

Where possible, a 50 cm deep soil pit was dug near the center of each plot and the profile described. In addition, a representative soil core was taken from the upper 30 cm of the profile; soil cores were sifted and dried on the same day. In the first field season, soil pH and conductivity were determined using an Accumet pH meter (model 925) and an Orion Conductivity meter (model 160). In the second year, an Accumet pH-conductivity meter (model AR20) was used. A 1:1 soil-to-water mixture (e.g., 50g of soil to 50ml of water) was used for both pH and conductivity. Samples were stirred for 30 minutes and allowed to settle for 30 minutes. The pH electrode was immersed into the supernatant while stirring. pH values were recorded once readings had stabilized. Similar steps were taken for conductivity

readings. A subset of the 1997 soil samples were tested with the new instrument; both pH and conductivity readings were not significantly different compared to the 1998 readings.

Soil texture (percentage sand, silt, and clay) was determined using the Bouyoucos (1951 and 1961) hydrometer method and a Fisher Scientific Soil Hydrometer (model 14-331-58; procedure is outlined in **Appendix 6**). All soil cores were kept in cold storage in the Botany Department, University of Manitoba until the year 2000.

Solar Irradiance & Slope

For each plot, an estimate of total annual solar irradiance was obtained using Swift's (1976) algorithm. This approach uses the latitude, slope, and aspect of a plot to obtain daily measures of expected direct incident solar radiation. Daily values were summed to obtain a measure of annual irradiance (see **Fig. 4.3**). Although the influence of scatter and diffused light was not incorporated into the algorithm the results emphasize the important role topography plays in the energy budget of landscapes in mountain environments.

Since slope, like aspect is a 'circular statistic', measured slope values had to be re-expressed as percent slopes using:

$$\%Slope = [\tan(\theta \times \pi/180)] \times 100\% \text{ where } \theta = \text{measure slope}$$

Based on this equation measured values of 0 - 45° were expressed as 0 – 100%. Values much greater than 45° increased exponentially. Slope angles were converted to radian ($\pi/180$) in the calculation.

4.3.2 Data Analysis:

Vegetation Analysis and Vegetation-Environmental Relationships

The basic vegetation data set consisted of percent cover estimates of 171 species over 220 plots. In the exploratory multivariate analyses (ordination and cluster analysis), total cover of each tree species was obtained by summing its cover estimates over the four vertical strata (canopy, upper subcanopy, lower subcanopy, and sapling layers). Percent cover values were square-root transformed prior to multivariate analysis. Given the multitude of factors and conditions characterizing forest stands, a multivariate approach was used to summarize species relationships and environmental associations.

Delineation of Stand Types: Cluster Analysis

Cluster analysis refers to a family of numerical methods that classify plots into non-overlapping groups, based on a matrix of pairwise distances between plots (Orlóci 1978).

Most cluster analysis methods are hierarchical, producing an ordered tree or 'dendrogram' of the relationships between individuals, while others are non-hierarchical which produces a single partition that optimizes within group homogeneity (Legendre and Legendre 1998). Numerous clustering methods were tested using this dataset. In every case the correspondence between the results was high, only differing between 10% of the sampled plots. Agreement in a final method was based on the correspondence of the clustering results and the vegetation information of the 220 plots.

In this study, Ward's 'minimum increase in error sum of squares' clustering method (Ward 1963; Orłóci 1967) was used to obtain a dendrogram of the 220 plots. Ward's method is an hierarchical agglomerative clustering technique. The method 'finds the pair of objects or clusters whose fusion increases as little as possible the sum, over all objects (n), of the squared distances (D) between objects and cluster centroids (m)' (Legendre and Legendre 1998).

$$e_k^2 = \left(\sum_{h,i=1}^n D_{ij}^2 \right) / n_k$$

The sum of the squared errors E_k^2 for all k clusters is the portion of the calculation which must be minimized at each fusion:

$$E_k^2 = \sum_{k=1}^K e_k^2$$

Fusion distances are computed between new clusters based on:

$$D^2(ab, c) = \left(\frac{[n_a+n_c]}{[n_a+n_b+n_c]} \right) D^2(a, c) + \left(\frac{[n_b+n_c]}{[n_a+n_b+n_c]} \right) D^2(b, c) - \left(\frac{[n_c]}{[n_a+n_b+n_c]} \right) D^2(a, b)$$

where D^2 is the squared distances among objects (plots) and n is the number of objects in clusters $a-c$. The distances can be computed using a Euclidean distance formula:

$$D^2 = \sum_{j=1}^p [y_{ij} - m_j]^2$$

In this study chord distance was used:

$$D^2 = \left(\left[2 (1 - \cos\theta) \right]^{-1/2} \right)^2$$

Pairwise resemblance values between plots were measured using the 'chord distance' (Orłóci 1978), based on square-root transformed percent cover values of species. This measure has a maximum value of $\sqrt{2}$ for sites with no species in common a 0 when sites share the same species at the same proportion (Legendre and Legendre 1998). Chord distance is a standardized form of the familiar Euclidean distance of everyday experience, in which proportional rather than absolute abundances of species are emphasized. This has the effect

of alleviating discrepancies in percent cover estimates over the field season and between years. The cluster analysis was performed using program HEIERCLUS of the statistical package SYNTAX 5 (Podani 1994).

Ordination of Stands

Correspondence Analysis (CA)

Correspondence analysis (CA) is an ordination method that examines the redundant features of a data structure, by determining the 'duality' between the rows (plots) and columns (species) of a data set.

$$\mathbf{S} = \mathbf{U} \mathbf{U}'$$

Where \mathbf{S} is used to compute the component score for the objects (sites) as well as variables (species).

In this study, CA (program CANOCO, ter Braak 1986, 1988) was used to summarize the essential features of the vegetation structure (220 plots x 171 species) in a two-dimensional ordination diagram. CA produces a dual ordination of plots and species, which in this study are plotted separately to aid in their interpretation.

Vegetation-Environment Relationships: Canonical Correspondence Analysis (CCA)

Canonical correspondence analysis (CCA) is a 'constrained' variant of CA (ter Braak 1986). Specifically, the method performs a multiple regression of the environmental data and uses this to 'constrain' the vegetation-based CA ordination. For this reason, CCA is sometimes referred to as a method of 'direct' gradient analysis (ter Braak 1986). CCA determines the degree to which the environmental data 'predicts' variation in vegetation composition, and produces 'weights' for each environmental variable on each constrained CCA ordination axis. In this study, seven constraining environmental variables were used: soil pH, conductivity, percent sand, percent silt, and depth of organic layer; plot slope and incident solar radiation.

Physiognomic Profiles

Illustrative physiognomic profiles were created for each of three stand-types delineated by cluster analysis. These profiles were based on relative density and percent cover values of dominant tree and shrub species, as well as topographic and edaphic variation within each stand-type. Standard illustrative symbols were used to produce the physiognomic profiles (see Fig. 4.2).

Summary Tables

The following summary tables were produced for each of the three stand-types:

- Relative frequency of tree species, over five vertical strata (canopy, upper subcanopy, lower subcanopy, saplings, and seedlings). Similar tables were also produced for the stand-types in each of the four mountain parks.
- Mean tree density, over the same five vertical strata.
- Relative frequency and mean cover for common (frequency > 5%) shrub species.
- Relative frequency and mean cover for common (frequency > 5%) herbaceous and graminoid species.
- Relative frequency and mean cover for common (frequency > 5%) cryptogam (bryophyte and lichen) species .
- Mean values (\pm one standard deviation) for measured soil variables (pH, conductivity, depth of organic matter, and particle size, proportion of sand, silt, and clay).

Species Richness and Diversity

Species richness (the number of species encountered) was summarized for the entire data set. In addition, 'effective species richness' values (based on Simpson's index; *reformulation of Renyi's entropy of order two* [$H^{\alpha} = (\ln \sum p_i^{\alpha}) / (1 - \alpha)$]) for each stand-type were determined separately for the tree canopy and understory (shrubs, herbs, graminoids, forbs, and cryptogams) layers. To permit comparisons between stand-types (which had different sample sizes), effective richness was determined using a randomization procedure (Manly 1991). Random simulations were run in which 25 plots belonging to a given stand-type were randomly selected and the total cover of each species over these 25 plots determined. The total cover values were then expressed as proportions, and 'effective species richness' computed as:

$$N2 = e^H = 1 / \sum_{i=1}^q p_i^2$$

where q is the number of species in the random sample of 25 plots. Effective species richness was then averaged over 100 random iterations to give a 'mean expected effective species richness (e^H) for a random sample of 25 plots'. The upper limit of N_2 is q (the total number of species encountered), which would occur if all species had equal cover values. Conversely, N_2 approaches 1 if a single species has very high cover while the remaining $q-1$ species have very minimal cover; in this case, only one species is 'effectively' present. Effective species richness is thus a measure of relative 'dominance'. For example, in stand-type II mean expected effective species richness of all moss species was determined to be 2.92, the mean number of species encountered was 16.24 (actual number of species (N_2) in stand-type II = 21). Therefore, in these stands even though there were around 20 moss species encountered only 2.9 dominated (based on cover and frequency).

4.4 RESULTS/DISCUSSION

Douglas-fir stands within the four mountain parks typically occur on calcareous soils (mean pH = 7.3), but soils range from somewhat acidic (pH = 4.77) in cool-moist forests to somewhat alkaline (pH = 8.6) in dry open canopied stands. Soil conductivity ranges from 38 to 589 μS (mean 158 μS), indicating low to moderate nutrient conditions. Well drained stands tend to have lower conductivity values. Depth of the organic layer ranges 0 to 20 cm, and tends to increase with increasing canopy closure (**Table 4.1**). Minimum Douglas-fir tree age ranges from 85 to 380 years, with moist closed-canopied stands having the oldest trees. Douglas-fir tree age and bole diameter (DBH) are highly correlated ($r^2 = 71.9$; $P < 0.05$; **Fig. 4.4**). Herbivore browsing intensities varied considerably, but were greatest in stand-type II.

Results from the Swift (1976) algorithm demonstrate that expected direct radiation incident on south-facing 30° slopes (at 52°N latitude) is consistently high from April to early September. This suggests that spring snow melt and summer soil moisture deficiency occur much earlier than on northern-facing slopes. The direct radiation incident on north-facing 30° slopes is much lower: the mid-summer peak value only equals values for March on south-facing slopes (**Fig. 4.5 ; Fig. 4.3**).

4.4.1 Delineation of Stand Types

Cluster analysis of the 220 plots was used to delineate three stand-types I-III and seven sub-types (**Fig. 4.6**). These three stand-types and their sub-types are most similar to the following vegetation groups recognized by Achuff et al. (1993):

- O05 (Douglas-fir/common juniper/bearberry) = Ib.
- C01 (Douglas-fir/hairy wildrye) = IIa.
- C55 (Douglas-fir, lodgepole pine/buffaloberry/Pleurozium) = IIb & IIc.
- C05 (White spruce/Douglas-fir/Hylocomium) = IIIa.

Douglas-fir stands in the four Mountain Parks occur in two of the three biogeoclimatic zones recognized by Krajina (1969): the mesic (IDFb) and xeric (IDFa) interior Douglas-fir zones.

4.4.2 Stand-Type Descriptions

I: Douglas-Fir/Juniper/Bearberry, $n = 95$ (B = 29, J = 33, K = 23, Y = 10).

Stand Age

Douglas-fir maximum canopy ages range from 100 to 290 years (**Table 4.1**). Stand origin maps indicate that catastrophic fires occurred in these sites ca. 80 to 100 years ago. Most of the oldest trees per plot (75.8%) exceed these fire origin dates (**Fig. 4.7**). Dry conditions and low fuel accumulation of these stands create conditions favourable for frequent low severity burns (cf. Johnson 1992). Such fires would typically have the greatest effects on herbaceous species, bryophytes and lichens, low growing prostrate shrubs such as juniper and bearberry, white spruce, and Douglas-fir saplings. The high proportion of Douglas-fir exceeding the estimated fire origin date reflects the ability of mature individuals to tolerate low to moderate-intensity fires.

Soil-Environment

The majority of these stands occur on steep, south-facing slopes. Two-thirds of the stands sampled occurred on the eastern slopes of the Rocky Mountains, in Banff and Jasper National Parks. Most sites are characterized by very well to excessively-drained calcareous sandy loams most were classified as Eutric Brunisols and Regosols. Soils are slightly basic (mean pH = 7.6) and of low nutrient status (mean conductivity = 110.4 $\mu\text{S}/\text{cm}$). The organic layer, when present, averages only 1.7 cm (**Table 4.1**). Browsing intensity in these stands is low to moderate.

A relatively open canopy, dominated by Douglas-fir, characterizes the very xeric variant of this stand-type (see **Fig. 4.10, 4.11, 4.12 and 4.13**). Rocky Mountain juniper may occur on very steep, excessively-drained slopes. Less xeric sites are also dominated by Douglas-fir, but white spruce and lodgepole pine may also be present.

Vegetation

Douglas-fir typically dominates all the canopy layers of these open stands (**Table 4.2 & Table 4.3**). Canopy and subcanopy Douglas-fir densities averaged about 2 stems per plot, while all other tree species have densities ≤ 1 stems per plot. The open canopy was dominated almost exclusively by Douglas-fir (**Table 4.3**). Upper and lower subcanopy stem densities are low, and dominated by Douglas-fir. Mean basal area per plot is also low (**Table 4.4**). White spruce, lodgepole pine, and Rocky Mountain juniper occur infrequently in these stand. The effective tree species richness is only 1.5, which reflects both the low tree richness and dominance of Douglas-fir (**Table 4.1**).

When present, the regeneration layer (lower subcanopy and saplings) is dominated by Douglas-fir. Most regenerating stands had 1-2 Douglas-fir saplings per plot, but occasional high regeneration (> 50 saplings) was observed in less xeric sites that had experienced recent groundfires (Fig. 4.4). White spruce regeneration was observed in only 14% of stands. Douglas-fir dominates the regeneration layers of this stand-type, suggesting its continued persistence and canopy dominance. Occasional ground fires may eliminate regenerating white spruce, while favouring Douglas-fir.

These xeric sites are characterized by high bare ground cover (mean of 33%). The understory vegetation is dominated by low evergreen shrubs, graminoids, and small-statured forbs. Effective species richness of the understory is 10.25, which is slightly lower than that of stand-type II but considerably higher than that of stand-type III. Effective species richness of moss and lichen is 4.93 and 3.00 respectively (Table 4.1).

Understory

The shrub layer is dominated by *Juniperus communis* and *Arctostaphylos uva-ursi*; *Shepherdia canadensis* and *Rosa acicularis* are more occasional (Table 4.6). Where present, *R. acicularis* is often heavily browsed and seldom exceeds a height of 0.5 m.

Herbaceous cover is low to moderate. A number of graminoid species dominate the herb layer. *Elymus innovatus* is the most frequently encountered grass; other common grasses include *Calamagrostis rubescens*, *Koeleria macrantha*, and various fescues (*Festuca saximontana*, *F. campestris*, *F. occidentalis*). Sedges occur in many stands. Characteristic forb species include *Aster conspicuus*, *Achillea millefolium*, *Allium cernuum*, *Solidago spathulata* and *Astragalus miser*. In less xeric sites *Fragaria virginiana* is also common (Table 4.7). Less common species that only occur in open, xeric areas include *Artemisia* sp., *Astragalus* sp., *Apocynum androsaemifolium*, and *Hedysarum sulphurescens*. A number of locally rare plants are exclusive to this stand-type, including *Calochortus apiculatus*, *Sisyrinchium montanum*, *Sedum laceolatum*, *Arabis lyallii* and *Selaginella densa*. Non-native species include *Medicago lupulina*, *Sonchus arvensis*, *Taraxacum officinale* and *Trifolium pratense* (Appendix 2).

Cryptogam cover is low and dominated by bryophytes. The moss *Tortula ruralis* is the most frequently encountered species on very dry, exposed sites. Other common mosses include *Thuidium abitinum* and *Hypnum revolutum*. Lichen cover is generally low, but *Peltigera canina* and *Cladonia* spp. are commonly encountered (Table 9.8).

Subtype Variants

Subtype Ia: Highly Xeric (n = 34)

These stands typically occur on very steep, south-facing slopes. The driest sites occur in extreme western portion of Kootenay National Park, British Columbia, where stands have a 'savanna-like' appearance with sparse, open-canopy Douglas-fir cover. Tree-sized specimens of Rocky Mountain Juniper are occasionally encountered. Bareground cover in these stands is high. The sparse understory is dominated by graminoids and low-growing forbs; shrubs may be present, but their cover is low. Similar stands occur on colluvial slopes in the Kicking Horse valley (Yoho National Park), and in the 'hoodoo' regions of Banff and Yoho National Parks. Limber pine is occasionally encountered in these sites (**Table 4.9**).

Regeneration in these very xeric sites is low (**Table 4.9**). It appears likely that this sub-type will undergo very little compositional change; the extreme environmental conditions are such that interspecific interactions with other species will be minimal, regardless of fire history.

Subtype Ib: Xeric (n = 61)

These stands are typically found on moderately steep, south-facing slopes. The discontinuous canopy is dominated by Douglas-fir, but white spruce may also be present and lodgepole pine is occasional. Douglas-fir dominates the regeneration layers; white spruce regeneration also occurs, but at much lower frequency. Shrubs are common in the understory, the most frequently encountered species being *Juniperus communis* and *Arctostaphylos uva-ursi*; *Shepherdia canadensis* is more occasional. Graminoids and low-growing forbs are common understory components (**Table 4.10**).

Regeneration in these stands is much higher than in stands of sub-type Ia. Douglas-fir seedlings and saplings are most frequently encountered in more sheltered microsites. The abundance of Douglas fir regeneration, together with limited regeneration of white spruce, suggests that these stands are self-replacing.

Forest Structure and Compositional Summary of Stand-Type I

These are xeric sites characterized by open, 'savanna-like' stands of Douglas-fir. Low site productivity results in a discontinuous fuel, which reduces fire severity and frequency. Should a severe catastrophic fire spread in from an adjoining area, these stands may revert to a treeless stage dominated by re-sprouting shrubs and herbaceous vegetation (Bradley et al. 1992). Re-establishment of Douglas-fir following fire requires a nearby seed source, typically mature trees that have managed to escape the fire. The ability of individual Douglas-fir trees to survive catastrophic fires on the landscape has been documented in several fire-history studies (Rogeanu 1994; Tymstra 1991; Tande 1979). Indeed, the numerous fire scars evident

on such mature 'relict' trees have facilitated the reconstruction of fire histories and historic climate trends (Tande 1979). The mean age of the oldest Douglas-fir trees in these stands (about 140 years) exceeds the mean 'stand origin' date (about 100 years), indicating that at least a few pole-sized trees in each stand survived the catastrophic fires that occurred at the turn of the century (Masters 1990).

The low levels of tree regeneration in these stands is likely attributable to a combination of soil moisture deficiency, high soil temperatures, and light stress (Stringer 1966); optimal germination and establishment of Douglas-fir occurs under semi-shaded conditions. In the absence of stand-replacing fires, recruitment of Douglas-fir in these stands is expected to be highly episodic. Masting occurs about every 10 years, and must be accompanied by optimal environmental conditions (i.e., cool, wet years) for successful germination and establishment to occur. Interior Douglas-fir achieves maximum seed production at about 200 years of age, and trees may live for over 400 years. Therefore, successful recruitment needs only occur a few times over this 400 year lifespan to perpetuate the stand-type. Since recruitment events are expected to be highly episodic, the low levels of regeneration in many stands should not be interpreted as a sign of possible stand 'degeneration'.

In these stands, canopy replacement by the shade-tolerant white spruce is unlikely. White spruce requires a dependable supply of well-aerated water (Nienstaedt and Zasada 1990), but these stands generally occur on steep, well drained, south-facing slopes that are not conducive to white spruce establishment. Differences in species longevity and fire tolerance must also be considered. White spruce seldom exceeds 200 years in age, and is not adapted to surviving ground fires. By contrast, Douglas-fir is a long-lived species (400 years or more), and established trees have adaptations (thick bark, high branches) that renders them tolerant of surface fires. In these stands, Douglas-fir tends to form a long-lived 'super-canopy' (c.f. Heinselman 1996) that is largely immune to the occasional ground-fires that remove regenerating white spruce. Regenerating white spruce thus poses little threat to the continued canopy dominance of Douglas-fir.

The presence of a cryptogam 'crust' (e.g. *Tortula ruralis*) in these stands serves to stabilize the soil and promote seedling establishment by reducing soil water loss (Johansen and St Clair 1986). 'Crust-forming' cryptogam species typically occur in sites with low organic matter accumulation on calcareous, nitrogen limited soils. They thrive under very xeric conditions, and may remain in a dormant state for up to 70 years following desiccation (McCune 1977). *Tortula ruralis* is a characteristic species of stand-type I.

II: Douglas-fir/Lodgepole pine/Buffaloberry $n = 80$ (B = 32, J = 7, K = 36, Y = 5)

Stand age

Maximum estimated Douglas-fir tree ages range from 85 to 305 years (**Table 4.1**). About two thirds of the plots (64%) exceeded the estimated fire origin date (**Fig. 4.8**). The multi-cohort age structure of these stands indicates a complex fire history. In about a third (36%) of the plots, all the Douglas-fir tree present established following the last catastrophic fire (i.e. there were no 'relict' trees present). This value is higher than those of the other two stand-types, suggesting that these stands burn with greater severity. Physiography and physiognomic stand characteristics may promote more complex and severe fire behaviours. The legacy of past fires is apparent from the numerous fire-scarred Douglas-fir trees encountered, and their presence is telling of the complicated behaviour and differential effects of fire in these stands.

Soil-Environment

Most of these stands occur on moderately steep, south-facing slopes in Banff and Kootenay National Parks (**Fig. 4.5**). Soils are pH neutral, (mean pH = 7.03) silty to sandy loams of intermediate nutrient status (mean conductivity = 179 $\mu\text{S}/\text{cm}$) classified as Orthic Eutric Brunisols. Surface organic matter accumulation is low (mean organic layer depth = 4.6 cm). Ungulate browsing levels vary, being highest in stands near roadways and townsites.

The more xeric variants of this stand-type generally occur on steep, well-drained slopes. The canopy is dominated by Douglas-fir in mixture with lodgepole pine. Shrub cover is high and dominated by buffaloberry and/or common juniper. Sub-mesic stand variants typically occur on lower slopes and are characterized by a diverse, multi-layered canopy. Douglas-fir and lodgepole pine are usually codominant in the canopy; trembling aspen is occasional. When present, white spruce usually occurs in the lower sub-canopy. Mesic stand variants are characterized by codominance of Douglas-fir and white spruce in the canopy and subcanopy layers; trembling aspen is occasional (**Fig 4.14, 4.15 & 4.16**).

Vegetation

This stand-type is characterized by a mixed-species, multi-layered canopy. Open-canopy stands are similar to those found of stand-type I, but lodgepole pine is generally present in the canopy and/or upper subcanopy. Closed-canopy stands are typically co-dominated by lodgepole pine and Douglas-fir in the canopy. In more mesic sites, white spruce (and occasionally trembling aspen) may also occur in the subcanopy. When present, mature trembling aspen trees often had wind-damaged upper stems, and were weakened by fungal infections. Douglas-fir regeneration is variable, being highest in more open-canopied stands in mesic sites. White spruce regeneration is low, and mostly occurs in more mesic sites (**Table**

4.11). Mean per-plot effective tree species richness is 2.15, which is intermediate between stand-types I and III (**Table 4.1**).

Mean stem density for canopy and subcanopy trees is highest for Douglas-fir (ca. 3 stems per plot) followed by lodgepole pine at ca. 2 stems per plot (**Table 4.11 & 4.12**). The mean density per canopy averaged about 3 stems, indicating a highly stratified physiognomic structure. Seventy-one percent of the total basal area in this stand-type was comprised by Douglas-fir. At 22%, lodgepole pine accounted for most of the remaining basal area (**Table 4.13**). Canopy cover was dominated by Douglas-fir (mean = 38%), lodgepole pine (mean = 14%), with some white spruce present (**Table 4.14**).

Douglas-fir had the highest mean regeneration per plot, averaging about 2 stems in the lower subcanopy and about 5 stems in the sapling layer (**Table 4.11**). Regeneration of other species averaged less than 1 stem per plot. Douglas-fir regeneration was highest in sub-type IIc, intermediate in sub-type IIa, and low in sub-type IIb.

Understory

These stands are characterized by an understory vegetation dominated by prostrate and tall shrubs, and high graminoid, forb and cryptogam cover. The understory per-plot effective species richness is 12.8, which is the highest of the three stand-types. Moss and lichen effective species richness are 2.92 and 3.04 respectively (**Table 4.1**).

These stands are characterized by a relatively high shrub cover. *Shepherdia canadensis* and *Juniperus communis* are the dominant species, in terms of both frequency and mean cover. *Arctostaphylos uva-ursi* is also frequently encountered, but typically occurs at low cover. *Rosa acicularis*, *Spiraea betulifolia*, *Symphoricarpos albus* and/or *Amelanchier alnifolia* may also be present. In some stands, ungulate browsing of *Rosa acicularis*, *Spiraea betulifolia* and *Shepherdia canadensis* was moderate to severe (**Table 4.15**).

The herb layer of these stands is diverse, and cover is high. *Calamagrostis rubescens* is the most commonly encountered grass; *Elymus innovatus* is also frequently encountered. Common forbs include *Fragaria virginiana*, *Aster conspicuus*, *Hedyselum sulphurescens* and *Aster ciliolatus*; *Pyrola chlorentha*, *Orthilia secunda*, *Goodyera oblongifolia* and *Allium cernuum* may also be present (**Table 4.16**). Locally uncommon plant species occasionally encountered in these stands include *Dodecatheon pulchellum*, *Castilleja miniata*, *Lycopodium complanatum* and *Pedicularis groenlandica*. Non-native species were occasionally encountered, including *Tragopogon dubius*, *Taraxacum officinale*, and *Sonchus arvensis* (**Appendix 2**).

Bryophytes are a conspicuous component of the understory of most stands. *Pleurozium schreberi* and *Hylocomium splendens* are most commonly encountered species, but *Sanionia uncinata*, *Hypnum revolutum* and *Brachythecium* spp. may also be present. *Peltigera* lichens (mainly *P. canina* and *P. aphthosa*) are fairly common but occur at low cover (Table 4.17).

Subtype Variants

Subtype IIa: Sub-Xeric (n = 32)

These stands typically occur on well-drained, moderately steep south-facing slopes. The upper canopy is semi-closed, and usually codominated by lodgepole pine and Douglas-fir. White spruce is rare in the upper canopy, but may be present in the subcanopy. Douglas-fir regeneration is variable: it is low in exposed dry sites, but may be abundant in sheltered, moist micro-sites (Table 4.17).

Shrub cover is low to moderate. *Arctostaphylos uva-ursi*, *Juniperus communis* and *Shepherdia canadensis* are the most commonly encountered species. Mean forb and graminoid cover is low (bare ground cover high) compared to the other two sub-types. *Elymus innovatus* is the dominant graminoid, while *Aster conspicuus*, *Hedysarum sulphurescens*, *Galium boreale*, *Fragaria virginiana*, and *Solidago spathulata* are frequently encountered forbs. Mosses are common; species characteristic of xeric habitats, such as *Tortula ruralis*, *Hypnum revolutum*, *Thuidium abitinum* and *Orthotrichum speciosum*, are generally present. The lichen *Peltigera canina* is frequently encountered, but occurs at low cover.

Subtype IIb: Sub-Mesic (n = 30)

This variant is typically found on moderately steep, south-west and east-facing slopes. Douglas-fir and lodgepole pine are codominant in the canopy, but white spruce and trembling aspen may also occur. In some stands, mature lodgepole pine trees have been infected by dwarf mistletoe, and windthrow is common. This 'breaking up' of the pine canopy may eventually favour canopy dominance by Douglas-fir and white spruce. These stands often show a multi-cohort age structure. With a few notable exceptions, most lodgepole pine and trembling aspen trees established as a single cohort immediately following the last catastrophic fire. Some individuals of white spruce established soon after the fire, but most have remained in a suppressed state; others have established more recently. Most of the Douglas-fir trees in these stands established following the last fire. Interspersed amongst these younger trees are older, 'relict' individuals that survived the fire and were probably the seed source for the younger cohort (Table 4.19; Fig. 4.8). As a result, these stands have a complex physiognomic profile. Douglas-fir regeneration in most stands is low, which may be attributable to the sub-mesic environment and high shrub cover.

These stands are characterized by high cover of tall woody shrubs. *Shepherdia canadensis* is the most common species, but *Acer glabrum*, *Rosa acicularis* and *Spiraea betulifolia* may also occur. Prostrate shrubs such as *Arctostaphylos uva-ursi* and *Linnaea borealis* are also present. The herb layer is floristically rich, and bare ground cover is low. The dominant graminoid is *Calamagrostis rubescens*. In addition to the forbs already listed as common in sub-type IIa, *Thalictrum occidentale*, *Aster ciliolatus*, *Orthilia secunda*, *Smilacina racemosa*, *Viola canadensis*, and *Goodyera oblongifolia* are also present. Mosses are common, with *Pleurozium schreberi* frequently occurring at moderate to high cover. *Rhytidiadelphus triquetrus*, *Hylocomium splendens* and *Ptilium crista-castrensis* are also common, but species characteristic of xeric habitats (e.g. *Tortula ruralis*, *Hypnum revolutum* and *Thuidium abitinum*, *Orthotrichum speciosum*) are uncommon or absent. The most commonly encountered lichen is *Peltigera aphthosa*.

Sub-Type IIc: Mesic (n =18)

These are dense stands, characterized by a relatively high canopy cover. The dominant species in both the canopy and upper subcanopy are Douglas-fir, lodgepole pine and white spruce. Douglas-fir regeneration in these stands is high: saplings or young trees occurred in well over half of the 10 x 10 m plots (**Table 4.20**).

Shrub cover in this sub-type is low, which probably reflects the high canopy cover (i.e. low light at ground level). *Rosa acicularis*, *Shepherdia canadensis* and *Linnaea borealis* are the most common encountered species. The herb layer is also comparatively poorly developed, with *Fragaria virginiana*, *Aster conspicuus* and *A. ciliolatus*, *Arnica cordifolia* and *Orthilia secunda* occurring at low to moderate frequency and cover. The lower light conditions favour the development of a cryptogram layer. The dominant moss species is *Hylocomium splendens*, a species characteristic of moderately shaded habitats. Dogpelt lichen (*Peltigera aphthosa*) is frequently encountered.

Selective ungulate browsing may alter potential successional pathways in stands located near townsites, where ungulate densities may reach 5-10 individuals/km². Localized heavy browsing of Douglas-fir saplings was evident in such areas. However, ungulate browsing of saplings was rare in other regions.

Forest Structure and Compositional Summary of Stand-Type II

These stands are of recent fire origin (late 1800's to early 1900's, Rogeau 1996; Weir et al. 1995; Tymstra 1991; White 1985; Tande 1979), as indicated by the presence of lodgepole pine, trembling aspen, *Shepherdia canadensis*, and *Calamagrostis rubescens* (Bradley et al. 1992). Many of the Douglas-fir trees in these stands are also of post-fire origin. However,

most stands also contain a few scattered 'relict' individuals of Douglas-fir (well over 100 years in age) that survived the catastrophic fires that swept through the area near the turn of the century. These surviving 'relict' trees were probably critical to the post-fire recruitment of Douglas-fir, and their presence indicates a complex fire regime for the region. The presence of *Acer glabrum* in sub-types IIb and IIc suggests locally mesic, mesotrophic conditions (Krajina et al. 1982).

Many stands have substantial understory fuel loads (e.g., high shrub cover), as well as 'thickets' of regenerating Douglas-fir and/or white spruce that may further increase the fire hazard by encouraging 'laddering' of a surface fire into the crown (Johnson 1992). A catastrophic crown fire will favour lodgepole pine and/or trembling aspen recruitment, whereas lower-intensity ground fires are more favourable to the fire-tolerant Douglas-fir. Such ground fires will 'kill the competition' while at the same time favouring germination and establishment of Douglas-fir on the residual duff layer.

In the absence of fire, recruitment into these stands may be driven by small-scale canopy disturbances such as individual tree mortality. The life-history characteristics of Douglas-fir are well-suited to such periodic, fine-scale disturbances. Douglas-fir is a semi-shade tolerant species, particularly in xeric and mesic habitats. Under low light conditions, established Douglas-fir saplings are suppressed and take on a sympodial rather than conical growth form. These suppressed individuals respond well to canopy release (Williams et al. 1999). By contrast, under full light (e.g., immediately following fire) shade-intolerant species such as lodgepole pine have greater terminal and lateral growth rates than Douglas-fir (Chen et al. 1996). Furthermore, cone serotiny in lodgepole pine is a favourable life-history trait in stands characterized by regular, large-scale catastrophic fires (Muir and Lotan 1985).

III: Douglas-fir/White Spruce/Feathermoss $n = 45$ (B = 2, J = 19, K = 10, Y = 14)

Stand age

Douglas-fir trees range in age from 115 to 380 years (**Table 4.1**). The vast majority of these stands (89%) had trees present whose age exceeded the estimated fire origin date (**Fig. 4.9**). Most of these stands occur in topographically 'sheltered' locations, such as north-facing slopes and depressions, that are somewhat protected from catastrophic fires (**Fig. 4.5**). The relatively coarse scale of most stand origin maps fail to consider these finer-scaled sheltered stands. Fire behaviour is modified by numerous physiographic factors, including natural fire breaks, proximity to water table, topography, wind, and fuel moisture content. Topographically 'protected' sites may therefore escape the cumulative effects of the recurrent catastrophic fires that sweep through the region. The presence in these stands of species not adapted to frequent burning (e.g., western redcedar) offers further evidence of site protection.

Soil-Environment

Most of these stands occur on low basal slopes or in depressions (**Fig. 4.5**), but some are found on steeper north or south-facing slopes. Soils are slightly basic (mean pH = 7.4), silty-loams to clay loams of relatively high nutrient status (conductivity = 223 $\mu\text{S}/\text{cm}$) classified as Brunisolic soils often gleyed in local depressions. The soil organic horizon is well developed (mean depth = 7.4 cm), and herbivore browsing is low (**Table 4.1**).

Sub-hygic stands, which generally occur on north or south-facing lower slopes, are characterized by a mixed canopy of mature Douglas-fir and white spruce; subalpine fir is occasionally present. Sapling and shrub cover is highest on south-facing slopes. The hygic variant occurs in cool-moist topographic depressions. The canopy of these stands consists of a mixture of mature Douglas-fir, white spruce and subalpine fir; western red cedar may also be present in British Columbia (i.e., the western slopes of the Rockies). Subcanopy trees in these stands are uncommon or absent (**Fig. 16, 17 & 18**).

Vegetation

In most stands, Douglas-fir and white spruce form a dense, co-dominant canopy (**Table 4.21 & 4.22**). Subalpine fir and western red cedar occur less frequently, and are restricted to cool-mesic sites west of the Cordillera. Lodgepole pine is rarely encountered as scattered 'over-mature' individuals within the mixed canopy. Mean density of canopy and subcanopy Douglas-fir is about 3 stems per plot, followed by white spruce (2 stems) and subalpine fir (1 stems; **Table 4.22**). Large relic Douglas-fir trees account for 71% of the total basal area

(Table 4.23). Canopy cover is dominated by Douglas-fir (mean = 32%), followed white spruce (22%). Mean per plot effective tree species richness is 2.85, which is considerably higher than the other two stand-types (Table 4.1).

Regeneration of Douglas-fir (beyond the seedling stage) in these stands is low. White spruce is the most common species in the regeneration layer, although western redcedar and subalpine fir saplings are also occasionally encountered. Seedlings are common, as most species germinate or vegetatively propagate readily on the rich organic seedbeds characteristic of these stands. White spruce and subalpine fir seeds germinate on decomposing wood, while western redcedar propagates vegetatively by layering. Douglas-fir seedlings are also present, but they rarely reach the sapling stage. Presumably they are suppressed and are eventually killed as a result of the deep shade cast by the canopy and subcanopy.

Understory

Low light conditions prevail in these stands. The soil organic layer is well-developed, and bare ground cover is very low. Understory mean effective species richness is 3.02. Lichen and moss effective species richness are 1.66 and 1.51 respectively (Table 4.1).

Shrub cover is typically low. *Linnaea borealis* is the dominant low-shrub species. The most common tall shrubs are *Rosa acicularis*, *Symphoricarpos albus*, and *Amelanchier alnifolia*. Unlike the other two stand-types, *Shepherdia canadensis* is relatively uncommon. *Viburnum edule* may occur in closed canopy stands. Locally rare shrubs such as *Lonicera utahensis*, *Menziesia ferruginea*, *Chimaphila umbellata*, *Oplopanax horridus*, and *Mahonia aquifolium* are usually found in association with western redcedar and subalpine fir (Table 4.25).

Herb species diversity and cover are low. *Elymus innovatus* occurs in about half the plots, but is never abundant. *Aster conspicuus*, *Fragaria virginiana*, *Comandra umbellata*, *Pyrola chlorentha* and *Orthilia secunda* are commonly encountered, but they generally occur at low cover. Locally rare understory plants include *Spiranthes romanzoffiana*, *Platanthera obtusata*, and *Listera cordata*. The only non-native species encountered was *Linaria dalmatica* (Table 4.26; Appendix 2).

The understory of these stands is typified by a thick bryophyte mat. *Hylocomium splendens* is the most frequently encountered moss and forms extensive 'carpets'. Other commonly encountered mosses include *Pleurozium schreberi*, *Rhytidiadelphus triquetrus*, *Timmia austriaca*, and *Plagiomnium drummondii*; most of these species are characteristic of mesic, shaded habitats. *Thuidium abitinum*, *Hypnum revolutum*, and *Tortula ruralis* are generally restricted to higher-light areas such as canopy gaps. The dominant lichen is *Peltigera aphthosa* (Table 4.27).

Subtype Variants

Two sub-types are recognized. About two-thirds of stands belonging to the sub-hygric variant occur on east-facing slopes in Banff and Jasper National Parks. Stands of the hygic variant are all located west of the Cordillera (Kootenay and Yoho National Park).

Sub-Type IIIa: Sub-Hygic (n = 31)

These stands typically occur on basal slopes and in depressions. Douglas-fir and white spruce are canopy codominants: canopy cover is moderate to high. The oldest Douglas-fir trees range in age from 110 to 298 years (Table 4.28).

Shrub cover is generally low. The dominant species are *Linnaea borealis*, *Rosa acicularis* and *Symphoricarpos albus*. *Juniperus communis* may occur in more open stands. Graminoids and forbs are uncommon, but feathermoss cover is high. The most commonly encountered species is *Hylocomium splendens*, which forms extensive mats.

White spruce is common in the regeneration layer (lower subcanopy and saplings) of these stands, suggesting that in the absence of fire it will become an increasingly important canopy component. However, the greater longevity of Douglas-fir will ensure its continued dominance in the foreseeable future. Furthermore, canopy openings (resulting from white spruce mortality) may facilitate future recruitment of Douglas-fir. Canopy openings may also increase shrub cover .

Sub-Type IIIb: Hygic (n =14)

Eleven of these fourteen stands are located in Yoho National Park, on south-facing basal slopes or depressions in the Upper and Lower Kicking Horse watersheds. These stands are characterized by a dense mixed canopy of Douglas-fir, white spruce, western red cedar and subalpine fir. Douglas-fir canopy tree ages range from 118 to 380 years. Regeneration of white spruce, western cedar and subalpine fir is occurring in some stands. Douglas-fir seedlings are commonly found near parent trees, but they rarely reach the sapling stage (Table 4.29).

Shrub cover is highest in open-canopy stands. *Linnaea borealis*, *Lonicera utahensis*, *Viburnum edule*, *Ribes lacustre*, and *Menziesia ferruginea* are the most commonly encountered species. *Chimaphila umbellata*, *Oplopanax horridus*, *Lonicera involucrata*, and *Mahonia aquifolium* are more common in closed-canopy stands. Graminoid cover is low. The most common forbs are *Aralia nudicaulis*, *Fragaria virginiana*, *Galium trifolium*, *Smilacina racemosa*, *Cornus canadensis*, and *Streptopus amplexifolius*. A feathermoss carpet

dominated by *Pleurozium schreberi* and *Hylocomium splendens* is characteristic. Other common mosses include *Timmia austriaca* and *Polytrichum juniperinum*.

In the absence of fire, it is anticipated that these stands will undergo little compositional change. Active regeneration of white spruce suggests its continued dominance. Subalpine fir and western redcedar, both long-lived species, are also regenerating and will likely continue to be important canopy components where they are present. Douglas-fir regeneration may be favoured by small-scale canopy disturbances, such as individual tree mortality. Prolific Douglas-fir seedling establishment was noted in many stands, but the deep shade cast by the closed canopy is apparently fatal, as very few saplings are present. Canopy gap openings may result in sufficient light reaching the forest floor to allow survival and growth of Douglas-fir seedlings.

Site physiography probably affords some protection from catastrophic fires, as evidenced by the absence of fire-adapted species (e.g., lodgepole pine) in these stands. Should a crown fire occur, species such as white spruce and Douglas-fir would likely be favoured, while a severe fire could result in the local extirpation of western redcedar and subalpine fir.

Forest Structure and Compositional Summary of Stand-Type III

These stands occur in somewhat 'protected' locations such as depressions (creek valleys) and basal slopes, which have a moderating effect on microclimate. The microenvironment is cool and moist, which reflects high canopy closure as well as physiographic position; most sites are shaded by the surrounding mountains. These factors have two important effects on floristics: (a) fire frequency and severity are lower (Romme and Knight 1981), favouring establishment of a fire-intolerant flora; (b) the moderated cool-moist microclimate favours 'coastal' species.

The presence of white spruce, western redcedar and subalpine fir indicates that these stands are infrequently burned; all three species are shade-tolerant and vulnerable to catastrophic fires (Minore 1990; Neinstaedt and Zasada 1990). The mean age of Douglas-fir individuals in these stands is 180 years, suggesting that they have escaped the large fires of the mid-1880s (Tymstra 1991). The 'relict' Douglas-fir trees present in these stands may be of fire origin. Another possibility is that these trees establish episodically, in canopy gaps created by individual tree mortality. Because Douglas-fir regenerates poorly in deep shade (Williams et al. 1999), the species may be locally extirpated if canopy gaps are not created.

A moderate microclimate, and the cool-wet conditions characteristic of these sites, has facilitated the establishment of 'coastal' species such western redcedar and *Oplopanax horridus*. These species are at their eastern distributional limit west of the Cordillera. Western

redcedar requires adequate nutrients (particularly nitrogen and calcium) and soil moisture for successful establishment (Minore 1990). The presence of extensive feathermoss mats (primarily *Pleurozium schreberi* and *Hylocomium splendens*) is also indicative of site conditions and disturbance history. *P. schreberi* occurs in semi-closed coniferous forests over a wide range of substrate types, from humus to exposed mineral soil to rock fragments. This shade-tolerant species is susceptible to desiccation. *H. splendens* is a highly shade-tolerant species that occurs in closed canopy situations. It is subject to evapotranspirational stress: growth is thus enhanced in sheltered shaded habitats and humid microenvironments (Busby et al. 1978; Binkley and Graham 1981). Post-fire recovery of a dense feathermoss mats can take several decades.

4.4.3 Vegetation-Environmental Relationships

Correspondence Analysis (CA)

Stand Ordination

The CA ordination of the 220 plots shows a clear separation of the three stand-types (as delineated by the cluster analysis), while at the same time recognizing that the cluster analysis has 'partitioned' a vegetation continuum (Fig. 4.20). The high affinity between the ordination and classification results confirms the 'robustness' of the delineated stand-types. The three stand-types are well separated along the first (primary) ordination axis. Based on the distribution of indicator species (Figs. 4.21 & 4.22), the first ordination axis is interpreted as a complex moisture-light gradient. The mean coordinate position of each of the seven sub-types was therefore projected onto this first axis gradient (Fig. 4.20). Sites characterized as 'xeric' were represented by stand-type I (Ia & Ib), those of intermediate light and moisture status ('mesic') by stand-type II (IIa, IIb & IIc), and moist ('hygric') low-light sites by stand-type III (IIIa & IIIb).

Species Ordination

The 'dual' species ordination (Figs. 4.21 & 4.22) confirms the interpretation of the first ordination axis as a complex light-moisture gradient. Species adapted to xeric, full light conditions (left side of the ordination) include Rocky Mountain juniper, limber pine, common rabbit-bush, ground and common juniper, sage, and the moss *Tortula ruralis*. At the opposite end of the gradient are species characteristic of moist, shaded conditions, including western redcedar, subalpine fir, devil's club (*Oplopanax horridus*), high-brush cranberry (*Viburnum edule*), false-azalea (*Menziesia ferruginea*), wild-lily-of-the-valley (*Maianthemum canadensis*), common mitrewort (*Mitella nuda*), false haircap moss (*Timmia autriaca*), and Drummond's leaf moss (*Plagiomnium drummondii*). Species located near the center of the ordination diagram (e.g., Douglas-fir) are either 'generalist' species (i.e., found along the entire light-moisture gradient), or species that occur in areas of intermediate light and soil moisture conditions.

Percent cover values of selected common species along the first ordination axis (light-moisture gradient) are summarized in Fig. 4.23-4.25. The raw data were smoothed using robust locally weighted regression analysis (Cleveland 1979). Douglas-fir is found in all stands, but percent cover peaks in the sub-xeric sites. Lodgepole pine cover is highest in intermediate sites (stand sub-types Ib, IIa, & IIc), but this species is virtually absent from sub-types Ia, IIIa and IIIb. White spruce cover increases with increasing soil moisture, peaking in stand-type III. Amongst the common shrub species, bearberry and common juniper both achieve highest cover in xeric sites. Buffaloberry cover peaks in intermediate sites, while twinflower cover is highest in the most mesic sites. Graminoid cover peaks in the intermediate

sites, and is lowest in moist, shaded sites. Total cover of forbs, lichens and feathmosses increases with increasing soil moisture and lower light levels.

Canonical Correspondence Analysis (CCA)

Direct gradient analysis (CCA) was used to determine the degree to which measured environmental variables can 'predict' variation in species composition (ter Braak 1986; Okland 1999). The inferred light-moisture gradient from the unconstrained (CA) ordination was substantiated by the CCA results (Fig. 4.26). Indeed, the CCA site ordination is very similar to the unconstrained CA ordination (compare Figs. 4.26 & 4.20), indicating that the dominant gradient in species space has a strong underlying environmental component: species are good indicators of site conditions. Mesic sites (stand-type III) are positively correlated with soil nutrients (conductivity), organic matter accumulation, and finer-textured soils (i.e., higher silt content). By contrast, the most mesic sites (stand-type I) are positively correlated with coarse-textured soils (i.e., higher sand content), greater incident solar radiation, and steeper slopes.

The direct gradient ordination confirms that species assemblages in these Douglas-fir stands are closely linked to environmental conditions. Previous studies have noted that gradients of soil factors (moisture, nutrients, acidity) and/or light conditions 'are important determinants of species composition and relative competitive abilities' (Kenkel and Watson 1998). Tree diversity (effective species richness per plot) increases with increasing soil moisture and nutrients (i.e., highest in stand-type III, lowest in stand-type I). Understory diversity shows almost the opposite trend, however, being highest in stand-types II and I, and lowest in stand-type III. The more open-canopied forests of stand-types I and II allows more light to reach the forest floor, increasing species diversity. By contrast, fewer species are tolerant of the shaded conditions characteristic of stand-type III.

In the CCA, only about 14% of the 'total inertia' (or variation) in the species data was explained by the seven measured environmental variables. However, 'total inertia' is not a particularly meaningful (or readily interpretable) measure of variation in multivariate data (Okland 1999). Nonetheless, it is clear that much of the species variation is unexplained by the measured environmental variables. Other factors that may contribute to species composition include unmeasured environmental variables (e.g., soil moisture deficit, soil nitrogen status), long-term fire history, herbivory and granivory, fungal pathogens and insect pests, and stochastic factors related to stand history (Houston and Smith 1987; McCune and Allen 1985).

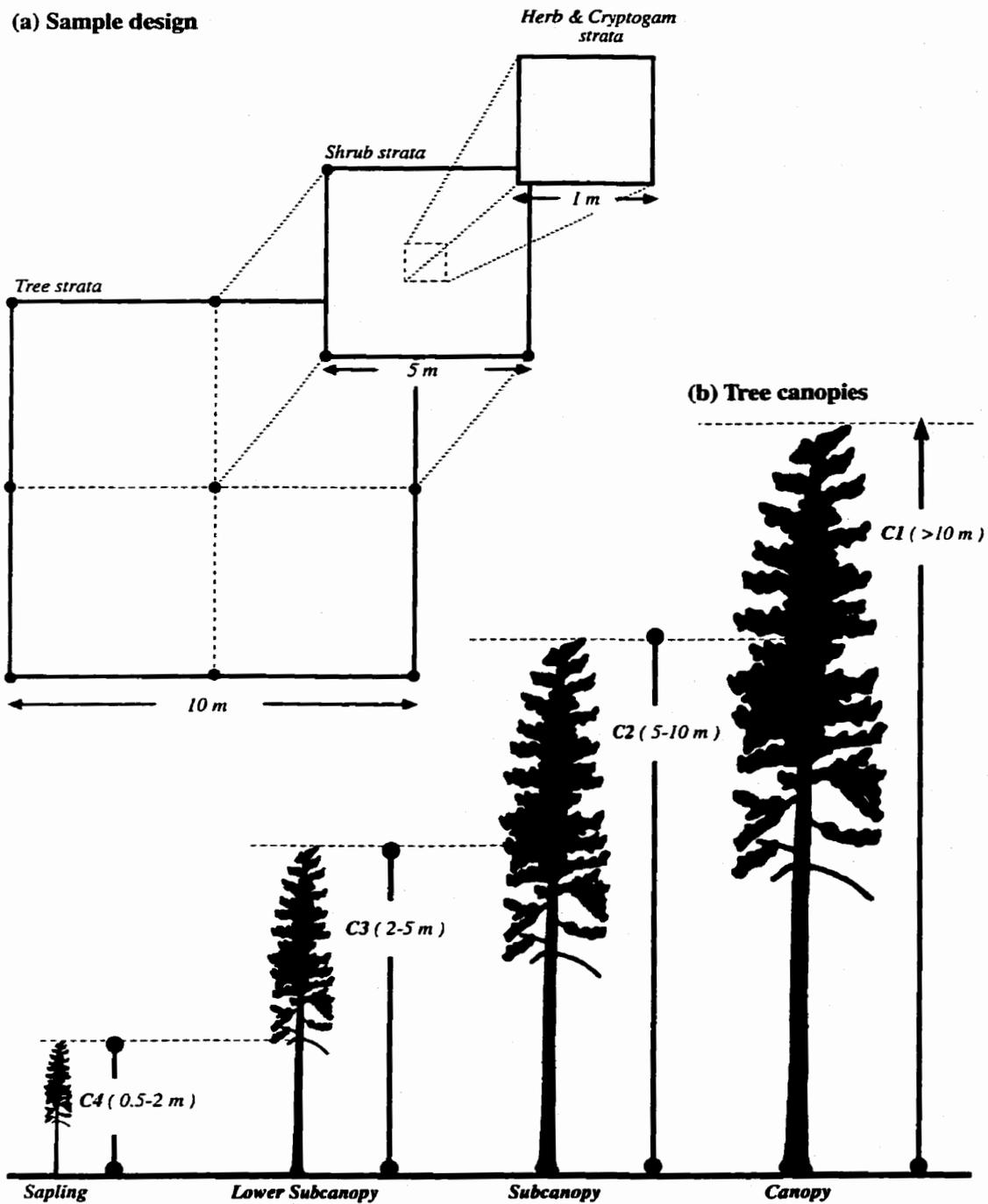


Figure 4.1 (a) Layout of sample plots for the tree, shrub and herb/cryptogam strata. (b) Canopy classes used to describe vegetation layers in each site. The herb-dwarf shrub, seedling and bryoid layers are $<0.5\text{m}$ and are denoted as canopies 5 and 6 respectively.

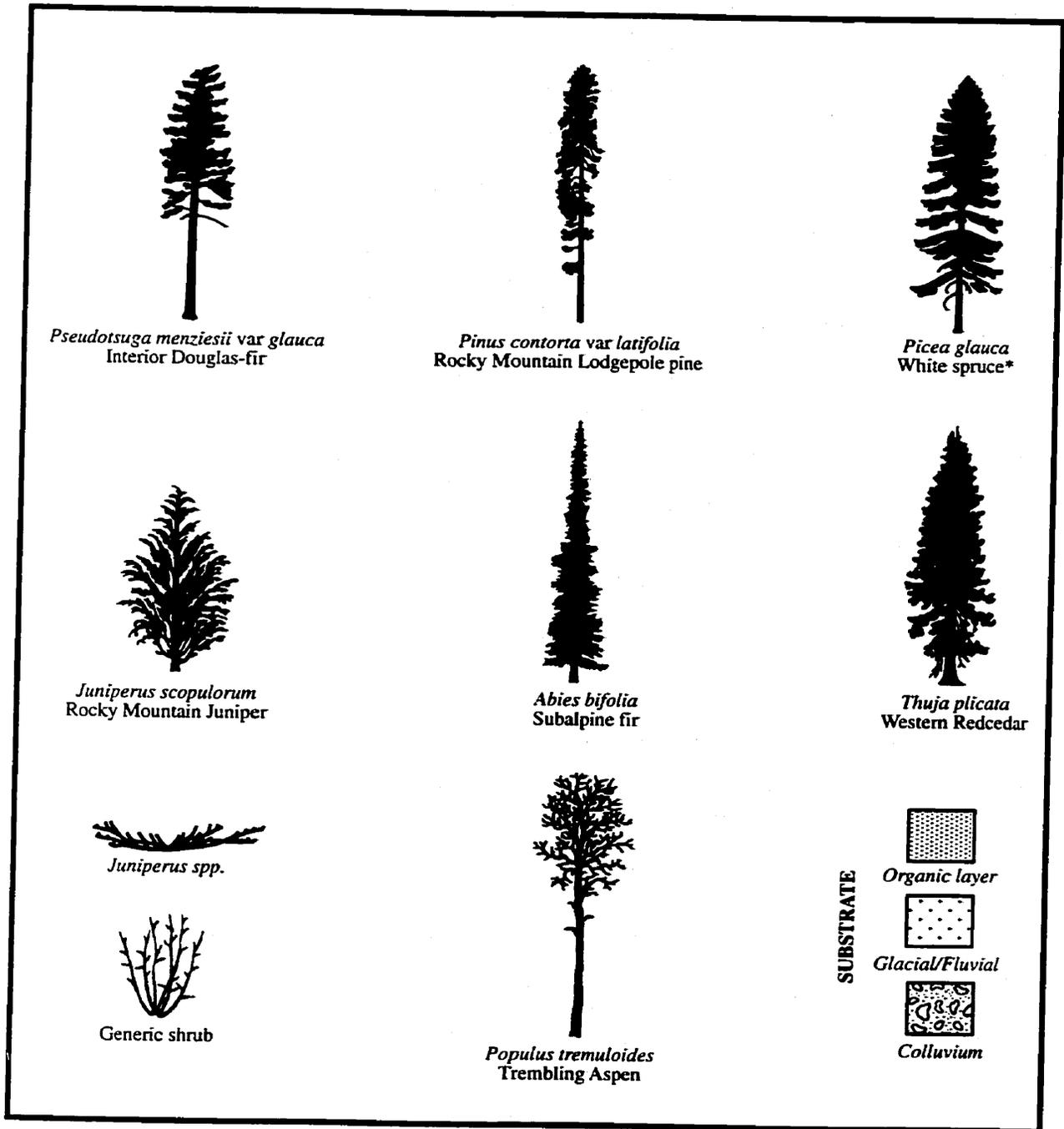


Figure 4.2. Icons used in the description of the physiognomic profiles. White spruce icon (*) may represent Engelmann spruce, white spruce or their hybrids.

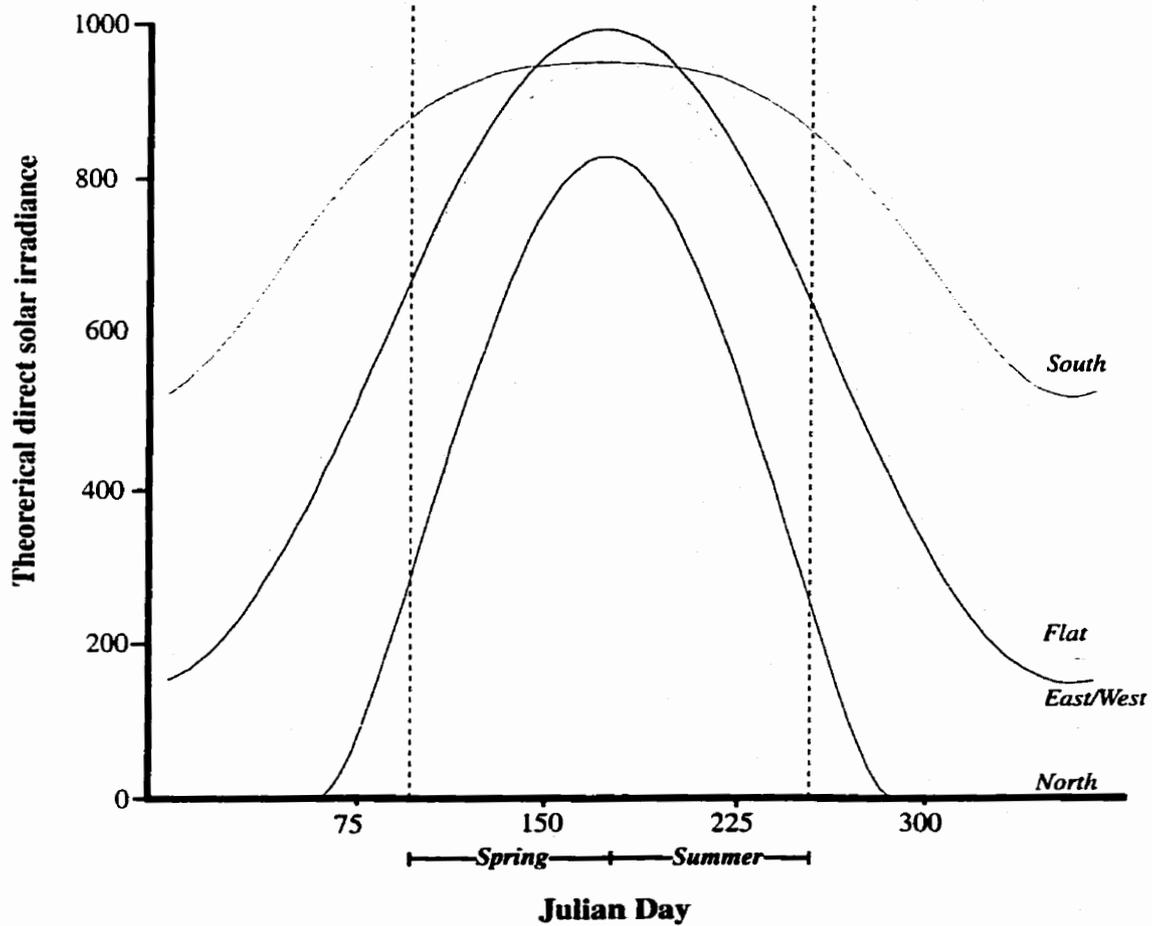


Figure 4.3. Theoretical direct solar radiation calculated for north, south, east and west facing aspects at 52°N and 30° slope. For example on March 30, a north-facing slopes receives approximately 46% of the total direct radiation compared to an equivalent south-facing slope. This has important implications for the snow melt period, start of fire season and growing degree days. This model does not take into account the heat budget of mountain slopes. Thermal models would show a difference between east and west facing slopes.

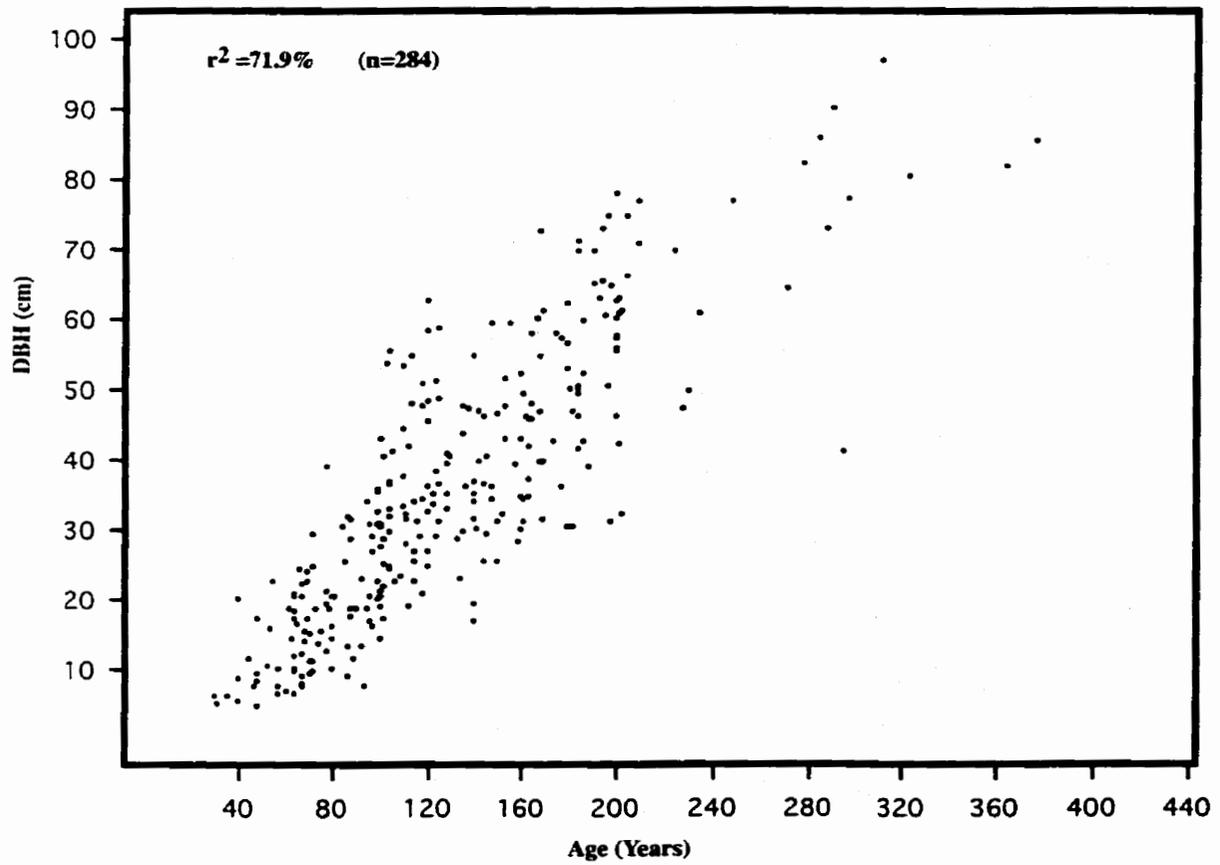


Figure 4.4 Age, DBH (Diameter at breast height) relationship for 284 Douglas-fir trees sampled in the four mountain parks.

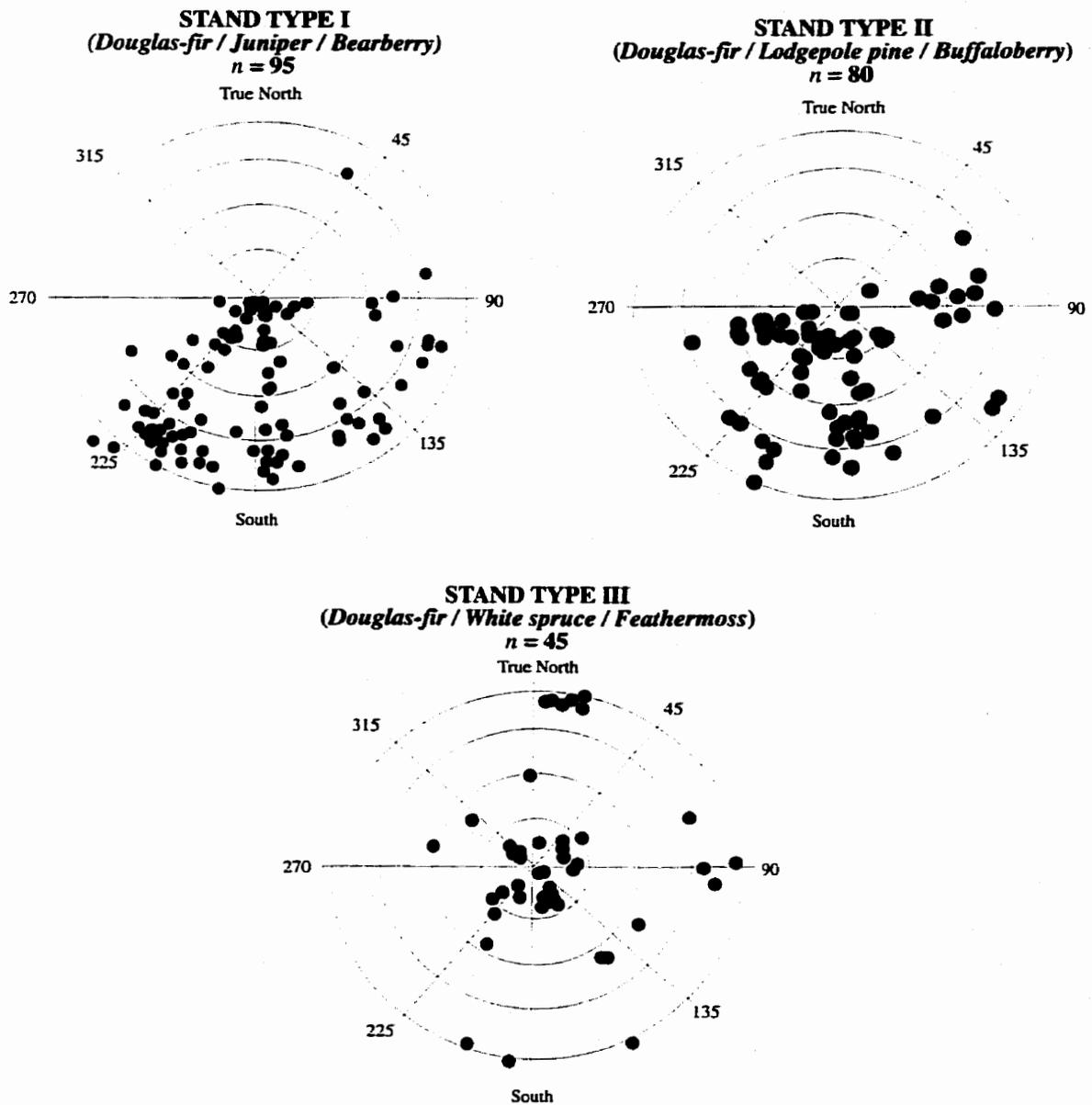


Figure 4.5. Percent slope and aspect diagram for each stand type. Each concentric circle represents 25% slope. Aspect values have been adjusted for true north.

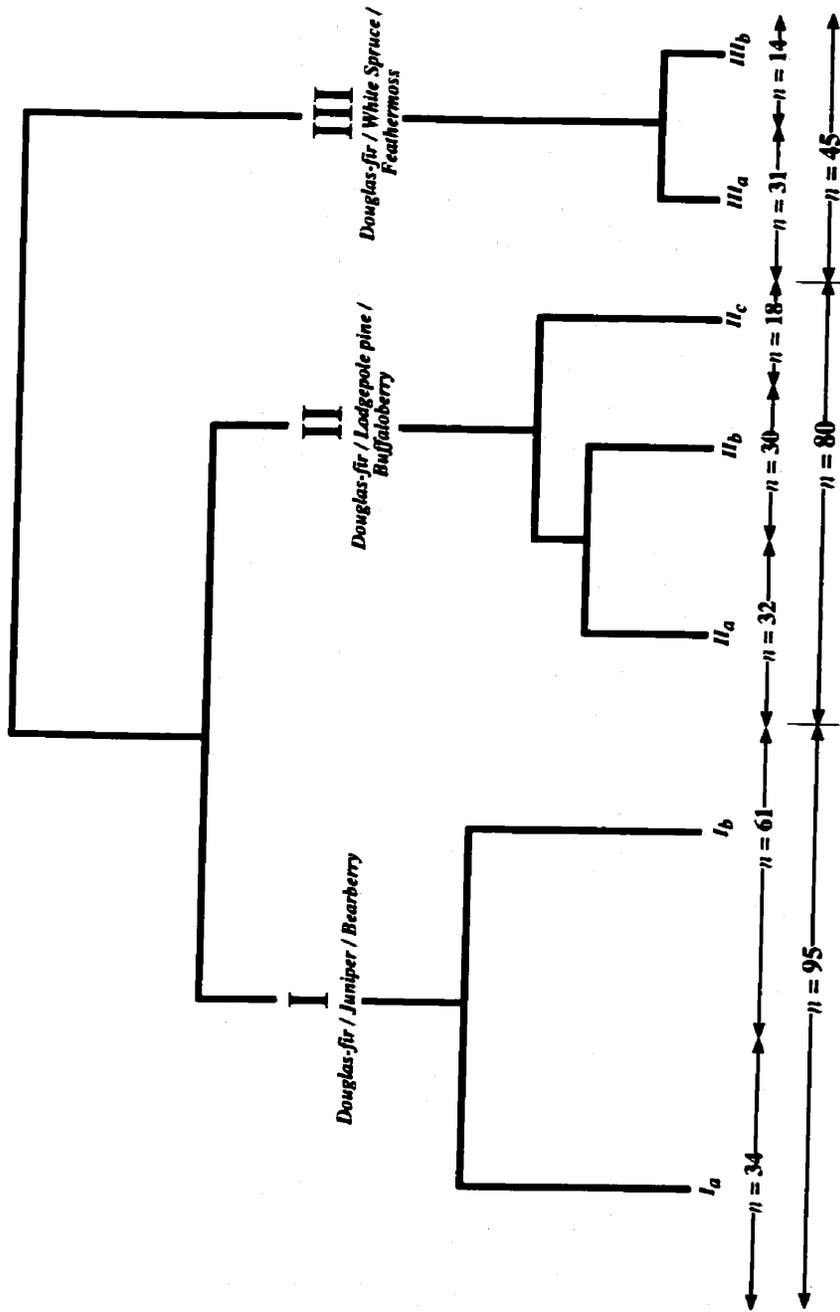


Figure 4.6. Cluster analysis(Ward's method) dendrogram of 220 Douglas-fir stands in Banff, Jasper, Yoho and Kootenay National Park. Wards clustering method based on a chord distance matrix.

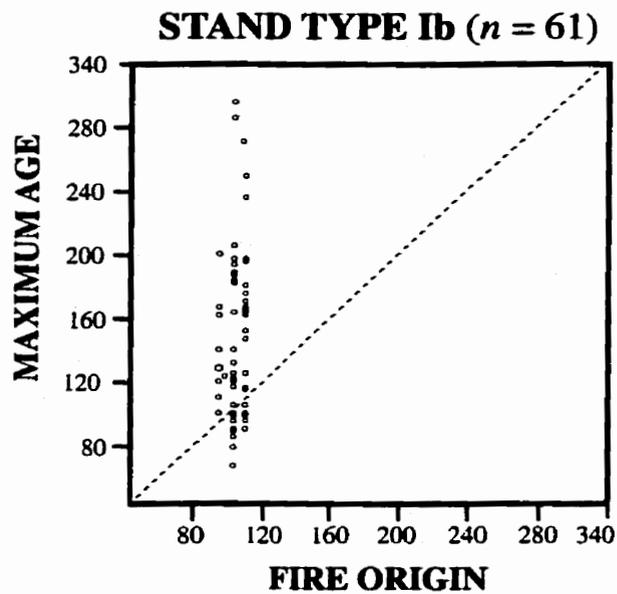
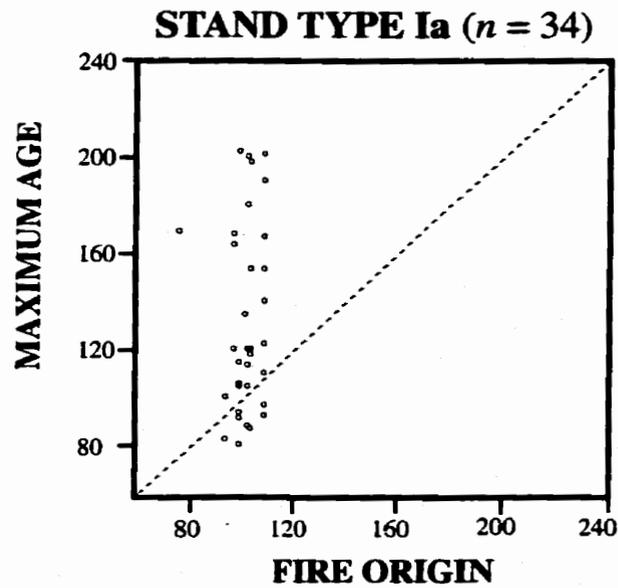


Figure 4.7. The relationship between fire origin date and maximum tree age for stand type I. The Diagonal line represents a one-to-one relationship between MAXIMUM AGE and FIRE ORIGIN. Points above the line represent sites in which the maximum age exceeds the estimated fire origin date.

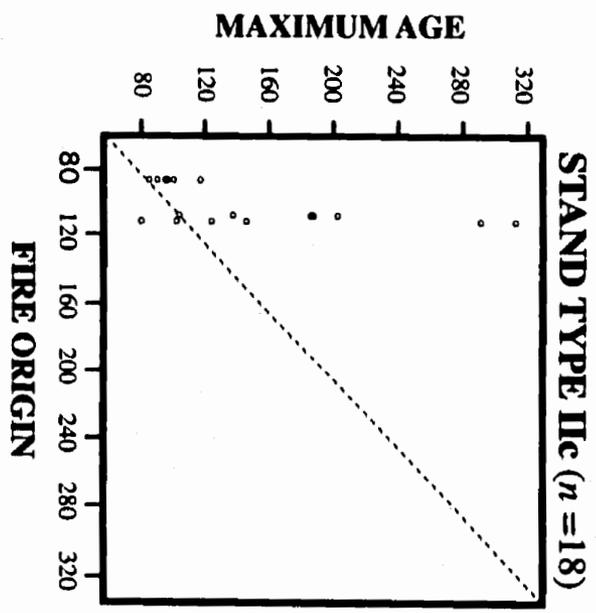
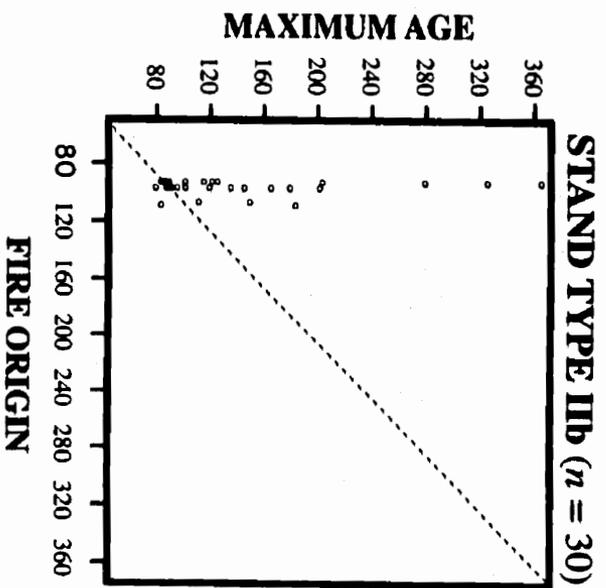
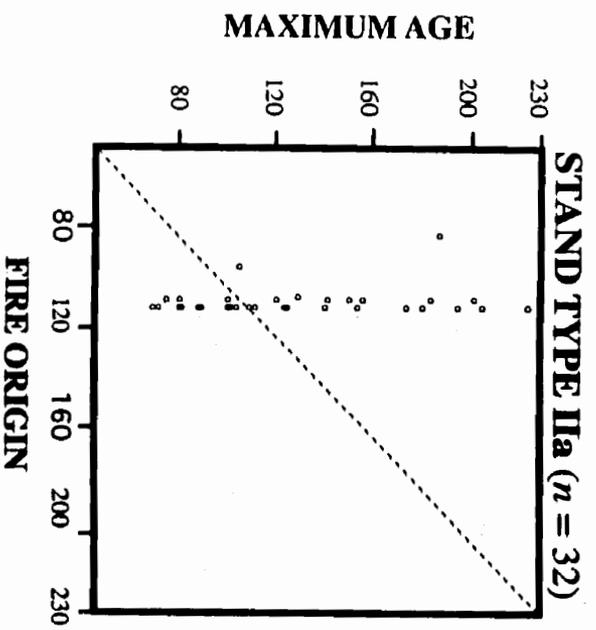


Figure 4.8. The relationship between fire origin date and maximum tree age for stand type II. The Diagonal line represents a one-to-one relationship between MAXIMUM AGE and FIRE ORIGIN. Points above the line represent sites in which the maximum age exceeds the estimated fire origin date.

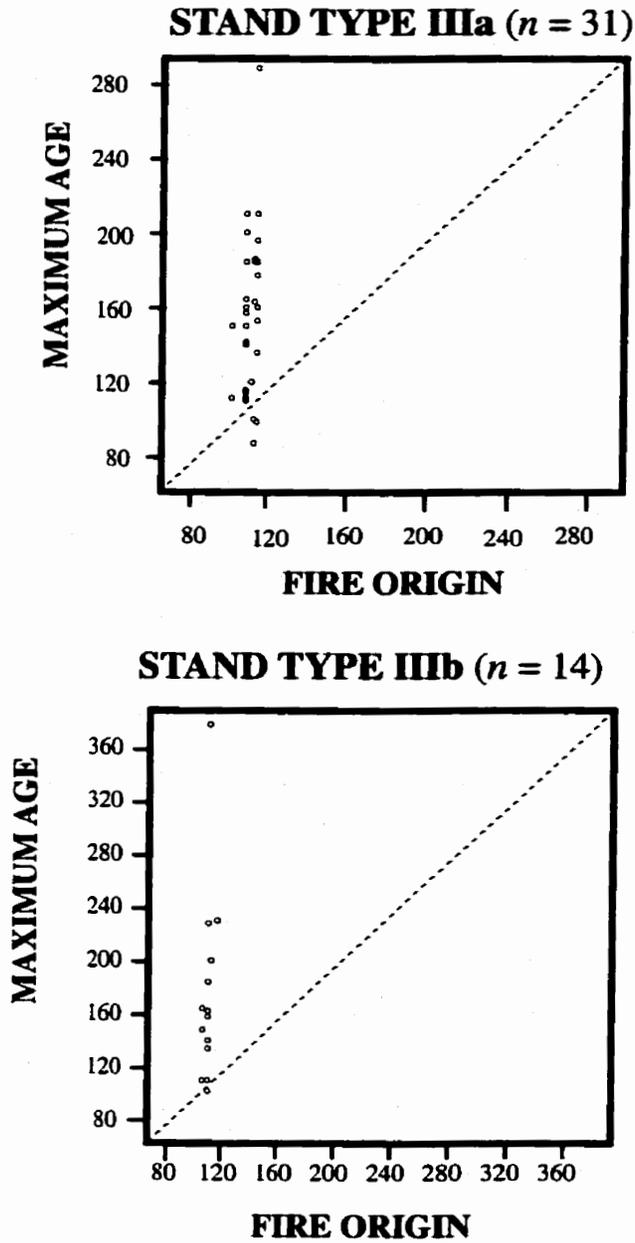


Figure 4.9. The relationship between fire origin date and maximum tree age for stand type III. The Diagonal line represents a one-to-one relationship between MAXIMUM AGE and FIRE ORIGIN. Points above the line represent sites in which the maximum age exceeds the estimated fire origin date.

Table 4.1.(a) Mean, and range (parenthesis) of edaphic and environmental variables.(b) Effective per plot species richness (H') is included for both the canopy and understory species.

| | STAND TYPE | | | | | | Mean | Range |
|---|------------|-------------|--------|---------------|---------|-------------|--------|-------------|
| | I | | II | | III | | | |
| <i>n</i> | 95 | | 81 | | 45 | | | |
| Environmental | | | | | | | | |
| pH | 7.6 | (6.4 - 8.6) | 7.03 | (5.7 - 8.0) | 7.4 | (4.7 - 8.2) | 7.33 | 4.7 - 8.6 |
| Conductivity (μ S/cm) | 110.4 | (53 - 240) | 179 | (55 - 526) | 223 | (38 - 589) | 158.34 | 38 - 589 |
| %silt | 39.9 | (22.5 - 63) | 43.9 | (28.6 - 73.9) | 48 | (32 - 69) | 43.02 | 22.5 - 73.9 |
| %sand | 39.5 | (21.1 - 73) | 34.9 | (8.5 - 71.4) | 32.6 | (20 - 58) | 36.4 | 8.5 - 71.4 |
| Organic depth (cm) | 1.7 | (0 - 6) | 4.6 | (0 - 12) | 7.2 | (1 - 20) | 3.8 | 0 - 20 |
| %Bareground | 33.3 | | 11.7 | | 2.8 | | 19.2 | 0 - 80 |
| % slope | 55 | | 35 | | 30 | | 45.6 | 0 - 142 |
| Aspect (deviation from N) | 141 | | 131 | | 87 | | - | - |
| Browse (rank scale 1-5) | 1.5 | | 1.8 | | 1.1 | | - | - |
| Max Age Range | 100-290 | | 85-305 | | 115-380 | | - | 85 - 380 |
| Diversity (e^H) | | | | | | | | |
| <i>Effective species richness(per plot)</i> | | | | | | | | |
| Tree | 1.5 | | 2.15 | | 2.85 | | - | - |
| understory | 10.25 | | 12.82 | | 3.02 | | - | - |
| Mosses | 4.93 | | 2.92 | | 1.51 | | - | - |
| Lichens | 3 | | 3.04 | | 1.66 | | - | - |



Figure 4.10 (a) Xeric open canopied stand (ST Ia) located in Jasper National Park. (b) Seedling Regerating on an exposed well-drained south-facing slope in Kootenay National Park, dominant graminoid is *Festuca saximontana*.



Figure 4.11 Xeric open-canopied stand (ST Ia) located in Kootenay National Park.



Figure 4.12 Sub-Xeric stand (ST Ib) located in Banff National Park.

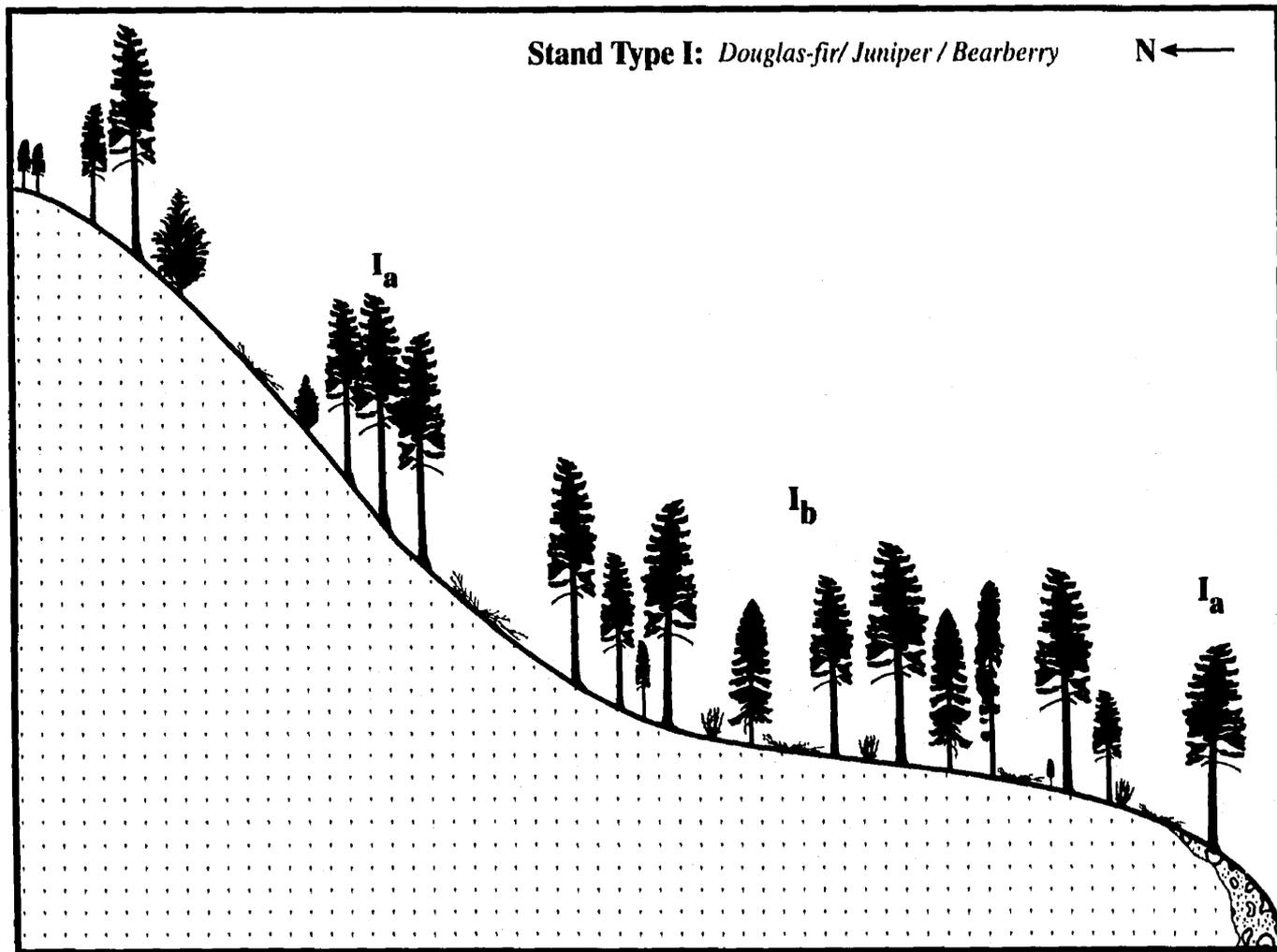


Figure 4.13. Physiognomic profile for stand type I (*Ia* and *Ib*). Sub-types are represented based on mean cover, density and slope estimates.

STAND TYPE I (DOUGLAS-FIR/JUNIPER/BEARBERRY), $n = 95$.

Table 4.2 Relative frequency

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.89 | 0.55 | 0.47 | 0.58 | 0.75 |
| <i>Picea glauca</i> | White Spruce | 0.44 | 0.13 | 0.22 | 0.14 | 0.14 | 0.22 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.22 | 0.09 | 0.11 | 0.06 | 0.04 | 0.05 |
| <i>Pinus flexilis</i> | Limber pine | 0.04 | 0.02 | 0.02 | 0.01 | 0.02 | |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.04 | | 0.02 | | 0.03 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.12 | 0.02 | 0.04 | 0.05 | 0.06 | 0.06 |

Table 4.3 Mean Density Per 100 m²; Stand-type I.

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|-------------|-------------|-------------|-------------|-------------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 18.53 | 3.21 | 1.77 | 1.82 | 5.23 | 6.49 |
| <i>Picea glauca</i> | White Spruce | 2.18 | 0.20 | 0.57 | 0.31 | 0.47 | 0.63 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 1.07 | - | 0.18 | - | 0.89 | - |
| <i>Pinus contorta</i> | Lodgepole pine | 0.58 | 0.15 | 0.19 | 0.08 | 0.06 | 0.09 |
| <i>Pinus flexilis</i> | Limber pine | 0.13 | 0.02 | 0.05 | 0.01 | 0.04 | - |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 1.08 | 0.02 | 0.16 | 0.22 | 0.15 | 0.54 |
| | | 23.56 | 3.60 | 2.92 | 2.44 | 6.85 | 7.76 |

Table 4.4 Mean Basal Area Per Plot (m² per 100 m²; Stand-type I)

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|-------------|-------------|-------------|-------------|-------------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 0.385 | 0.330 | 0.024 | 0.003 | 0.016 | 0.012 |
| <i>Picea glauca</i> | White Spruce | 0.015 | 0.009 | 0.005 | - | - | - |
| <i>Pinus contorta</i> | Lodgepole pine | 0.008 | 0.005 | 0.003 | - | - | - |
| <i>Pinus flexilis</i> | Limber pine | 0.002 | 0.001 | 0.001 | - | - | |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | - | | - | | - | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.003 | 0.001 | 0.001 | - | - | 0.001 |
| | | 0.41 | 0.35 | 0.03 | 0.00 | 0.02 | 0.01 |

TABLE 4.5. Frequency, mean cover and variance of tree species (Stand-type I).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|---|------------------------|-----------|----------------|----------|
| Conifers | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 41.20 | 354.29 |
| <i>Picea glauca</i> | White Spruce | 0.44 | 4.29 | 77.16 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.22 | 1.16 | 10.67 |
| <i>Pinus flexilis</i> | Limber pine | 0.04 | 0.22 | 1.77 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.04 | 2.44 | 45.88 |
| Deciduous | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.12 | 0.64 | 6.81 |
| <i>Betula papyrifera</i> | Paper Birch | 0.05 | 0.25 | 1.54 |
| <i>Acer glabrum</i> var. <i>douglasii</i> | Rocky Mountain Maple | 0.04 | 0.24 | 1.51 |
| <i>Salix</i> spp | Willow | 0.03 | 0.02 | 0.01 |
| <i>Populus balsamifera</i> | Balsam poplar | 0.02 | 0.03 | 0.10 |

TABLE 4.6. Frequency, mean cover and variance of common shrub species ($f \geq 5\%$; Stand-type I).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|--------------------------------|-----------------------------|-----------|----------------|----------|
| Tall Shrubs | | | | |
| <i>Shepherdia canadensis</i> | Buffalo berry (Soopolallie) | 0.60 | 1.88 | 19.23 |
| <i>Spiraea betulifolia</i> | Birch-leaved spirea | 0.28 | 0.54 | 2.49 |
| <i>Rosa acicularis</i> | Prickly rose | 0.59 | 0.52 | 0.48 |
| <i>Symphoricarpos albus</i> | Common snowberry | 0.35 | 0.51 | 1.18 |
| <i>Amelanchier alnifolia</i> | Saskatoon | 0.25 | 0.21 | 0.30 |
| <i>Ribes lacustre</i> | Blackgoose berry | 0.12 | 0.13 | 0.37 |
| <i>Potentilla fruticosa</i> | Shrubby cinquefoil | 0.06 | 0.10 | 0.29 |
| Low Shrubs | | | | |
| <i>Juniperus communis</i> | Common juniper | 0.69 | 8.35 | 137.37 |
| <i>Arctostaphylos uva-ursi</i> | Bearberry (Kinnikinnick) | 0.48 | 4.56 | 55.45 |
| <i>Juniperus horizontalis</i> | Creeping juniper | 0.18 | 0.33 | 1.32 |

TABLE 4.7. Frequency, mean cover and variance of common herb species ($f \geq 5\%$; Stand-type I).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|----------------------------------|-----------------------|-----------|----------------|----------|
| Graminoid | | | | |
| <i>Elymus innovatus</i> | Wildrye | 0.80 | 6.21 | 106.17 |
| <i>Calamagrostis rubescens</i> | Pinegrass | 0.31 | 1.23 | 14.32 |
| <i>Koeleria macrantha</i> | Junegrass | 0.23 | 0.69 | 6.09 |
| <i>Agropyron spp.</i> | Wheatgrass | 0.09 | 0.59 | 5.23 |
| <i>Carex spp.</i> | Sedge | 0.28 | 0.29 | 1.26 |
| <i>Festuca saximontana</i> | Rocky Mountain fescue | 0.11 | 0.07 | 0.09 |
| <i>Stipa occidentalis</i> | Stiff needlegrass | 0.06 | 0.05 | 0.09 |
| <i>Muhlenbergia richardsonis</i> | Mat Muhly | 0.06 | 0.02 | 0.01 |
| <i>Poa pratensis</i> | Kentucky bluegrass | 0.09 | 0.01 | 0.00 |
| Dicot Herbs | | | | |
| <i>Aster conspicuus</i> | Showy aster | 0.31 | 1.26 | 11.58 |
| <i>Solidago spathulata</i> | Spikelike goldenrod | 0.37 | 0.35 | 0.53 |
| <i>Fragaria virginia</i> | Wild strawberry | 0.40 | 0.35 | 0.55 |
| <i>Astragalus miser</i> | Timber milk-vetch | 0.31 | 0.35 | 0.67 |
| <i>Achillea millefolium</i> | Yarrow | 0.37 | 0.25 | 0.22 |
| <i>Galium boreale</i> | Northern bedstraw | 0.37 | 0.24 | 0.26 |
| <i>Aster ciliolatus</i> | Lindley's aster | 0.17 | 0.21 | 0.41 |
| <i>Anemone multifida</i> | Cut-leaf anemone | 0.31 | 0.18 | 0.16 |
| <i>Hedysarum sulphurescens</i> | Yellow Hedysarum | 0.16 | 0.17 | 0.44 |
| <i>Vicia americana</i> | American vetch | 0.09 | 0.14 | 0.27 |
| <i>Senecio canus</i> | Woolly groundsel | 0.11 | 0.14 | 0.27 |
| <i>Solidago multifida</i> | Northern goldenrod | 0.09 | 0.11 | 0.21 |
| <i>Taraxicum officinale</i> | Common dandelion | 0.22 | 0.10 | 0.12 |
| <i>Oxytropis splendens</i> | Showy locoweed | 0.11 | 0.10 | 0.18 |
| <i>Artemisia frigida</i> | Pasture sage | 0.16 | 0.09 | 0.09 |
| <i>Apocynum androsaemifolium</i> | Spreading dogbane | 0.09 | 0.09 | 0.14 |
| <i>Viola adunca</i> | Early blue violet | 0.14 | 0.07 | 0.05 |
| <i>Campanula rotandifolia</i> | Common harebell | 0.15 | 0.06 | 0.03 |
| <i>Artemisia dracunculus</i> | Tarragon | 0.06 | 0.05 | 0.04 |
| <i>Oxytropis campestris</i> | Field locoweed | 0.07 | 0.04 | 0.04 |
| <i>Antennaria mycophylla</i> | Rosy pussytoes | 0.12 | 0.03 | 0.02 |
| <i>Veronica americana</i> | American brooklime | 0.12 | 0.02 | 0.01 |
| <i>Pyrola chlorantha</i> | Green wintergreen | 0.06 | 0.02 | 0.01 |
| <i>Aster laevis</i> | Smooth aster | 0.06 | 0.02 | 0.01 |
| Monocot Herb | | | | |
| <i>Allium cernuum</i> | Nodding onion | 0.28 | 0.09 | 0.05 |

TABLE 4.8. Frequency, mean cover and variance of common bryophyte and lichen species ($f \geq 5\%$; Stand-type I).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|-------------------------------|----------------------|-----------|----------------|----------|
| Pleurocarpous mosses | | | | |
| <i>Thuidium abietinum</i> | Wiry fern moss | 0.32 | 1.74 | 27.67 |
| <i>Hypnum revolutum</i> | Rusty claw moss | 0.32 | 0.98 | 7.92 |
| <i>Sanionia uncinata</i> | Sickle moss | 0.27 | 0.78 | 6.33 |
| <i>Pleurozium schreberi</i> | Shrebers's red stem | 0.12 | 0.53 | 7.51 |
| <i>Hylocomium splendens</i> | Stem moss | 0.13 | 0.23 | 0.82 |
| <i>Brachythecium spp.</i> | lawn moss | 0.12 | 0.10 | 0.21 |
| Acrocarpous mosses | | | | |
| <i>Tortula ruralis</i> | Rusty stem moss | 0.49 | 0.83 | 2.87 |
| <i>Orthotrichum speciosum</i> | Hooded moss | 0.12 | 0.08 | 0.08 |
| Lichens | | | | |
| <i>Cladonia spp.</i> | Club lichen | 0.43 | 0.46 | 1.44 |
| <i>Peltigera canina</i> | Dog Pelt lichen | 0.31 | 0.44 | 1.03 |
| <i>Peltigera aphthosa</i> | Freckled Pelt lichen | 0.11 | 0.23 | 1.04 |

TABLE 4.9. Relative frequency of trees in sub-type Ia.

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.47 | 0.32 | 0.41 | 0.47 |
| <i>Picea glauca</i> | White Spruce | 0.18 | 0.00 | 0.03 | 0.03 | 0.06 | 0.09 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.12 | 0.06 | 0.06 | 0.03 | | 0.03 |
| <i>Pinus flexilis</i> | Limber pine | 0.03 | | | | 0.03 | |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.09 | | 0.06 | | 0.06 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.09 | 0.03 | | | 0.03 | 0.06 |

TABLE 4.10. Relative frequency of trees in sub-type Ib.

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.84 | 0.59 | 0.56 | 0.67 | 0.85 |
| <i>Picea glauca</i> | White Spruce | 0.59 | 0.20 | 0.33 | 0.18 | 0.16 | 0.28 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.28 | 0.11 | 0.13 | 0.08 | 0.07 | 0.07 |
| <i>Pinus flexilis</i> | Limber pine | 0.05 | 0.03 | 0.03 | 0.02 | 0.02 | |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.02 | | | | 0.02 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.13 | 0.02 | 0.07 | 0.08 | 0.08 | 0.07 |



Figure 4.14. (above) Mixed Aspen/Douglas-fir/ and white spruce site located near Cory Pass, Banff. Note the spatial distribution of the three different 'ecosites' is strongly influenced by topography. (Bottom) Douglas-fir mix stand composed of young aspen and spruce (ST IIa).



Figure 4.15. 120 year old mesic Douglas-fir stand located near Johnson lake, Banff National Park.

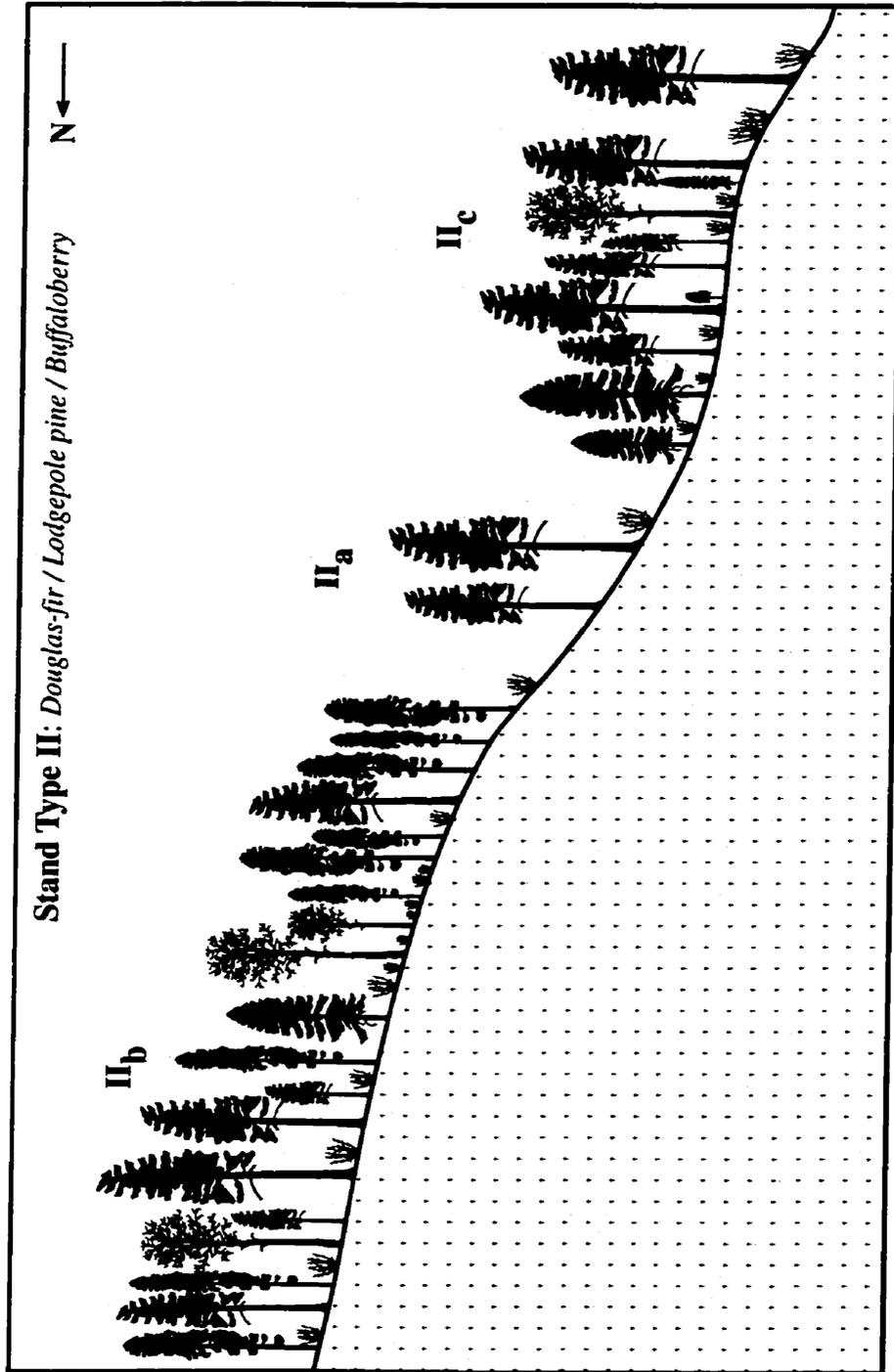


Figure 4.16. Physiognomic profile for stand type II (*IIa*, *IIb* and *IIc*). Sub-types are represented based on mean cover, density and slope estimates.

STAND TYPE II (DOUGLAS-FIR/LOGEPOLE PINE/BUFFALOBERRY), n= 80.

Table 4.11 Relative frequency

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.91 | 0.66 | 0.61 | 0.54 | 0.73 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.86 | 0.73 | 0.35 | 0.26 | 0.05 | 0.09 |
| <i>Picea glauca</i> | White Spruce | 0.64 | 0.19 | 0.20 | 0.21 | 0.20 | 0.21 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.05 | | | | 0.05 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.39 | 0.15 | 0.16 | 0.01 | 0.18 | 0.21 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.10 | | 0.03 | | 0.09 | 0.01 |
| <i>Salix</i> spp. | Willow | 0.05 | | 0.03 | 0.03 | 0.01 | |
| <i>Betula papyrifera</i> | Paper Birch | 0.04 | 0.01 | 0.03 | | 0.01 | |

Table 4.12 Mean Density Per 100 m² (Stand-type II).

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|-------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 22.01 | 3.30 | 3.23 | 2.40 | 4.86 | 8.23 |
| <i>Pinus contorta</i> | Lodgepole pine | 5.10 | 3.39 | 1.10 | 0.39 | 0.06 | 0.16 |
| <i>Picea glauca</i> | White Spruce | 1.89 | 0.31 | 0.34 | 0.35 | 0.44 | 0.45 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.10 | | | | 0.10 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 2.91 | 0.25 | 0.38 | 0.01 | 1.08 | 1.20 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.79 | | 0.03 | | 0.75 | 0.01 |
| <i>Betula papyrifera</i> | Paper Birch | 0.18 | 0.09 | 0.08 | | 0.01 | |
| <i>Salix</i> spp. | Willow | 0.06 | | 0.03 | 0.03 | 0.01 | |
| | | 33.04 | 7.34 | 5.16 | 3.18 | 7.31 | 10.05 |

Table 4.13 Mean Basal Area Per Plot (m² per 100 m²; Stand-type II).

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|-------|-------|-------|-------|-------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 0.347 | 0.283 | 0.023 | 0.003 | 0.010 | 0.029 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.109 | 0.099 | 0.008 | 0.001 | | |
| <i>Picea glauca</i> | White Spruce | 0.012 | 0.009 | 0.003 | | | |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.015 | 0.007 | 0.006 | | 0.001 | 0.001 |
| <i>Betula papyrifera</i> | Paper Birch | 0.002 | 0.002 | | | | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.001 | | | | 0.001 | |
| <i>Salix</i> spp. | Willow | | | | | | |
| | | 0.49 | 0.40 | 0.04 | 0.00 | 0.01 | 0.03 |

* Values ≤ 0.0005 are indicated by a slash (-).

TABLE 4.14. Frequency, mean cover and variance of tree species (Stand-type II).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|---|------------------------|-----------|----------------|----------|
| Conifers | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 38.21 | 300.12 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.86 | 13.98 | 147.08 |
| <i>Picea glauca</i> | White Spruce | 0.64 | 4.53 | 77.46 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.05 | 0.14 | 0.42 |
| Deciduous | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.39 | 2.42 | 24.65 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.10 | 0.74 | 6.49 |
| <i>Betula papyrifera</i> | Paper Birch | 0.05 | 0.20 | 1.55 |
| <i>Salix</i> spp | Willow | 0.04 | 0.04 | 0.03 |

TABLE 4.15. Frequency, mean cover and variance of common shrub species ($f \geq 5\%$; Stand-type II).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|--------------------------------|-----------------------------|-----------|----------------|----------|
| Tall Shrubs | | | | |
| <i>Shepherdia canadensis</i> | Buffalo berry (Soopolallie) | 0.81 | 4.43 | 29.23 |
| <i>Rosa acicularis</i> | Prickly rose | 0.80 | 1.56 | 3.29 |
| <i>Spiraea betulifolia</i> | Birched-leaved spirea | 0.71 | 1.10 | 1.99 |
| <i>Amelanchier alnifolia</i> | Saskatoon | 0.33 | 0.32 | 0.33 |
| <i>Symphoricarpos albus</i> | Common snowberry | 0.33 | 0.83 | 5.21 |
| <i>Lonicera utahensis</i> | Utah honeysuckle | 0.21 | 0.47 | 1.52 |
| <i>Ribes lacustre</i> | Blackgoose berry | 0.08 | 0.05 | 0.04 |
| <i>Viburnum edule</i> | High-brush cranberry | 0.06 | 0.08 | 0.14 |
| Low Shrubs | | | | |
| <i>Juniperus communis</i> | Common juniper | 0.74 | 5.63 | 83.66 |
| <i>Linnaea borealis</i> | Twinflower | 0.60 | 3.26 | 29.88 |
| <i>Arctostaphylos uva-ursi</i> | Bearberry (Kinnikinnick) | 0.50 | 2.70 | 31.22 |
| <i>Chimaphila umbellata</i> | Princes-pine | 0.13 | 0.15 | 0.32 |
| <i>Juniperus horizontalis</i> | Creeping juniper | 0.10 | 0.12 | 0.24 |

TABLE 4.16. Frequency, mean cover and variance of common herb species ($f \geq 5\%$; Stand-type II).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|-----------------------------------|----------------------------|-----------|----------------|----------|
| Graminoid | | | | |
| <i>Calamagrostis rubescens</i> | Pinegrass | 0.85 | 9.37 | 101.88 |
| <i>Elymus innovatus</i> | Wildrye | 0.76 | 7.17 | 94.84 |
| <i>Carex spp.</i> | Sedge | 0.21 | 0.13 | 0.12 |
| <i>Carex concinnoides</i> | Northwestern sedge | 0.08 | 0.05 | 0.06 |
| Dicot Herbs | | | | |
| <i>Fragaria virginiana</i> | Wild strawberry | 0.75 | 1.49 | 4.85 |
| <i>Aster conspicuus</i> | Showy aster | 0.65 | 2.45 | 14.57 |
| <i>Hedysarum sulphurescens</i> | Yellow Hedysarum | 0.45 | 0.56 | 0.74 |
| <i>Aster ciliolatus</i> | Lindley's aster | 0.41 | 0.87 | 3.07 |
| <i>Pyrola chlorantha</i> | Green wintergreen | 0.36 | 0.29 | 0.29 |
| <i>Orthilia secunda</i> | One-sided wintergreen | 0.33 | 0.27 | 0.32 |
| <i>Achillea millefolium</i> | Yarrow | 0.28 | 0.18 | 0.22 |
| <i>Astragalus miser</i> | Timber milk-vetch | 0.26 | 0.28 | 0.84 |
| <i>Arnica cordifolia</i> | Heart-leaved arnica | 0.19 | 0.64 | 3.99 |
| <i>Viola adunca</i> | Early blue violet | 0.19 | 0.09 | 0.05 |
| <i>Galium boreale</i> | Northern bedstraw | 0.18 | 0.12 | 0.22 |
| <i>Lathyrus ochroleucus</i> | Creamy peavine | 0.16 | 0.14 | 0.18 |
| <i>Solidago spathulata</i> | Spikelike goldenrod | 0.16 | 0.07 | 0.06 |
| <i>Goodyera oblongifolia</i> | Rattlesnake plantain | 0.15 | 0.12 | 0.20 |
| <i>Anemone multifida</i> | Cut-leaf anemone | 0.14 | 0.04 | 0.03 |
| <i>Veronica americana</i> | American brooklime | 0.10 | 0.03 | 0.01 |
| <i>Vicia americana</i> | American vetch | 0.09 | 0.15 | 0.40 |
| <i>Goodyera repens</i> | Dwarf rattlesnake plantain | 0.09 | 0.05 | 0.03 |
| <i>Taraxicum officinale</i> | Common dandelion | 0.08 | 0.02 | 0.00 |
| <i>Thalictrum occidentale</i> | Western meadowrue | 0.08 | 0.38 | 5.39 |
| <i>Cornus canadensis</i> | Bunchberry | 0.08 | 0.19 | 0.90 |
| <i>Aster laevis</i> | Smooth aster | 0.06 | 0.11 | 0.52 |
| <i>Epilobium angustifolium</i> | Fireweed | 0.06 | 0.02 | 0.01 |
| <i>Solidago multifida</i> | Northern goldenrod | 0.06 | 0.04 | 0.03 |
| <i>Trifolium repens</i> | White clover | 0.06 | 0.10 | 0.25 |
| <i>Clematis occidentalis</i> | Blue clematis | 0.06 | 0.05 | 0.07 |
| Monocot Herb | | | | |
| <i>Allium cernuum</i> | Nodding onion | 0.15 | 0.10 | 0.14 |
| <i>Disporum trachycarpum</i> | Rough-fruited fairybells | 0.11 | 0.10 | 0.12 |
| <i>Lilium philadelphicum</i> | Wood lily | 0.08 | 0.05 | 0.04 |
| <i>Zigadenus elegans</i> | Mountain death-camas | 0.06 | 0.04 | 0.03 |
| <i>Smilacina racemosa</i> | False soloman's seal | 0.06 | 0.13 | 0.33 |
| <i>Sirempotopus amplexifolius</i> | Bronze bells | 0.06 | 0.05 | 0.04 |

TABLE 4.17. Frequency, mean cover and variance of common bryophyte and lichen species ($f \geq 5\%$; Stand-type II)

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|----------------------------------|---------------------|-----------|----------------|----------|
| Pleurocarpous mosses | | | | |
| <i>Pleurozium schreberi</i> | Shrebers's red stem | 0.75 | 6.90 | 137.19 |
| <i>Hylocomium splendens</i> | Stem moss | 0.64 | 8.10 | 144.63 |
| <i>Sanionia uncinata</i> | Sickle moss | 0.34 | 0.41 | 0.96 |
| <i>Brachythecium spp.</i> | Lawn moss | 0.31 | 0.19 | 0.19 |
| <i>Hypnum revolutum</i> | Rusty claw moss | 0.24 | 0.46 | 3.25 |
| <i>Thuidium abietinum</i> | Wiry fern moss | 0.23 | 0.67 | 3.83 |
| <i>Dicranum scoparium</i> | Broom moss | 0.19 | 0.27 | 0.75 |
| <i>Ptilium crista-castrensis</i> | Knight's plume | 0.14 | 0.23 | 0.91 |
| <i>Rhytidadelphus triquetrus</i> | Hanging basket moss | 0.11 | 0.10 | 0.11 |
| <i>Dicranum fuscescens</i> | | 0.09 | 0.13 | 0.21 |
| <i>Brachythecium albicans</i> | Common lawn moss | 0.08 | 0.06 | 0.08 |
| Acrocarpous mosses | | | | |
| <i>Tortula ruralis</i> | Rusty stem moss | 0.28 | 0.77 | 3.96 |
| <i>Orthotrichum speciosum</i> | Hooded moss | 0.09 | 0.05 | 0.10 |
| Lichens | | | | |
| <i>Peltigera canina</i> | Dog pelt lichen | 0.50 | 0.88 | 3.07 |
| <i>Peltigera aphthosa</i> | Freckle pelt lichen | 0.46 | 0.72 | 1.45 |
| <i>Cladonia spp.</i> | Club lichen | 0.41 | 0.37 | 0.67 |
| <i>Peltigera spp.</i> | Pelt Lichen | 0.08 | 0.13 | 0.32 |

TABLE 4.18. Relative frequency of trees in sub-type IIa

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|--------|-------|-----|-----|-----|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.9 | 0.5 | 0.5 | 0.5 | 0.7 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.94 | 0.8 | 0.4 | 0.4 | 0.1 | 0.1 |
| <i>Picea glauca</i> | White Spruce | 0.65 | 0.2 | 0.2 | 0.2 | 0.3 | 0.2 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.25 | 0.0625 | 0.125 | - | 0.1 | 0.2 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |

TABLE 4.19. Relative frequency of trees in sub-type IIb

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.90 | 0.77 | 0.67 | 0.63 | 0.83 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.73 | 0.57 | 0.23 | 0.20 | | 0.07 |
| <i>Picea glauca</i> | White Spruce | 0.63 | 0.27 | 0.23 | 0.17 | 0.07 | 0.17 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | 0.13 | | | | 0.13 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.67 | 0.27 | 0.27 | 0.03 | 0.40 | 0.37 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.23 | | 0.07 | | 0.20 | 0.03 |
| <i>Salix</i> spp. | Willow | 0.10 | | 0.07 | 0.07 | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.10 | 0.03 | 0.07 | | 0.03 | |

TABLE 4.20 Relative frequency of trees in sub-type IIc

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.83 | 0.78 | 0.50 | 0.61 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.94 | 0.78 | 0.50 | 0.11 | 0.00 | 0.06 |
| <i>Picea glauca</i> | White Spruce | 0.61 | 0.11 | 0.11 | 0.28 | 0.17 | 0.33 |
| <i>Juniperus scopulorum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.17 | 0.11 | 0.06 | | | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.06 | | | | 0.06 | |
| <i>Salix</i> spp. | Willow | 0.06 | | | | 0.06 | |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |

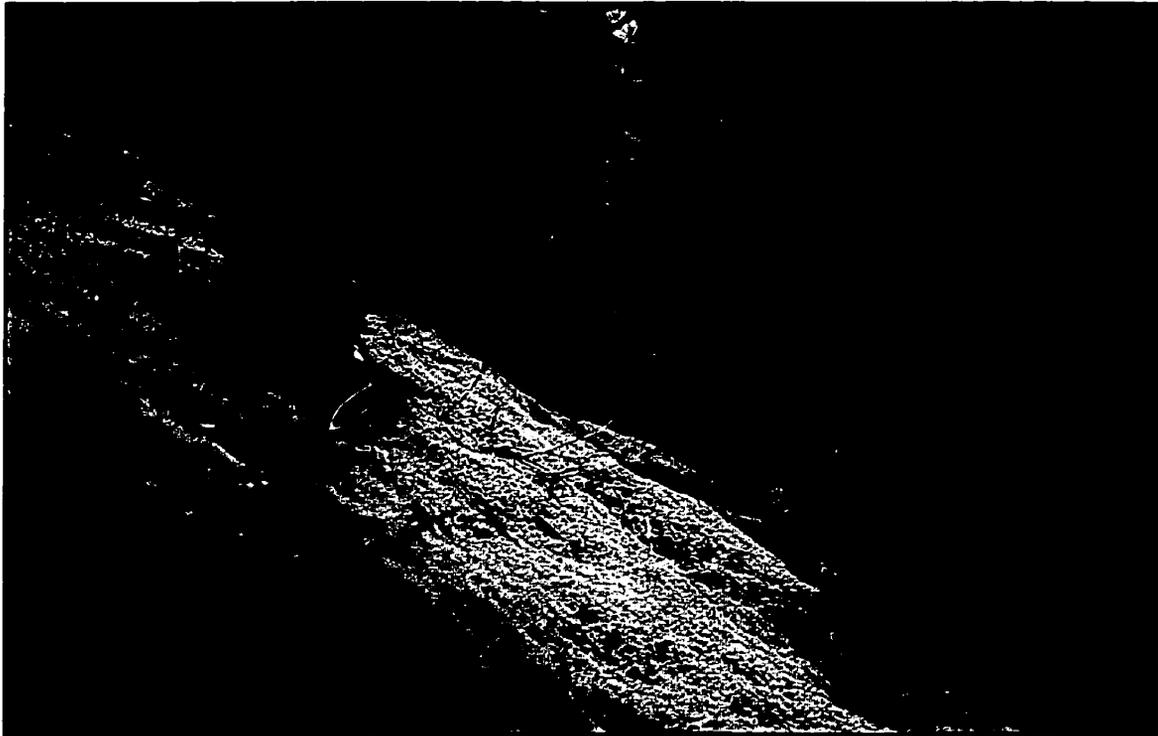


Figure 4.17 Stand-type IIIa, located near Morboerly flats in Jasper National Park. Ground cover was characterized by a thick organic layer (around 25cm thick) composed of feather moss, woody material and a well developed humic layer. The dominant moss was *Hylocomium splendens* which had a mean cover of 90% followed by *Thuidium abitinum* which was only common along ridges and upper slopes. Parasitic plants such as *Commandra livida* were present throughout the stand. Douglas-fir seedlings were only encountered on the upper slopes, individuals rarely exceeded 0.35m in height and 20 years of age. The canopy had a maximum age of 205 years (based on the oldest tree). Evidence of Douglas-fir bark beetle mortality and damage was common on mature trees throughout the sites.

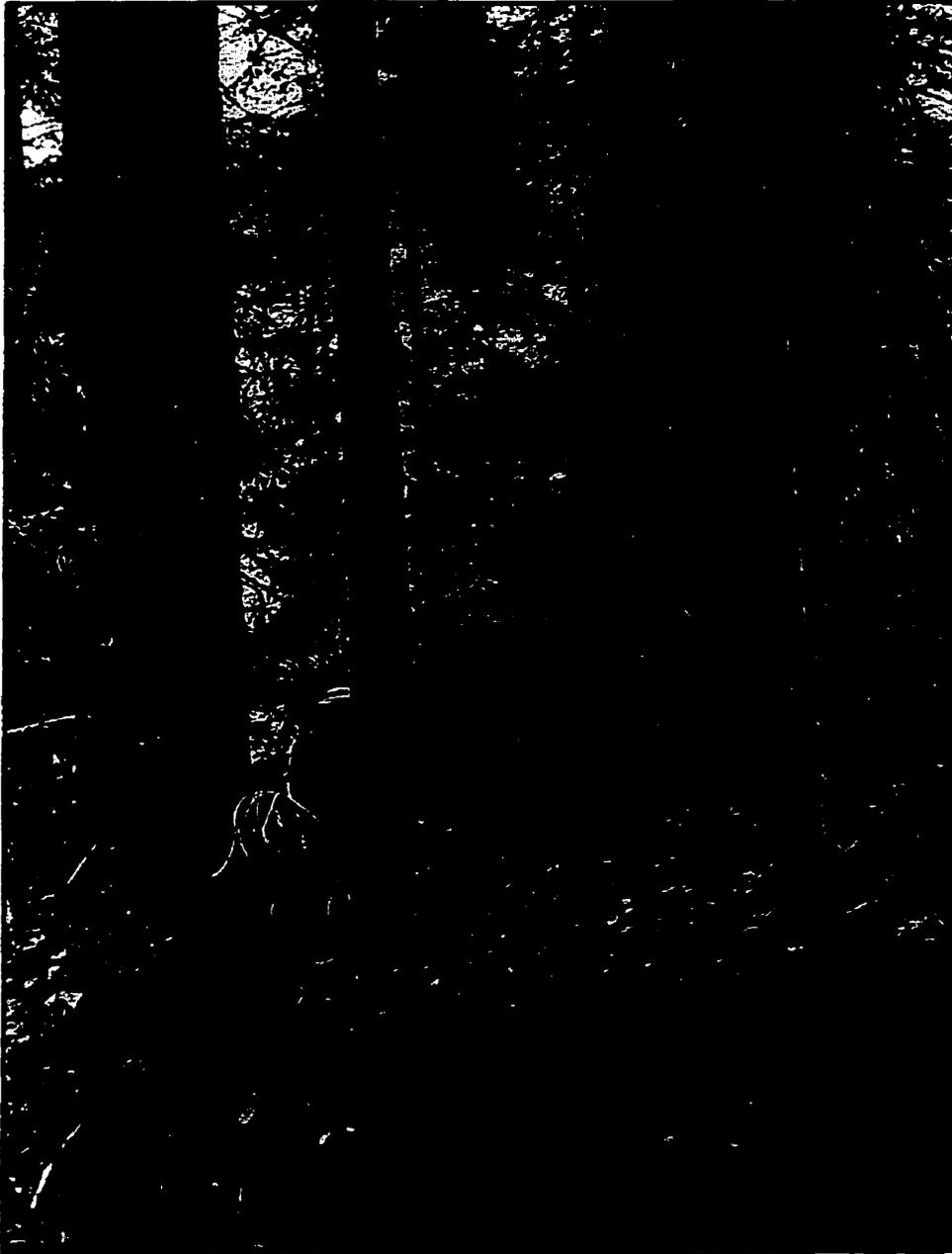


Figure 4.18 Stand-type IIIb, located in the Kicking Horse valley (Yoho National Park). The stand was co-dominated with subalpine fir, western redcedar, and white spruce. The forest floor was characterized by a thick moss layer composed of 90% cover of *Hylocomium splendens*.

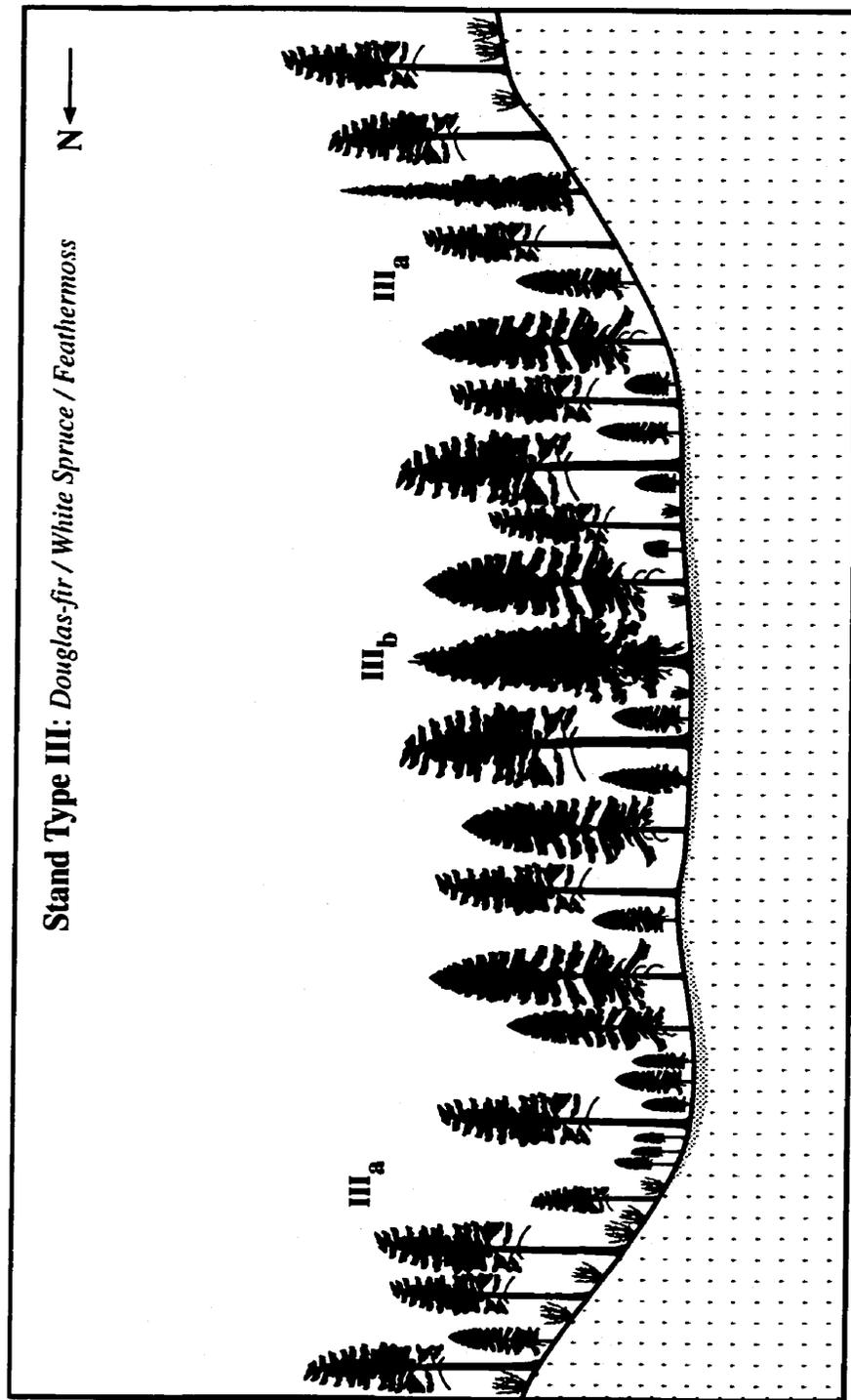


Figure 4.19 . Physiognomic profile for stand type III (*IIIa* and *IIIc*). Sub-types are represented based on mean cover, density and slope estimates.

STAND TYPE III (DOUGLAS-FIR/WHITE SPRUCE/FEATHERMOSS), $n = 45$

Table 4.21 Relative frequency

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 0.82 | 0.67 | 0.47 | 0.67 | 0.67 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.44 | 0.33 | 0.56 | 0.96 |
| <i>Abies bifolia</i> | Subalpine fir | 0.38 | 0.16 | 0.16 | 0.31 | 0.31 | 0.20 |
| <i>Thuja plicata</i> | Western red cedar | 0.18 | 0.07 | 0.09 | 0.04 | 0.07 | 0.11 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.18 | 0.16 | | 0.02 | | 0.02 |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.16 | | 0.04 | 0.09 | 0.09 | 0.02 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.04 | | | 0.04 | 0.04 | |
| <i>Salix</i> spp. | Willow | 0.04 | | | | 0.04 | |
| <i>Populus tremulooides</i> | Trembling aspen | 0.02 | | | | | 0.02 |

Table 4.22 Mean Density Per 100 m² (Stand-type III).

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|-------|-------|-------|-------|-------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 24.13 | 4.60 | 1.13 | 0.71 | 2.62 | 15.07 |
| <i>Picea glauca</i> | White Spruce | 13.22 | 2.40 | 2.13 | 1.47 | 3.33 | 3.89 |
| <i>Abies bifolia</i> | Subalpine fir | 6.91 | 0.96 | 0.56 | 1.20 | 2.82 | 1.38 |
| <i>Thuja plicata</i> | Western red cedar | 1.00 | 0.133 | 0.156 | 0.067 | 0.222 | 0.422 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.33 | 0.29 | - | 0.02 | - | 0.02 |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.49 | | 0.07 | 0.16 | 0.20 | 0.07 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.20 | | | 0.04 | 0.16 | |
| <i>Salix</i> spp. | Willow | 0.04 | | | | 0.04 | |
| <i>Populus tremulooides</i> | Trembling aspen | 0.02 | | | | | 0.02 |
| | | 46.35 | 8.38 | 4.04 | 3.67 | 9.40 | 20.87 |

Table 4.23 Mean Basal Area Per Plot (m² per 100 m²; Stand-type III).

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|-------|-------|-------|-------|-------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 0.4632 | 0.412 | 0.013 | 0.001 | 0.001 | 0.036 |
| <i>Picea glauca</i> | White Spruce | 0.1387 | 0.111 | 0.019 | 0.002 | 0.003 | 0.004 |
| <i>Abies bifolia</i> | Subalpine fir | 0.0341 | 0.026 | 0.003 | 0.002 | 0.003 | 0.001 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.0079 | 0.008 | | - | - | - |
| <i>Thuja plicata</i> | Western red cedar | 0.0050 | 0.003 | 0.001 | - | - | - |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.0009 | | - | - | - | - |
| <i>Acer glabrum</i> | Rocky Mountain Maple | - | | | - | - | - |
| <i>Salix</i> spp. | Willow | - | | | | - | - |
| <i>Populus tremulooides</i> | Trembling aspen | - | | | | | - |
| | | 0.65 | 0.56 | 0.04 | 0.00 | 0.01 | 0.04 |

* Values ≤ 0.0005 are indicated by a slash (-).

TABLE 4.24. Frequency, mean cover and variance of tree species (Stand-type III).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|---|----------------------|-----------|----------------|----------|
| Conifers | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 21.67 | 182.22 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 31.84 | 166.22 |
| <i>Abies bifolia</i> | Subalpine fir | 0.38 | 8.89 | 247.77 |
| <i>Thuja plicata</i> | Western red cedar | 0.18 | 2.72 | 73.08 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.18 | 0.83 | 5.47 |
| Deciduous | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.16 | 0.74 | 10.67 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.04 | 0.46 | 2.37 |
| <i>Salix</i> spp. | Willow | 0.04 | 0.18 | 0.94 |
| <i>Populus tremuloides</i> | Trembling aspen | 0.02 | 0.02 | 0.02 |

TABLE 4.25. Frequency, mean cover and variance of common shrub species ($f \geq 5\%$; Stand-type III).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|------------------------------|-----------------------------|-----------|----------------|----------|
| Tall Shrubs | | | | |
| <i>Rosa acicularis</i> | Prickly rose | 0.69 | 1.18 | 1.49 |
| <i>Symphoricarpos albus</i> | Common snowberry | 0.51 | 0.58 | 0.68 |
| <i>Amelanchier alnifolia</i> | Saskatoon | 0.42 | 0.43 | 0.50 |
| <i>Spiraea betulifolia</i> | Birched-leaved spirea | 0.40 | 0.46 | 0.69 |
| <i>Lonicera utahensis</i> | Utah honeysuckle | 0.33 | 0.67 | 3.22 |
| <i>Shepherdia canadensis</i> | Buffalo berry (Soopolallie) | 0.29 | 1.21 | 5.92 |
| <i>Ribes lacustre</i> | Blackgoose berry | 0.27 | 0.25 | 0.21 |
| <i>Lonicera ciliosa</i> | Orange honeysuckle | 0.20 | 0.22 | 0.42 |
| <i>Viburnum edule</i> | High-brush cranberry | 0.20 | 0.31 | 0.67 |
| <i>Menziesia ferruginea</i> | False-azalea | 0.13 | 0.23 | 0.63 |
| <i>Lonicera involucrata</i> | Honeysuckle | 0.07 | 0.07 | 0.08 |
| Low Shrubs | | | | |
| <i>Linnaea borealis</i> | Twainflower | 0.80 | 5.28 | 46.00 |
| <i>Juniperus communis</i> | Common juniper | 0.53 | 2.86 | 31.57 |
| <i>Chimaphila umbellata</i> | Princes-pine | 0.07 | 0.06 | 0.07 |
| <i>Vaccinium scoparium</i> | Grouseberry | 0.07 | 0.11 | 0.19 |

TABLE 4.26. Frequency, mean cover and variance of common herb species ($f \geq 5\%$; Stand-type III).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|---------------------------------|----------------------------|-----------|----------------|----------|
| Graminoid | | | | |
| <i>Elymus innovatus</i> | Wildrye | 0.58 | 1.52 | 4.33 |
| <i>Carex spp.</i> | sedge | 0.36 | 0.20 | 0.17 |
| <i>Calamagrostis rubescens</i> | Pinegrass | 0.33 | 0.79 | 2.35 |
| <i>Oryzopsis asperifolia</i> | Rough-leaved ricegrass | 0.13 | 0.41 | 2.76 |
| Dicot Herbs | | | | |
| <i>Pyrola chlorentia</i> | Green wintergreen | 0.51 | 0.28 | 0.14 |
| <i>Orthilia secunda</i> | One-sided wintergreen | 0.51 | 0.47 | 0.60 |
| <i>Aster conspicuus</i> | Showy aster | 0.47 | 2.64 | 27.25 |
| <i>Fragaria virginiana</i> | Wild strawberry | 0.38 | 0.36 | 0.32 |
| <i>Comandra umbellata</i> | Pale commandra | 0.38 | 0.28 | 0.31 |
| <i>Goodyera repens</i> | Dwarf rattlesnake plantain | 0.29 | 0.14 | 0.08 |
| <i>Cornus canadensis</i> | Bunchberry | 0.29 | 1.21 | 9.77 |
| <i>Aster ciliolatus</i> | Lindley's aster | 0.27 | 0.17 | 0.17 |
| <i>Galium boreale</i> | Northern bedstraw | 0.13 | 0.04 | 0.02 |
| <i>Goodyera oblongifolia</i> | Rattlesnake plantain | 0.13 | 0.21 | 0.46 |
| <i>Aralia nudicaulis</i> | Wild sarsaparilla | 0.09 | 0.47 | 6.01 |
| <i>Galium triflorum</i> | Sweet-scented bedstraw | 0.09 | 0.12 | 0.45 |
| <i>Mitella nuda</i> | Common mitrewort | 0.09 | 0.16 | 0.39 |
| <i>Osmorhiza chilensis</i> | Mountain sweet-cicely | 0.07 | 0.05 | 0.06 |
| Monocot Herb | | | | |
| <i>Calypso bulbosa</i> | Fairyflipper | 0.13 | 0.07 | 0.06 |
| <i>Maianthemum canadensis</i> | Wild lily-of-the-valley | 0.09 | 0.02 | 0.01 |
| <i>Smilacina racemosa</i> | False soloman's seal | 0.09 | 0.12 | 0.23 |
| <i>Disporum trachycarpum</i> | Rough-fruited fairybells | 0.07 | 0.02 | 0.00 |
| <i>Streptopus amplexifolius</i> | Clasping twisted stack | 0.07 | 0.06 | 0.09 |

TABLE 4.27. Frequency, mean cover and variance of common bryophyte and lichen species ($f \geq 5\%$; Stand-type III).

| Species | Common name | Frequency | Mean Cover (%) | Variance |
|-----------------------------------|-----------------------|-----------|----------------|----------|
| Pleurocarpous mosses | | | | |
| <i>Hylocomium splendens</i> | Stem moss | 1.00 | 52.26 | 773.77 |
| <i>Pleurozium schreberi</i> | Shrebers's red stem | 0.47 | 6.22 | 98.13 |
| <i>Thuidium abietinum</i> | Wiry fern moss | 0.36 | 3.21 | 49.41 |
| <i>Ptilium crista-castrensis</i> | Knight's plume | 0.24 | 0.81 | 4.64 |
| <i>Hypnum revolutum</i> | Rusty claw moss | 0.20 | 0.36 | 0.91 |
| <i>Rhytidiadelphus triquetrus</i> | Hanging basket moss | 0.18 | 0.53 | 2.52 |
| <i>Saniona uncinata</i> | Sickle moss | 0.13 | 0.08 | 0.06 |
| Acrocarpous mosses | | | | |
| <i>Tortula ruralis</i> | Rusty stem moss | 0.22 | 0.25 | 0.33 |
| <i>Timmia austriaca</i> | False haircap moss | 0.16 | 0.18 | 0.31 |
| <i>Dicranum scoparium</i> | Broom moss | 0.11 | 0.31 | 1.53 |
| <i>Mnium spinulosum</i> | Flapper moss | 0.07 | 0.04 | 0.05 |
| <i>Plagiomnium drummondii</i> | Drummond's leafy moss | 0.07 | 0.09 | 0.18 |
| <i>Polytrichum juniperinum</i> | Juniper haircap moss | 0.07 | 0.05 | 0.05 |
| Liverwort | | | | |
| <i>Barbilophozia spp.</i> | Barbilophozia | 0.13 | 0.21 | 1.26 |
| Lichens | | | | |
| <i>Peltigera aphthosa</i> | freckled pelt | 0.78 | 2.01 | 5.17 |
| <i>Cladonia spp.</i> | club lichen | 0.31 | 0.21 | 0.31 |
| <i>Peltigera canina</i> | dog pelt | 0.18 | 0.41 | 1.57 |

TABLE 4.28. Relative frequency of trees in sub-type IIIa

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 0.81 | 0.65 | 0.52 | 0.68 | 0.71 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.0 | 0.6 | 0.4 | 0.5 | 0.9 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.16 | 0.1 | | | | |
| <i>Abies bifolia</i> | Subalpine fir | | | | | | |
| <i>Thuja plicata</i> | Western red cedar | | | | | | |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.16 | | 0.10 | 0.06 | 0.03 | |
| <i>Salix</i> spp. | Willow | 0.06 | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.03 | | | | | 0.03 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |

TABLE 4.29. Relative frequency of trees in sub-type IIIb

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 0.86 | 0.71 | 0.36 | 0.64 | 0.50 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.93 | 0.14 | 0.21 | 0.64 | 0.93 |
| <i>Abies bifolia</i> | Subalpine fir | 0.38 | 0.50 | 0.50 | 0.79 | 0.86 | 0.57 |
| <i>Thuja plicata</i> | Western red cedar | 0.18 | 0.21 | 0.29 | 0.14 | 0.21 | 0.36 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.18 | 0.21 | | 0.07 | | 0.00 |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.16 | | 0.07 | 0.07 | 0.14 | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.04 | | | 0.14 | 0.14 | |
| <i>Salix</i> spp. | Willow | 0.04 | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.02 | | | | | - |

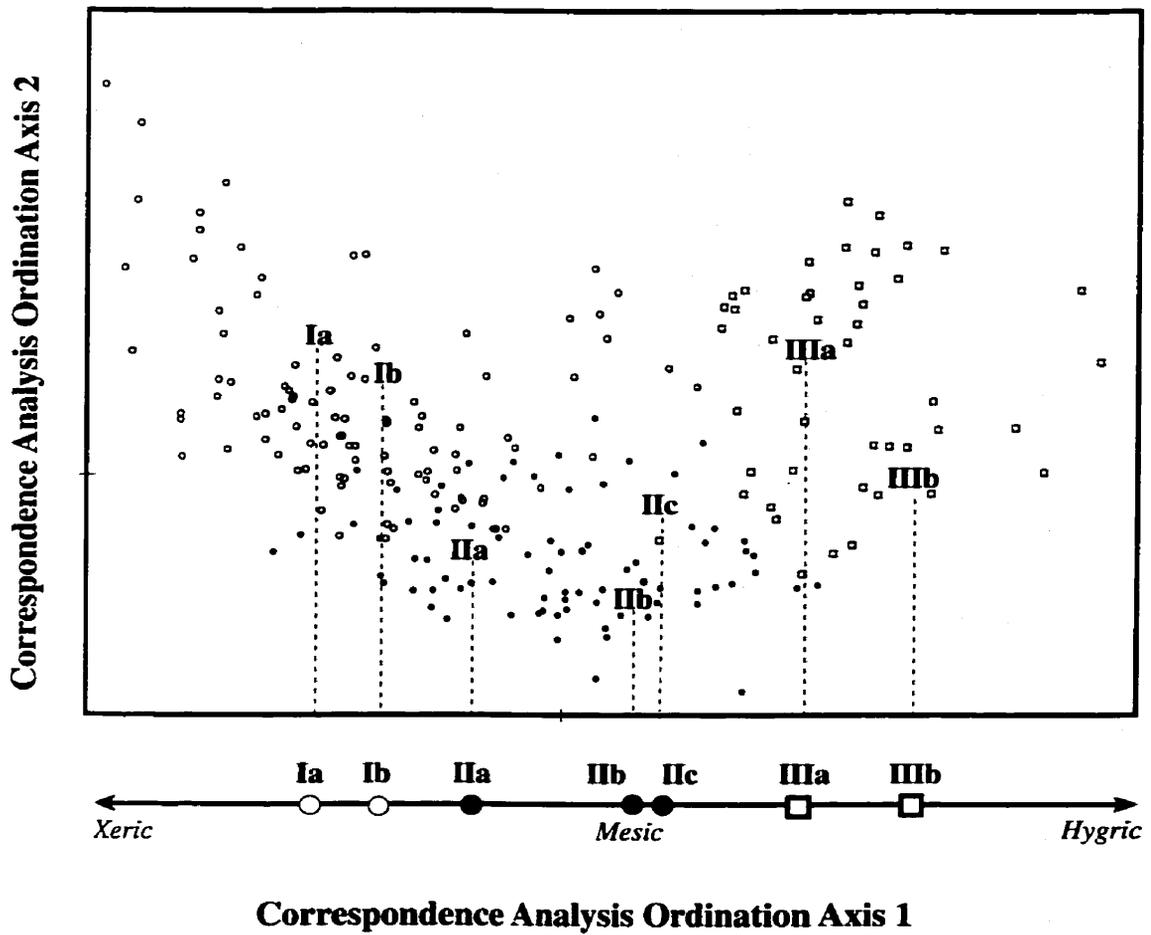
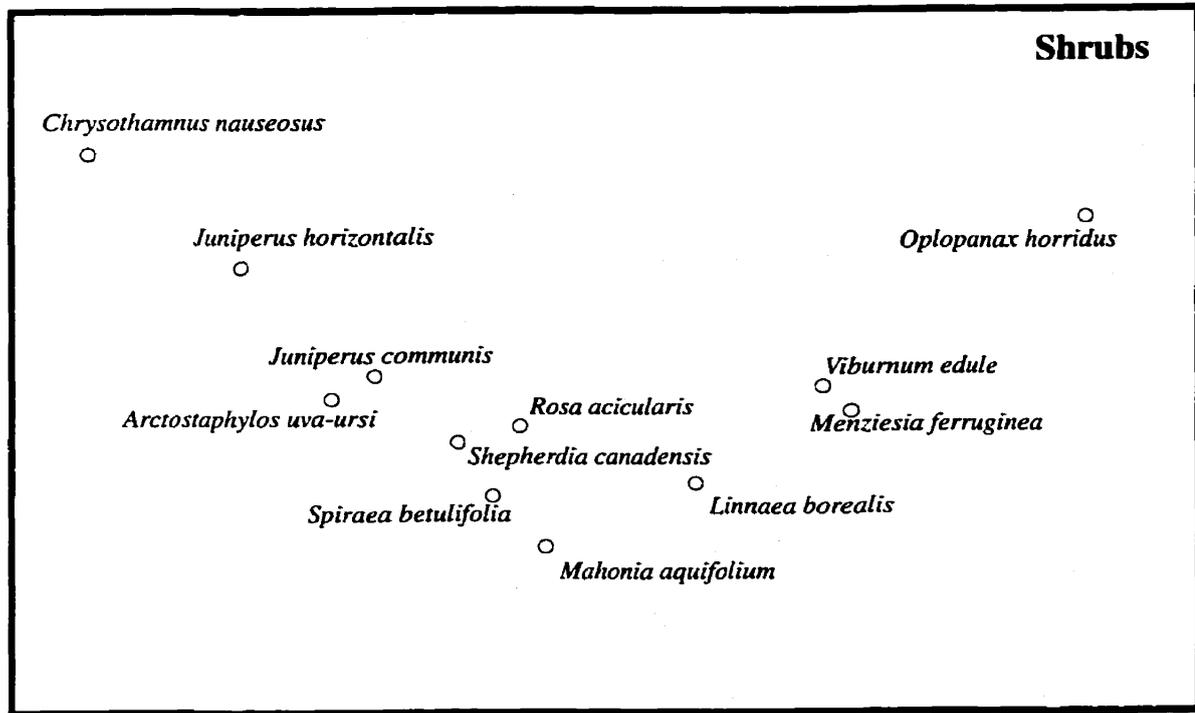
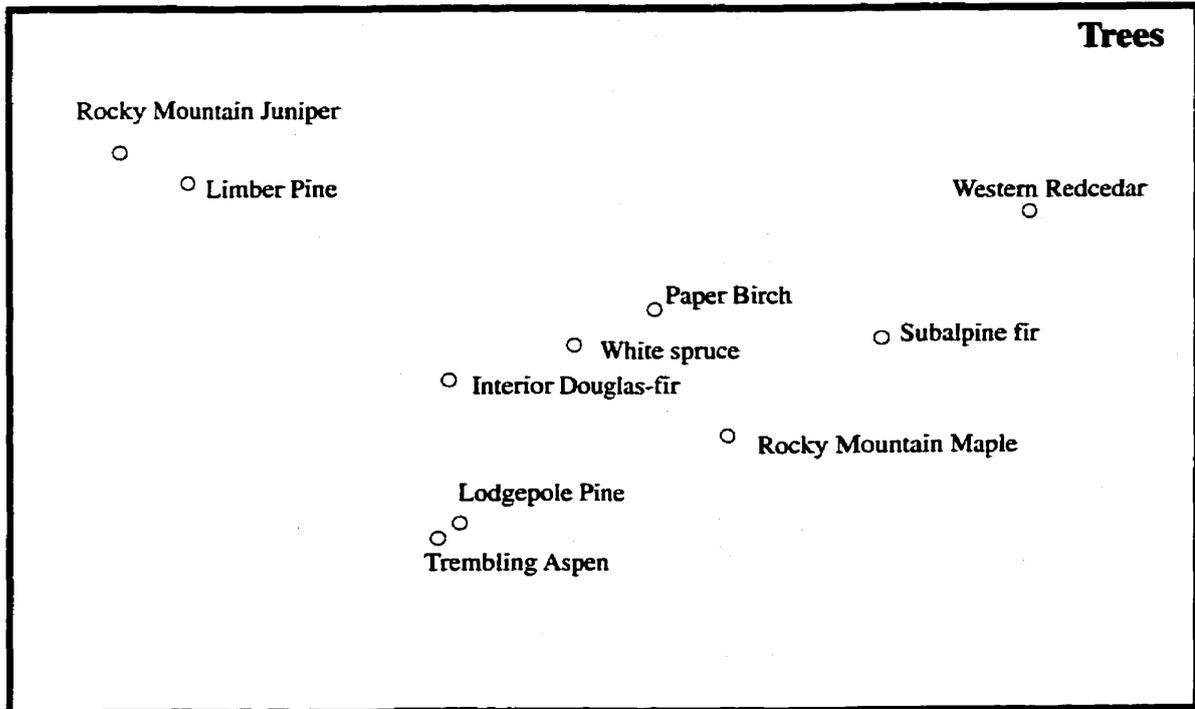


Figure 4.20. Correspondence analysis (CA) ordination of the 220 plots. Symbols indicate stand type affinities. The projected vertical lines represent the mean eigenvector location of each stand type along the first ordination axis.

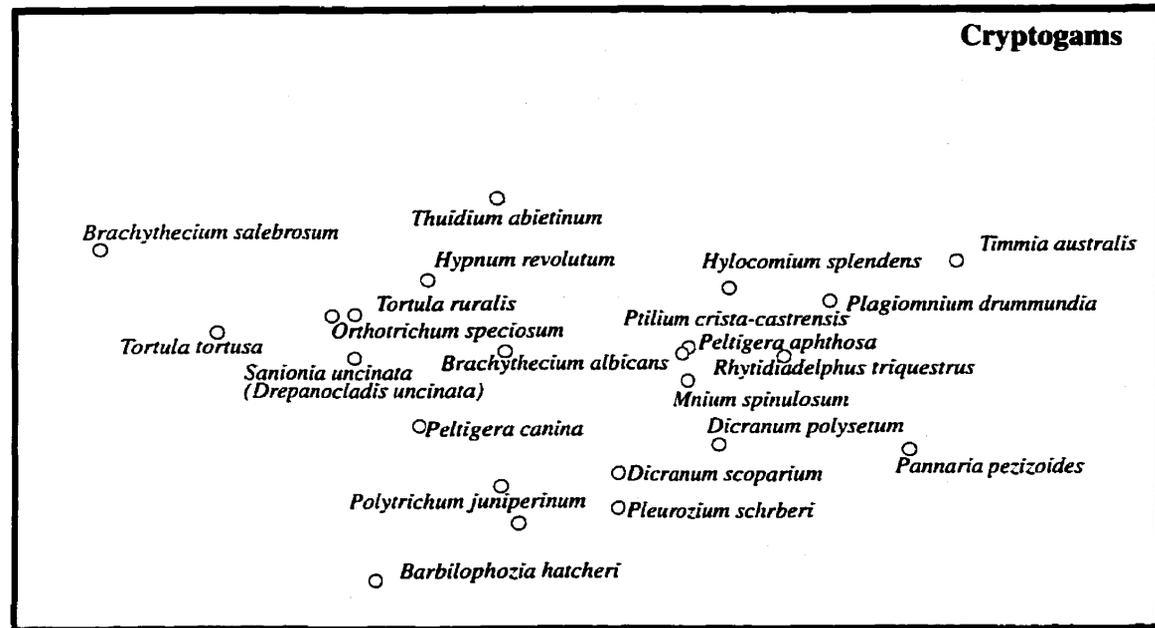
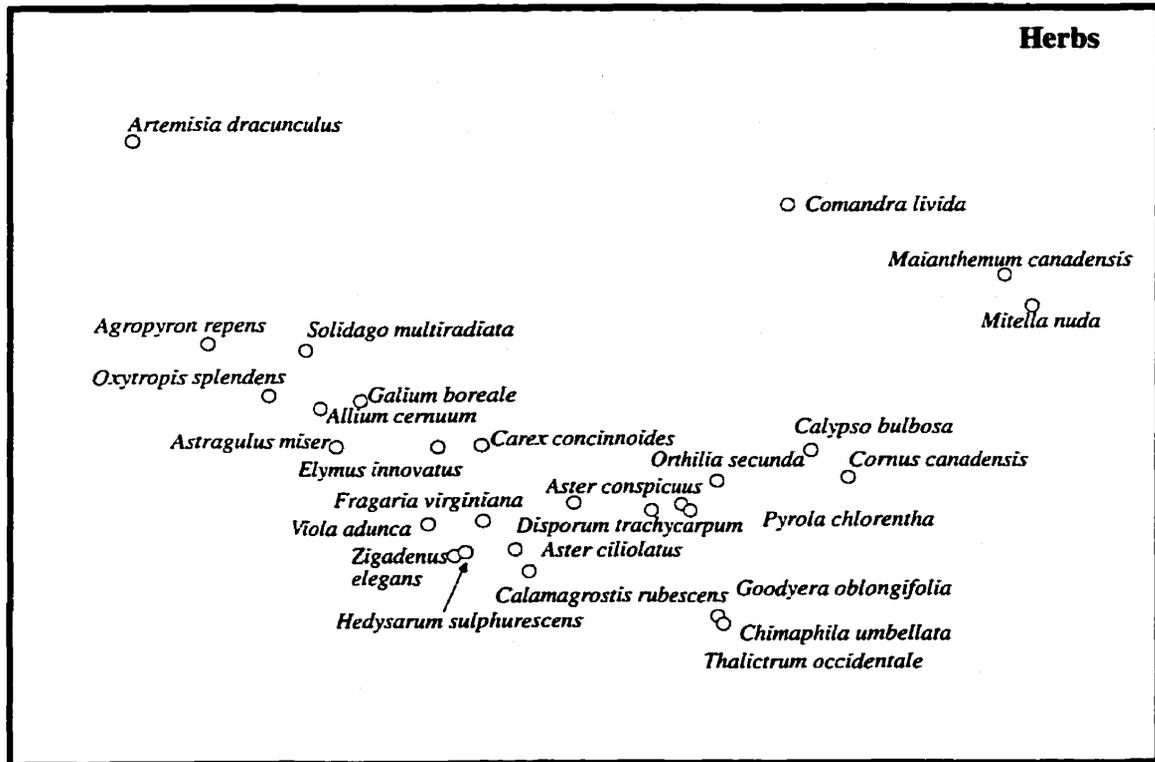
Correspondence Analysis Ordination Axis 2



Correspondence Analysis Ordination Axis 1

Figure 4.21. Correspondence analysis ordination (axis I and II) biplots of selected trees shrubs.

Correspondence Analysis Ordination Axis 2



Correspondence Analysis Ordination Axis 1

Figure 4.22. Correspondence analysis ordination (axis I and II) biplots of selected herbs and cryptogam species.

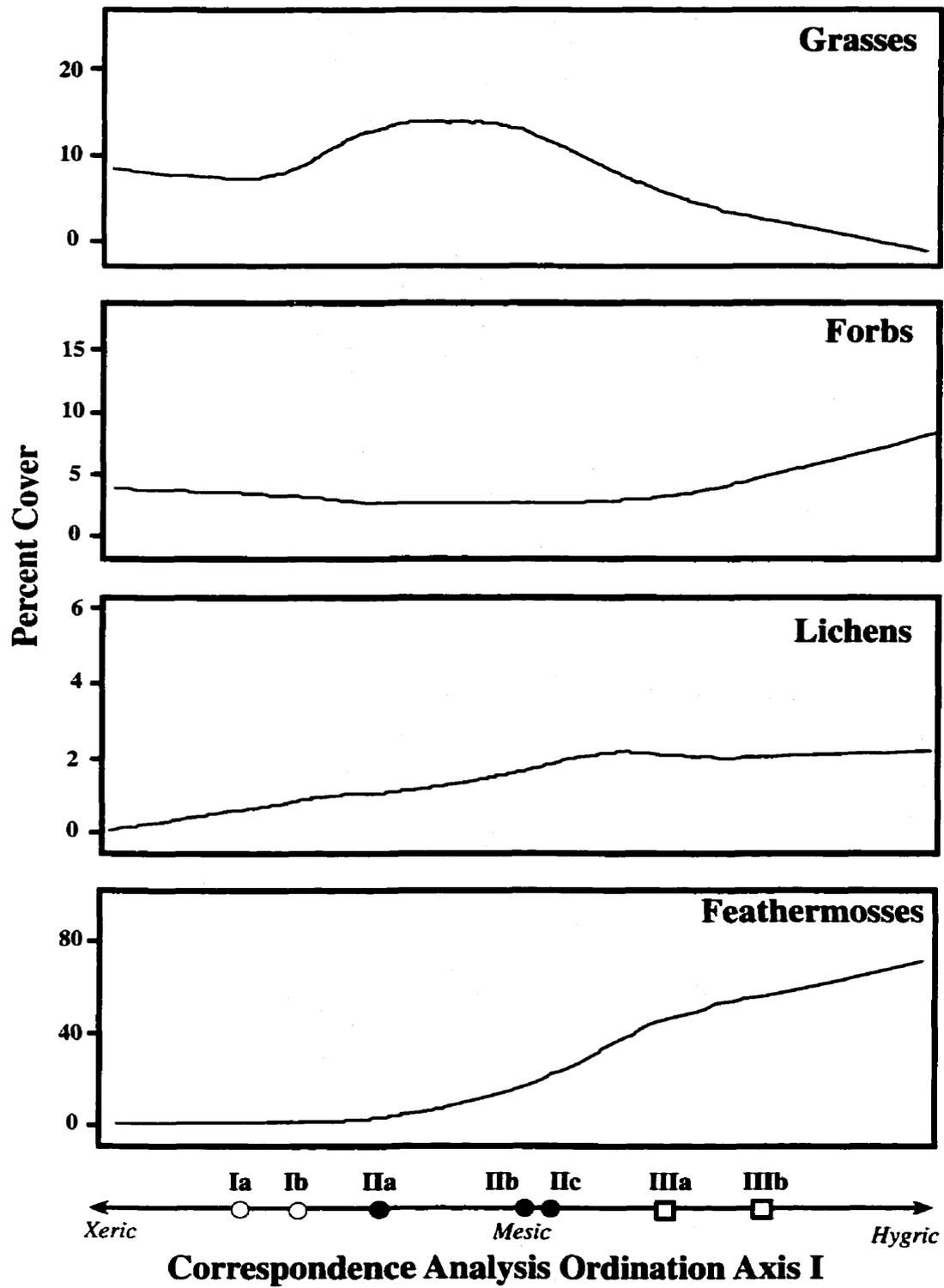


Figure 4.23. Changes in total herb/cryptogam cover along the first ordination axis. Lines were fitted using weighted regression analysis. Lower line represents the mean position of the seven sub-types on the first ordination axis.

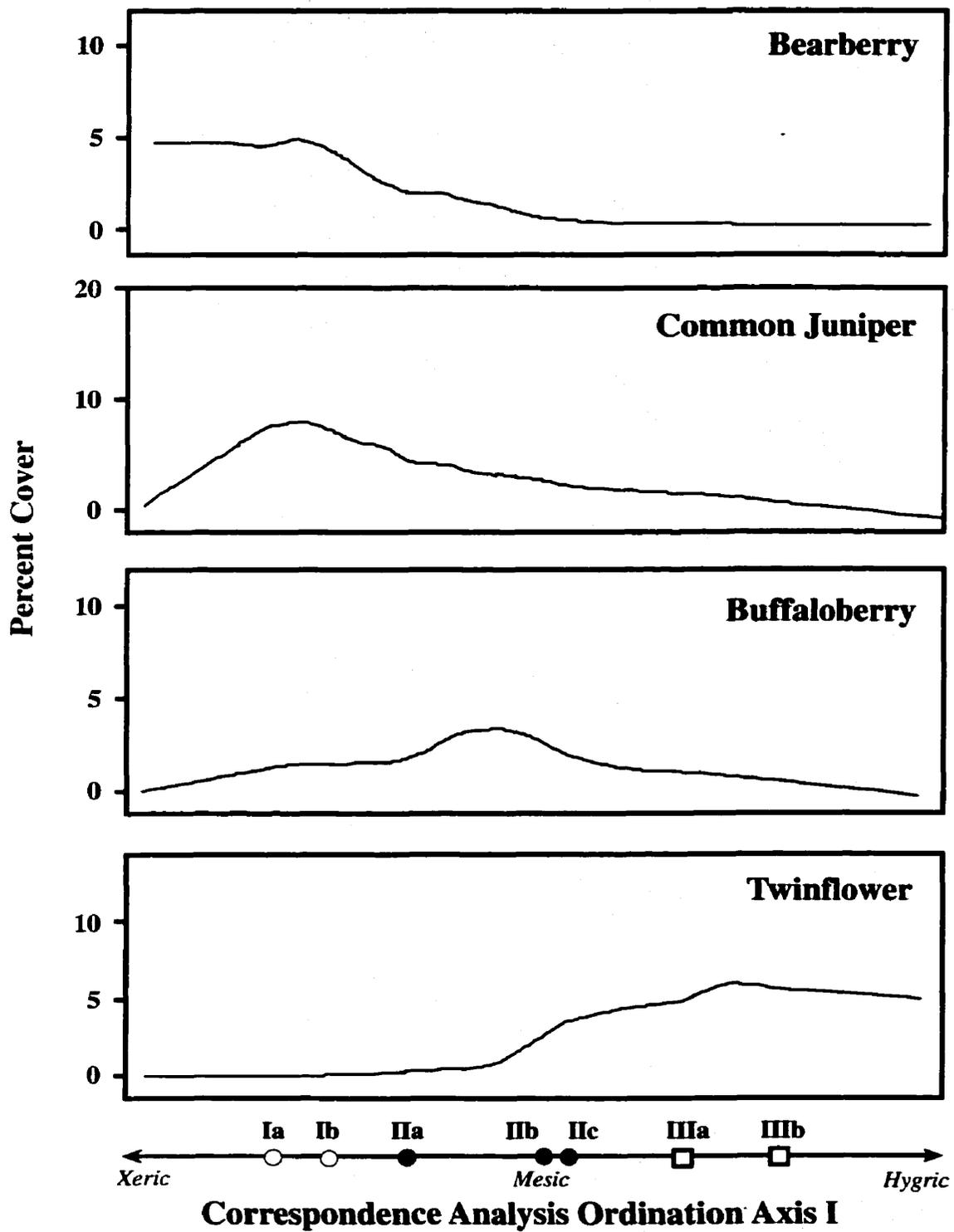


Figure 4.24. Changes in total shrub cover along the first ordination axis. Lines were fitted using weighted regression analysis. Lower line represents the mean position of the seven sub-types on the first ordination axis.

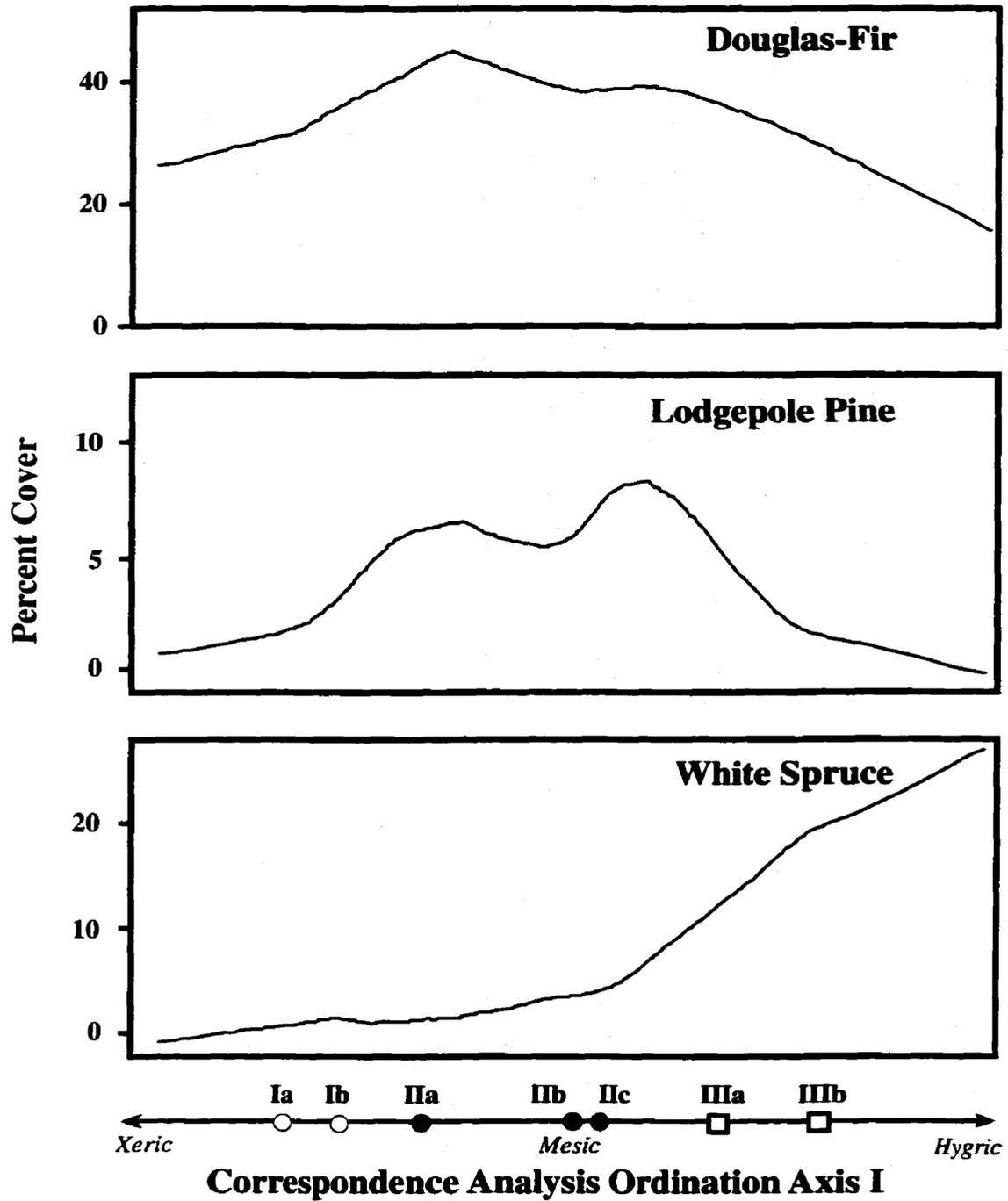


Figure 4.25. Changes in total tree cover along the first ordination axis. Lines were fitted using weighted regression analysis. Lower line represents the mean position of the seven sub-types on the first ordination axis.

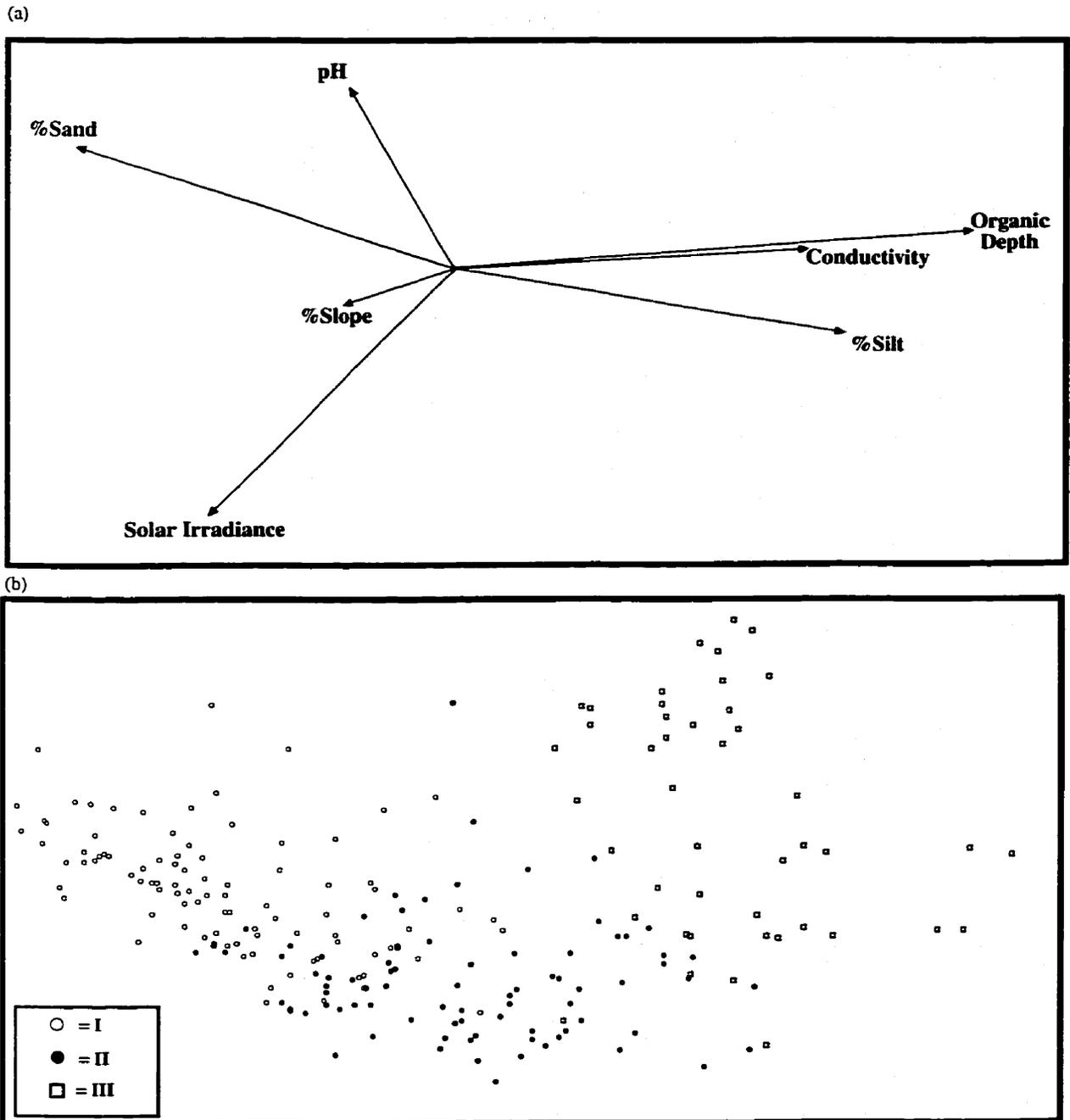


Figure 4.26. Canonical correspondence analysis (CCA) of $n = 220$ plots, $p = 171$ species and 7 environmental variables. (a) environmental biplot scores. (b) Site weighted Average scores, subdivided by the three stand types derived from the cluster analysis; standtype I, Stand type II, and Stand type III. The horizontal axis is axis one. Eigenvalues and canonical correlations: $\lambda_1 = 0.168$, $R^2 = 0.755$; $\lambda_2 = 0.062$, $R^2 = 0.682$. The amount of explained variation along the first axis is ca. 14% (the ratio of the *canonical inertia*:*total inertia* = $0.345/2.593 \cdot 100\% = 13.3\%$).

CHAPTER 5

GROWTH RATES OF INTERIOR DOUGLAS-FIR (*Pseudotsuga menziesii* var. *glauca*) WITHIN THREE COMMUNITY TYPES IN CANADA'S FOUR MOUNTAIN PARKS

5.1 INTRODUCTION

5.1.1 Differential growth and the Stand dynamics paradigm

Stand dynamic models inferred from static age-size distributions (e.g., Stewart 1986; McCune and Allen 1985) often fail to determine the likelihood of canopy replacement based on the growth and mortality rates of individuals within a stand (Johnson et al. 1994; Johnson and Fryer 1989). Population studies have indicated that recruitment, growth, and mortality rates are important determinants of stand dynamics differing not only between canopy and understory cohorts but also within a single cohort (Johnson et al. 1994). The vertical stratification of a stand, defined by the regeneration ecology of a species and its growth rate, often results from the competitive interactions between individuals (c.f. Ishii et al. 2000). The development of multi-tiered stands in post-fire Douglas-fir communities in the western Cascades results from differences in height growth rates (Stewart 1989). The probability of an individual reaching the canopy depends on a number of factors, which include disturbance frequency (e.g., fire), canopy residence time, competition, below ground resource allocation, climatic conditions, and stochastic events (Lorimer et al. 1988; Franklin and DeBell 1988). Temporal changes in growing conditions result in the shifting of competitive hierarchies within a stand, with the outcome determined by a species life-history characteristics (Ishii et al. 2000; Wright et al. 1998; Kobe 1996). These ideas have been associated with the concept of initial floristics (Egler 1954) and with the successional mechanisms of tolerance and inhibition (Connell and Slatyer 1977). Both the stand dynamics of a species within a region and its differential success at the landscape level is contingent on the "processes of juvenile tree growth and survivorship" (Kobe 1996; Stewart 1989). In this study it is therefore critical to assess the growth of interior Douglas-fir saplings before determining the regeneration patterns and long-term successional trajectories of the population (c.f. Wright et al. 2000; Wright et al. 1998 Kobe and Coates 1997; Pacala et al. 1994).

5.1.2 Factors and conditions affecting tree growth

Tree growth often incorporates a broad suite of factors and conditions which include the spatial and temporal distribution of photosynthetically active radiation (PAR), air temperature, below ground resources, ambient CO₂ concentration, length of growing season, precipitation, snow depth, age- height related changes in growth potential, pathogens, and herbivory

(McKenzie et al. 2001; Drobyshev and Nihlgård 2000; Olszyk et al. 1998; Fritts 1974). Slope, aspect, altitude, latitude, microtopography, and stand structure are important parameters controlling tree growth. Such abiotic/biotic parameters are important determinants of heat flux and microclimate, and are critical in defining the temperature and moisture regime of a given area (Fritts 1974). Temperature and precipitation affects on tree growth vary at both spatial and temporal scales: For example, above average temperatures in June favor rapid growth in mesic sites, whereas temperatures above freezing in the winter may trigger the resumption of metabolic activity which can be detrimental to an individual once temperatures drop below freezing (Fritts 1974). Fall and spring precipitation may promote growth, but high summer precipitation may inhibit following year growth by prolonging meristematic activity so that a greater proportion of stored photosynthates are utilized (Fritts 1974). Tree ring chronologies have enabled researchers to elucidate information about species recruitment patterns, disturbance history, population and successional dynamics, and reconstruct historic climatic data (Abrams 2000; Fritts 1982; Fritts 1976). Dendrochronological studies in the southern Canadian Rockies revealed that tree ring chronologies for Douglas-fir are highly and positively correlated with previous June and current May precipitation but negatively correlated with summer temperatures (Luckman and Watson 1999). Case and McDonald (1995) also found correlations between precipitation and growth in limber pine, however the growth-response of the species was more sensitive to previous August and current July precipitation levels, indicating a species specific growth-response to precipitation patterns: Such species specific growth responses to climate are one of the major mechanisms determining the spatial distribution of species (Krajina 1969). The impact of climate on growth is not ubiquitous, as canopy cover tends to modify annual temperature and precipitation extremes. Drobyshev and Nihlgård (2000) found that saplings growing in gaps or in clearings are more sensitive to environmental extremes compared to individuals growing under a closed canopy: under these conditions light and not precipitation becomes a limiting factor.

Growth response to varying light environments

Tree growth patterns along a light gradient depends on the moisture-holding capacity and nutrient levels of the soil (Chen et al. 1996). Within arid open savanna like systems, light exposure can be detrimental to sapling growth and survival since it tends to increase soil surface temperature and evapotranspiration stress. In mixed or closed canopied forests, increases in light are often associated with increases in height and radial growth across species. In general, altitude, elevation, microclimatic conditions and stand structure determine the light environment of a forest understory. Light levels can change along numerous temporal and spatial scales: For example i) diurnal and annual variations in light levels associated with solar angle, day length and phenology of vegetation and ii) the spatial

attenuation of understory light decreased by the presence of canopy gaps as well as stem-branch density, and crown architecture (Lieffers et al. 1999; Chen et al. 1996). Furthermore, light quality can change as it gets scattered by the atmosphere within a canopy (Walker and Kenkel 2000) or transmitted through foliage (Lieffers et al. 1999).

Fire frequencies in Canada's four mountain parks have decreased since the early 1930's (White 1985), partly in response to climatic conditions (Luckman 1998; Flannigan et al. 1998) but mainly as a result of active fire management policies. The reduction in the total area burned in these parks has shifted age-classes creating structurally old-growth forests characterized by high understory fuel loads, complex canopy structures, and a multi-tiered canopy (Johnson et al. 1995). Within these systems the dynamics of the understory cohorts are driven by the dual interaction of low light survival and high light growth (Wright et al. 2000). The presence of canopy gaps creates opportunities for increased growth of understory cohort trees contingent on factors such as sun angle, height of neighboring canopy trees, and the areal extent of the disturbance. Clearings created by gaps also provide habitat for ungulates, as well as increase diurnal temperature extremes and wind patterns which may cause damage to terminal shoots (Messier et al. 1999). The low temporal and spatial frequency of gap formation within montane forests means that an adaptive strategy for low light survival is critical for the persistence of a species in the absence of stand replacing fires. The ability of species to sustain low growth rates under light limiting conditions is dependent on its morphological and physiological adaptations to low irradiance (Wright et al. 2000; Awada and Redmann 2000; Abrams et al. 2000). Nearly all boreal-montane tree species are able to tolerate some degree of shading. Within species response to low light is often related to the size, age, and growing condition of the individual. For example, low light survival and growth of understory Douglas-fir is associated with drier habitat conditions as well as smaller size classes (Krajina 1969). The variation of species specific responses to shade tolerance corresponds to the minimum light levels necessary to trigger morphological and physiological changes (Wright et al. 2000; Lieffers and Stadt 1994). For instance, shade intolerant lodgepole pine requires $\approx 40\%$ full sun in order to achieve 50% of maximum radial growth compared to more shade tolerant species which require $\approx 20\%$ full sun, levels considered 'lethal' for most pines (Wright et al. 1998; Kobe and Coates 1997). Once the growth rate of a species falls below a critical point defined as the 'Radial Growth Threshold (RGT)' the likelihood of mortality increases (Kobe and Coates 1997). Kobe and Coates (1997) reported species-specific RGT thresholds ranging from 0.25mm/yr for western redcedar, 0.6mm/yr for white spruce and 0.9mm/yr for lodgepole pine. Foresters have long recognized that the probability of sapling mortality increases with a decrease in growth rates. This has important implications for the long-term successional trajectory and population dynamics of a stand (Wyckoff and Clark 2000).

5.2 OBJECTIVES

The objective of this study was to examine the growth of interior Douglas-fir regeneration across three stand types in the four mountain parks.

- Quantify changes in growth rates between the three Douglas-fir stand-types (mesoclimatic & light affects).
- Examine the effects of within stand canopy heterogeneity on tree growth (changes in light levels).

5.3 METHODS

5.3.1 Site Description

To assess radial growth, 85 interior Douglas-fir saplings (0.5-3m) were sampled within Banff, Jasper, Yoho, and Kootenay National Park. The selection of sites for this study was determined from the classified 220, 10x10 m plots sampled between 1997/98. Light and moisture regimes were inferred from the stand ordination (see **Chapter 4**): based on the minimum increase in error sum of squares clustering method (See Ward 1963). Three stand-types and seven sub-types (e.g., Ia, Ib, IIa, IIb, IIc, IIIa and IIIb) were defined from the analysis. The stand-types were classified as:

- *Stand-type I (Xeric) = Douglas-fir/Juniper/Bearberry - Open forest savanna.*
- *Stand-type II (Mesic) = Douglas-fir/Lodgepole pine/Buffaloberry - Heterogeneous canopy structure.*
- *Stand-type III (Hygric) = Douglas-fir/White spruce/feathermoss - Closed canopy.*

5.3.2. Sampling protocol

26 Representative 5 x 5m plots from each stand-type were selected a priori as 'sample-sites' based on their location along the first ordination axis. Only the driest (Ia) and wettest (IIIb) variants of stand-type I and III were sampled. In order to gauge the variation of canopy structure on sapling growth (e.g., presence of canopy gaps) all three variants of stand-type II were sampled. The regeneration cohort included all saplings between 0.5 and 5 meters in height. Regeneration was further partitioned into 'recent' (<30 yrs since initial fire cohort) and 'advanced' (≥30 yrs from the initial fire cohort) age classes. In this paper protected microsites were defined as areas that ameliorate stressful environmental conditions: for example in stand-type I protected microsites include microtopographical depressions as well as local vegetation cover.

Within each sample-site, information on local vegetation and canopy structure was recorded for each sapling. 'Local sapling information' was collected within a 2m radius from a sampled individual and included understory and canopy cover. The presence of indicator understory species along with local topography and canopy cover were used as determinants of local light and moisture conditions (Bridge and Johnson 1999). Vegetation cover classes were ranked on a 5 point ordinal scale (1 = low to 5 = high cover) and partitioned according to height classes. In addition, stem densities for all individuals between seedling to canopy height classes were determined. The vegetation information was used to verify that sample plot characteristics matched those of the stand-type. Tree canopy percent cover was estimated and canopy structure was determined based on the presence or absence of canopy openings.

Canopy gaps were defined on the basis of two criteria:

- Distance from the center of the "gap" to the four nearest neighbor canopy projections (minimum distance of 2.0 meters was used).
- Presence of two or more felled canopy trees.

Tree saplings were harvested within a 1.5 meters radius from the center of the opening.

5.3.3 Tree ring growth measurements

For each sapling height, basal diameter, crown architecture as well as evidence of past damage was recorded. Ages were determined by removing basal discs from saplings or by extracting 30 cm basal cores from mature trees. Basal sections and cores were taken back to the lab where they mounted and sanded using 400 and 600 grit sand paper. Only symmetrical tree sections were used in the analysis to avoid errors associated with discerning ring structure from compression wood. Ring width measurements were done with the aid of a hand held nomameter and a dissecting microscope. Ring measurements were recorded down to 0.025 mm accuracy along four perpendicular radii (see **Fig. 5.1**) using a 40x stereoscope. The measurements were later averaged. The outer most tree ring of individuals sampled in 1999 were removed from the analysis in order to ensure that measurements were from a complete growing season.

5.3.4 Data Analysis

Data format

Tree ring widths were expressed as cumulative tree increments ($T_i + T_{i-1} \dots + T_n$). Results were grouped according to stand-type and expressed as cumulative radial growth curves. Other authors have used relative incremental growth instead of absolute growth in order to remove the confounding effects of tree size on growth (Wright 1999). In order to ensure that that the response of sampled trees corresponded to environmental information recorded at the time of harvesting, growth rates were determined on the last five years of growth. Linear regression was used on the last 5 years in order to determine sapling growth rate (mm/yr): the coefficient of determination (r^2) for the fitted linear regression line ranged from 0.84 to 1.00. Richard's growth function (nonlinear growth model) was used in the initial analysis but was deemed unsuccessful based on the lack of inflection points in many of the growth curves: for example several of the saplings growing in gaps show non-asymptotic growth. Since comparisons were made on only the last five years of growth and given the fact that the range in mean sapling age was narrow (between 42-50 years of age) there was no need to express growth in relative terms. Although there was evidence of moderate size dependency on

growth, dividing radial growth by radius did not produce size independent results (See Wright et al. 1998).

Box plots of each stand-type illustrated the relationship in growth rate between each stand-type as well as the influence of canopy gaps. Suppression was defined as three or more consecutive years with growth rates below 0.60 mm/yr (the radial growth threshold of white spruce, considered slightly more shade tolerant than Douglas-fir). Release events were defined as growth periods exceeding 0.60 mm/yr (Wright et al. 2000). Yearly growth rates determined for each individual were calculated as a 4 year running slope function using a linear regression model.

Growth Model

A conceptual model was derived illustrating the correspondence between light, moisture and radial growth rate across each stand type. A quantitative model was developed using mean radial growth rates and multivariate analysis (correspondence analysis) results. Plot ordination results from the 220 plots were summarized and interpreted. The mean positions of each sub-type in two-dimensional ordination space were determined. The first ordination axis was used since this was interpreted as a complex moisture-light gradient. The mean positions of each sub-type along the first ordination axis could be used to infer relative light and moisture availability.

Canopy profile

A growth rate profile was created for canopy, lower subcanopy, and advanced recruitment within stand-type I (located near Tunnel Mountain, Banff National Park). Mature canopy Douglas-fir was cored near the base ($\approx 30\text{cm}$) using an increment borer. Lower subcanopy and regeneration cohort was cut at the base and at breast height ($\approx 1.4\text{m}$; **Fig. 5.4**).

Spatial distribution map of seedlings/saplings and mature canopy trees

Three 20x20 m plots for each of the three stand-types were mapped in order to display the spatial distribution of recent and advanced regeneration as well as mature canopy Douglas-fir. Seedlings were excluded from the map (**Fig. 5.7**).

5.4 RESULTS

5.4.1 Changes in Growth Rates of Douglas-fir between Stand-types

Results indicate that within stand-type I regeneration is clumped and often not associated with mature canopy trees. In contrast, stand type III regeneration tends to occur in proximity of mature canopy trees. Given the more favorable growth conditions encountered in stand type II, regeneration is spatially more complex, with more robust individuals normally occurring within forest openings (**Fig. 5.2** and **5.7**).

Growth in Stand-Type I

The well-drained south-facing slopes of stand-type I result in low stand productivity, under-dispersed landcover and low asymptotic growth of regenerating Douglas-fir (**Fig. 5.2**). Protected microsites created by local depressions and vegetation cover break up an otherwise sparse landcover. These refugia sites provide relief from seasonal temperature extremes and evapotranspiration stress enabling saplings to endure and prosper within harsh growing conditions (**Fig. 5.2**). Individuals growing in open-light environments tend to be older (35 to 73 years) and more diminutive (mean height = 2.49m and mean diameter = 2.63cm) than those growing in protected microsites (40 to 52 years; mean height = 3.22m and mean diameter = 3.1cm; **Table 5.1**). Mean radial growth rates between the two are significantly different, with a mean ranging from 0.12 mm/yr in openings and 0.45 mm/yr in microsites (**Fig. 5.3**). The number of suppression events are similar (mean 1.35, ranging from 1 to 2 years). However, the mean number of years of suppression are greater in openings (mean = 34 years, range = 5 to 65 years) compared to microsites (mean = 19 years, range = 6 to 27 years; **Table 5.1**). The mean number of years of release between individuals growing in the open (10.2 years, range = 3 to 19 years) and in microsites (8.4 years, ranging 5 to 18 years) are similar. Results from the canopy growth profile indicate that growth patterns are different between post-fire canopy trees and the recent regeneration cohort (**Fig. 5.4**).

Growth in Stand-Type II

The mixed forest and heterogeneous canopy structure of stand-type II communities results in varied growing conditions for Douglas-fir saplings. Much like the modifying effect of the protected microsites in stand-type I, the increased canopy cover of IIa ameliorates the effects of what would otherwise be considered adverse growing conditions (**Fig. 5.2**). Sub-type IIa has the highest mean radial growth rate (0.95 mm/yr) individuals range in age between 36 to 54 years and attain the tallest height (mean = 3.74 m, range from 3 to 4.8m) and basal diameters (mean = 6.6 cm, range from 5.3 to 8cm) of any other group (**Fig 5.3**). The mean number of suppression events (1.1 years) and the mean number of years of suppression (7 years, ranging from 4 to 12 years) are one of the lowest. However the mean number of release events (1.5 years, ranging from 1 to 2) and the mean number of years of release (20.7

years, ranging from 7 to 30 years) are the highest of any group. Increased canopy complexity within IIb and IIc results in greater spatial and temporal heterogeneity in understory light levels. Growth is either asymptotic or linear depending on understory light levels (**Fig. 5.2**). Sapling growth is largely dependent upon asynchronous small scale disturbances such as canopy gaps. Mean radial growth of Douglas-fir saplings in both IIb (0.15 mm/yr) and IIc (0.12mm/yr) are significantly lower compared to individuals growing in gaps (0.78 mm/yr and 0.68 mm/yr respectively; **Fig. 5.3**). The age of saplings in both subtypes including those found in gaps range from 42 to 50 years: no clear trends in age are detected (**Table 5.1**). Mean sapling height and diameter is greater for saplings growing in gaps in both IIb (height = 3.25m, basal diameter = 5.07cm) and IIc (height = 2.5m, basal diameter = 5.45cm) compared to counterparts growing in the shade. Individuals in gaps within subtypes IIb and IIc experienced a greater number of years in a rapid growth phase (Mean No. of yrs of release = 12.5 and 14.8) compared to those found in the shade (Mean No. of yrs of release = 6.8 and 4.8 respectively). Conversely individuals growing beneath a closed canopy undergo a longer duration in suppression (**Table 5.1**).

Growth in Stand-Type III

The high canopy cover and physiographic position of these stands increases the quality and quantity of light attenuated by the canopy. Given that the average canopy height exceeds 30m and that most sites typically occur on north-facing basal slopes the absence of one or two trees (i.e., the presence of gaps) did not seem to have an effect in species composition or the growth of Douglas-fir (pers. obs.). High understory moisture levels enhanced by decomposing organic material and bryophytes creates favourable conditions for shade tolerant conifers but unfavourable conditions for Douglas-fir sapling growth: A majority of individuals achieved asymptotic growth by 20 years of age (**Fig. 5.2**). Mean radial growth is less than 1 mm/yr (**Fig. 5.3**). The age of saplings range from 25 to 54 years (**Table 5.1**). Most individuals are near the seedling to sapling transition stage, none were encountered greater than 1m height (mean height = 0.63 m; basal diameter = 1.34 cm; **Table 5.1**). All sampled trees are undergoing prolonged suppression (**Table 5.1**).

5.4.2 Growth rate age/size relationship

The relationship between age, stem height, and growth rate was evaluated using locally weighted regression. The locally weighted regression line suggests that sapling stem height increases and age decreases at higher growth rates (**Fig. 5.5**). The age and growth rate relationship peaks around 54 years (corresponds to stand-type I) and declines as rates decrease. This can be misleading since the lowest growth rates corresponds to younger individuals sampled from stand-type III. Growth rates >0.60 mm/yr are associated with younger sapling ages (<45 yrs) and stem height ranging from 3 to 4.8m in height.

Conversely growth rates < 0.60 mm/yr are associated with older saplings (54 years) and a wider variation in stem height (ranging from 0.55 to 3.2m; **Fig. 5.5**).

5.4.3 Interior Douglas-fir Growth Rate Model

The trade-off in growth between low vs. high light and moisture regimes is critical to understanding the competitive ability of a species (**Fig. 5.6**).

Based on the mean position of each stand-type along the growth rate and ordination axes, mean radial growth as a function of light and moisture could be interpreted as a trade off between limiting resources. Within 'light-enriched' environments seasonal temperature extremes can be detrimental to sapling growth and survival. 'Light-enriched' environments like those of stand-type I also tend to be characterized by well drained nutrient poor substrates, which can limit the growth of species such as white spruce. Based on our results, the mean radial growth of stand-type I saplings is < 0.25 mm/yr, this almost doubles in moist sheltered microsites. 'Light-limiting' environments similar to stand-type III, tend to favour the regeneration of late-successional species which rely on vegetative propagation as a means of reproduction (e.g., western redcedar). Light levels can be below the critical threshold necessary to maintain a positive carbon balance in semi-shade tolerant species. Unlike stand-type I, the small variation in understory seasonal temperatures, relatively high humidity levels, and moist organic seed beds (e.g., bryophytes or moist decomposing logs) favour seedling germination. However based on the low mean radial growth rates of individuals in stand-type III, the long-term survival and growth of interior Douglas-fir seedlings seems unlikely. Douglas-fir sapling annual growth is maximized under relatively high light and moderate moisture levels. Similar trends are seen for gap driven systems where growth rates are nearly tripled compared to understory-grown saplings (**Fig. 5.6**).

5.5 DISCUSSION

5.5.1 Changes in growth rates between stand-types

Results from our study clearly indicate that the growth rates of regenerating interior Douglas-fir vary as a function light and edaphic conditions. The differential growth of Douglas-fir in the xeric to hygric stand-types implies that the long-term successional trajectories of these communities are contingent on the competitive ability of individuals. Radial stem growth is most variable in stand-type II where spatio-temporal perturbations to the upper canopy results in a heterogeneous light environment. Growth rates are highest in stands of intermediate soil moisture, associated with canopy gaps and lowest in areas where canopy cover is intact. Stand-type I is moisture and nutrient limited: growth of recent Douglas-fir recruitment is compromised by a combination of excessively well-drained soils, high daily summer temperatures and sparse vegetation cover which causes a cessation in growth early in the growing season. Stand-type III is light limited: the combination of canopy cover, organic matter accumulation and seasonally water saturated soils results in reduced understory light levels and seedbed conditions which decrease the likelihood of seedling survival. Douglas-fir growth rates are below the minimum threshold required to maintain more shade tolerant species (see Wright et al. 2000; Kobe and Coates 1997).

Growth in Stand-type I

The radial growth rate of interior Douglas-fir in the dry open forests of stand-type I is compromised by the early onset of drought conditions brought about by excessive drainage, depth and coarse fragment content of soil, high evapotranspiration, and belowground competition (Simpson 2000; Janz and Storr 1977; Krajina 1969; Stringer 1966). The combination of exposed mineral soils, high summer temperatures, and south-facing slopes significantly reduces the establishment of saplings by increasing competitive interactions among individuals. In these stands, edaphic limitations in soil moisture and nutrients increases asymmetric competition between previously established individuals (competitive dominants) and new recruits (competitive subordinates; see Keddy 1990). Recruitment of competitive subordinates in these xeric stands are often characterized by low stem productivity (e.g., shorter stature and small radial diameters) and survival (Karakatsoulis and Kimmin 1993). Post-fire recruitment within moisture limited stands is often restricted to marginal locations as most of the more optimal 'micro-sites' are already occupied by mature trees. A notable shift in radial growth was observed between the two fire cohorts and post-fire cohort. The demand of essential nutrients and water created by larger individuals produces a 'depletion-zone' around mature trees and shrubs, which limits the growth of non-contemporaneous individuals (Kimmins 1987). Trees with larger crowns have greater sapwood areas and are expected to utilize more water (Simpson 2000). Nutrient cycling within these mature stands is limited by

low microbial activity and slow decomposition rate of Douglas-fir woody debris (Gartner et al. 1999). Thus the cover provided by an existing canopy may ameliorate the effects of light and temperature stress but has no effect in releasing resources. Bi-directional and asymmetric competition among species is cited as one of the most important factors limiting growth (Keddy 1990). In early post-fire communities, rapid colonization by forbs and grasses compromises the establishment and growth of seedlings (Rose et al. 1999): for example, the proliferation of root biomass by *Calamagrostis canadensis* in central Alberta is cited as the limiting factor controlling the growth and survival of white spruce seedlings (Leiffers et al. 1999). In xeric Douglas-fir stands, the benefits of vegetation cover in ameliorating the effects of heat stress are greater than the associated competitive interactions among species. These trade-offs in growing conditions are critical for the long-term survival of individuals: reductions in needle-transpiration results in increased diurnal stomatal conductance, leading to greater carbon allocation to belowground structures. Sapling competition with forbs and graminoids plays a lesser role in the establishment and survival of individuals in stand-type I, compared to more moderate sites. Given the heterogeneous distribution of belowground resources in these stands, the growth habit of graminoids are characterized by tufted grasses with a clumped distributions such as *Elymus innovatus* instead of the creeping rhizomatous growth habit of *C. canadensis*. Nonetheless, water loss as a function of grass water use and direct evapotranspiration can not be over looked. For dry open-canopied interior Douglas-fir stands, Simpson (2000) found water use to 1.08-1.59 mm/day, with the smallest trees (<10cm diameter) using 21-42% and larger trees (>20cm diameter) using 44-75% of the average daily stand water use (Simpson 2000). By comparison, water loss in a grass-covered forest clear-cut averages 80% of the equilibrium evapotranspiration rate with measured values as high as 4.1mm/day (Adams et al. 1991). Water loss resulting from vegetation and bare ground may account for significant soil moisture depletion in dry open-canopied forests (Simpson 2000). The inequitable division of resources in these stands is the underlying factor controlling the spatial distribution of canopy, tree regeneration, shrubs, forbs, and graminoid species. It is within these growing conditions that Douglas-fir is able attain a self-perpetuating stand.

The slow growing Douglas-fir in these open-canopied forests often show signs of cumulative damage to their leader resulting from frost or ungulate injury. Open-grown saplings are exposed to a wider range of temperatures, often resulting in stem dieback (Fritts 1976; Fritts 1974). Wright et al. (1998) found that conifer growth was poorest for individuals growing in exposed high light environments, as environmental conditions tend to be more extreme. In Banff and Jasper National Park, the effects of warm dry 'chinook' winds on long-term sapling survival are greater in open-environments. Above-freezing temperatures,

may trigger the onset of metabolic activity which can be detrimental to the survival of sapling buds and stems once temperatures return to normal (Fritts 1974).

Mechanisms of survival

The survival of open-grown Douglas-fir saplings is dependent on water use efficiency (Simpson 2000). Removal or damage to photosynthetic tissues can have detrimental effects on growth since a reduction of leaf area often leads to a reduction in sapwood production and hence a loss in water use efficiency (Simpson 2000). This often leads to a negative feedback process whereby growth is further compromised by the inability of the individual to sustain growth in the following year. Reduction in stored carbon results in a greater dependence on newly assimilated carbon as well as depletion of secondary defensive compounds (Fritts 1974). Seedling exposure to temperature extremes results in a reduction of shoot length (with no loss of needle density per branch), and inhibition of lammas flush. Very high temperatures (>35°C) may cause bud injury in the summer resulting in the abnormal development of bud scales and needle primordia (Olszyk et al. 1998).

The open-canopied forests of stand-type I are composed of sparse vegetation, punctuated by forest thickets (McGuire et al. 2001; Canham et al. 1994). Much like gaps in closed-in forests, the presence of mature trees within savanna-like communities increases the spatial heterogeneity in an otherwise homogeneous landcover type. These local refugia provide relief from high daily summer temperatures, evapotranspiration, fluctuations in winter extremes, and ungulate herbivory. Furthermore, sheltered microsites composed of deciduous shrubs may enrich soils by drawing up nutrients and depositing it as litter beneath a canopy (c.f. McGuire et al. 2001). Although beneficial for sapling survival, growth may still be compromised through competitive interactions. Protected-microsites are critical for ensuring the survival and growth of advance regeneration by not only reducing the effects of diurnal temperature extremes, evapotranspiration and ungulate herbivory but also increasing local soil moisture and nutrient levels (Canham et al. 1994). Although not examined in this study the presence of ectomycorrhizal fungi is considered to be critical for the growth and survival of Douglas-fir saplings growing in marginal sites. Ectomycorrhizal fungi are known to transport essential nutrients and water (Harley and Smith 1983) to their hosts, provide resistance to pathogens (Barham et al. 1974) and are normally found associated with 'refuge' plants. Species such as *Arctostaphylos uva-ursi* are considered important for maintaining a diverse ectomycorrhizal community within open-canopied dry forests (Hagerman et al. 2001). The prostrate growth form of *A. uva-ursi* makes it an effective refuge plant since it not only reduces evapotranspiration stress but also does not smother seedlings (Horton et al. 1999). Hagerman et al. (2001) found that many of the ectomycorrhizal species associated with *A. uva-ursi* were also found in Douglas-fir.

Growth in Stand-type II

The growth response of Douglas-fir understory regeneration is most variable within stand-type II. What accounts for this variability in growth rate? Unlike stand type I, soils in these forests are seldom exposed to drought conditions. Both shrub and canopy cover along with moderate slopes tend to offset the evapotranspirational stress and heating loads characteristics of the more xeric open-canopied stands. Thus the overriding factor limiting or enhancing growth is light availability. In the Canadian Rockies, unlike the boreal plains, shrub cover seems to play a minor role in the suppression of conifer regeneration. For example, in boreal mixedwood stands, beaked hazelnut can drastically limit the recruitment of white spruce by reducing light levels and smothering seedlings. By comparison, the shrub layer within mature Douglas-fir stands seldom achieve the density and height necessary to have a significant impact on seedling survival. Most if not all of overstory cover is generated by canopy and subcanopy trees. Progressive self thinning and differential mortality of pioneer species increases with age (Walker and Kenkel 1998). Thus a once continuous forest canopy is broken up, creating a spatially complex mosaic dotting the landscape in an asynchronous manner. It is within these local openings or gaps that Douglas-fir regeneration and growth is the highest. Natural forest openings also promote the growth of other species, thus increasing competition as well as increasing the likelihood of ungulate activity and exposure to climatic extremes during the growing season.

The growth pattern of Douglas-fir is not consistent within stand-type II. Mesoclimatic differences promoted by local topography and vegetation cover are evident among the three sub-variants. Sub-type IIa is considered the driest of the three and characterized as a Douglas-fir/lodgepole pine dominated stand. Douglas-fir regeneration and growth is enhanced within protected microsites. Within these sub-xeric stands natural forest openings and gaps may create conditions which are unfavourable for rapid growth (Kimmins 1987). Vegetation cover tends to ameliorate otherwise adverse growing conditions. Why then does this drier sub-variant contain trees with the highest growth rates? Although this sub-type is considered sub-xeric, the low to moderate slopes which characterize these forests allow for less run off and greater deposition of organic matter and litter. The higher cover and moderate topography results in greater snow accumulation during the winter and a longer melt period in the spring. Thus during the critical phase of growth early in the season the soils of these stands are saturated. The moderate cover provided by the understory and tree canopy is enough to reduce water loss through evapotranspiration in the summer and sublimation in the winter. Thus these stands are less prone to severe drought conditions common to stand-type I. Furthermore, the higher moisture levels in the spring gives these trees a competitive advantage over their counterparts growing in the open. Nonetheless, these stands are drier than the other

sub-variants in stand type II. This can be advantageous for Douglas-fir seedlings as drier conditions trigger a greater allocation of carbon to belowground structures (Chen et al. 1996). The establishment of a well developed taproot can offset the effects of water loss in the upper soil horizons and give the species a competitive advantage. Seedlings of co-dominant species such as white spruce which normally do not produce a deep tap root can not persist in these drier habitats (Nienstaedt and Zasada 1990). Those that do survive are normally smaller and have lower radial growth compared to Douglas-fir (pers. obs.). Although Douglas-fir growth is enhanced by cover, light attenuation is low enough to prevent low-light growth or suppression. Individuals growing beneath a canopy were almost 5m in height. Williams et al. (1999) suggest that in sub-xeric habitats there may be an advantage in maintaining a few short lateral branches distributed equally along the stem. In the absence of competing vegetation a spindled vertical growth form intercepts more light (Williams et al. 1999).

The other two subvariants of stand-type II are considered sub-mesic to mesic and characterized as a Douglas-fir/lodgepole pine/spruce and aspen forest. Growth and survival in these stands is driven by the differential mortality within the canopy created by either extensive branch die back or felled trees. Individuals from IIb and IIc seem to undergo two distinct growth phases, low-light and high-light growth. Increased canopy cover created by a multi-tiered tree canopy dramatically attenuates the amount of light reaching the forest floor. Within these stands light is the limiting factor controlling the growth and survival of Douglas-fir. Radial growth rates of individuals growing beneath an established canopy was around 0.25mm/year. Most of the sampled trees were described as 'oskars' characterized by a non-conical growth habit with heights seldom exceeding 1.7m. Low stem stature has been demonstrated to be advantageous for survival under low light conditions. Hiura et al. (1996) found an inverse relationship between height growth and survival in some tree species growing beneath a closed canopy. Even though growth rates were below the radial growth threshold of white spruce (e.g., 0.6mm/yr), all of the sampled trees were at least 35 years of age with most undergoing suppression for an extensive portion of their lives. This suggests that Douglas-fir is able to grow and develop beneath an established canopy for an extensive period of time. Furthermore, the presence of a multi-tiered Douglas-fir subcanopy and the high density of the upper canopy indicates that survivorship is high within these stands. Although considered a semi-shade tolerant species, Douglas-fir is able to maintain its self under low light conditions in drier habitats (Krajina 1969). The ability to increase lateral branch growth over terminal leader growth within low light environments such as these is indicative of shade tolerance (Williams et al. 1999; Wright et al. 1998; Chen et al. 1996). Slow annual growth and low above ground productivity are critical for the survival of suppressed trees as this maintains a positive carbon balance (Williams et al. 1999).

In both sub-types IIb and IIc increases in growth are associated with canopy gaps. Canopy gaps replace the synchronous large-scale effects of fire in old-growth forests by promoting greater spatial heterogeneity through cumulative small scale perturbations (Wright et al. 2000; Drobyshev and Nihlgård 2000; Weiss 2000; Wright et al. 1998; William et al. 1997; Chen and Klinka 1997; Grey and Spies 1996; Lertzman et al. 1996; Poulson and Platt 1989; Lorimar et al. 1988). In the Pacific Northwest, increased light levels within canopy-gaps has been shown to promote the establishment and growth of recent regeneration (Stewart 1986). Frazer et al. (2000) noted that the "key process distinguishing old-growth from earlier stages of stand development is the mortality of canopy dominants". Although the chronological ages of sub-types IIb and IIc would not constitute the traditional definition of 'old-growth', the structural components and functional characteristics of these stands would qualify them as old-growth stands (Johnson et al. 1995). The presence of fallen and standing dead lodgepole pine as well as branch die back in numerous mature Douglas-fir has created a spatially heterogeneous canopy. This discontinuous canopy creates numerous interstitial spaces which allow light to reach the forest floor (McGire et al. 2001). The response of trees to these openings is dependent on the gap size, within gap position, sun angle (affects canopy crown projection), and canopy height. The benefit of gaps on tree growth is not restricted to light levels alone: a positive relationship was found to exist between gap size, rainfall amount, and water availability in the upper mineral soil (Nihlgård 1971; Anderson et al. 1969). This has important implications for sub-mesic Douglas-fir stands where intense below ground competition may limit growth beneath a closed canopy.

Although in most cases it is difficult to determine when a canopy gap developed it seems likely that most of the individuals in sub-type IIb and IIc established before an opening occurred. Recruitment generated by the gap itself is difficult to determine, and seems to be a contentious area in gap-dynamic research (E. Johnson, 2000 pers. comm.; Clark 1991). In the absence of disturbance, the duration of gaps within coniferous forests may take as long as 50-100 years to close, compared to 5 years in temperate deciduous forest and as little as 2 years in tropical forests (c.f. Gray and Spies 1996).

One of the striking differences between gaps and nongaps is the average, growth rate, size and crown architecture of saplings (Ishii et al. 2000). The response of increasing light levels on tree growth is a function of shade-tolerance. Chen et al. (1996) found that the less shade tolerant lodgepole pine growing in an opening has greater terminal and lateral growth response compared to the more shade-tolerant Douglas-fir. However the growth response of Douglas-fir is better adapted to alter its crown morphology under low-light (0-15% of photosynthetic photon flux density (PPFD)), by decreasing its terminal/lateral branch ratios

(Williams et al. 1999). The lateral branch growth of interior Douglas-fir was reported to be much greater than pines at similar low light levels.

Most of the trees sampled were at least twice as tall as those encountered beneath the intact canopy. Crown architecture also differed, with open grown tree showing greater canopy depth (pers. obs.). Williams et al. (1999) found that increasing light levels and crown depth of interior Douglas-fir are directly related. They proposed using crown depth as an index of tree vigor. Greater sapling heights in gaps leads to a positive feed back between increasing light and accumulation of foliage area (Ishii et al. 2000). In addition, mean radial growth rates of all the sampled trees were three times greater than suppressed individuals. This implies that light is one of the most important resources for predicting tree performance (Coates and Burton 1999; Leiffers et al. 1999; Messier 1999; Williams et al. 1999). Results for sub-type IIc were interesting since these stands tended to have the highest regeneration densities within canopies three and four but not the highest growth rates. Part of the answer lies in the fact that non-conspecific species competition was high. Although a competitive index was not calculated for this study results based on stem densities and static size-classes imply that gaps created in IIc not only benefited Douglas-fir growth but also much faster growing species such as understory lodgepole pine and white spruce (Nienstaedt and Zasada 1990). Furthermore, the growth response to climate is more pronounced in openings compared to a closed forest. Wright et al. (1998) found that the growth of lodgepole pine beneath an intact canopy was unrelated to regional climate, but its growth was more variable within openings, reflecting local differences in mesoclimatic conditions.

Growth in Stand type III

Stand type III is characterized as a Douglas-fir/white spruce and feathermoss forest. There are currently no published studies on the growth of interior Douglas-fir within hygric old-growth forests in the Canadian Rockies. In contrast to stand type I, these forest are light limited. Seedbed and soils conditions are characteristic of old-growth hygric forests (Edmonds et al 1993). Organic substrates are composed mainly of bryophytes (\approx 30cm deep) with a humic layer made up largely of decomposing wood, overtop water saturated soils. All of the Douglas-fir regeneration encountered in these stands are $<$ 50 cm in height. Most of the sampled seedlings have their rooting systems suspended within a bryophyte organic matrix overtop mineral soil. The inability of most seedlings to penetrate the upper soil horizons has a pronounced effect on root development since seedling survival is precariously dependent on moisture availability. Fluctuations in forest floor humidity levels results in the rapid desiccation of organic seedbeds thus increasing seedling mortality. Close proximity to the robust stems of shade-tolerant species inhibits Douglas-fir seedling development by further attenuating lower subcanopy light levels. The dramatic decrease in stem density from

seedlings to lower subcanopy trees within these stands implies that understory mortality rates of interior Douglas-fir is high, assuming that evidence of smaller size-class mortality has not been destroyed. The paradox of high seedling density and low annual growth rates (<10mm/yr) is explained by the presence of large seed producing relic trees in the stands. Within these closed forests wind dispersal is minimized by the presence of tall neighboring trees. Seed rain generated by mature trees tends to create a cascade affect of seeds descending from the upper canopy to the forest floor. Those that survive germinate on organic seedbeds, where they are protected from the effects of diurnal and seasonal extremes in temperature. However, the small seed size of Douglas-fir necessitates both light and warm seedbed conditions to trigger germination and survival (Li et al. 1994; Hermann and Lavender 1990). Conditions favorable for germination may not occur until late spring or early summer when substrate temperatures are more favourable. Furthermore development is compromised by low light levels and increasing respiratory cost associated with growth. Reduction of photosynthetic tissue is required in order to maintain a positive carbon balance. The loss of productive tissue further depletes stored reserves now needed to sustain the individual in a perpetual state of animation. Wright et al (1998) found that the growth rates of more tolerant species growing in 5% full light is enhanced in cooler meso-climates. Conversely the growth and shade tolerance of Douglas-fir increases under drier climatic conditions. Thus low-light growth of Douglas-fir within these cool moist forests increases the likelihood of seedlings mortality (Kobe and Coates 1997). Most Douglas-fir seedlings growing in low-light succumb to fungal pathogens such as Armillaria root rot, or needle cast fungus. Edmonds et al. (1993) found that insect induced mortality accounted for 18% of the standing dead while suppression induced mortality accounted for 56%. Although mortality is high, seedlings/saplings range in age from 25 to 54 years, indicating that individuals maybe able to maintain themselves for a long period of time at a suppressed juvenile state. In the more open forests of stand-type IIIa, seedling mortality evident along upper slopes and ridges was dated at around 20 years of age (unpublished data).

5.5.2 Growth Rates of Douglas-fir and their Implication to Forecast Canopy Change

Differential growth of interior Douglas-fir is deemed to be the overriding factor controlling the population and stand dynamics of this species. Changes in growing conditions brought about through fluctuations in climate, as well as local variability in canopy development, and recession alters the growth potential of the species and thus its competitive ability (Wright et al 2000; Pacala et al. 1994). Competition among tree species plays an important role in the establishment, growth, and survival of individuals (Ishii et al 2000; Kobe 1996).

In stand type I, mesoclimatic and edaphic conditions are deemed to be too extreme to support a vast contingent of tree species. Most are unable to establish and survive, those that

do are normally characterized by low growth and low stem productivity. Furthermore, initial establishment following a catastrophic fire takes advantage of the non-sequestered belowground resources once utilized by live stems. Subsequent recruitment into the stand must withstand intensive belowground competition sequestered by the spatial occupation of mature stems, which severely compromise the growth, and survival of subordinate trees. Results from this study suggest that 'successional development' will be cyclic rather than linear even in the absence of disturbance. The low productivity of these open-canopied forests limits the accumulation of coarse woody debris thus maintaining the 'historic fire regime'.

The more favourable conditions encountered in stand type II are offset by greater competition for light of faster growing species. Douglas-fir growth is highest in the sub-xeric stands of IIa, where it is able to outcompete white spruce and lodgepole pine. However its growth is compromised by either canopy shading or stem competition within forest openings in more mesic conditions. Based on the growth rate results from this study canopy-turnover will favour Douglas-fir in more xeric stands and a Douglas-fir/white spruce mixed in more mesic conditions.

The low percent of light transmitted through the canopy in stand-type III significantly reduces the growth and likelihood of survival of understory Douglas-fir regeneration. Irrespective of the neighborhood, effects of understory crown 'shading' produced by shrub and late-successional tree species, the cover generated by the tall (>35m in height) upper canopy is too pervasive in extent and duration to allow for light competition within the lower tree strata. Thus like stand type I, species more adapted to grow and prosper within marginal growing conditions will tend to outcompete ill-adapted subordinate species. In this case Douglas-fir is outcompeted by more shade tolerant late successional species.

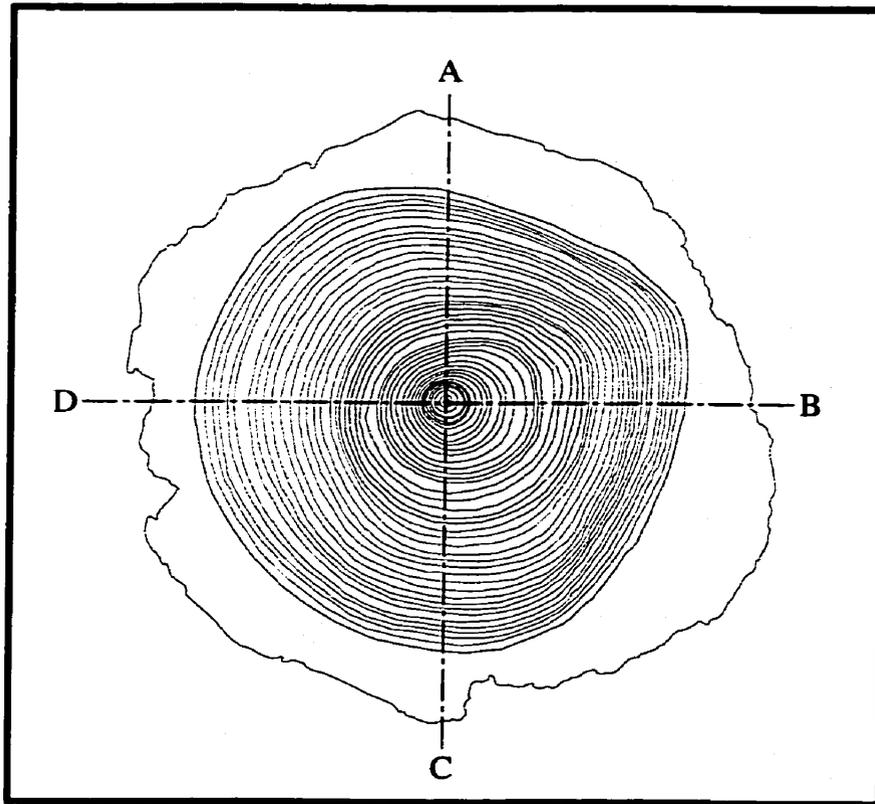


Figure. 5.1. Douglas-fir tree cross-section illustration depicting the four perpendicular axis to determine annual tree ring width. Measurements were made along each of the four axis from the core to the outer most complete ring. Current year growth was omitted from the analysis as most samples had not yet completed seasonal growth. The four measurements were averaged and re-expressed as cumulative growth. Only symmetrically grown trees were used to avoid problems with compression wood. The darkened inner region represents the aerial extent of the non-functional heartwood, with the clear region representing the sapwood. The darker outer region represents the phloem(cork) and outer bark.

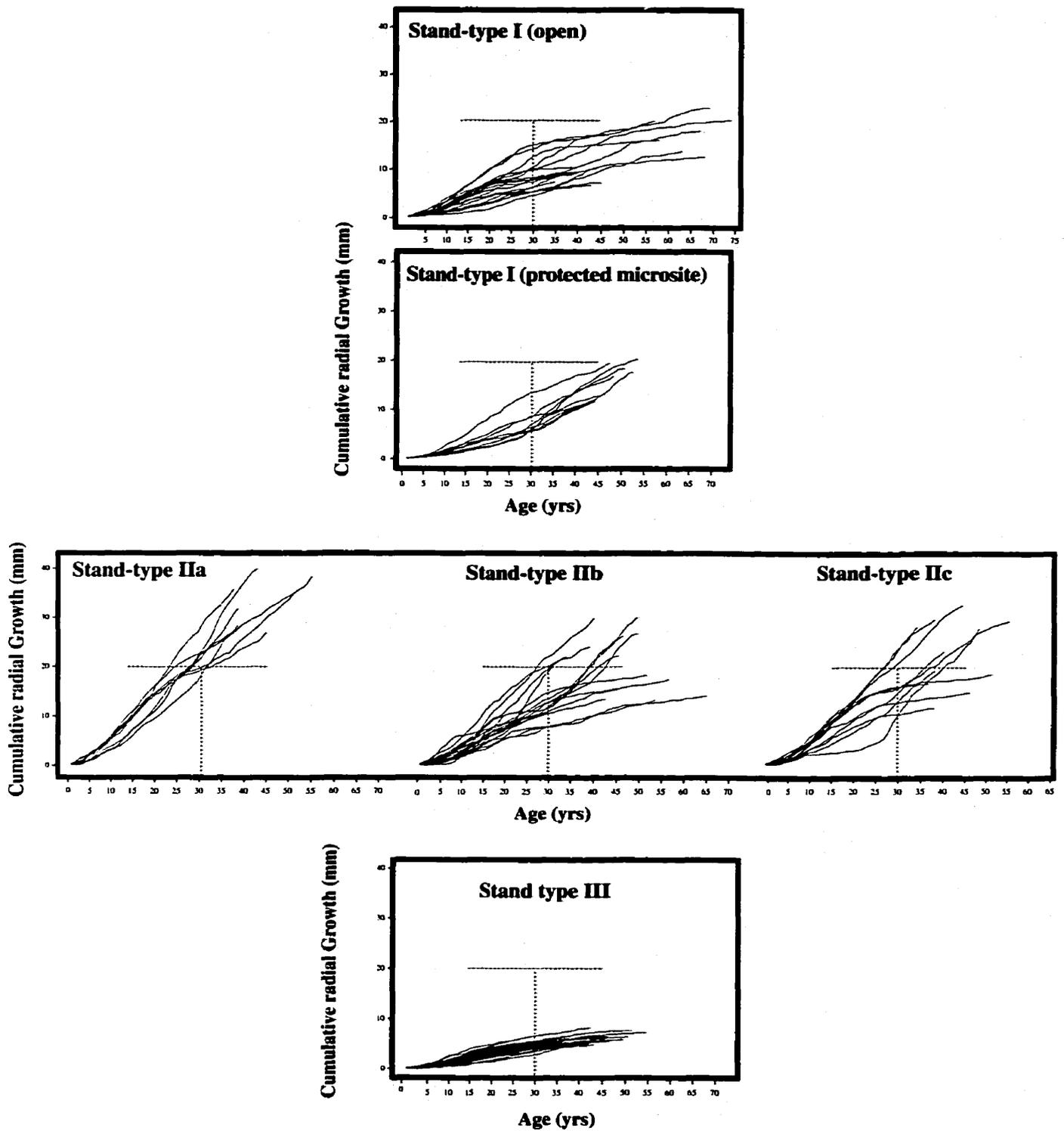


Figure 5.2. Cumulative incremental growth of interior Douglas-fir regeneration (0.5 - 5m in height) across stand-type I, II (including its variants IIa, IIb and IIc) and III. For subtypes IIb and IIc growth was determined for regenerating individuals underneath an established canopy (dark line) and for individuals growing within gaps (grey line). Line demarking radial growth at 30 years of age was superimposed on all graphs for comparison purposes.

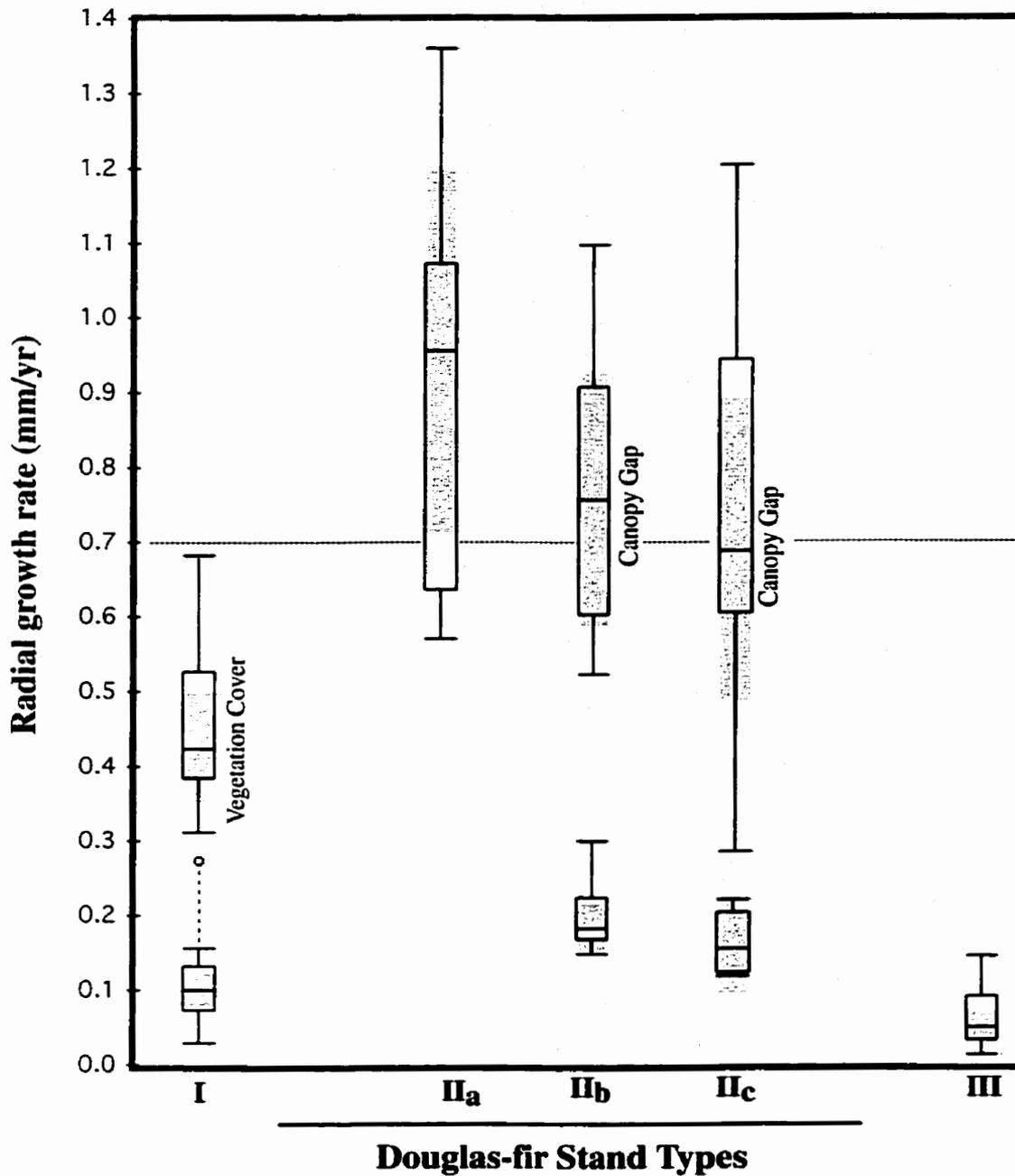


Figure 5.3. Radial growth rate distribution of douglas-fir regeneration (0.5-5m in height) across the three stand-types and sun-types. Radial growth rates were calculated for the last 5 year of growth of all sampled individuals ($n = 85$).

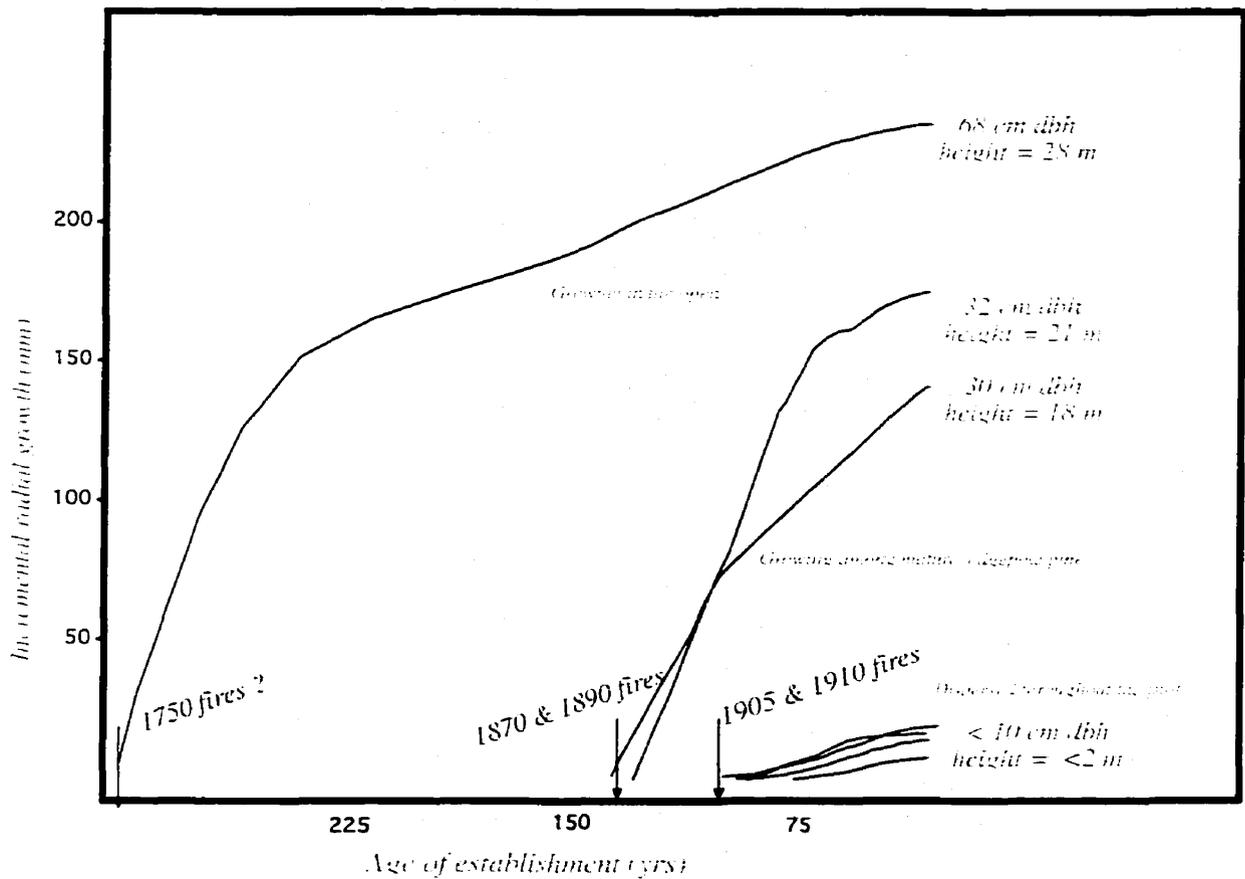


Figure 5.4. Forest profile of stand-type Ib taken from a 10 x10m plot near Tunnel Mountain, Banff National Park. Canopy and subcanopy Douglas-fir were cored 30-60 cm from the base. The oldest individual aged at 248 years in a relict tree, extensive dead back at the top and a 2.4m fire scar along the south-face of the tree. Saplings growing beneath an established canopy showed a notable decline in growth rate compared to canopy and subcanopy trees. Intense below ground competition for resources seriously compromises productivity.

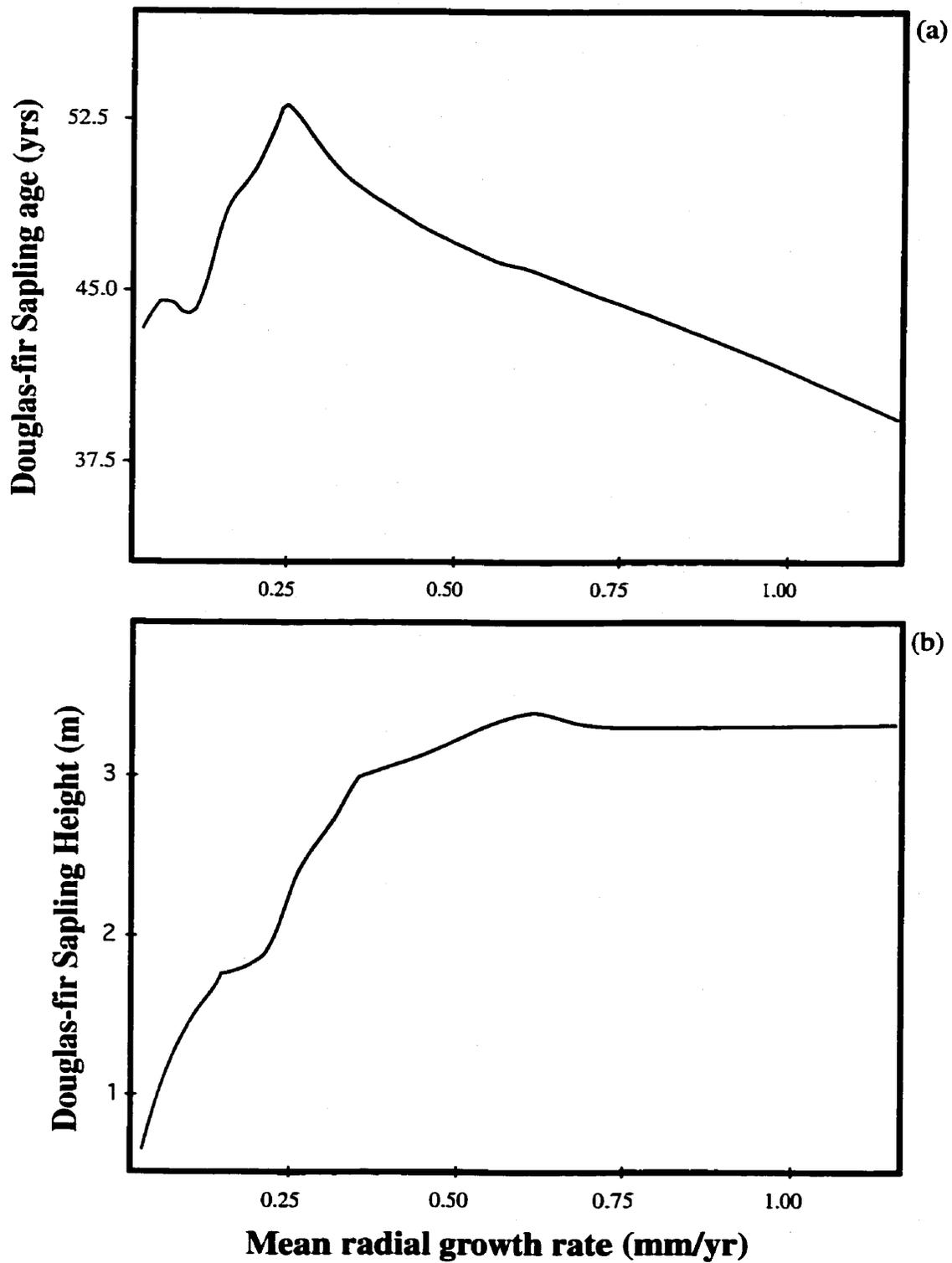


Figure 5.5. Douglas-fir sapling height (a), age (b) and radial growth rate relationships. the data points were smoothed using locally weighted regression.

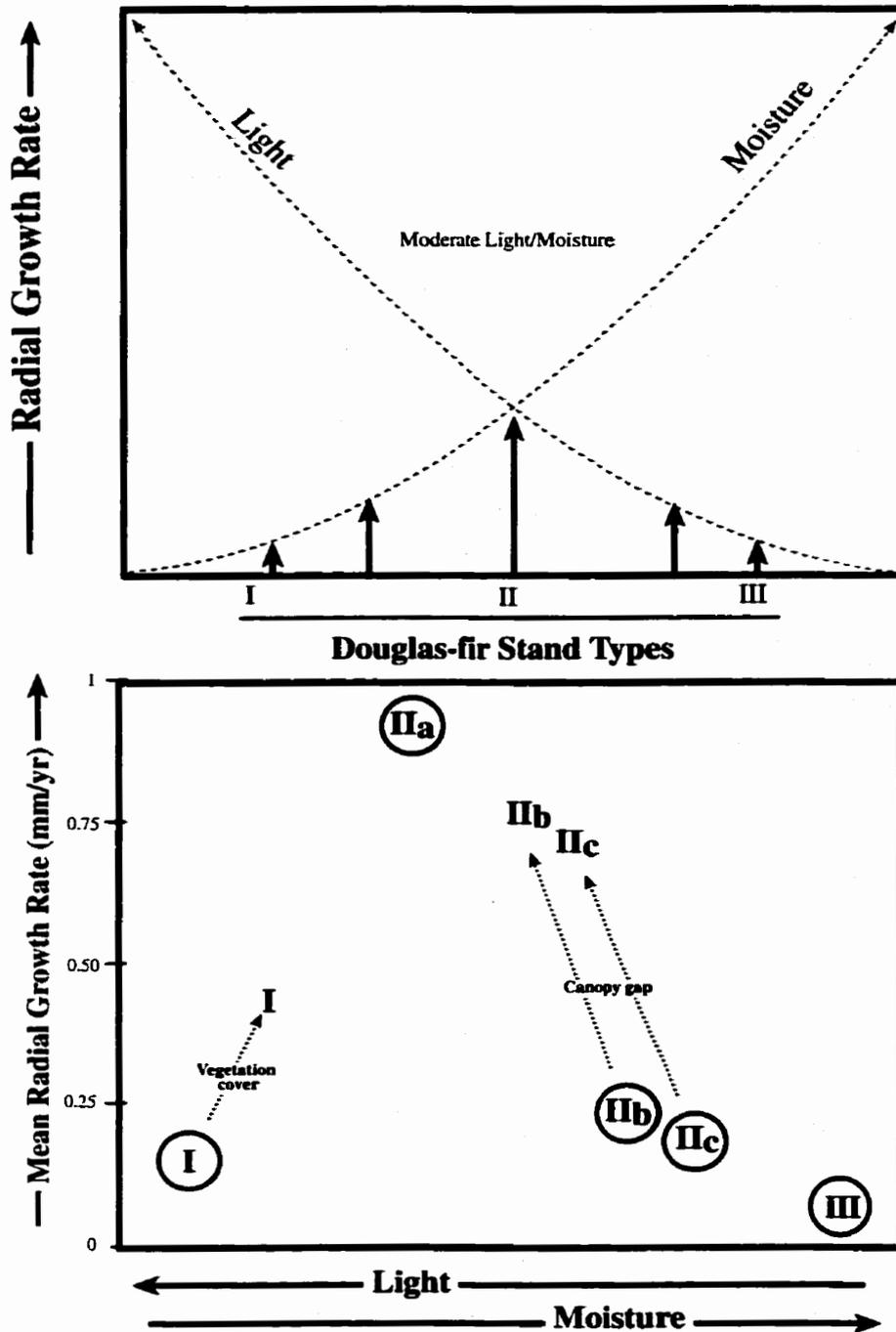


Figure 5.6. Douglas-fir radial growth rate model. Position of stands are based on the mean CA scores for each stand-type along the first ordination axis (x-axis) and the mean radial growth rates per stand-type (y-axis).

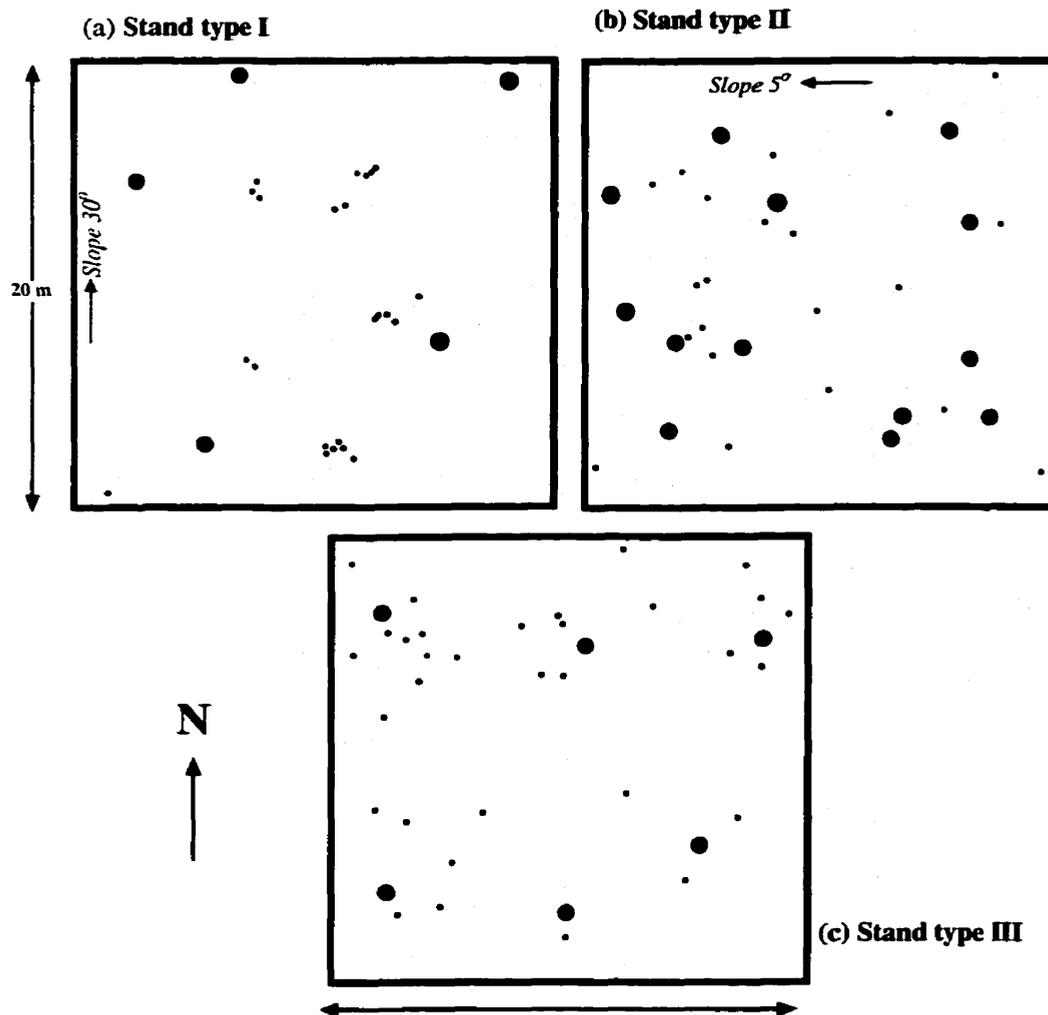


Figure 5.7 Spatial Distribution of Douglas-fir saplings ($\leq 5\text{m}$) and mature trees (subcanopy and canopy individuals $> 5\text{m}$) from representative sites of each of the three stand types. (a) Pyramid lakes, Jasper National Park: xeric stand, with most of the regeneration relegated to protected microsites (microtopographic depressions or vegetation cover). (b) Dier Pitts, Kootenay National Park: Mesic mixed-stand of white spruce, aspen, lodgepole pine and Douglas-fir, regeneration scattered throughout, tallest individuals found in canopy openings. (c) Mount Burgess, Yoho National Park: Hygric old-growth forest, most of the Douglas-fir regeneration ranges from 0.25 -0.95 m in height, and relegated to the base of mature trees

Table 5.1. Douglas-fir tree regeneration characteristics, the mean and range (in parenthesis) of Age, Height, DbaseH, as well as growth rate patterns of suppression and release for all sampled individuals.

| Stand-type | Forest Structure | <i>n</i> = | Age (yrs) | Height (m) | Basal Diameter (cm) | No. of periods of suppression | No. of Yrs of suppression | No. of periods of release | No. of Yrs of release |
|------------|------------------|------------|------------|-----------------|---------------------|-------------------------------|---------------------------|---------------------------|-----------------------|
| I | open | 17 | 50 (35-73) | 2.49 (1.1-5.1) | 2.63 (1.4-4.6) | 1,4 (1-2) | 34 (5-65) | 0.38 (0-1) | 10.2 (3-19) |
| I | Vegetation cover | 9 | 46 (40-52) | 3.22 (2.8-3.7) | 3.1 (2.1-4.1) | 1,3 (1-2) | 19 (6-27) | 0.6 (0-1) | 8.4 (5-18) |
| | | 26 | | | | | | | |
| IIa | Canopy cover | 8 | 42 (36-54) | 3.74 (3-4.8) | 6.6 (5.3-8) | 1,1 (0-2) | 7 (4-12) | 1.5 (1-2) | 20.7 (7-30) |
| IIb | Gap | 8 | 42 (32-49) | 3.25 (3-4.2) | 5.07 (4.2-6) | 0.75 (0-2) | 9.7 (6-14) | 1.5 (0-2) | 12.5 (3-22) |
| IIc | Gap | 7 | 42 (34-55) | 2.5 (1.4-4.1) | 5.45 (3.8-6.5) | 0.71 (0-2) | 7 (4-12) | 1 (0-1) | 14.8 (10-21) |
| IIb | Canopy cover | 7 | 50 (35-64) | 1.74 (1-3.4) | 2.89 (1.7-3.7) | 1.57 (1-3) | 28.4 (6-50) | 0.71 (0-2) | 6.8 (2-12) |
| IIc | Canopy cover | 4 | 43 (37-51) | 1.38 (1.1-1.8) | 3.11 (2.3-3.7) | 1.25 (1-2) | 19.4 (4-24) | 1 (0-1) | 4.8 (2-10) |
| | | 34 | | | | | | | |
| III | Canopy cover | 25 | 40 (25-54) | 0.63 (0.5-0.95) | 1.34 (1.1-1.8) | 1 (-) | 40 (25-54) | - | - |
| | | 85 | | | | | | | |

Suppression : GR < 0.60 mm/yr sustained for ≥ 4 years

CHAPTER 6

REGENERATION & STAND DYNAMICS OF DOUGLAS-FIR

6.1 INTRODUCTION

6.1.2 Stand Dynamics

Disturbance is the single most important factor driving vegetation dynamics in boreal-montane forests of western Canada (Johnson et al. 1998; Johnson and Gutsell 1994). In the Canadian Rockies, the pervasive influence of fire determines forest structure, composition, and equilibrium. Fire behaviour in turn is influenced by spatially heterogeneous landscapes resulting in differential fire effects. Variation in wind conditions, topography, and firebreaks (e.g., water bodies, low fuel loads) all contribute to the heterogeneous nature of fire on the landscape and ultimately to vegetation pattern (Lertzman et al. 1998). The complex age- and size-structure of boreal mixedwood and montane systems is a result of frequent spatially complex fire behavior and can have important implications for stand dynamics (Lieffers et al. 1996; Cumming et al. 1996; Turner and Romme 1994). Survival of mature seed bearing trees is an important factor controlling seed source availability following fire (Eberhart and Woodard 1987). The likelihood of encountering residual vegetation following fire not only depends on landscape attributes but also species attributes. Live crown height and thermal insulation of the vascular cambium are considered critical characteristics for being able to tolerate the effects of low to moderate intensity fires. Differences in stand productivity may also offset the impact of fire. Marginal sites such as those found on excessively well-drained slopes limit the 'homogenizing' effect of a fire by reducing fuel loads. The composition and age structure of forest stands in the Canadian Rockies is a result of the synergistic interactions between disturbance types of varying intensities, episodic 'interdisturbance' recruitment events, climate, and species-attributes (Parish et al. 1999).

Most studies that have looked at forests dynamics in western Canada have either examined fire initiated stands or old-growth forests (Ishii et al. 2000; Johnson et al. 1994; Lieffers and Stadt 1993; Edmonds et al. 1992; Franklin and DeBell 1988). The complex vertical development of mature boreal-montane systems is often not a result of successional development but rather the differential growth response of contemporaneous individuals undergoing competition. The probability of canopy turnover is thus dependent on fire (Johnson et al. 1999), the potential longevity of subordinate species, and their tolerance of understory conditions (Johnson et al. 1994). Since average tree expectancy of boreal species is related to mean fire frequency, canopy replacement of understory individuals will be rare (Johnson et al. 1998; Johnson, et al. 1994; Johnson and Miyanishi 1991). Given the pervasiveness of fire in boreal-montane ecoregions a majority of the landscape will be

maintained at the initial cohort phase (Johnson et al. 1994). In the case of interior Douglas-fir stands, the ability of mature trees to survive low-intensity ground fires enables them to maintain canopy and subcanopy dominance for hundreds of years. Thus, in the Rockies older age classes exist not only as a function of differential fire behaviour but also as a function of differential life history and species attributes. Few studies have addressed the dynamics of fire dependent forest communities characterized by complex age structures. In this study we examined the regeneration and successional development of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) stands in Canada's four mountain parks (Banff, Jasper, Kootenay, and Yoho National Park).

6.2 OBJECTIVES

The objectives of this study are to elucidate the patterns of regeneration and stand dynamics of the three interior Douglas-fir stand types.

- To determine and quantify the factors and conditions affecting the regeneration dynamics of interior Douglas-fir in the four mountain parks. The age-size structure of stands will be determined and used to develop a synoptic regeneration model.
- To develop a predictive forest regeneration model for determining the future composition and structure of interior Douglas-fir stands.
- To discuss the implications of disturbance history, differential mortality, and management on the long term stand dynamics of Douglas-fir communities in Canada's four mountain parks.

6.3 METHODS

6.3.1 Regeneration

Proportional Canopy Index

Proportion frequencies were computed for all Douglas-fir tree canopies classes within each sub-variant. Index values range from 0 (absence) to 1 (high frequency). For example an index value of 0.85 for canopy 5 means that within these stands Douglas-fir seedlings occurred in 85% of the sampled plots.

Canonical Correspondence Analysis

Canonical correspondence analysis was used to determine the regeneration requirements of 5 tree species associated with Douglas-fir. For each species, three pseudospecies were created to represent seedlings (canopy 5), samplings (canopy 4), and low subcanopy (canopy 3) individuals. The analysis was constrained by 8 'site variables' defined as factors or conditions associated with high recruitment within each stand.

6.3.2 Regeneration model

The regeneration model was developed using the proportion of stands containing Douglas-fir regeneration in canopies 3 and 4. Positions of each the stand-type variants were determined based on the ordination results and canopy cover. Since the first axis of the Correspondence Analysis (see **Fig 4.20**) is interpreted as a complex moisture gradient, the relative positions of the 7 sub-type were superimposed along the x-axis. Total canopy cover was used to determine the degree of light availability, results were ranked on an ordinal scale and superimposed along the y-axis. Elliptical concentric regeneration density contours were

developed based on the proportion of stands contains recruitment in canopy 3 (2-5m in height) and 4 (0.5-2m in height). Lower canopies were omitted from the analysis to decrease the probability of stem mortality.

6.3.3 Successional model

Successional trajectories based on age-size relationships assume that life-history traits and demographic parameters (mortality, natality and growth rates) are similar both within and between species (Bergeron and Dubuc 1989). Temporal changes in growth conditions within a stand often results in the differential development of individual trees making it difficult to interpret age-size relationships (Johnson et al. 1998; Ishii et al. 2000). Selective biotic disturbances, such as browsing as well as the suppression of the regenerating trees by an established canopy can mask successional trends (Williams et al. 1999).

The observed vertical stratification of canopy tree species was used to infer probable successional 'trajectories' for seven stand sub-types delineated by cluster analysis (see **chapter 4**). For each sub-type, frequencies of occurrence of the three dominant tree species (Douglas-fir, white spruce and lodgepole pine) were determined in each of the three upper canopy layers (canopy, height > 10m; upper sub-canopy, 5-10m; and lower subcanopy, 2 - 5 m). Saplings (0.5 – 2 m) and seedlings (< 0.5 m) were not included in the analysis, since high mortality rates are characteristic of these lower canopies (Bergeron and Dubuc 1989).

The data set thus incorporates frequency values of Douglas-fir, lodgepole pine and white spruce in each of 21 'pseudo-stands': seven sub-types (Ia, Ib, IIa, IIb, IIc, IIIa, & IIIb), each with three tree canopies. Size-class ordination (using correspondence analysis, CA) was used to summarize a three species x 21 'pseudo-stands' data set (see McCune and Allen 1985; Bergeron and Dubuque 1989). Successional vectors were created for each of the 7 sub-types by sequentially linking the coordinate positions of the 3 canopy strata for each sub-type. Pseudo-stands were linked in the order canopy - upper subcanopy - lower subcanopy, under the assumption that subcanopy trees will successively enter the canopy as the current canopy trees die (barring a catastrophic disturbance). Ordination scores for the three tree species were superimposed on the ordination biplot to aid interpretation. Successional trajectories were interpreted based on vector linearity, direction, and length: a short, non-linear vector implies self-replacement, where as a long, linear vector indicates a shift in tree species composition between strata (Carleton and Maycock 1978). It is important to note that this approach fails to account for climatic change, differences in species growth rates, and differential mortality between canopy layers (both density-dependent and density-independent). For example, ungulate browsing may alter theoretical trajectories if some species saplings are favoured over others.

6.4 RESULTS

6.4.1 Regeneration

Proportional Canopy Index

Results clearly indicate a wider dispersion in canopy index values within moisture and light limited sites. Sub-type Ia, was characterized by mature canopy trees with <50% of plots having individuals in the understory. Protected micro-sites within Ib promoted the recruitment of seedlings into these stands resulting in their high frequency values. Canopy index values of intermediate stands (e.g., IIa-IIc) were more aggregated. Sub-type IIa and IIb were unique based on the fact that not all plots in these stands had Douglas-fir present in the upper canopy. Since canopy classes were based on heights, the low incidence of large canopy trees in a few of the plots maybe a result of subcanopy Douglas-fir individuals being scattered among larger mature lodgepole pine. Sub-type IIc, is a slightly older stand (maximum age of relic Douglas-fir tree around 300 years), thus the upper canopy is dominated by the presence of mature Douglas-fir. Sub-type IIIa and IIIb, clearly show high seedling recruitment but low subcanopy and low subcanopy stem frequencies (**Fig. 6.1**).

Canonical Correspondence Analysis

Results from the CCA indicate that white spruce, western redcedar, and subalpine fir require old-growth conditions for regeneration. Most of the seedlings and saplings of these species were encountered on decaying wood and/or on extensive feathermoss layers. *Hylocomium splendens* was a good indicator of stand conditions (see **Appendix 5**) and was chosen based on its requirement of high forest floor humidity and nutrient levels. Douglas-fir regeneration seems to favour conditions with moderate moisture/nutrients levels as well as canopy cover. On the otherhand species such as aspen and lodgepole pine seems to be 'recruiting' into sites characterized by south-facing steep slopes. Most of these individuals were present in recently burned stands (**Fig. 6.2**).

6.4.2 Regeneration model

The regeneration model indicates that understory Douglas-fir recruitment is limited by light and moisture availability (**Fig. 6.3**). Within stand-type I, regeneration is often limited by soil moisture deficiency early in the growing season. Subtype Ia has the lowest percentage of plots with regeneration present in canopy 3 and 4 (25-40%). Subtype Ib has higher vegetation cover, which tends to offset evapotranspirational stress. In these stands 41-55% of plots have lower subcanopy regeneration present. Stand Type II displays a wide range in lower subcanopy recruitment. Sub-type IIa, has similar regeneration patterns to Ia, even though moisture levels are high, recruitment tends to be limited by competitive interactions among species. Sub-type IIb, has 41-55% of its plots containing lower subcanopy

recruitment, with growing conditions similar to those encountered in Ib (**Fig. 6.3**). Sub-type IIc, has the highest recruitment levels of any stand type variant, with more than 55% of its plots containing recruitment in the lower subcanopy. Moderate moisture and light levels seem to promote seedling establishment and growth within these stands. Stand type III has the lowest recruitment of any stand type. In these forests, light attenuated by a tall canopy significantly limits regeneration densities in the lower subcanopy. Subtype IIIa has similar recruitment compared to Ia (moisture limited) and IIa (competitive interactions) with only 21-55% of plots containing lower subcanopy recruitment. Sub-type IIIb has the lowest recruitment levels of any stand variant with less than 25% of plots containing lower subcanopy regeneration (**Fig 6.1**).

6.4.3 Succession Model

Results of the successional trajectories developed for each of the stand types indicate that canopy development will continue to favor Douglas-fir canopy dominance (**Fig 6.4**). Cyclic successional vectors are only present in stand-type I, indicating the persistence of current canopy conditions. Stand-type II show the greatest variation in stand development. The successional vectors of the three stand-type II variants indicate a shift in canopy composition; characterized by relatively long linear vectors. Both sub-type IIa and IIc were initially characterized by a lodgepole pine dominated canopy: in the absence of disturbance successful understory recruitment and growth will favor the development of a Douglas-fir canopy. The successional trajectory of Sub-type IIb is similar, however the starting point of these stands are different compared to the other two sub-variants. Instead of a pine dominated post fire stand, IIb is characterized by a mixed pine/aspen post-fire forest altering the initial starting point of the successional vector. Stand Type III is clearly undergoing a shift from a Douglas-fir dominated forests to one dominated by white spruce. The presence of other late successional species such as western redcedar and subalpine fir tend to offset what would otherwise be a linear shift in canopy composition (**Fig. 6.4**).

6.5 REGENERATION DYNAMICS OF DOUGLAS-FIR

6.5.1 Regeneration Model for Interior Douglas-fir

The regeneration model, which is based on recruitment in the sapling and lower subcanopy layers, reveals that Douglas-fir recruitment is dependent on both available understory light (a function of canopy closure and shrub cover) and soil moisture conditions (Fig. 6.3). Recruitment is greatest in sites of intermediate soil moisture and moderate understory light conditions (particularly sub-type IIc, and to a lesser extent sub-types IIa & IIb). Douglas-fir recruitment in sub-type Ia is compromised by the combination of low soil moisture and high incident light, which creates highly xeric, 'droughty' seedbed conditions. In these stands, saplings and lower subcanopy trees were generally restricted to 'protected' (shaded) microsites. In sub-type IIb, soil moisture conditions are adequate, but high shrub and subcanopy cover results in shaded conditions and reduced Douglas-fir recruitment even though growth is maximize in openings. Similarly, high canopy closure in stand type III (sub-types IIIa & IIIb) results in greatly reduced light levels in the regeneration layer. Douglas-fir seedlings are often abundant, suggesting that seedbed conditions are ideal for germination. However, light levels are so low that these seedlings rarely reach the sapling stage (see Chapter 5).

Regeneration Dynamics in Stand-Type I

Douglas-fir recruitment in this stand-type is low (very xeric, sub-type Ia) to moderate (xeric, sub-type Ib; Fig 6.3). Regeneration in these stands appears to be limited by a combination of soil moisture deficiency, high summer soil temperatures, and low nutrients (c.f. Rose et al. 1999; Stringer and La Roi 1970; Stringer 1966). Nitrogen is often the most limiting nutrient in xeric sites within Banff and Jasper National Parks (Stringer 1996). Low nutrient status, together with evapotranspirative stress, appears to limit recruitment (Stringer and La Roi 1970). Under xeric conditions, regeneration is relegated to sheltered microsites where the physiological effects of excessive light stress are reduced. The importance of refuge plants is critical not only for reducing the effects of open-conditions but also for providing essential connections to ectomycorrhizal fungi. Horton et al (1999) found that the survival of Douglas-fir advance regeneration was improved for individuals growing near patches of *Arctostaphylos glandulosa* spp. *glandulosa* in chaparral communities in the central coast of California. The presence of ectomycorrhizal fungi associated with *Arctostaphylos* is critical for the growth and survival of Douglas-fir seedlings (Hagerman et al. 2001). Most of the advance Douglas-fir regeneration encountered in stand-type I occurred in the proximity of *A. uva-ursi* (see Fig 6.2).

Factors such as evapotranspiration stress, high daily temperatures and low soil nutrients limits Douglas-fir regeneration, but they have an even greater effect on limiting the recruitment of less drought-tolerant species such as white spruce (Hogg and Schwarz 1997).

Historically, frequent low-intensity fires (less than 30 year return cycles) in these xeric sites maintained open 'parkland-like' Douglas-fir stands, by limiting conspecific regeneration and incursion of potential competitors. Mild winter chinooks followed by a return to sub-zero temperatures may increase frost-induced dieback of seedlings and stems on these exposed southwest-facing slopes. Douglas-fir is near its northeastern distributional limit in the Alberta Rockies, suggesting that climatic extreme such as severe frosts or drought may play an important role in the long-term population dynamics of these forests.

Regeneration Dynamics in Stand-Type II

Regeneration of Douglas-fir in this stand-type may be low, moderate, or high (Fig. 6.3). In the most xeric sub-type (IIa), regeneration is moderate and limited primarily by low available soil moisture. Regeneration in sub-type IIb may be limited by canopy cover (the result of a denser canopy and much higher shrub cover). Canopy gaps promote the growth of already existing understory regeneration, but seems to have no impact of regeneration density. Some of these stands also have high graminoid cover, dominated almost exclusively by *Calamagrostis rubescens*. This species forms extensive rhizomatous mats that physically interfere with seedling root development and compete for soil moisture and nutrients (Rose et al. 1999). Douglas-fir regeneration density is greatest in the most mesic variant of this sub-type (IIc), however stem competition with other species reduces growth (see chapter 5).

Regeneration patterns in this stand-type are complex: the combination of two limiting conditions (light and soil moisture) has synergistic effects on seed germination, establishment, growth, and survival. While higher herb and shrub cover may provide protection from excessive moisture loss, herbs and shrubs also compete for soil water and light with tree seedlings. The canopy cover provided by 'early-successional' species such as lodgepole pine may reduce soil water loss, while also reducing understory wind conditions and minimizing exposure to climatic extremes (Kimmins 1987). Shrub and/or advanced regeneration cover also decrease the amount of light energy reaching the ground thus reducing the effects of light stress (the nurse-plant effect). However, if light levels are too low, Douglas-fir saplings enter a suppressed state (Williams et al. 1999; Chen and Klinka 1997) responding only when light levels increase. Variations in soil moisture content resulting from small-scale changes in topography, vegetation cover and/or soil texture may also be important. The presence of isolated feathermoss patches in sub-xeric sites is indicative of the complex physiographic variability encountered in this stand.

Regeneration Dynamics in Stand Type III

A deeply shaded understory (the result of high canopy cover, particularly in sub-type IIIb) strongly limits Douglas-fir advance regeneration and growth in this stand-type. In old-growth coastal Douglas-fir stands, the size of canopy gap openings is an important determinant of recruitment (Stewart 1989). Small openings created by windthrow of single trees favour shade-tolerant species such as *Abies amabilis* and *Tsuga heterophylla*. Indeed, Douglas-fir does not regenerate in dense old-growth forests (Stewart 1989). More shade-tolerant species (e.g., white spruce, western redcedar) were most commonly represented in the lower subcanopy of stand-type III, although Douglas-fir seedling densities were high. The presence of an organic seedbed, together with extensive canopy cover, may favour germination by reducing the effects of seasonal and diurnal temperature and light extremes (Chen et al. 1996; Stringer 1966). Douglas-fir seed germination is favoured on organic 'bryophytic' substrates (Li and Burton 1994; Rose et al. 1999), possibly because they have high 'biologic activity' by serving as a substrate for nitrogen fixation (Hope and Li 1997). However, the benefits of an organic seedbed may be offset by the tendency for feathermoss mats to desiccate rapidly: their moisture status changes in response to fluctuations in humidity. Furthermore, feathermosses may also 'tie up' nutrients, hinder root-to-soil contact, and increase pathogenic fungal activity (Li and Burton 1994).

In these stands, the combination of low photosynthetic capacity (deeply shaded conditions), high substrate, and atmospheric moisture, and decomposing organic matter greatly increases the susceptibility of Douglas-fir seedlings and saplings to fungal infection. Needle cast fungus and *Armillaria* root disease commonly affect seedlings (and mature trees). In addition, seedling-to-sapling growth of Douglas-fir is severely compromised by prolonged subcanopy light suppression, particularly under hygric conditions (Williams et al. 1999; Carter and Klinka 1998). Under low-light conditions, increasing the leader height imposes much greater maintenance costs, thus decreasing the viability of pole-sized individuals (Williams et al. 1999; Waring 1987).

6.5.2 Spatial and Temporal Dynamics of Recruitment

The spatio-temporal patterns of recruitment in Douglas-fir are determined by numerous environmental and biotic stressors, which either decrease successful seed germination and establishment or reduce sapling survivorship:

Dispersal, Germination and Establishment Stage

In northern forests, tree recruitment tends to be highly episodic and temporally infrequent (McCune and Allen 1985). Establishment of tree seedlings is a function of three factors:

1. Seed Availability

In trees, seed production is proportional to stand basal area (Green et al. 1999). Douglas-fir is a prolific seed producer that 'masts' (i.e. produces large to medium cone crops) at least once every ten years. Seed dispersal is mainly by wind and gravity, although granivores such as red squirrels may also play a role. In low cone-production (non-masting) years, seed depredation by small mammals often depletes the entire seed crop (Silvertown and Doust 1993). In the four mountain parks, high levels of Douglas-fir cone depredation by red squirrels were often observed. Effective seed dispersal (and germination) may therefore only occur during mast years.

2. Seed Bed Conditions

Seed germination and early establishment are strongly affected by seedbed conditions, including litter type and depth (Williams et al. 1990; Collins 1990), soil moisture (Collins and Good 1987), soil nutrients (Chanway and Holl 1992; Stringer 1966) and substrate compaction (Stringer and La Roi 1970). Regeneration of interior Douglas-fir is favoured under conditions of adequate soil moisture and available nitrogen levels (Stringer 1966). Seeds will germinate under a variety of edaphic conditions, but non-organic (mineral) substrates or those with minimal organic matter accumulation (less than 5 cm depth) are preferred. Decomposing logs are normally an important seedbed for species such as white spruce. However no seedlings were encountered growing on decomposing wood, since in most stands dry conditions tend to slow down microbial activity associated with decomposition. Well-aerated sandy loam soils are particularly favoured (Stringer 1966). Soils of low albedo (e.g., those blackened following fire) are unfavourable for seedling development due to high temperature stress. Seedlings also fare poorly on anaerobic substrates such as compacted gleyed soils often encountered in stand-type III (Stringer and La Roi 1970).

3. Climatic Conditions

Growth of interior Douglas-fir seedlings is often slowed by water and nutrient deficiency, and seedling dormancy may be initiated when soil moisture levels are low. This dormant period can extend from midsummer until the following spring (Hermann and Lavender 1990). Drought conditions may prevent germination, or may kill seedlings early in the establishment stage. In addition, early seasonal frosts may kill newly established seedlings (Riech and van der Kamp 1993). Fungal pathogens and insect pests may also severely damage or kill seedlings.

Survival Stage

Seed germination and early seedling establishment are only the first of many stages in tree recruitment. Growing seedlings soon enter the 'survival stage', and a number of factors can affect successful recruitment into the canopy:

1. Ungulate Browsing

Tree saplings are vulnerable to ungulate damage, including browsing and trunk-rubbing (Engelmark 1993; van Egmond 1990). Browsing of Douglas-fir saplings generally occurs in winter when alternate browse is not available; the extent of tissue removal is dependent on snow depth (Stringer 1966). While browsing seldom results in direct mortality, it greatly reduces photosynthetic potential and renders saplings more susceptible to pest and pathogen attack (Webb 1981; Franklin et al. 1987). The effect of photosynthetic tissue removal has a lag affect of growth, with most trees showing a reduction in growth the following year. Dry years tend to increase herbivore pressure on seedlings/saplings during the winter. Stored carbohydrates normally utilized as backup for root growth, needle production, and secondary defensive compounds must now be reallocated to repair damaged tissue. This can have detrimental affects on the long term growth and survival on individuals.

2. Interspecific Competition

Shrubs and herbaceous vegetation may compete with tree saplings for light, soil moisture, and/or soil nutrients (Shafi and Yarranton 1973). Interspecific competition from shrubs and herbaceous vegetation has been shown to reduce the survivorship of Douglas-fir saplings (Rose et al. 1999; Karakatsoulis and Kimmins 1993).

3. Light Quantity and Quality

The deep shade cast by established tree canopies results in a low-light understory environment (Li and Burton 1994). Douglas-fir is 'moderately' shade-tolerant, since established saplings require low-moderate light conditions to survive. Shade-tolerance may be greater under more xeric conditions (Carter and Klinka 1992; Krajina 1969). Heavily shaded

Douglas-fir saplings maintain a limited number of healthy branches in the live crown, and allocate more resources to lateral growth (Chen and Klinka 1997). The resulting 'umbrella-like' growth form is efficient in capturing diffuse light and sunflecks while keep respiratory cost low (Williams et al. 1999). At 5% of full light, sixty year old interior Douglas-fir saplings may grow only a few millimeters per year (see **chapter 5**; Williams et al. 1999; Messier et al. 1999). Such highly light-suppressed saplings often respond poorly to canopy openings (i.e., a sudden increase in understory light conditions). Furthermore, long-term suppression increases the susceptibility of older saplings to fungal pathogens and/or insect pests (Mitchell et al. 1993). Suppressed saplings are also more vulnerable to snow compaction, and to disturbances that may result in damage or removal of the apical dominant stem or 'leader'. Removal of the leader greatly reduces the likelihood that an individual will make it into the upper canopy (Weir and Johnson 1998).

4. Disturbance Frequency

Rapidly growing, shade-intolerant trees species such as lodgepole pine are favoured in areas where large-scale catastrophic disturbances are frequent (i.e., within the mean lifespan of tree species; Johnson and Miyanishi 1995). By contrast, more localized regions of the landscape that evade the ravages of these disturbances will be succeeded by slower-growing, more shade-tolerant species such as Douglas-fir. However, tree recruitment may be compromised in areas where low-intensity disturbances (e.g., ground fires) are frequent. Most Douglas-fir saplings develop a thick outer bark and relatively high (around 2m) crown height by 40-50 years of age. Recurrent low-intensity ground-fires with intervals matching the 'survival-age' of Douglas-fir regeneration may not have a significant impact on understory tree mortality.

6.6 VEGETATION DYNAMICS OF DOUGLAS-FIR STANDS

6.6.1 Forest Succession Model

Long-term successional trends are determined by a multitude of factors, including site history, disturbance regime, habitat type, the propagule pool, seed sources and seed dispersal, resource availability, differential species performance, and the legacy of pre-disturbance species composition (Pickett et al. 1987; McCune and Allen 1985; Shafi and Yarraton 1973; Heinselman 1973). Asynchronous, stochastic events often result in non-linear successional pathways, making it difficult to predict a stable end point.

Static size-class ordination is an effective method for summarizing probable successional trajectories in the absence of a catastrophic disturbance regime. This approach assumes that species composition and abundance in the subcanopy and regeneration layers is indicative of the future forest canopy. The sapling and seedling layers are not normally used in such analyses, since these layers are characterized by high differential mortality (Bergeron and Dubuc 1989; McCune and Allen 1985). Knowledge of growth rates is critical in order to determine the likelihood of survival. In most Douglas-fir stands recruitment densities and growth rates are correlated. In our analysis, only 'well-established' trees (those in the canopy and subcanopy layers, greater than 2 m in height) were used. The resulting ordination (Fig. 6.4) is summarized below.

Succession in Stand-Type I

These stands (both subtypes Ia and Ib) are undergoing little change in terms of their canopy-subcanopy dynamics. Both sub-type vectors are relatively short and non-directional, suggesting that these Douglas-fir stands are self-perpetuating (Fig. 6.4). Other tree species are infrequent on the subcanopy layers. The suppression of periodic groundfires in these stands may alter understory composition and structure, and eventually result in more multi-aged and closed-canopied Douglas-fir stands. However, because recruitment is highly episodic and generally limited to topographically protected 'safe-microsites' (e.g., shaded depressions), the vast majority of these stands will likely retain their open-canopied physiognomy for many years to come.

During the Little Ice Age, open-canopied Douglas-fir stands were maintained for centuries by recurrent, low intensity fires (Arno 1976, 1980; Hall 1976). The geographic expansion and contraction of these forests during the last 8,000 years reflect changes in climatic conditions and regional fire regimes (Hallet 1996; Richie 1996; Luckman and Kearney 1986). During the warm Hypsithermal period, Douglas-fir forests dominated much of the montane and lower subalpine ecoregions (Hallet 1996; Luckman and Kearney 1986; Stringer 1966; Patton 1963). The cooler and wetter conditions of the Neoglacial period 'forced'

Douglas-fir onto marginal sites characterized by dry and warm south-facing slopes: to this day, the species is most commonly found in such areas. These 'refugial' stands are an important seed source for potential colonization into more mesic habitats. These stands may serve as a genetic pool during cooler and wetter periods or dispersal nuclei during warmer, drier conditions. The long-term presence of Douglas-fir on the landscape under various regional climate change models is strongly dependent on factors such as microclimate, disturbance history, and seed source proximity.

Most of these stands are located in major valleys near 'high-use' areas (visitor use, park infrastructure), where fire suppression has been practiced since the turn of the century. As a result, increased fuel loads may in some cases increase the risk of a stand-replacing fire. For example, the incursion of white spruce (mainly sub-type Ib) may shift the local fire regime from non-lethal surface burns to catastrophic stand-replacing fires (Johnson 1992). However, this is not expected to occur in most stands, since 'sub-optimal' site conditions (low soil moisture and nutrients) have resulted in a very limited establishment of white spruce and fuel accumulation.

Succession in Stand-Type II

The succession vectors for this stand-type (particularly sub-types IIb and IIc, and to a lesser extent IIa) are strongly directional, and indicate a shift in canopy dominance from early-successional lodgepole pine (occasionally trembling aspen) towards dominance by interior Douglas-fir (Fig. 6.4). Lodgepole pine currently dominates the canopy of most of these stands, but it is rarely present in the regeneration layers. By contrast, interior Douglas-fir is present in both the canopy/sub-canopy and regeneration layers of most stands. In the absence of fire, a mixed multi-storied forest will develop as the lodgepole pine canopy 'breaks apart' and suppressed individuals of Douglas-fir are released. The abundance of shade-tolerant trees, particularly white spruce, will increase over time and eventually dominate the regeneration layers. As the density of the canopy-subcanopy increases, the potential of fungal pathogen or pest outbreaks may increase (Herman and Lavender 1990). Greater vertical stratification of the canopy may also increase the chances of a catastrophic fire. Should such a fire occur, lodgepole pine would again be favoured.

Understory composition and structure are expected to change as forest canopy density increases. Shade-intolerant shrubs such as buffaloberry (*Shepherdia canadensis*) will decline in abundance. Buffaloberry is a food source by both black and grizzly bears, and is an important nitrogen fixer in nutrient-poor sites (Bormann 1988). Graminoid cover (particularly *Calamagrostis rubescens*) is also expected to decline as canopy cover increases (Lieffers et al. 1999). By contrast, feathermoss cover (particularly *Pleurozium schreberi*) is expected to increase.

The majority of Douglas-fir individuals in this stand-type established after the last major fire event, probably from seed produced by 'relict' trees that survived the last fire within the burn area or mature trees from surrounding regions that did not burn. The abundance of lodgepole pine (a pyric species) indicates that the fire regime of these stands is characterized by catastrophic burns (by contrast, ground-fires are characteristic of stand-type I). However, the mosaic of stand ages and the presence of 'relict' interior Douglas-fir trees indicates a complex fire history.

Succession in Stand-Type III

The successional vectors for this stand-type (both sub-types IIIa and IIIb) are short, and are converging toward white spruce. Low light levels in the understory prevent Douglas-fir seedlings from entering the regeneration layer (based on their current growth rates), with the result that Douglas-fir will continue to be a minor component of these stands. The deeply shaded conditions are more conducive to white spruce regeneration, although western redcedar and/or subalpine fir may also regenerate successfully depending on the proximity of parental trees. The success of white spruce in these stands is primarily attributed to seedbed conditions (see Fig.6.2). Although spruce prefers to establish on mineral substrates, rotten logs have been documented to be a suitable substrates for white spruce seedling establishment and growth (Lieffers et al. 1996). Unlike stand type I and II, the moisture and low light levels of Stand type III results in higher decomposition rates of felled trees. Exposure to sunlight can bleach wood making it harder to decompose rapidly. Organic substrates such as rotten wood elevate seedlings above the litter accumulation zone preventing smothering and increasing local light levels. In the boreal-mixwood region of Alberta advance recruitment of white spruce is often encountered on decomposing wood (Lieffers et al. 1996; Nienstaedt and Zasada 1990). Although capable of establishing on organic seedbed, Douglas-fir is unable to sustain growth under low-light conditions (Krajina 1969). When present the regeneration of western redcedar relies heavily on vegetative propagation (Minor 1990). This resulted in high and low-density phases of cedar. Vegetative layering seemed to be promoted through physical damage to the main stem, or by the partial burial of low lying horizontal branches caused by felled trees or tall shrubs (Owens and Molder 1980). In these areas Douglas-fir seedling growth was choked out by extensive cedar branch cover promoted through vegetative layering.

These stands may represent remnants of a fire-initiated stand, with relics that established before or during the Little Ice Age (ca. 500 years BP). The physiographic characteristics of these stands reduce both fire frequency and severity, thus favouring the regeneration of shade-tolerant, late-successional tree species. A fire would have to be of very high intensity,

and be preceded by a blocking high-pressure system, to have significant effects on the canopy mortality and replacement (Heinselman 1996).

6.6.2 Alternative Trajectories

Alternative successional trajectories are expected when a natural disturbance (e.g., fire) is taken into account. Depending on their extent and intensity, fires may slow or reverse linear successional trends (Romme and Knight 1981). Low to moderate intensity surface fires facilitate subcanopy and canopy thinning, leaving fire-resistant mature trees intact while killing fire-susceptible species (e.g., white spruce, lodgepole pine) and most of the advance and recent regeneration.

Mature spruce/fir forests are characterized by high fuel densities, and therefore burn at high intensity under dry conditions (Johnson 1992). Catastrophic crown fires kill trees in both the canopy and regeneration layer, and in extreme cases may result in reversion to a herb/shrub-dominated system (Bradley et al. 1992). The recruitment of both early and later-successional species (e.g., Douglas-fir) is dependent upon the proximity of a seed source. Tree seeds may enter from adjacent unburned forest patches, or from scattered 'relict' trees that survive the burn. The type of burn (convective vs. wind driven) and seedbed condition are also important in determining recruitment trends.

Selective ungulate browsing may also slow down canopy succession. In areas with high ungulate densities, Douglas-fir saplings are damaged by either selective browsing during the winter or stem girdling during the rutting season. At high elk densities (>4 animals km^{-2}), palatable conifers such as Douglas-fir are selected over less palatable species such as white spruce (White et al. 1998). Browsing affects sapling performance and survival, and thus has long-term impacts on successional pathways. The 'vagaries of seed production' (McCune and Allen 1985), climatic variation, and the synergistic effects of fire, herbivory, insects and disease may dramatically alter the future composition of a stand for thousands of years. These stochastic processes are, by definition, difficult to predict.

6.5.3 Spatio-Temporal Variation in Fire Mortality Within Douglas-Fir Stands

The persistence of Douglas-fir in the four mountain parks is ultimately dependent on a complex of factors related to disturbance, species vital attributes, and site characteristics. Scattered, long-lived 'relict' individuals that survive catastrophic fires are a critical parental seed source (Lertzman et al. 1998; Tande 1979).

Population Age Distribution of Douglas-Fir

The age distribution of Douglas-fir in the four mountain parks reflects its longevity (greater than 400 years), its ability to survive low-intensity surface fires, and the frequency of stand-replacing burns in the region. Recurrent fires have shaped the age and compositional mosaic of the landscape. Most of the fire initiated stands which established in the late 1800's have fire-scarred individuals of Douglas-fir (and more rarely lodgepole pine) which predate the last major fire event (Rogean 1996; Weir et al. 1995, Tymstra 1991; Masters 1990; White 1985; Tande 1979). Indeed, the largest trees aged in this study generally exceed the estimated 'stand origin' dates (see Fig. 4.7-4.8). This is not particularly surprising, as 'stand origin' is a landscape-scale concept based on data compiled from fire-scars on relict trees (Tande 1979; Masters 1990; Tymstra 1991; Rogean 1996). What follows is a discussion of mechanisms of differential mortality in Douglas-fir stands, and how these may explain the age and spatial distributions of the species in the four mountain parks.

Differential Mortality Theory

Effect of Fire Behaviour on Tree Survival

The spatial heterogeneity of fire behaviour within a burn is complex. Fires often create their own environmental conditions (e.g., convective winds or eddies) and therefore behave in a 'chaotic' manner (Turner 1994). Burned areas form a matrix of two hierarchical spatial scales. At the landscape level, residual patches of unburned vegetation form a mosaic of cohort classes. At finer scales, internal variability within a burned area creates a mosaic of burn intensities (Fig. 6.6; Lertzman et al. 1998; Turner 1994; DeGrandpre et al. 1993; Romme and Knight 1981; Rowe and Scotter 1973; Ritchie 1956). Variations in fire intensity usually reflect changes in stand structure and composition, weather, and topography (Arno 1980).

The shape and extent of large intense burns is determined primarily by wind (Turner et al. 1994; Johnson 1992). In most cases, the burn-pattern created by very intense ($>40,000 \text{ kWm}^{-1}$) and fast spreading ($>10 \text{ m min}^{-1}$) fires is independent of landscape spatial heterogeneity (Johnson et al. 1995; Johnson 1992). Natural fire breaks created by vegetation, topography, drainage, and even roads are often overcome by 'flame spotting' (e.g., Vermillion Pass Fire in Kootenay National Park; Heinselman 1996). Under such a scenario, tree survivorship within a burn will be reduced irrespective of the 'fire-tolerance' of a species. Such fires tend to 'homogenize' the landscape, but relatively minor changes in wind speed/direction and fuel conditions may reduce the intensity of the burn. In the subalpine ecoregion, the probability of burning is independent of stand age, since the fire regime is

characterized by infrequent, high intensity fires (Weir et al. 1995). By contrast, frequent low intensity burns are more typical of the montane ecoregion (Tande 1979).

Propagation of less severe fires is influenced by the condition and contagion of ground fuel, as well as by fine-scale variation in slope, aspect, and wind speed/direction. The intensity and severity of small fires generally decreases with increasing topographic heterogeneity (Larsen 1997). If wind conditions are relatively constant, the heterogeneity of these burns will closely mimic the spatial heterogeneity of the landscape. However, if winds increase or the canopy crown architecture changes, a low-intensity burn can rapidly develop into an intense catastrophic canopy fire (Heinselman 1996). The biological legacy of low intensity fires is reflected in the scattered survivors ('relict' trees) encountered within a stand. Topographic features (slope and aspect) are also important. South-facing slopes burn more frequently than do north-facing ones (Rogean 1996), and the probability of burning is reduced near cool ravines, canyons, depressions and water bodies (Heinselman 1981; Romme and Knight 1981).

The majority of stand-type III sites occur in depressions or north-facing slopes, where the effects of historic fires are expected to be reduced. The presence of mature (>160 years) fire-intolerant species such as subalpine fir, white spruce, and western redcedar in these stands is indicative of the local fire frequency and microclimatic conditions. Higher fire frequencies are characteristic of southwest facing aspects (stand-types I & II); this is attributable to a long duration of high daily maximum temperatures and solar irradiance (see Fig. 4.3; Rogean 1996). The resultant high heat index increases evapotranspiration rates, reducing site productivity and fuel buildup. In addition, soil moisture reserves are generally low since precipitation is limited: low herbaceous cover and slope drainage further increases soil moisture deficiency. Together, these factors increase fire frequency, but reduce fire severity. As a result, periodic fires leave behind a greater number of surviving trees and at the same time reduce competitive pressures (Nash and Johnson 1996; McCune and Allen 1985).

A high frequency of low-intensity fires, together with 'harsh' site conditions, results in a less diverse forest canopy on south-facing slopes (stand-types I & II). The relatively short (<30 years) fire return interval on these slopes results in high sapling mortality. Successful recruitment is therefore often restricted to 'sheltered' microsites, or to episodic periods when the fire interval is increased. Fine-scale topographic irregularities may reduce the local effects of a surface fire, and rocky outcrops may evade fires altogether for much longer periods as they do not have the combustible resources needed to propagate a fire. For example, the ages of Douglas-fir trees on colluvial substrates near Mt. Burgess (Yoho National Park) well exceeded the estimated stand origin date (Tymstra 1991). In Yellowstone National Park, interior Douglas-fir and whitebark pine stands often occur on substrates that evade the effects of fire for long periods (Barrett 1994).

The distribution of 'relict' trees on the landscape is related to site characteristics. On dry, steep south-facing slopes such as stand-type I, individuals are aggregated, whereas they tend to be more randomly located on more mesic, flatter sites (see Fig 5.7). At the landscape level, the highly aggregated spatial distribution of Douglas-fir in the four mountain parks appears to be the result of topographic variability and differential fire behaviour. A combination of low severity fires, topographic heterogeneity, and climatic fluctuations may explain the age-structure distribution of Douglas-fir in the region.

Adaptations to Fire Survival

The vital-attributes of Douglas-fir have enabled the species to endure sub-lethal conditions created by variable fire behaviour. These traits are particularly important in stand-types I and II, which are characterized by naturally high fire frequencies but low intensity (Tymstra 1991; Tande 1979). The architectural and anatomical characteristics of mature Douglas-fir enable the species to evade the potentially lethal effects of fire. Critical surface intensities required for crowning typically increase with increasing live crown base height. For example, a live crown base height of 5 meters with a foliar moisture content (FMC) of 100 requires an intensity of about $2,000 \text{ kWm}^{-1}$ to cause crowning (Johnson 1992). By contrast, a lower crown base of 1.5 m (characteristic of spruce/fir forests) results in crowning at fire intensities as low as $1,000 \text{ kWm}^{-1}$. In mature Douglas-fir trees, the combination of a thick bark, large stem diameter, high crown base (5m or greater), sparse ground fuels, and a non-conical crown architecture reduce the impact of recurrent fires. The probability of surviving a fire is thus related to both the physical characteristics of the tree and site conditions. Thus a crown fire in a spruce stand may revert to a surface fire in a Douglas-fir stand (Bessie and Johnson 1995; Johnson 1992; Ryan et al. 1988). Douglas-fir thus has a much higher probability of surviving a 'catastrophic' fire event.

A higher residence time (i.e., lower 'spread rate') of a fire increases the chances of tree mortality or severe damage, since differential heating of the bark occurs when the spread rate is slow (Gutsell and Johnson 1996). Cambial damage (fire scarring) is most pronounced on the leeward side of larger trees, where flame height, temperature, and flame residence time are all higher. Trees of small diameter do not appreciably increase the residence time of a leeward flame: if temperatures are high enough, complete cambial mortality will occur around the base of small trees. For fires with very fast spread rates, the time to kill windward and leeward cambium will be the same irrespective of stem size (Gutsell and Johnson 1996). Even if Douglas-fir is killed by cambial heating, the crown may not be fully consumed and a viable seed crop will remain (Greene et al. 1999). Very low fire spread rates (high fuel consumption) can also damage near-surface lateral roots in Douglas-fir, resulting in greater soil moisture stress and/or reduced resistance to pest or pathogen attacks (Ryan et al. 1988).

The presence of cumulative fire scars on mature Douglas-fir is indicative of fire behaviour characteristic of these stands (Rogean 1996; Tymstra 1991; Masters 1990; Tande 1979). Predicting fire behaviour on the landscape is difficult, since it is often determined by dynamic and stochastic environmental conditions. Thus spatio-temporal patterns in fire behaviour as well as the physical characteristics of mature trees determine the scattered survivability of Douglas-fir on the landscape.

The ability to endure or evade fires allows Douglas-fir to persist in pyric systems. The aged Douglas-fir trees often exceeds the mean fire return interval (MFRI) for surface or stand replacing burns. Post-burn (non-serotinous) seed source availability is influenced by the differential effects of fire behaviour: fire 'patchiness' on the landscape leaves behind scattered 'relict' seed trees (Fig. 6.5; McCune and Allen 1985). Disturbance-driven systems are characterized by a small proportion of older forest stands intermixed in a complex mosaic of younger age classes. Douglas-fir is restricted to discrete areas of the landscape where fire effects are evaded or diminished. The combination of species longevity and fire-adaptations enable Douglas-fir to persist on the landscape for much longer periods of time than most of its associates.

To summarize, scattered survivability of Douglas-fir on the landscape is favoured under the following conditions:

- *Differential Fire Behaviour*: The spatial heterogeneity of fires, and of fire intensity, facilitates the recolonization of Douglas-fir into recently disturbed habitats. The physiographic complexity of montane sites results in multi-aged landcover classes. Scattered survivability is favoured by complex fire behaviour.
- 2. *Physical Adaptations*: Fire-induced mortality is reduced by the adaptive characteristics (vital attributes) of Douglas-fir. Stem diameter and bark thickness both increase over time, resulting in higher temperatures for lethal cambium heating.
- 3. *Site Characteristics*: Lower buildup of ground fuel reduces fire severity and propagation. Site productivity and interspecific competition are reduced on dry, well-drained sites.

6.7 THE MANAGEMENT PARADIGM

The population dynamics of Douglas-fir can be defined at various temporal and spatial scales. Variations in climate and disturbance regimes that occur over the lifespan of a tree are correlated with mortality and recruitment rates (Johnson et al. 1994). The synergistic interaction of biotic and abiotic stressors over such a time scale can alter successional trajectories. Longer-term shifts in climate and disturbance regimes affect site conditions and change habitat suitability, thereby altering species distributions and abundances.

The management of Douglas-fir stands is dependent on our understanding of 'natural' states and processes that have shaped these forests over the past 8,000 yrs. A long-term management philosophy is appropriate, given the longevity of the species (>400 yrs) and the persistence of Douglas-fir stands on the landscape (>5,000 yrs). Short-term changes in habitat conditions are unlikely to have a significant long-term effect on population dynamics. A temporary hiatus in recruitment or short-term increases in mortality may well be within the normal range of population variability (Johnson et al. 1994). Without a historic 'benchmark', it is difficult to determine whether the natural variability of a system has been exceeded. Since climate is in a constant state of flux it would be difficult if not impossible to define what environmental condition(s) would constitute a benchmark. Creating a scenario using long-term mean climate removes the important affects of extreme conditions, which are normally the limiting factors for many species. Hallet (1996) postulated that the present-day vegetation mosaic in Kootenay National Park "is within its natural variability according to the paleoecological record". Given the climatic shifts that have occurred over the past 1,000 years and current changes in climate during the 20th century, attempts to restore disturbance regimes to pre-1900 (or even pre-Columbian) conditions seems naive if not erroneous.

Climatic conditions in the four mountain parks have changed since Europeans first settled in the region (Luckman 1999). Regardless of the impacts that recent landuse patterns have had on ecosystem function, natural variation, and synergistic interactions of climate, disturbance regime and resource availability make each point in time ecologically unique. It follows that subtle changes in initial conditions following disturbance may result in divergent successional pathways (Kenkel et al. 1997; van Hulst 1997). Restoration of an ecosystem to its 'natural' state is therefore meaningless, since the natural state is by definition a moving target. The goal of vegetation management should not be restoration of the 'natural' state at some arbitrary point in time; instead, an attempt should be made to recognize and understand the natural variability of vegetation change. The fact that most if not all major plant taxa that migrated since the Hypsothermal are still represented in the flora of the Canada Rockies, testifies to the resilience of these systems. However the loss of important corridors in most of Canada's western parks has important implications on gene flow. Furthermore, loss of land to

agriculture, resource extraction, and urban development during the 20th century has created barriers to the migration of not only species but also the spread of natural disturbances such as fires. Since these factors are irreversible (at least during our lifetime) attempts to better understand the complex interactions of natural systems will be essential. Considerations should be given to the effects of natural fire, pest or pathogen attacks, and herbivory/granivory on stand development, since the synergistic interaction of these factors gives rise to complex spatial and temporal vegetation patterns. Natural disturbance increases landscape heterogeneity, promotes species diversity at the stand level, and increases genetic diversity at the population level (Bonan and Shugart 1989).

The mandate of Parks Canada is to maintain ecological integrity (e.g., preserve native biodiversity) and minimize interference of natural processes (Parks Canada 1993; Woodley 1993). It must be remembered that protected areas are not pristine vestiges of wild habitat: resource extraction, development, wildlife management, and the introduction of non-native species has imposed some stress on these ecosystems (Achuff et al. 1996). In some cases, a hands-off approach is inappropriate given the level of ecological intervention that has occurred since the turn of the century. Losses in habitat connectivity, decreases in frequent low-intensity fires, and the influence of exotic species on the native biodiversity all warrant management consideration. The effects of prehistoric aboriginal landuse practices on ecosystem structure and function should also be carefully evaluated. In theory, Parks Canada guidelines dictate a 'hands-off' approach to large catastrophic fires, but in practice such a policy is unrealistic: a balance between public safety, park infrastructure, and ecological integrity must be struck. Natural processes are important in maintaining ecological integrity (Parks Canada 1997), and current policy allows natural disturbances (e.g., naturally ignited or planned fires) to occur provided that public safety and existing facilities are not compromised (Achuff et al. 1996).

Both long-term and short-term variations in vegetation dynamics should be considered when establishing management guidelines for Douglas-fir stands in the four mountain parks. Important issues include:

- *Habitat Fragmentation:* The loss of wildlife habitat connectivity in Jasper and Banff National Parks has resulted in the displacement of large carnivores such as wolves. The result has been a steady increase in elk populations in predator-refuge zones, increasing the severity of elk-induced vegetation damage. It is probably safe to assume that this imposed ecological condition is beyond the realm of natural variability in predator-prey and plant-animal interactions. The reduction in photosynthetic capacity resulting from elk browsing decreases the vigor of Douglas-fir saplings and may severely compromise stand regeneration. Cumulative ungulate browsing may result in tree death, thus adding to

the fuel load and increasing the probability and severity of a stand-replacing fire. In addition, changes in composition of the regeneration layer induced by selective browsing may alter successional development.

- *Fire Suppression:* Fire suppression has been effective in 'controlling' the small, low-intensity natural burns that are characteristic of open-canopied Douglas-fir stands. Such suppression has resulted in a loss of ungulate habitat (Van Egmond 1990) and increased dead and live fuel loads (Johnson 1992). Suppression has been less effective in controlling large high intensity burns (Weir et al. 1995).
- *Exotic Species:* The native biodiversity of Douglas-fir stands may be compromised by competitively aggressive non-native species. Such species may outcompete or suppress the growth of the native flora. A complete inventory of non-native plant species and their abundance is required in order to monitor this potential problem.
- *Prehistoric Anthropogenic Landuse:* An acknowledgement and understanding of pre-Columbian human occupation and landuse practices is important to understanding the potential role that humans have had on the region. But attempts to mimic the effects of aboriginal practices are problematic: the lack of empirical data relating to the impacts of aboriginal burning makes it difficult to accurately test or recreate its ecological effects.
- *Climate Change:* The structure of montane forests has changed dramatically over the past 7,000 years, resulting in a geographic 'shifting' of ecosystems (Achuff et al. 1996). The cooler-moister conditions of the Neoglacial period favoured late-succession species such as white spruce and subalpine fir, while warmer-drier conditions during the Holocene Hypsithermal and Medieval Optimal favoured fire-adapted species such as lodgepole pine and Douglas-fir (Hallet 1996). Long-term shifts in forest cover reflect the inherent dynamics of these communities as they respond to changing climate conditions.

6.8 SUMMARY

This study is concerned with describing the structure, composition and dynamics of interior Douglas-fir stands in Canada's four Mountain Park. Ward's clustering method was used to classify the 220 plots into three stand-types & 7 sub-types. The classification was similar to those derived by Krajina (1969) Achuff et al. (1993). The following is a summary of the major findings encountered in this study.

Stand-Type I: Douglas-fir/Juniper/Bearberry ($n = 95$)

1. Canopy and Subcanopy: "Savanna-like" stands occurring on steep south-facing well-drained slopes of low nutrient status. Canopy is composed of mature Douglas-fir (100-290 yrs), *Juniperus scopulorum* and *Picea contorta*. Diverse understory (effective species richness around 10). *Tortula ruralis* is considered an indicator species in these stands. Browsing was low-moderate and restricted to ungulate high use areas (e.g., near Banff and Jasper townsites).

2. Recruitment and Growth: Recruitment and growth is favoured in "protected microsites" (e.g., vegetation cover or moderate topography). Mean annual growth rates are low ranging from 0.13 mm/yr (open) to 0.50 mm/yr (vegetation cover) with most individuals ranging in age between 23-45 years.

3. Stand-Dynamics: These stands are self-perpetuating, the combination of high fire frequency (low-intensity), low soil moisture and nutrients results in low establishment rates of other tree species (e.g., *Picea glauca*). It is possible that these stands have persisted here for well over 5,000 years, serving as a potential seed and genetic pool when climatic conditions favour the expansions of the species distribution.

Stand-Type II: Douglas-fir/Lodgepole pine/ Buffaloberry ($n = 85$)

1. Canopy and Subcanopy: Mixed-canopy stands, occurring on moderate south-facing slopes on low-moderate nutrient soils. Canopy is composed of Douglas-fir with a mean age of 85 years although several "relic" fire scarred trees were encountered around 305 years. Understory diversity was highest in these stands (effective species richness 12). Although browsing was evident on shrub species such as *Rosa acicularis* it was rarely encountered on understory Douglas-fir.

2. Recruitment and Growth: Recruitment is more ubiquitous throughout these stands, development is often limited by faster growing contemporaneous species such as *Pinus Contorta* (forming a canopy dominant before Douglas-fir) as well as a more developed shrub layer. In the absence of fire, "canopy gaps" seem to favour the growth of the advance Douglas-fir regeneration cohort, with radial growth rates exceeding 1 mm/year in openings. Based on the cumulative growth curves most of these individuals have undergone

numerous suppression (e.g., mean number of suppression events = 3) and release events. The longest suppression event lasting 28 year.

3. Stand-Dynamics: These stands are characterized by a more "severe" fire regime resulting from greater productivity compared to Stand-type I. The presence of relic fire scarred Douglas-fir indicates that historic fire behaviour was complex in these stands. These stands are heading from a fire initiated *Pinus contorta* canopy towards a Douglas-fir dominated system.

Stand-Type III: Douglas-fir/White Spruce/Hylocomium (n = 45)

1. Canopy and Subcanopy: Mixed-canopy stands, occurring but not restricted to north-facing nutrient rich low-moderate slopes. Canopy is composed of mature Douglas-fir (110-380 yrs), *Picea glauca*, *Thuja plicata*, and *Abies bifolia*. Understory diversity is low (effective species richness 3). *Hylocomium splendens* is an indicator species. No evidence of browsing.

2. Recruitment and Growth: Recruitment is high with mean seedling densities around 15 stems per m². However, sapling densities are low (0.40 stems per m²) indicating an increase in understory recruitment mortality. Annual growth rates for regenerating Douglas-fir average 0.075 mm/yr.

3. Stand-Dynamics: These stands are characterized by a low frequency high intensity fire regime. The presence of *Picea glauca* and *Thuja plicata* (>100 years) as well as a thick organic layer indicates that fire have been rare. Low light conditions favour *Picea/Thuja* establishment and growth (most seedlings occurring on rotten wood). Most of the existing Douglas-fir established in the mid to late 1700's. In the absence of fire these stands are heading towards a *Picea/Abies* dominated forest.

Future Considerations

- A genetic study should be conducted in order to determine if differences exist between interior Douglas-fir populations occurring on xeric south-facing slopes compared to hygric north-facing slopes.
- Stand reconstruction should be done in order to quantify recruitment and mortality rates of canopy and the advance regeneration cohort.
- Permanent plots should be established in order (e.g., biosphere reserve) to monitor changes in stand structure and composition as well as impacts of ungulates and pathogens.

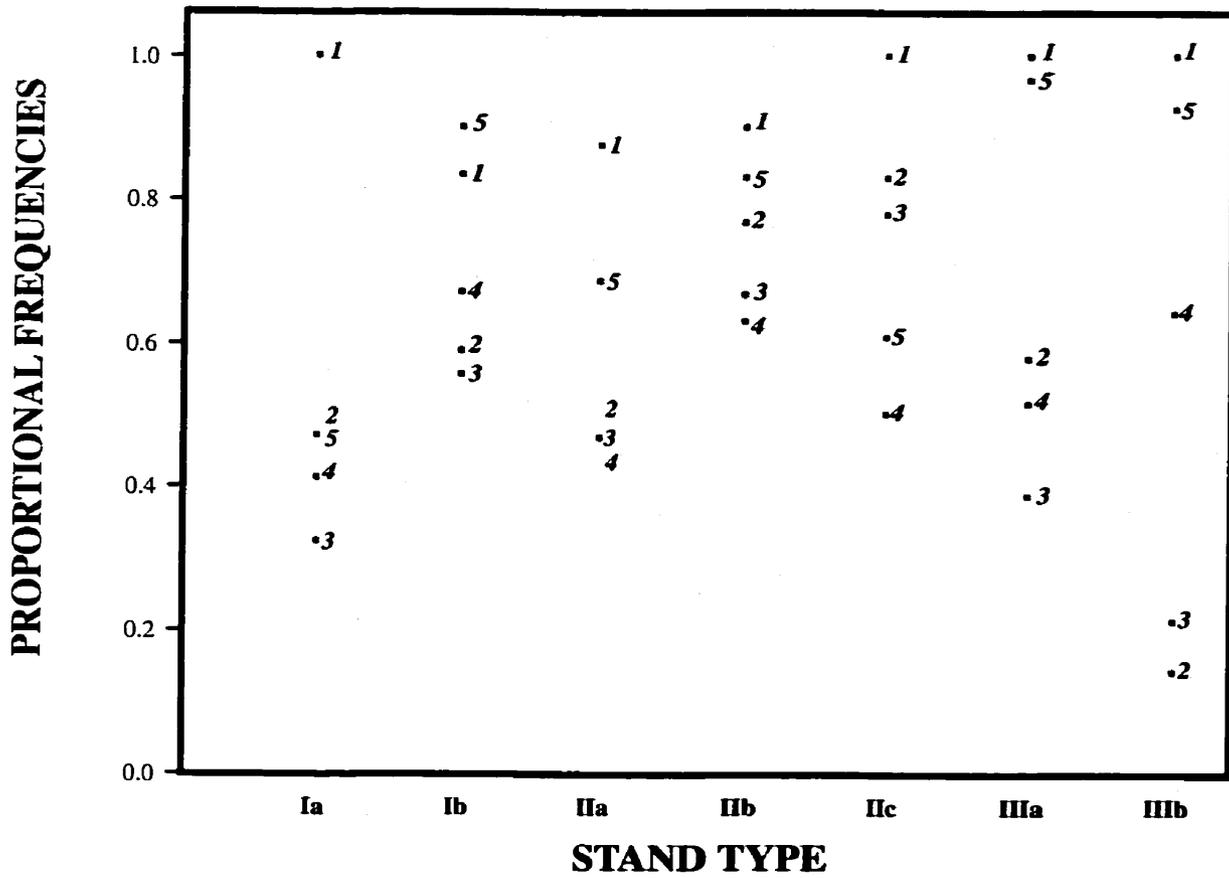


Figure 6.1. Proportional frequency of plots containing Douglas-fir in each of five canopy classes 1-5 , by stand sub-type. For example, 100% of the 34 plots belonging to sub-type Ia contain Douglas-fir in canopy 1.

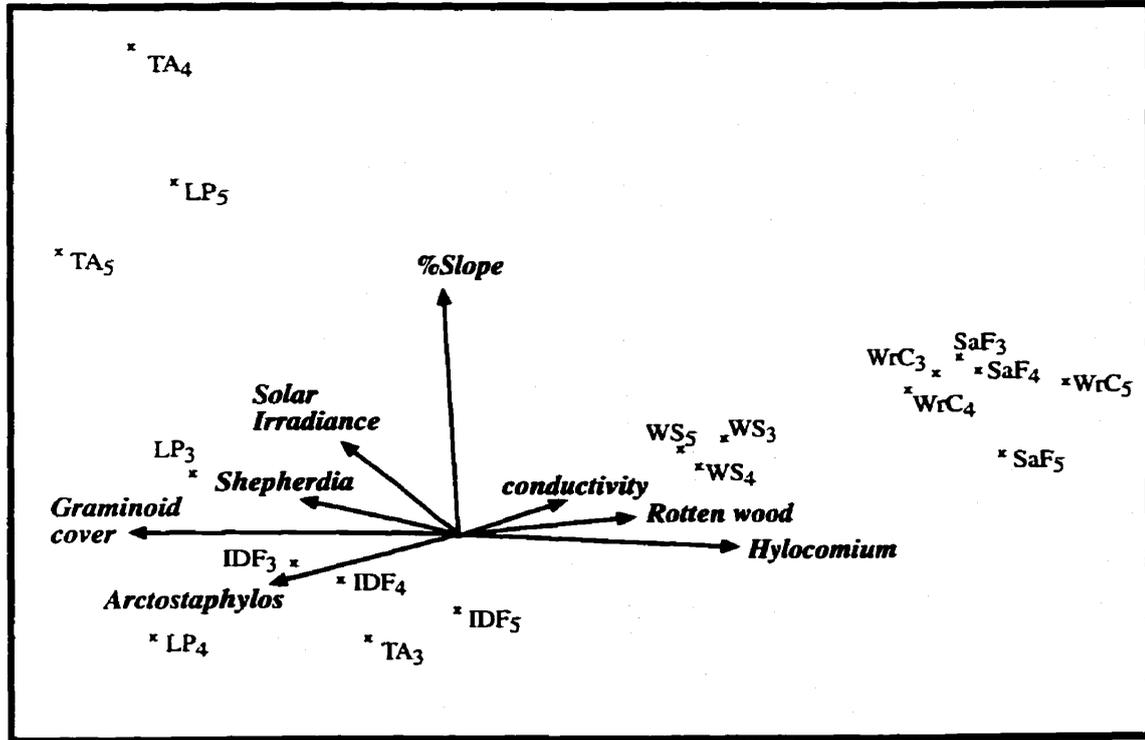


Figure 6.2. Canonical correspondence analysis (CCA) of tree regeneration constrained by biotic and abiotic stand variables across the 220 sampled plots. The six tree species used were further partitioned into three canopy classes (canopy 3 = 2-5m, canopy 4 = 0.5-2m and canopy 5 = seedlings). Canonical correlations: $R_1^2 = 0.709$, $R_2^2 = 0.589$. Redundancy (ratio of the canonical inertia/ total inertia) = $0.689/3.832 * 100\% = 17.9\%$. Amount of explained variance along the first and second axis: $\lambda_1 = 7.5\%$ and $\lambda_2 = 12\%$. Species code: IDF = interior Douglas-fir, LP = Lodgepole pine, TA = trembling aspen, WS = White spruce, SaF = Subalpine Fir and WrC = Western redcedar.

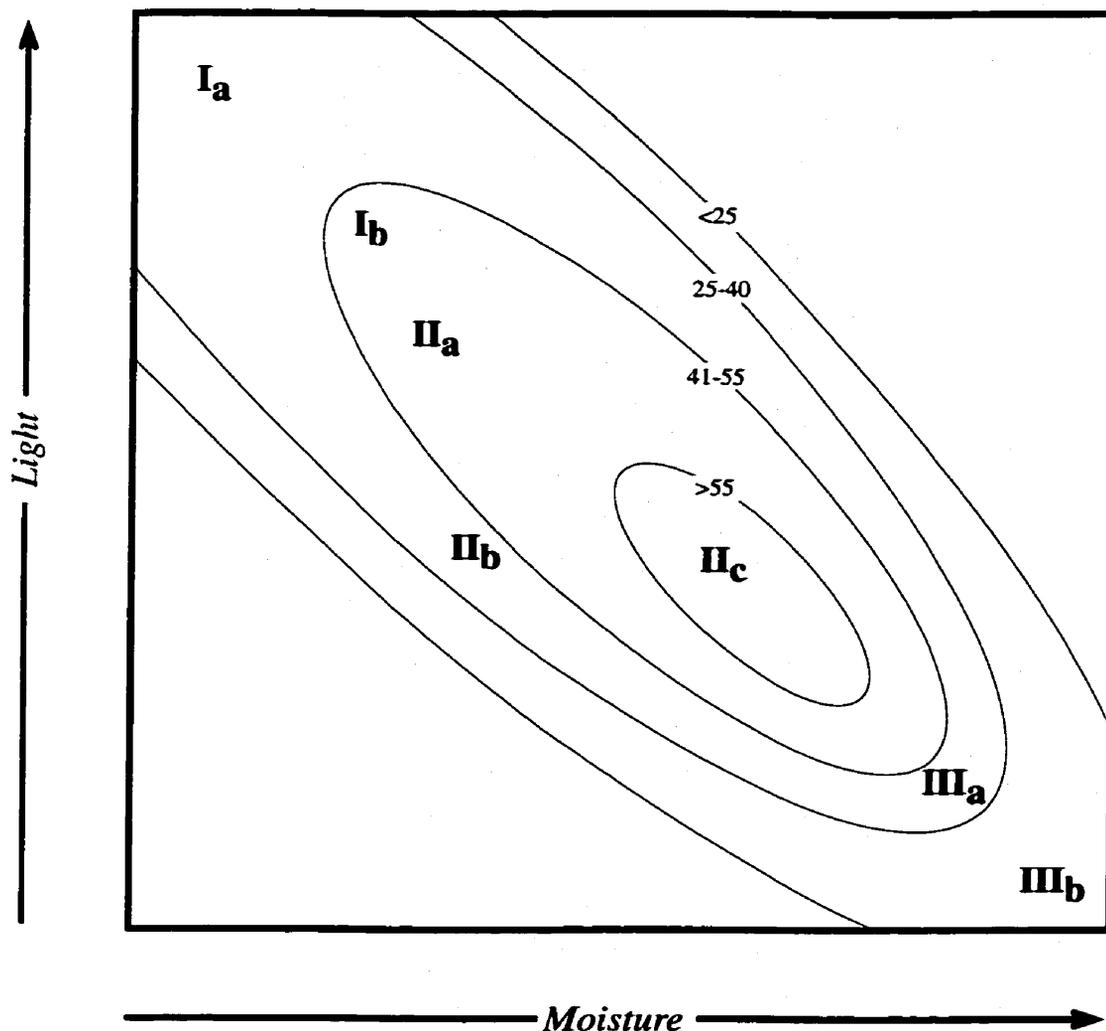


Figure 6.3 Douglas-fir regeneration in the seven stand sub-types. Subtypes are placed in a two dimensional environmental (light and moisture) space; refer to text for details. Superimposed on this space are percentages of plots in each subtype containing at least one Douglas-fir tree in both regeneration canopies 3 (2-5m height) and 4 (0.5-2m height). For example over 55% of plots in subtype IIc contained trees in both canopies 3 and 4.

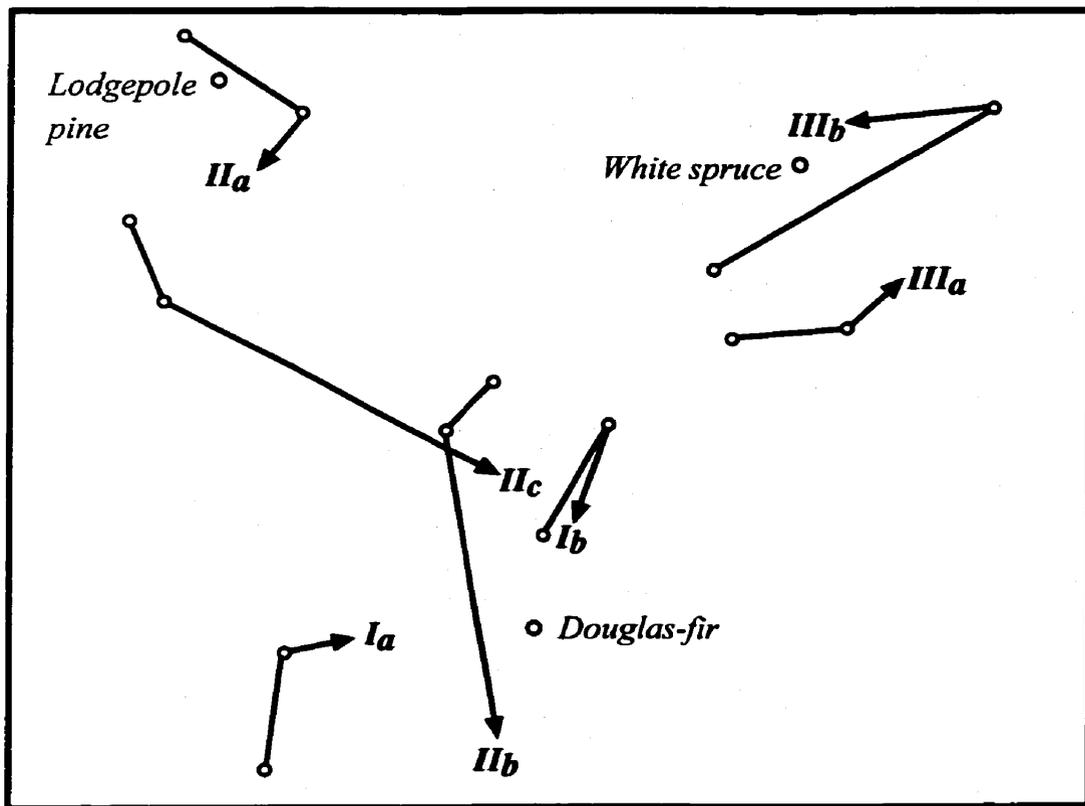


Figure 6.4. Successional trajectories for the seven Douglas-fir sub-types. Size-class ordination based on frequency value were used to create successional vectors. Each node (open circle) represents a canopy layer. The lower subcanopy (arrow tip) and canopy are sequentially linked. The assumption is that lower subcanopy trees will eventually replace the canopy. Vegetation dynamics were inferred from vector linearity and length. Long linear vectors represent canopy turn-over while short non-linear vectors represent self-replacing stands.



Figure 6.5. Differential fire behaviour of the Minnewanka prescribe burn.

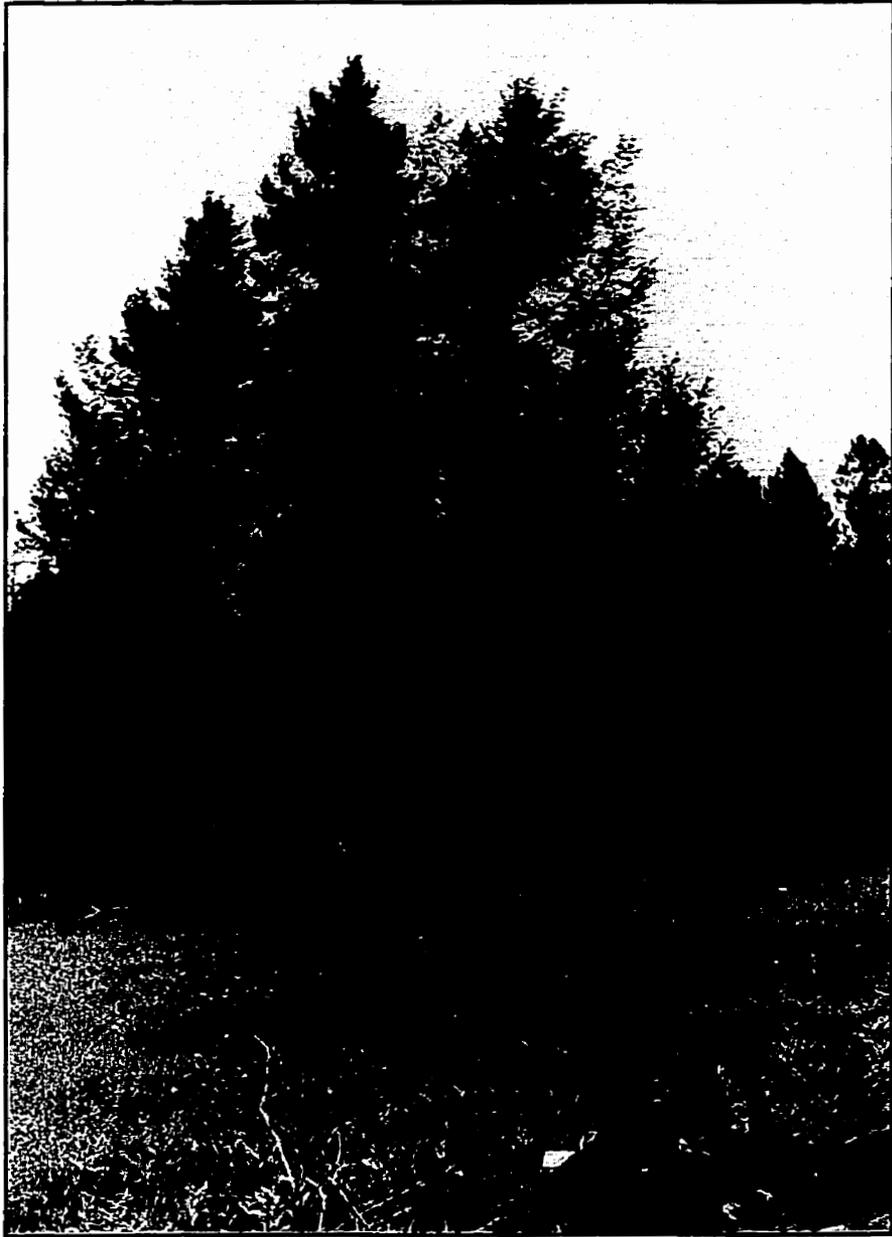


Figure 6.6. Differential fire behaviour of the Sawback range prescribe burn.

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Appendix 1. Final species list of the 220 Douglas-fir sites enumerated between 1997 and 1998 and Banff, Jasper, Kootenay and Yoho National Park. Species most commonly encountered in Douglas-fir stands are indicated by an asterisk (*). Nomenclature of vascular plants follows Parish et al (1996), Budds (1990) and Moss (1983) for cryptogams Crum (1976), Schofield (1992) & Vitt et al. (1988).

| | GENUS | SPECIES | COMMON NAMES |
|---------------|-----------------------|--|-----------------------------|
| TREES | | | |
| Conifers | <i>Abies</i> | <i>bifolia</i> | Subalpine fir |
| | <i>Juniperus</i> | <i>scopulorum</i> | Rocky Mountain Juniper |
| | <i>Picea</i> | <i>glauca</i> | White spruce * |
| | <i>Pinus</i> | <i>contorta</i> var. <i>latifolia</i> | Lodgepole pine * |
| | <i>Pinus</i> | <i>flexilis</i> | Limber pine |
| | <i>Pseudotsuga</i> | <i>menziesii</i> var. <i>glauca</i> | Interior Douglas-fir * |
| | <i>Thuja</i> | <i>plicata</i> | Western Redcedar |
| Deciduous | <i>Betula</i> | <i>papyrifera</i> | Paper birch |
| | <i>Populus</i> | <i>balsamifera</i> spp. <i>trichocarpa</i> | Balsam poplar |
| | <i>Populus</i> | <i>tremuloides</i> | Trembling aspen |
| SHRUBS | | | |
| | <i>Acer</i> | <i>glabrum</i> var. <i>douglasii</i> | Rocky Mountain maple |
| | <i>Alnus</i> | <i>crispa</i> | Sitka alder * |
| | <i>Amelanchier</i> | <i>alnifolia</i> | Saskatoon |
| | <i>Arctostaphylos</i> | <i>uva-ursi</i> | Bearberry (Kinnikinnick) |
| | <i>Chimaphila</i> | <i>umbellata</i> | Princes-pine |
| | <i>Chrysothamnus</i> | <i>nauseosus</i> | Common rabbit-brush |
| | <i>Cornus</i> | <i>stolonifera</i> | Red-osier Dogwood |
| | <i>Elaeagnus</i> | <i>commutata</i> | Wolf-willow |
| | <i>Juniperus</i> | <i>communis</i> | Common juniper |
| | <i>Juniperus</i> | <i>horizontalis</i> | Creeping juniper |
| | <i>Ledum</i> | <i>groenlandicum</i> | Labrador tea |
| | <i>Linnaea</i> | <i>borealis</i> | Twinflower |
| | <i>Lonicera</i> | <i>ciliata</i> | Orange honeysuckle |
| | <i>Lonicera</i> | <i>dioica</i> | Red honeysuckle * |
| | <i>Lonicera</i> | <i>involucrata</i> | honeysuckle |
| | <i>Lonicera</i> | <i>utahensis</i> | Utah honeysuckle |
| | <i>Mahonia</i> | <i>aquifolium</i> | Tall Oregon-grape |
| | <i>Oplopanax</i> | <i>horridus</i> | Devil's club |
| | <i>Menziesia</i> | <i>ferruginea</i> | False azalea |
| | <i>Potentilla</i> | <i>fruticosa</i> | Shrubby cinquefoil * |
| | <i>Ribes</i> | <i>lacustre</i> | Blackgoose berry |
| | <i>Rosa</i> | <i>acicularis</i> | Prickly rose * |
| | <i>Rosa</i> | <i>gymnocarpa</i> | Baldhip rose |
| | <i>Rubus</i> | <i>parviflorus</i> | Thimbleberry |
| | <i>Salix</i> | <i>bebbiana</i> | Bebb's willow |
| | <i>Salix</i> | <i>sitchensis</i> | Willow * |
| | <i>Shepherdia</i> | <i>canadensis</i> | Buffalo berry (Soopolallie) |
| | <i>Sorbus</i> | <i>scopolina</i> | Western mountain-ash * |
| | <i>Spiraea</i> | <i>betulifolia</i> | Birched-leaved spirea * |
| | <i>Spiraea</i> | <i>pyramidata</i> | Pyramid spirea * |
| | <i>Symphoricarpos</i> | <i>albus</i> | Common snowberry |
| | <i>Vaccinium</i> | <i>caespitosum</i> | |
| | <i>Vaccinium</i> | <i>myrtilus</i> | Low bilberry |
| | <i>Vaccinium</i> | <i>parvifolium</i> | Red huckleberry |
| | <i>Vaccinium</i> | <i>scoparium</i> | Grouseberry |
| | <i>Vaccinium</i> | sp. | Blueberry |
| | <i>Viburnum</i> | <i>edule</i> | High-brush cranberry |

| | GENUS | SPECIES | COMMON NAMES |
|-------------------|----------------------|---|----------------------------|
| GRAMINOIDS | | | |
| Grasses | <i>Agropyron</i> | <i>spicatum</i> | Bluebunch wheatgrass |
| | <i>Agropyron</i> | sp. | Wheatgrass |
| | <i>Calamagrostis</i> | <i>rubescens</i> | Pinegrass |
| | <i>Elymus</i> | <i>lanceolatus</i> | Northern wheatgrass |
| | <i>Elymus</i> | <i>glaucus</i> | Blue wildrye |
| | <i>Elymus</i> | <i>innovatus</i> | Wildrye |
| | <i>Festuca</i> | <i>campestris</i> | Rough fescue |
| | <i>Festuca</i> | <i>saximontana</i> | Rocky Mountain fescue |
| | <i>Koeleria</i> | <i>macrantha</i> | Junegrass |
| | <i>Muhlenbergia</i> | <i>richardsonii</i> | Mat Muhly |
| | <i>Oryzopsis</i> | <i>asperifolia</i> | Rough-leaved ricegrass |
| | <i>Poa</i> | <i>palustris</i> | Fowl bluegrass |
| | <i>Poa</i> | <i>pratensis</i> | Kentucky bluegrass |
| | <i>Poa</i> | sp. | Bluegrass |
| | <i>Schizachne</i> | <i>purpurascens</i> | Purple oat grass |
| <i>Stipa</i> | <i>occidentalis</i> | Stiff needlegrass | |
| <i>Stipa</i> | <i>richardsonii</i> | Richardson's needlegrass | |
| Sedges | <i>Carex</i> | <i>concinna</i> | Low Northern sedge |
| | <i>Carex</i> | <i>concinnoides</i> | Northwestern sedge |
| | <i>Carex</i> | sp. | Sedge |
| FORBS | | | |
| Dicotyledons | <i>Achillea</i> | <i>millefolium</i> | Yarrow |
| | <i>Actaea</i> | <i>rubra</i> | Baneberry |
| | <i>Androsace</i> | <i>septentrionalis</i> | Fairy candelabra |
| | <i>Anemone</i> | <i>multifida</i> | Cut-leaf anemone |
| | <i>Antennaria</i> | <i>umbrinella</i> | Umber pussytoes |
| | <i>Antennaria</i> | <i>racemosa</i> | Racemose pussytoes |
| | <i>Antennaria</i> | <i>microphylla</i> | Rosy pussytoes |
| | <i>Apocynum</i> | <i>androsaemifolium</i> | Spreading dogbane |
| | <i>Arabis</i> | <i>holboellii</i> | Holboell's rockcress |
| | <i>Aralia</i> | <i>nudicaulis</i> | Wild sarsaparilla |
| | <i>Arnica</i> | <i>cordifolia</i> | Heart-leaved arnica |
| | <i>Artemisia</i> | <i>dracunculus</i> | Tarragon |
| | <i>Artemisia</i> | <i>frigida</i> | Pasture sage |
| | <i>Artemisia</i> | <i>norvegica</i> | |
| | <i>Aster</i> | <i>ciliolatus</i> | Lindley's aster |
| | <i>Aster</i> | <i>conspicuus</i> | Showy aster |
| | <i>Aster</i> | <i>ericoides</i> | |
| | <i>Aster</i> | <i>laevis</i> | Smooth aster |
| | <i>Astragalus</i> | <i>agrestis</i> | Field milk-vetch |
| | <i>Astragalus</i> | <i>miser</i> | Timber milk-vetch |
| | <i>Astragalus</i> | <i>tenellus</i> | Pulse milk-vetch |
| | <i>Campanula</i> | <i>rotundifolia</i> | Common harebell |
| | <i>Castilleja</i> | <i>miniata</i> | Scarlet paint brush |
| | <i>Clematis</i> | <i>occidentalis</i> | Blue clematis |
| | <i>Clematis</i> | <i>occidentalis</i> | Blue clematis |
| | <i>Commandra</i> | <i>umbellata</i> | Pale commandra |
| | <i>Cornus</i> | <i>canadensis</i> | Bunchberry |
| | <i>Crepis</i> | <i>atrabarba</i> | Slender hawkbeard |
| | <i>Dodecatheon</i> | <i>pulchellum</i> | Few-flowered shooting star |
| | <i>Dryas</i> | <i>drummondii</i> | Yellow Mountain-Avens |
| | <i>Epilobium</i> | <i>angustifolium</i> | Fireweed |
| | <i>Erigeron</i> | <i>compositus</i> var. <i>glabratus</i> | Cut-leaved daisy |
| | <i>Fragaria</i> | <i>virginiana</i> | Wild strawberry |
| | <i>Gaillardia</i> | <i>aristata</i> | Brown-eyed Susan |
| | <i>Galium</i> | <i>boreale</i> | Northern bedstraw |

| | GENUS | SPECIES | COMMON NAMES |
|----------------|---------------------|---|----------------------------|
| | <i>Galium</i> | <i>triflorum</i> | Sweet-scented bedstraw |
| | <i>Goodyera</i> | <i>oblongifolia</i> | Rattlesnake plantain |
| | <i>Goodyera</i> | <i>repens</i> | Dwarf rattlesnake plantain |
| | <i>Hedysarum</i> | <i>sulphurescens</i> | Yellow Hedysarum |
| | <i>Heterotheca</i> | <i>villosa</i> | Golden aster |
| | <i>Lathyrus</i> | <i>nevadensis</i> | Purple peavine |
| | <i>Lathyrus</i> | <i>ochroleucus</i> | Creamy peavine |
| | <i>Linaria</i> | <i>genistifolia</i> spp. <i>dalmatica</i> | Dalmatian toadflax |
| | <i>Linum</i> | <i>lewisii</i> | Western blue flax |
| | <i>Listera</i> | <i>cordata</i> | Heart-leaved twayblade |
| | <i>Lithospermum</i> | <i>ruderale</i> | Lemonweed |
| | <i>Medicago</i> | <i>lupulina</i> | Black medick |
| | <i>Mitella</i> | <i>nuda</i> | Common mitrewort |
| | <i>Moneses</i> | <i>uniflora</i> | Single delight |
| | <i>Oplopanax</i> | <i>horridus</i> | Devil's club |
| | <i>Orthilia</i> | <i>secunda</i> | One-sided wintergreen |
| | <i>Osmorhiza</i> | <i>chilensis</i> | Mountain sweet-cicely |
| | <i>Oxytropis</i> | <i>splendens</i> | Showy locoweed |
| | <i>Oxytropis</i> | <i>campestris</i> | Field locoweed |
| | <i>Pedicularis</i> | <i>bracteosa</i> | Bracted lousewort |
| | <i>Penstemon</i> | <i>confertus</i> | Yellow penstemon |
| | <i>Potentilla</i> | <i>ledebouriana</i> | Cinquefoil |
| | <i>Potentilla</i> | <i>pennsylvanica</i> | Prairie cinquefoil |
| | <i>Pyrola</i> | <i>chlorantha</i> | Green wintergreen |
| | <i>Saxifraga</i> | <i>bronchialis</i> | Spotted saxifrage |
| | <i>Saxifraga</i> | <i>ferruginea</i> | Alaska saxifrage |
| | <i>Sedum</i> | <i>lanceolatum</i> | Lance-leaved stonecrop |
| | <i>Senecio</i> | <i>canus</i> | Woolly groundsel |
| | <i>Silene</i> | <i>menziesii</i> | Menzie's campion |
| | <i>Solidago</i> | <i>multiradiata</i> | Northern goldenrod |
| | <i>Solidago</i> | <i>spatulata</i> | Spikelike goldenrod |
| | <i>Sonchus</i> | <i>arvensis</i> | Perennial sow-thistle |
| | <i>Taraxacum</i> | <i>officinale</i> | Common dandelion |
| | <i>Thalictrum</i> | <i>occidentale</i> | Western meadowrue |
| | <i>Tragopogon</i> | <i>dubius</i> | Goat's-Beard |
| | <i>Trifolium</i> | <i>pratense</i> | Red clover |
| | <i>Trifolium</i> | <i>repens</i> | |
| | <i>Veronica</i> | <i>americana</i> | American brooklime |
| | <i>Vicia</i> | <i>americana</i> | American vetch |
| | <i>Viola</i> | <i>canadensis</i> | Viola canadensis |
| | <i>Viola</i> | <i>renifolia</i> | Kidney-leaved violet |
| | <i>Viola</i> | <i>adunca</i> | Early blue violet |
| Monocotyledons | | | |
| | <i>Allium</i> | <i>cernuum</i> | Nodding onion |
| | <i>Calochortus</i> | <i>apiculatus</i> | Sagebrush mariposa lily |
| | <i>Calypto</i> | <i>balbosa</i> | Fairy slipper |
| | <i>Disporum</i> | <i>hcokeri</i> | Hookers fairybells |
| | <i>Disporum</i> | <i>trachycarpum</i> | Rough-fruited fairybells |
| | <i>Lilium</i> | <i>columbianum</i> | Tiger lily |
| | <i>Lilium</i> | <i>philadelphicum</i> | Wood lily |
| | <i>Listera</i> | <i>cordata</i> | Heart-leaved twayblade |
| | <i>Maianthemum</i> | <i>canadensis</i> | Wild lily-of-the-valley |
| | <i>Platanthera</i> | <i>obtusata</i> | One-leaved rein-orchid |
| | <i>Sisyrinchium</i> | <i>idahoense</i> | Idaho blue-eyed-grass |
| | <i>Spiranthes</i> | <i>romanzoffiana</i> | Lady's tresses |
| | <i>Smilacina</i> | <i>racemosa</i> | False soloman's seal |
| | <i>Stenanthium</i> | <i>occidentale</i> | Bronze bells |
| | <i>Streptopus</i> | <i>amplexifolius</i> | Clasping twisted stack |
| | <i>Zigadenus</i> | <i>elegans</i> | Mountain death-camas |
| Ferns | | | |
| | <i>Gymnocarpium</i> | <i>dryopteris</i> | oak fern |
| Clubmosses | | | |
| | <i>Lycopodium</i> | <i>complanatum</i> | Ground-cedar |
| | <i>Selaginella</i> | spp. | Selaginella |

| | GENUS | SPECIES | COMMON NAMES | |
|-----------------------------|--------------------------|--------------------------|----------------------------|---|
| BRYOPHYTES | | | | |
| Pleurocarpous Mosses | | | | |
| | <i>Brachythecium</i> | <i>albicans</i> | Common lawn moss | • |
| | <i>Brachythecium</i> | <i>rivulare</i> | Waterside feather moss | |
| | <i>Brachythecium</i> | <i>salebrosum</i> | Rough lawnmoss | |
| | <i>Bryoerthrophyllum</i> | <i>recurvirostrum</i> | | |
| | <i>Climacium</i> | <i>dendroroides</i> | | |
| | <i>Hylocomium</i> | <i>splendens</i> | Stem moss | • |
| | <i>Hypnum</i> | <i>revolutum</i> | Rusty claw moss | • |
| | <i>Leskea</i> | <i>polycarpa</i> | | |
| | <i>Metaneckera</i> | <i>menziesii</i> | | |
| | <i>Pleurozium</i> | <i>schreberi</i> | Shrebers's red stem | • |
| | <i>Ptilium</i> | <i>crista-castrensis</i> | Knight's plume | • |
| | <i>Pylaisiella</i> | <i>polyantha</i> | Stocking moss | |
| | <i>Rhytidiadelphus</i> | <i>triquetrus</i> | Hanging basket moss | • |
| | <i>Rhytidium</i> | <i>rugosum</i> | | |
| | <i>Sanionia</i> | <i>uncinata</i> | Sickle moss | • |
| | <i>Thuidium</i> | <i>abietinum</i> | Wiry fern moss | • |
| | <i>Thuidium</i> | <i>recognitum</i> | Lacy fern moss | |
| Acrocarpous Mosses | | | | |
| | <i>Barbula</i> | <i>convoluta</i> | | |
| | <i>Ceratodon</i> | <i>purpureus</i> | Fire moss | |
| | <i>Dicranum</i> | <i>Fuscissens</i> | | |
| | <i>Dicranum</i> | <i>polysetum</i> | Electric eels | |
| | <i>Dicranum</i> | <i>scoparium</i> | Broom moss | |
| | <i>Distichium</i> | <i>capillaceum</i> | Erect-fruited iris moss | |
| | <i>Distichium</i> | <i>flexicaulis</i> | | |
| | <i>Encalypta</i> | <i>rhaptocharpa</i> | Grooved gnome moss | |
| | <i>Mnium</i> | <i>spinulosum</i> | Flapper moss | |
| | <i>Ornhotrichum</i> | <i>speciosum</i> | Hooded moss | |
| | <i>Plagiomnium</i> | <i>cuspidatum</i> | Woodsy leafy moss | |
| | <i>Plagiomnium</i> | <i>drummondii</i> | Drummond's leafy moss | |
| | <i>Pohlia</i> | <i>nutans</i> | Nodding Pohlia | |
| | <i>Polytrichum</i> | <i>juniperinum</i> | Juniper haircap moss | |
| | <i>Polytrichum</i> | sp. | Haircap moss | |
| | <i>Pseudoleskella</i> | <i>tectorum</i> | | |
| | <i>Timmia</i> | <i>austriaca</i> | False haircap moss | |
| | <i>Tortula</i> | <i>brevipes</i> | Short twisted moss | |
| | <i>Tortula</i> | <i>mucronifolia</i> | Sword's point twisted moss | |
| | <i>Tortula</i> | <i>tortuosa</i> | Twisted moss | • |
| | <i>Tortula</i> | <i>ruralis</i> | Rusty stem moss | |
| Liverworts | | | | |
| | <i>Barbilophozia</i> | <i>hatcheri</i> | Hatcher's fan wort | |
| | <i>Barbilophozia</i> | <i>lycopodioides</i> | Barbilophozia | |
| | <i>Barbilophozia</i> | sp. | Barbilophozia species | |
| Hair Lichen | | | | |
| | <i>Bryoria</i> | <i>fremontii</i> | Horsehair lichen | |
| Club Lichen | | | | |
| | <i>Cetraria</i> | sp. | Cetraria species | |
| | <i>Cetraria</i> | <i>ericetorum</i> | Icelandmoss | |
| | <i>Cladonia</i> | sp. | Club lichen | • |
| | <i>Letharia</i> | <i>vulpina</i> | Wolf lichen | |
| Leaf Lichen | | | | |
| | <i>Pannaria</i> | <i>pezizoides</i> | Pannaria | • |
| | <i>Peltigera</i> | <i>aphthosa</i> | Freckle pelt | • |
| | <i>Peltigera</i> | <i>canina</i> | Dog pelt | |
| | <i>Peltigera</i> | <i>neckeri</i> | Pelt lichen | |
| | <i>Peltigera</i> | <i>neopolydactyla</i> | Frog pelt | |
| | <i>Xanthoparmelia</i> | <i>coloradoensis</i> | Colorado rockfrog | |

Appendix 2. Non-native species encountered in the 220 Douglas-fir plots enumerated in the four mountain parks

| GENUS | SPECIES | COMMON NAMES | Stand Type | | |
|-------------------|---|-----------------------|------------|----|-----|
| | | | I | II | III |
| <i>Linaria</i> | <i>genistifolia</i> spp. <i>dalmatica</i> | Dalmatian toadflax | | | † |
| <i>Medicago</i> | <i>lupulina</i> | Black medick | † | | |
| <i>Poa</i> | <i>pratensis</i> | Kentucky bluegrass | † | † | |
| <i>Sonchus</i> | <i>arvensis</i> | Perennial sow-thistle | † | † | |
| <i>Taraxacum</i> | <i>officinale</i> | Common dandelion | † | † | |
| <i>Tragopogon</i> | <i>dubius</i> | Goat's-Beard | | † | |
| <i>Trifolium</i> | <i>pratense</i> | Red clover | † | | |

Appendix 3a. STAND TYPE I (DOUGLAS-FIR/JUNIPER/BEARBERRY), n= 95.

(i) Relative frequency for Banff National Park, n=29

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.93 | 0.52 | 0.38 | 0.38 | 0.59 |
| <i>Picea glauca</i> | White Spruce | 0.55 | 0.14 | 0.34 | 0.21 | 0.14 | 0.21 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.21 | 0.14 | 0.07 | | | 0.07 |
| <i>Pinus flexilis</i> | Limber pine | 0.10 | 0.07 | 0.07 | 0.03 | 0.03 | |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.17 | 0.03 | 0.07 | 0.14 | 0.10 | 0.17 |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp | Willow | | | | | | |
| <i>Populus balsamifera</i> | Balsam poplar | | | | | | |

(ii) Relative frequency for Jasper National Park, n=33

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.85 | 0.55 | 0.52 | 0.70 | 0.94 |
| <i>Picea glauca</i> | White Spruce | 0.39 | 0.15 | 0.15 | 0.03 | 0.06 | 0.24 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.39 | 0.15 | 0.21 | 0.18 | 0.12 | 0.03 |
| <i>Pinus flexilis</i> | Limber pine | | | | | | |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.03 | | | | | 0.03 |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp | Willow | | | | | | |
| <i>Populus balsamifera</i> | Balsam poplar | | | | | | |

(iii) Relative frequency for Kootenay National Park, n=23

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.57 | 0.39 | 0.48 | 0.61 |
| <i>Picea glauca</i> | White Spruce | 0.26 | | 0.09 | | 0.09 | 0.17 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.09 | | 0.04 | | | 0.09 |
| <i>Pinus flexilis</i> | Limber pine | | | | | | |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | 0.17 | | 0.09 | | 0.13 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.04 | | | | 0.04 | |
| <i>Salix</i> spp | Willow | | | | | | |
| <i>Populus balsamifera</i> | Balsam poplar | | | | | | |

(iv) Relative frequency for Yoho National Park, n=10

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.70 | 0.60 | 0.80 | 1.00 | 0.90 |
| <i>Picea glauca</i> | White Spruce | 0.70 | 0.30 | 0.40 | 0.60 | 0.50 | 0.30 |
| <i>Pinus contorta</i> | Lodgepole pine | | | | | | |
| <i>Pinus flexilis</i> | Limber pine | 0.10 | | | | 0.10 | |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.30 | | 0.20 | 0.10 | 0.10 | |
| <i>Betula papyrifera</i> | Paper Birch | 0.50 | | 0.30 | 0.30 | 0.10 | 0.10 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.30 | | | 0.30 | | |
| <i>Salix</i> spp | Willow | 0.30 | | 0.10 | 0.10 | 0.20 | |
| <i>Populus balsamifera</i> | Balsam poplar | 0.20 | | 0.10 | | 0.10 | |

Appendix 3b. STAND TYPE II (DOUGLAS-FIR/LODGEPOLE PINE/BUFFALOBERRY), *n* = 80.

(i) Relative frequency for Banff National Park, *n*=32

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.88 | 0.44 | 0.41 | 0.34 | 0.59 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.94 | 0.84 | 0.28 | 0.34 | 0.09 | 0.09 |
| <i>Picea glauca</i> | White Spruce | 0.72 | 0.22 | 0.25 | 0.28 | 0.34 | 0.16 |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.22 | 0.06 | 0.09 | 0.00 | 0.03 | 0.19 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |

(ii) Relative frequency for Jasper National Park, *n*=7

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.86 | 0.86 | 1.00 | 1.00 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.85 | 0.43 | 0.43 | 0.43 | 0.14 | 0.29 |
| <i>Picea glauca</i> | White Spruce | 0.29 | 0.00 | 0.00 | 0.14 | 0.29 | 0.14 |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | | | | | | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.14 | | 0.14 | | 0.14 | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |

(iii) Relative frequency for Kootenay National Park, *n*=36

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 0.92 | 0.83 | 0.75 | 0.58 | 0.83 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.78 | 0.64 | 0.42 | 0.17 | 0.00 | 0.06 |
| <i>Picea glauca</i> | White Spruce | 0.64 | 0.19 | 0.19 | 0.17 | 0.08 | 0.31 |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | 0.08 | | | | 0.08 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.58 | 0.28 | 0.25 | 0.03 | 0.28 | 0.31 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.22 | 0.00 | 0.06 | 0.00 | 0.19 | 0.03 |
| <i>Salix</i> spp. | Willow | 0.11 | | 0.06 | 0.06 | 0.03 | |
| <i>Betula papyrifera</i> | Paper Birch | 0.06 | 0.03 | 0.06 | | | |

(iv) Relative frequency for Yoho National Park, *n*=5

| Species | Common name | Canopy layer | | | | | |
|---|------------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.60 | 0.60 | 0.80 | 0.40 |
| <i>Pinus contorta</i> | Lodgepole pine | 1.00 | 1.00 | 0.20 | 0.20 | 0.00 | 0.00 |
| <i>Picea glauca</i> | White Spruce | 0.60 | 0.20 | 0.20 | 0.20 | 0.00 | 0.00 |
| <i>Juniperus scopularum</i> | Rocky Mountain Juniper | 0.20 | | | | 0.20 | |
| Deciduous | | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.40 | | | | 0.40 | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.20 | 0.00 | 0.00 | 0.00 | 0.20 | 0.00 |

Appendix 3c. STAND TYPE III (DOUGLAS-FIR/WHITE SPRUCE/FEATHERMOSS). n = 45

(i) Relative frequency for Banff National Park, n=2

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 0.50 | 1.00 | 1.00 | 1.00 | 0.00 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.50 | 0.50 | | 0.50 |
| <i>Abies bifolia</i> | Subalpine fir | 0.50 | 0.50 | | 0.50 | 0.50 | |
| <i>Thuja plicata</i> | Western red cedar | | | | | | |
| <i>Pinus contorta</i> | Lodgepole pine | 0.50 | 0.50 | | 0.50 | | |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | | | | | | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | | | | | | |

(ii) Relative frequency for Jasper National Park, n=19

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 0.74 | 0.53 | 0.37 | 0.79 | 0.84 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.58 | 0.16 | 0.32 | 1.00 |
| <i>Abies bifolia</i> | Subalpine fir | | | | | | |
| <i>Thuja plicata</i> | Western red cedar | | | | | | |
| <i>Pinus contorta</i> | Lodgepole pine | 0.50 | 0.05 | | | | |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.16 | | 0.05 | 0.11 | | 0.05 |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | | | | | | |

(iii) Relative frequency for Kootenay National Park, n=10

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 1.00 | 0.70 | 0.70 | 0.40 | 0.50 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.50 | 0.60 | 0.80 | 0.90 |
| <i>Abies bifolia</i> | Subalpine fir | 0.40 | 0.20 | | 0.40 | 0.30 | |
| <i>Thuja plicata</i> | Western red cedar | 0.10 | | 0.10 | | | |
| <i>Pinus contorta</i> | Lodgepole pine | 0.30 | 0.20 | | | | 0.10 |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.20 | | | | 0.20 | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | 0.20 | | | 0.20 | 0.20 | |
| <i>Salix</i> spp. | Willow | 0.20 | | | | 0.20 | |
| <i>Populus tremuloides</i> | Trembling aspen | 0.10 | | | | | 0.10 |

(iv) Relative frequency for Yoho National Park, n=14

| Species | Common name | Canopy layer | | | | | |
|---|----------------------|--------------|------|------|------|------|------|
| | | Total | 1 | 2 | 3 | 4 | 5 |
| Conifers | | | | | | | |
| <i>Picea glauca</i> | White Spruce | 1.00 | 0.86 | 0.79 | 0.36 | 0.64 | 0.64 |
| <i>Pseudotsuga menziesii</i> var. <i>glauca</i> | Interior Douglas-fir | 1.00 | 1.00 | 0.21 | 0.36 | 0.79 | 1.00 |
| <i>Abies bifolia</i> | Subalpine fir | 0.86 | 0.29 | 0.50 | 0.64 | 0.71 | 0.64 |
| <i>Thuja plicata</i> | Western red cedar | 0.50 | 0.21 | 0.21 | 0.14 | 0.21 | 0.36 |
| <i>Pinus contorta</i> | Lodgepole pine | 0.21 | 0.21 | | | | |
| Deciduous | | | | | | | |
| <i>Betula papyrifera</i> | Paper Birch | 0.14 | | 0.07 | 0.14 | 0.14 | |
| <i>Acer glabrum</i> | Rocky Mountain Maple | | | | | | |
| <i>Salix</i> spp. | Willow | | | | | | |
| <i>Populus tremuloides</i> | Trembling aspen | | | | | | |

APPENDIX 4. Regeneration summary table of interior Douglas-fir within each stand type.

| | STAND TYPE I | STAND TYPE II | STAND TYPE III |
|--|---|---|--|
| REGENERATION PRESENT (CANOPY 3 and 4) | <p>Vegetation:</p> <p>Moderate Canopy Cover Moderate Shrub cover • Moderate Buffalo-berry cover • Moderate Bearberry Cover</p> <p>High cover of <i>Elymus innovatus</i></p> <p>Low-Moderate Moss cover • High cover of <i>Hypnum revolutum</i></p> <p>Low-Moderate White spruce regeneration Moderate-high Regeneration of Douglas-fir in Canopy 3 Moderate Douglas-fir Seedling density</p> <p>Environment:</p> <p>Low-moderate bare ground Moderate slopes Low-Moderate Nutrient Levels</p> | <p>Vegetation:</p> <p>Low-Moderate Canopy Cover High Shrub Cover • High cover of Buffalo-berry • High cover of Bearberry • High cover of Common Juniper Moderate-high graminoid cover</p> <p>Moderate Moss Cover</p> <p>Low-Moderate White spruce regeneration Moderate-High Regeneration of Douglas-fir in Canopy 3 Moderate-high Douglas-fir Seedling density</p> <p>Environment:</p> <p>Low-moderate bare ground Moderate slopes Moderate-high Nutrient levels</p> | <p>Vegetation:</p> <p>Moderate-High Canopy cover Moderate-High Shrub Cover • Moderate cover of Buffalo-berry • Moderate cover of Twinflower</p> <p>Low-Moderate Graminoid cover</p> <p>Moderate-high Moss Cover • Moderate cover of <i>Pleurozium schreberi</i></p> <p>Moderate-High White spruce regeneration Low Regeneration of Douglas-fir in Canopy 3 High Douglas-fir Seedling density</p> <p>Environment:</p> <p>Low Bare Ground High Nutrient Levels</p> |
| REGENERATION ABSENT (CANOPY 3 and 4) | <p>Vegetation:</p> <p>Low Canopy Cover Low Shrub Cover</p> <p>Low graminoid cover</p> <p>Low moss cover • Moderate cover of <i>Tortula</i> species</p> <p>Low White spruce regeneration Low Regeneration of Douglas-fir in Canopy 3 Low-Moderate Douglas-fir Seedling density</p> <p>Environment:</p> <p>High bare ground High slopes Low-Moderate Nutrient Levels</p> | <p>Vegetation:</p> <p>Moderate-High Canopy cover Moderate-Low Shrub Cover • Moderate-high Twinflower cover Moderate-high graminoid cover</p> <p>Moderate cover of <i>Peltigera aphthosa</i> Moderate cover of <i>Drepanocladus uncinata</i> & <i>Dicranum scopularum</i></p> <p>Moderate White spruce regeneration Moderate Regeneration of Douglas-fir in Canopy 3 Low Douglas-fir Seedling density</p> <p>Environment:</p> <p>Low bare ground High-Moderate slopes Low-Moderate Nutrient Levels</p> | <p>Vegetation:</p> <p>High Canopy Cover Low Shrub Cover • Low-Moderate cover of <i>Lonicera / Cornus / Symphoricarpos</i> Low graminoid cover</p> <p>High Moss Cover • High cover of <i>Hylocomium splendens</i></p> <p>Moderate-High White spruce regeneration Low Regeneration of Douglas-fir in Canopy 3 High Douglas-fir Seedling density</p> <p>Environment:</p> <p>Low bare ground Moderate-High Nutrient Levels</p> |

MOISTURE →

← LIGHT

APPENDIX 5

INDICATOR SPECIES WITHIN DOUGLAS-FIR STANDS

INTRODUCTION

The use of indicator species to typify site conditions

In this study species associations were used to characterize the environmental conditions of each stand-type, based on the common ecological requirements shared by species within the three groups (see **chapter 4**; Legendre and Legendre 1998). Most of the species encountered were present in at least two out of the three groups, differing in their abundance not frequency (e.g., %cover). Only a hand full of species were 'unique' to any one of the classified stands. These species were considered indicators of environmental conditions and were characterized by low frequency and abundance values. Traditionally, indicator species have been used in management, conservation, and restoration to monitor habitat change, or characterize site conditions (Legendre and Legendre 1998; Jones and Kaly 1996). Indicator species add ecological meaning to groups of sites derived from clustering methods (Legendre and Legendre 1998). Indicator species differ from 'species associations' in that they are indicative of condition within groups. What constitutes a 'good indicator'? To begin with the species should be found in a single stand-type (group) of a typology and be present in most of the plots; in other words species with a clear ecological preference.

Computing Indicator species

Most studies which deal with indicators do so using apriori knowledge of site partitions. Two Way INDicator SPecies ANalysis (Twinspan; Hill 1979) has been used in the past to identify species fidelity based on the formation of a 'crude dichotomy' of a species data matrix. It is a polythetic divisive clustering method which uses dummy variables (pseudospecies) based on relative species abundance levels to model indicator species: a site x pseudospecies matrix is created. The dichotomy is computed utilizing the Correspondance Analysis (CA) centroid line to divide the samples into two groups (negative and positive) using the original site x species matrix. This dichotomy is then refined using a process comparable to iterative character weighting. The results are then ordered into a two-way table so that similar clusters are near to each other. In other words, species are scored according to their degree of preference, highly preferential species are those that are at least 3x more

common on one side. This procedure continues in hierarchical fashion until a minimum group size, selected by the user is obtained. Once all the samples have thus been classified, the species are classified according to their overall fidelity to the groups, and a sorted table is produced. One of the problems with the method is that it assumes a single underlying environmental gradient which is often not the case in natural systems (Legendre and Legendre 1998).

Another method used to measure the 'specificity' and 'fidelity' of a species is called the indicator value index (INDVAL; see Fleishman et al. 2000; Bruun and Ejrnæs 2000; Klinka and Song 1999; Dufrière and Legendre 1997). Unlike twinspan which relies on the identification of indicators from the partitioning of sites based on ordination results, INDVAL derives indicator species from any clustering (hierarchical and non-hierarchical) procedure based only on within species abundance's and frequencies (Legendre and Legendre 1998). Legendre and Legendre (1998) defined INDVAL based on the following:

For each species j encountered per stand-type k , one computes the product of its fidelity (A_{jk}) and specificity (B_{jk}).

(1) **Fidelity:** $A_{kj} = N_{\text{individuals}_{kj}} / N_{\text{individuals}_{+k}}$

where $N_{\text{individuals}_{kj}}$ = the mean abundance (%cover) of species j across plots pertaining to stand-type k and individuals_{+k} = The sum of mean abundances of species j across all the stand-types. A_{kj} is maximized when species j is encountered on in a single stand-type.

(2) **Specificity:** $B_{kj} = NSites_{kj} / NSites_{+k}$

Where $NSites_{kj}$ = Number of plots (frequency) in stand-type k in which species j is encountered and $NSites_{+k}$ = total number of plots in stand-type k .

(3) **INDVAL** = 100% $A_{kj} B_{kj}$

The index value is 100% when species j occurs on all plots belonging to stand-type k . INDVAL was computed for all understory species encountered within each of the three Douglas-fir stand-types, results are presented in Table A5.1 and partitioned into moss, graminoids, forbs, and shrubs categories.

Cryptogams

Hylocomium splendens had the highest computed INDVAL of any species (86.3%). Although it was marginally present in stand-type II (8.5%) its high index value in stand-type III made it a good indicator of stand conditions within mature closed-canopied hygric forests. Stand-type I was characterized by the presence of xerophytic mosses such as *Tortula* spp.. Although *T. ruralis* has its highest index value in stand-type I (22.3%) it is also present in stand-type II (11.4%) and III (3%). *T. tortula* is unique to stand-type I (5.2%). *Hypnum revolutum* was not unique to stand-type I it did have its highest index value (17%) compared to other two stand-types (6.1 and 4%; **Table A5.1**). *Pleurozium shreberi* is more indicative of mesic-hygric forest floor conditions. Its presence in Stand-type II (37.9%) and III (21.3%) testifies to its wider ecological amplitude compared to *H. splendens*. *Peltigera canina* is more indicative of stand-type II conditions with an index value of 25.5%.

Graminoid

Graminoids were better indicators of stand-type I and II. *Oryzopsis* sp. was the only species which was unique to stand-type III (12.9%). Indicator grasses of stand-type I include *Agropyron repens* (4.2%) *A. spicatum* (2.1%), *Stipe occidentalis* (6.3%), and *Muhlenbergia richardsonis* (6.3%). *Calamagrostis rubescens* is indicative of stand-type II with an index value of 69.9%. *Elymus innovatus* typifies more open canopied stands, its index value for stand-type I and II were almost identical (33.3 and 36.7%)

Forbs

Indicator species of stand-type I, include *Artemisia frigida* (15.8%), *Oxytropis campestris* (7.3%), *O. splendens* (10.5%), *Antennaria microphylla* (11.6%). Stand-type II indicators include *Hedysarum sulphurescens* (34.3%), *Fragaria virginia* (50.9%), *Lilium philadelphicum* (7.5%). and *Clematis occidentalis* (6.3%). Indicator species of Stand-type III include *Comandra livida* (37.5%), *Cornus canadensis* (24.9%), *Goodyera repens* (20.9%) and *Mitella nuda* (8.9%).

Shrubs

The shrub species computed as 'indicators' of stand-type I had low frequency and cover values, this is not surprising given the low productivity of these stands. With the exception of *Oplopanix horridus* (4.4%), there were no other shrub species which qualified as indicators for stand-type II or III. Species such as *Shepherdia canadensis* or *Lonicera utahensis* were either common in all stand-types or restricted to Stand-types II and III. Computed indicators

of stand-type I include *Potentilla fruticosa* (5.7%) *P. pensylvanica* (2.1%) , *Chrysothamnus nauseosus* (2.1%), and *Elaeagnus commutata* (2.1%).

Based on these results it seems that species which are dependent on belowground resources at the soil-humus interface or within the upper soil horizons are more sensitive to fluctuations in meso-climate and environmental gradients. The presence or abundance of these species is often limited by, inconsistent forest floor conditions (e.g., stem transpiration). Species turn-over resulting from competition is high resulting in either the presence of stress tolerators (e.g., *Tortula* sp.) or competitors (e.g., *Calamagrostis rubescens* and *Hylocomium splendens*) characterizing a site.

Longer lived species which are able to attain secondary stem and root growth as well as mycorrhizal associations are better adapted to withstand a wider range of growing conditions and disturbances. For example *Shepherdia canadensis* is a nitrogen-fixer (nodulation common in xeric soils) characterized by having varied root morphology: rhizomatous roots with deep underground structures, fibrous and shallow, and a taproot with no rhizomes (Alastair 1968). The lack of high turn-over in shrub species across the stand-types maybe scale dependent. Species which respond to larger scale climatic variation may require a wider ecological niche in order to show affinity to a given environmental conditions. This may explain why species who are more dependent on smaller-scale climatic variations such as moss and forbs show higher stand fidelity and specificity.

The following discussion will focus on the growth and general biology of bryophytes

Bryophytes: indicators of forest floor conditions

Poikilohydric species such as bryophytes are good indicators of forest floor conditions. The absence of internal conducting tissues, roots, and stomates makes them reliant on ground-level humidity and nutrients released from the LFH and organic horizons to ensure growth and survival. Ground moisture tends to fluctuate as a function of increasing light and temperature levels associated with a discontinuous canopy. Ephemeral increases in evapotranspiration resulting from high-pressure systems tend to have a greater impact on moisture reserves in the upper mineral soils and LFH horizons compared to deeper substrates. Episodic drying periods throughout the growing season dramatically limits bryophyte growth resulting in clumped distributions relegated to micro-sites. Within a closed-canopy forest the effects of seasonal climatic extremes are buffered, thus creating more stable lower sub-canopy environmental conditions. Highly persistent moisture conditions increase the effective growing period of bryophytes, leading to an increase in their dominance on the forest floor.

The fact that most bryophytes rely on high-humidity to sustain growth and survival, means that their spatial distribution is independent of underlying edaphic conditions and more dependent on ephemeral forest floor conditions such as moisture and light.

Vegetation cover in open-savannas and canopy gaps within closed-canopy forests tends to increase the complexity of light and moisture regimes within a given area. The distribution and abundance of moss species mimics the inherent spatial heterogeneity encountered within these communities resulting in either small clumps or extensive mats. Although all moss species have a strong dependence on moisture, the ability to tolerate high radiation levels and low water availability changes between species. The presence of mosses in excessively well drained xeric Douglas-fir stands are often restricted to micro-sites located beneath low postrate shrubs such as *Juniper communis* or *Arctostaphylos uva ursi* where micro-environmental conditions are atypical of the surrounding area. In these cases the presence of these individuals cannot be used to typify stand-level conditions. On the other hand, xerophytic mosses which can tolerate low moisture and desiccation by shutting down metabolic activity not only persist in these environments but help to reduce surface runoff, stabilize soil erosion, and create favorable micro-sites for vascular species.

The presence of extensive bryophytic mats indicates that growing conditions at the forest floor are more spatially and temporally consistent (Fig A5.1). The slow growth of most feathermosses testifies to the fact the extensive and thick moss carpet must have taken a long-time to develop and thus are often used as stand-age indicators. The presence of these "late-successional" moss species tend to be associated the certain substrate conditions such as rotten wood and organic substrates. Increases in *Pleurozium* mats within mature lodgepole pine stands in Banff are related to time since fire (around 80 yrs) as well as the development of a multitiered tree canopy (personal observation).

Ecological advantage of an acrocarpus vs pleurocarpus

The ability to growth in vertical tufts or spread-out laterally has certain advantages for organism growing on a homogenous or complex forest-floor conditions. Most of the acrocarpos (vertical stems) moss species encountered within Douglas-fir stands occurred in small clumps. All of the species in this group have are sparsely branched with the sporophyte located at the apex, Species such as *Tortula* sp., or *Timmia* sp. were often limited by moisture or a lack of suitable substrates (e.g., decaying wood). In either case this growth-habitat was not restricted to over-riding macroclimate conditions (see Fig A5.2 and A5.1). Individual growth consist of increasing stem height. In the case of *Tortula* sp. its growth seemed to be related to macro-climatic conditions (Lesca et al. 1991). Most of tufts encountered in open

xeric conditions were short in stature (<2 cm), sporophytes were rare compared to specimens which occur in protected micro-sites (personal observation). *Timmia* was encountered stand-types III, All of the collected specimens were growing exclusively on decomposing wood, stem height were <10 cm.

Unlike acrocarpus moss, pleurocarps tend to be more frequent and abundant in mesic to hygric stand-types (Fig A5.2). Feather moss species such *Thuidium abietium*, *Hypnum revolutum*, *Ptilium crist-castrensis*, *Pleurozium schreberi*, and *Hylocomium splendens* are slow growers characterized by a horizontal growth habit. *Thuidium* and *Hypnum* are one the few feathermosses which tend to occur in drier conditions (stand-type I and II). Lateral stem growth is beneficial for capturing more light under low-light conditions as well as creating a thick moss layer made up of live and decomposing material which serve to sequester essential nutrients and water (Busby et al 1978). The differences in growth form between the two groups has important implications on growth response. Acrocarpus species are more sensitive to micro-site conditions, explaining the presence of xerophytic mosses in stand-type II. In addition micro-site sensitivity decreases the likelihood of high dominance (high percent cover). Pleurocarpus mosses respond to stand-level climatic conditions. The dominance of pleurocarpus species such as feathermosses is a function of stable forest floor conditions. The high cover values of pleurocarpus species means that they are responding stand-level conditions instead of micro-site conditions (Busby et al. 1978).

The following is a summary of 'indicator' species encounter in Douglas-fir stands through the four mountain parks:

Indicator Species of Stand-type I

***Tortula ruralis* (Hedw.) Gaertn., Meyer, & Scherb. – Hairy Screw Moss**

Distribution

The species has a cosmopolitan distribution, occurring in North America, South America, Europe, Middle East, Africa, and Australia. In North America *T. ruralis* is more common to the western portion of the continent. The species has a wide ecological amplitude occurring from xeric to mesic forests, grasslands, to deserts, arctic-tundra and tundra,. The species grows on a wide range of substrates generally preferring calcareous rocks.

Species Biology

T. ruralis is a short plant (1-4 cm in height) with a acrocarpus growth habit (erect) forming robust tufts. The gametophyte is anchored to the soil by rhizoid. The species is considered a xerophytic moss, tolerant of drought and desiccation. During periods of low humidity the plants quickly dry entering a dormant phase which has been documented to last for upto 70 years. During the dormant phase the leaves are twisted around the stem turning dark brown in color, becoming brittle and are normally broken apart by ungulates. A resumption of Metabolic activity following re-hydration triggers a dramatic change in leaf orientation and color (leaves spread out in an 90° angle and turn green in color). The species can tolerate full sun as well as full shade. Cryptogamic soil crusts such as *T. ruralis* are important components of barren grasslands and xeric open-forests communities by reducing soil erosion, increasing water percolation, organic matter accumulation, decreasing runoff, as well as facilitate vegetation establishment by creating optimal growing conditions in micro-sites.

T. ruralis is a dioecous species which undergoes a distinctive annual reproductive phases. Vegetative propagation occurs through the dispersion of gemmae or the fragmentation of the sporophyte.

Indicator Species Common to Stand-type II

***Calamagrostis rubescens* Buckl. - Pinegrass**

Species Distribution

Calamagrostis rubescens occurs in western North America. In Canada it occurs from Manitoba to British Columbia and in the United States, from Idaho, Montana, Oregon, Wyoming, Utah, Colorado, and into California. Not to be confused with *C. canadensis* which is the most common *Calamagrostis* species in North America, most commonly occurring in climax riparian and cool, moist forest communities. *C. rubescens* is considered an important understory species within Aspen, Engelmann spruce, lodgepole pine, and Douglas-fir communities. It is the most abundant grass species in forested regions of southern British Columbia.

Species Biology

Calamagrostis rubescens is a perennial rhizomatous grass with rhizomes growing mostly in the upper 5 cm of the mineral soil. Beneath a forest canopy *C. rubescens* reproduces through the lateral extensions of rhizomes and only produces seeds in openings. The species grows in xeric as well as mesic conditions and can be found in open and closed-canopied forests. *C. rubescens* is shade tolerant and persists throughout all successional stages increasing site dominance with increased light levels. Early post-fire dominance of *C. rubescens* occurs through rhizome sprouts, so long as the fire does not consume the duff layer. Higher intensity fires which consume the duff layer kill off rhizomes, in these cases colonization occurs from seed dispersal. Generally *C. rubescens* responds positively to fire, increasing in dominance, it is seldom eliminated from fire driven systems. Soils which support high *C. rubescens* cover are usually nitrogen poor and undergo episodic moisture deficit. The species is considered an 'aggressive competitor' for soil moisture and can limit seedling recruitment into stands. High water usage enables the species to undergo rapid growth early in the season and photosynthesize at low leaf water potential levels. In British Columbia the species is most abundant in the interior Douglas-fir zone, where it occupies extremely xeric to hygric stands (Comeau et al. 1989).

Indicator Species of Stand-type III

Hylocomium splendens (Hedw.) B.S.G. – Stairstep moss

Species distribution

The species has a cosmopolitan distribution occurring in the cooler parts of the Northern Hemisphere from Greenland to Alaska, South to North Carolina, and west to Oregon and California (Schofield 1992). It also occurs in the West-Indies, Europe, Asia, Africa, Australia, and New Zealand. The species is indicative of stable old-growth conifer stands.

Species Biology

Hylocomium splendens is a perennial feather moss species with an average life span of around 8 years. The species is very closely related to microclimatic conditions, removal of canopy trees or shrubs can have prominent effects on growth. Busby et al (1978) found that within two weeks after transplanting feathermosses into an open fen, stem damage (bleaching) was noticed on all species with *Ptilium crista-castrensis* showing the most damage followed by *H. splendens* and *Pleurozium shreberi* showing the least damage. Studies such as these confirm that the growth and survival of the species is dependent on low-irradiance, rainfall frequency, and high nutrient levels. Growth rates are highest beneath a closed-canopy with high humidity and low evapotranspiration (LaRoi and Stringer 1976). Beneath a forest canopy maximum feathermoss production seems to occur near 'drip zones' (Tamm 1953). Busby et al. (1978) measured water deficiency levels between moss-dominated and moss-free zones beneath a forest canopy. They found that showers of less than 5 mm did not penetrate through the canopy down to the moss-free regions, by comparison nearly 78% of rainfall penetrated down to the moss-dominated zones. Thus they concluded that water rather than low light seems to limit feathermoss growth. Such information is important when using *H. splendens* as a moisture indicator. *H. splendens* establishes on humus, mineral or organic soils, and decaying wood. The sequestered moisture in the *Hylocomium* layers take only a few minutes to reach 'equilibrium moisture content' when relative humidity decreases, thus increasing the flammability of the feathermoss carpet during fire seasons (Nurum 1982). Johnson (1981) noted that it takes around 30-50 years for *Hylocomium* to return after a fire.

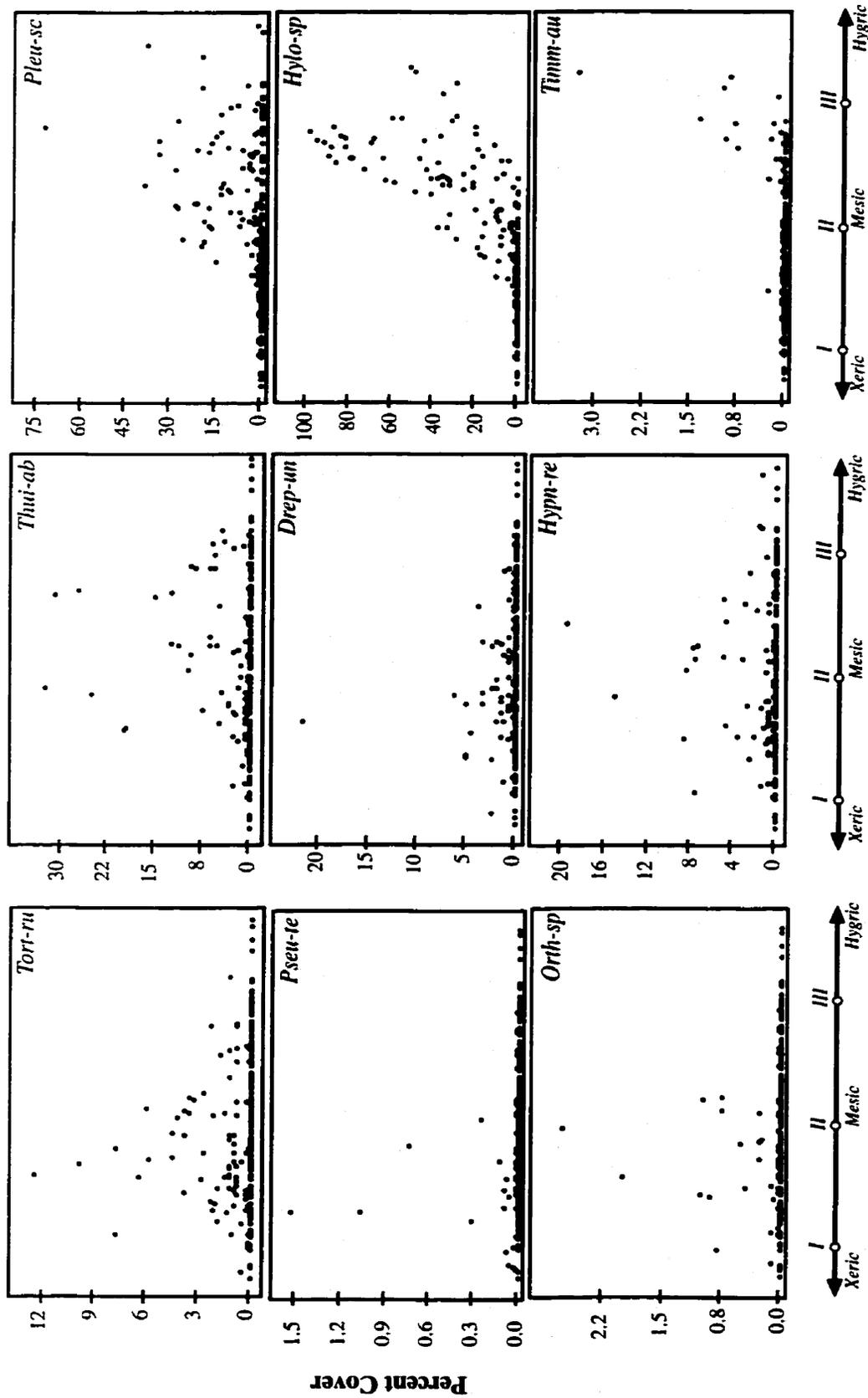


Figure A5.1. Percent cover (Y-axis) of moss species encountered in Douglas-fir stands (I-III) within the four mountain parks plotted against the species ordination scores along the 1st CA axis (X-axis). Abbreviations: Tor-ru = *Torula ruralis*, Pseu-te = *Pseudoleskeella tectorum*, Orth-spp = *Orithricum* spp., Thui-re = *Thuidium abietinum* (*Abietinella abietina*), Drep-un = *Drepanocladus uncinatus* (*Saniona uncinata*), Hypn-re = *Hypnum revolutum*, Pleu-sc = *Pleurozium schreberi*, Hylo-sp = *Hylocomium splendens* and Tinn-au = *Timmia austriaca*.

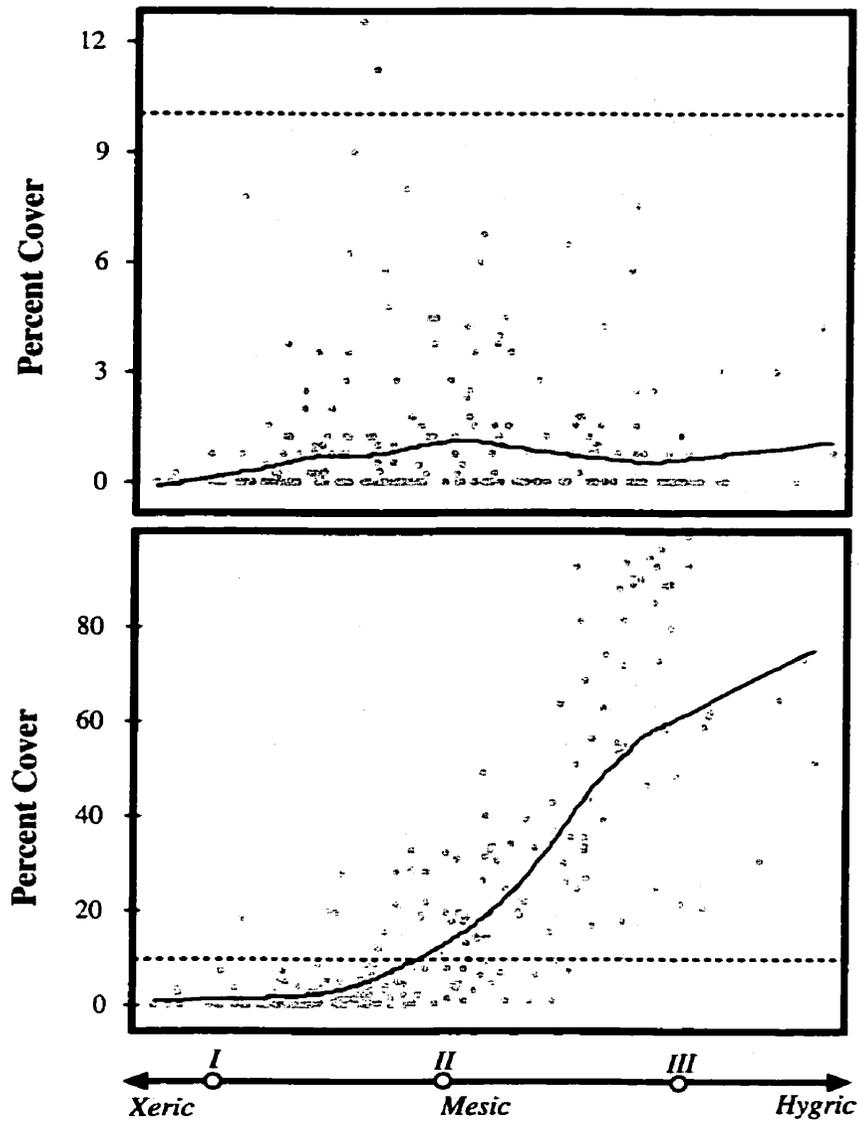


Figure A5.2. Changes in cover of *Acrocarpus* (TOP) and *Pleurocarpus* (BOTTOM) mosses across the three interior Douglas-fir stand-type. Lines were fitted using weighted regression analysis. Horizontal axis represents the first correspondence analysis axis, with mean location of stand-types I-III plotted on the line beneath

Table A5.1 INDVAL (Index values) of 'indicator species'. Values of 100% signifies high species affinity to a given stand-type

| Mosses/Lichens | I | II | III |
|-----------------------------------|----------|-----------|------------|
| <i>Hylocomium splendens</i> | 0.0 | 8.5 | 86.3 |
| <i>Peltigera aphthosa</i> | 0.8 | 11.3 | 52.7 |
| <i>Pleurozium shreberi</i> | 0.5 | 37.9 | 21.3 |
| <i>Thuidium abietinum</i> | 9.8 | 2.7 | 20.3 |
| <i>Ptilium crista-castrensis</i> | 0.8 | 2.5 | 15.4 |
| <i>Timmia austriaca</i> | 0.0 | 0.0 | 15.3 |
| <i>Rhytidiadelphus triquetrus</i> | 0.0 | 1.7 | 15.0 |
| <i>Dicranum scoparium</i> | 0.3 | 8.2 | 5.6 |
| <i>Peltigera canina</i> | 7.7 | 25.5 | 4.2 |
| <i>Hypnum revolutum</i> | 17.2 | 6.1 | 4.0 |
| <i>Tortula ruralis</i> | 22.3 | 11.4 | 3.0 |
| <i>Dicranum fuscissemis</i> | 0.0 | 6.3 | 1.2 |
| <i>Drepancladis uncinatis</i> | 16.9 | 10.9 | 0.8 |
| <i>Tortula torula</i> | 5.2 | 0.0 | 0.0 |
| <i>Orthitricum speciosum</i> | 7.0 | 3.5 | 0.0 |
| Grasses | | | |
| <i>Elymus innovatus</i> | 33.3 | 36.7 | 5.9 |
| <i>Koeleria macrantha</i> | 19.7 | 0.2 | 0.1 |
| <i>Festuca saximontana</i> | 8.9 | 0.4 | 0.0 |
| <i>Muhlenbergia richardsonis</i> | 6.3 | 0.0 | 0.0 |
| <i>Stipa occidentalis</i> | 6.3 | 0.0 | 0.0 |
| <i>Agropyron repens</i> | 4.2 | 0.0 | 0.0 |
| <i>Calamagrostis rubescens</i> | 3.3 | 69.9 | 2.3 |
| <i>Agropyron spicatum</i> | 2.1 | 0.0 | 0.0 |
| <i>Schizachne purpurascens</i> | 0.3 | 0.0 | 1.5 |
| <i>Carex concinna</i> | 0.0 | 6.8 | 0.2 |
| Forbs | | | |
| <i>Commandra umbellata</i> | 0.0 | 0.0 | 37.0 |
| <i>Orthilia secunda</i> | 0.0 | 11.8 | 32.5 |
| <i>Cornus canadensis</i> | 0.0 | 1.0 | 24.9 |
| <i>Pyrola chlorentha</i> | 0.0 | 17.6 | 24.4 |
| <i>Goodyera repens</i> | 0.0 | 2.4 | 20.9 |
| <i>Aster conspicuus</i> | 6.1 | 25.0 | 19.4 |
| <i>Calypso bulbosa</i> | 0.0 | 0.4 | 11.2 |
| <i>Mitella nuda</i> | 0.0 | 0.0 | 8.9 |
| <i>Maiantemum canadensis</i> | 0.0 | 0.0 | 8.9 |
| <i>Galium triflorum</i> | 0.0 | 0.0 | 8.7 |
| <i>Goodyera oblongifolia</i> | 0.0 | 5.4 | 8.4 |
| <i>Fragaria virginiana</i> | 6.4 | 50.9 | 6.1 |
| <i>Viola renifolia</i> | 0.0 | 0.0 | 4.4 |
| <i>Smilacina racemosa</i> | 0.0 | 3.2 | 4.4 |
| <i>Aster ciliolatus</i> 5 | 2.9 | 28.6 | 3.6 |
| <i>Streptopus amplexifolius</i> | 0.1 | 2.7 | 3.4 |
| <i>Galium borealis</i> | 21.9 | 5.4 | 1.3 |
| <i>Lathyrus ochroleucus</i> | 0.9 | 9.4 | 1.1 |
| <i>Disporum trachycarpum</i> | 0.1 | 9.2 | 0.9 |
| <i>Arnica cordifolia</i> | 0.1 | 16.3 | 0.5 |
| <i>Achillia millefolium</i> | 21.2 | 11.3 | 0.0 |
| <i>Hedyselum sulphurescens</i> | 3.6 | 34.4 | 0.0 |

| | | | |
|----------------------------------|------|------|------|
| <i>Taraxicum officinale</i> | 19.1 | 1.0 | 0.0 |
| <i>Astragalus miser</i> | 16.9 | 11.7 | 0.0 |
| <i>Viola adunca</i> | 5.7 | 10.9 | 0.0 |
| <i>Lilium philadelphicum</i> | 0.0 | 7.5 | 0.0 |
| <i>Trifolium repens</i> | 0.0 | 6.3 | 0.0 |
| <i>Clematis occidentalis</i> | 0.0 | 6.3 | 0.0 |
| <i>Solidago spathulata</i> | 30.5 | 2.8 | 0.0 |
| <i>Anemone multifida</i> | 25.1 | 2.4 | 0.0 |
| <i>Camanula rotundifolia</i> | 10.2 | 1.2 | 0.0 |
| <i>Senecio canina</i> | 9.8 | 0.1 | 0.0 |
| <i>Oxytropis campestris</i> | 7.3 | 0.0 | 0.0 |
| <i>Artemisia dracunculus</i> | 6.3 | 0.0 | 0.0 |
| <i>Apocynum androsaenifolium</i> | 9.5 | 0.0 | 0.0 |
| <i>Oxytropis splendens</i> | 10.5 | 0.0 | 0.0 |
| <i>Antennaria microphylla</i> | 11.6 | 0.0 | 0.0 |
| <i>Artemisia frigida</i> | 15.8 | 0.0 | 0.0 |
| SHRUBS | | | |
| <i>Shepherdia canadensis</i> | 15.0 | 47.8 | 4.6 |
| <i>Rosa acicularis</i> | 9.4 | 38.2 | 25.0 |
| <i>Spiraea betulifolia</i> | 7.3 | 37.4 | 8.8 |
| <i>Juniperus communis</i> | 34.5 | 24.7 | 9.0 |
| <i>Linnaea borealis</i> | 0.1 | 22.5 | 48.7 |
| <i>Arctostaphylos uva-ursi</i> | 30.2 | 18.4 | 0.1 |
| <i>Symphoricarpos albus</i> | 9.2 | 14.1 | 15.5 |
| <i>Amelanchier alnifolia</i> | 5.6 | 10.8 | 18.9 |
| <i>Chimaphila umbellata</i> | 0.0 | 8.9 | 1.9 |
| <i>Lonicera utahensis</i> | 0.0 | 8.7 | 19.4 |
| <i>Juniperus horizontalis</i> | 12.9 | 2.7 | 0.0 |
| <i>Spiraea pyramidata</i> | 0.0 | 1.4 | 1.0 |
| <i>Viburnum edule</i> | 0.1 | 1.2 | 15.1 |
| <i>Lonicera dioica</i> | 0.0 | 0.9 | 0.6 |
| <i>Ribes lacustre</i> | 3.6 | 0.8 | 15.6 |
| <i>Sorbus scoparium</i> | 0.0 | 0.5 | 1.4 |
| <i>Vaccinium caespitosum</i> | 0.0 | 0.3 | 3.8 |
| <i>Vaccinium scoparium</i> | 0.0 | 0.2 | 5.8 |
| <i>Menziesia ferruginea</i> | 0.0 | 0.1 | 11.8 |
| <i>Lonicera involucrata</i> | 0.0 | 0.1 | 5.9 |
| <i>Cornus stolonifera</i> | 2.4 | 0.1 | 0.8 |
| <i>Potentilla fruticosa</i> | 5.7 | 0.1 | 0.0 |
| <i>Chrysothamnus nauseosus</i> | 2.1 | 0.0 | 0.0 |
| <i>Elaeagnus commutata</i> | 2.1 | 0.0 | 0.0 |
| <i>Potentilla pensylvanica</i> | 2.1 | 0.0 | 0.0 |
| <i>Lonicera ciliosa</i> | 0.1 | 0.0 | 18.9 |
| <i>Oplopanax horridus</i> | 0.0 | 0.0 | 4.4 |

APPENDIX 6

BOUYOUCOS HYDROMETER METHOD: PARTICLE-SIZE ANALYSIS

The following summary is based on: (40.202. 1993. Laboratory Manual for Introductory Soil science; Kalra and Maynard 1991; Bouyoucos, 1951 and 1962;).

BACKGROUND

Particle size distribution is a stable soil characteristic related to the physical and chemical properties of the soil. Particle size distribution is a standard means for typifying the fine earth fraction of solid soil particles and helps determine the appropriate soil texture class. Soil texture often determines the water-holding capacity of soils. A mechanical analysis known as the Bouyoucos Hydrometer Method is used to determine the proportion of sand (0.05-2.00 mm), silt (0.002-0.05 mm) and clay (<0.002 mm) in a sample. The Hydrometer method works on the principals that larger particles fall more rapidly through a column of water than smaller particles. Before the percentage of particle size can be determined, individual soil particles must be separated from each other using both mechanical and chemical procedures. Mechanical separation is accomplished through stirring, this is an effective mean of separating larger particles from one another. Chemical dispersion is essential for separating smaller sized particles and requires a strong dispersing agent. Sodium hexametaphosphate (e.g., Calgon) is commonly used because it alters the chemical attraction between soil particles (particularly clay particles), causing them to repel each other. Soil colloids (finely divided particles dispersed in continuous medium) carry an inherent charge which is neutralized to some degree by cations in the soil. Depending on the type of cation present, soil colloids will tend to attract one another causing aggregations to form (flocculate) or the clay particles may disperse. If soil colloids flocculate the newly formed aggregates would simulate larger particle and settle at a faster rate.

The presence of cations such as Na^+ tend to disperse soils whereas the presence of H^+ and Ca^{2+} tend to cause soils to aggregate. Dispersal agents such as Sodium hexametaphosphate tend to replace Ca^{2+} ion often associated with negatively charged soil colloids with Na^+ . The phosphorus in the dispersal agent precipitates Ca^{2+} from the solution.

Once this is accomplished different soil particle sizes are separated in a 1000 ml column based on their differential sedimentation rate using the principals of Stokes Law:

$$(1) V = (2/9) [r^2 g (d_1 - d_2)/\eta],$$

where r = particle radius, g = natural acceleration due to gravity, d_1 = density of the particle and d_2 = density of the liquid. Equation (1) can be simplified to approximate velocity: $V = 8711 d^2$, where d is the diameter of the particle size in centimeters. One of the problems with Stokes Law is that it assumes that soil colloids are perfect spheres when in fact clay particles can be 'platelike in nature'. Furthermore, the hydrometers should be calibrated to 20°C, otherwise a correction factor is often required since both the density and viscosity of water change with increasing temperature (e.g. increase in temperature, decrease in viscosity).

PROCEDURE

- 50g of fine texture soil or 100 grams of sandy soil were transferred to a dispersal cup.
- Water was added to about 400 ml or to the 3/4 mark.
- 50 ml of 43g / 100ml of calgon solution was added and the soil solution was agitated in a 'milkshake' blender for 15 minutes. A shaking table can also be used, however soil solutions must remain on the table for at least 6 hrs. Its recommended that samples be stirred at least 2 times during this period.
- Once completed the soil suspension was transferred to a 1000 ml graduated cylinder. Water was added upto the 1000 ml mark.
- The soil suspension was stirred, in a gentle clockwise up and down manner.
- The soil suspension was allowed to sit for 40 seconds. 3-4 drops of alcohol were used to disperse fine organic debris. The hydrometer was placed gently into the solution, ensuring that organic debris was dispersed away from the hydrometer. A reading was taken from the top of the meniscus (mg/m^3).
- The cylinder was allowed to stand for 5 hours and then a second reading was taken.

The hydrometer readings from Cobb lake trail, in Kootenay National park range from 1.0250 (mg/m^3 ; 40 sec) to 1.0080 (mg/m^3 ; 300 min).

After the readings were measured the temperature of the solution was taken. For every 1°C change from 20°C a 0.36 graduation was added (increase in temperature) or subtracted (decrease in temperature) from the hydrometer reading.

The sanded settled out of the solution at the 40 second reading. Thus this reading is used to calculate the grams of silt and clay (W_s) in suspension:

$$W_s = V_t (D - D_w) / (1 - D_w / D_s)$$

Where V_t = total volume, D = density of soil suspension (hydrometer reading), D_w = Density of water (1.0 Mg m^{-3}) and D_s = Density of soil (assume 2.65 Mg m^{-3}). For the Cobb lake trail soil W_s would be:

$$\begin{aligned} \mathbf{WSi+C: W_s (40sec)} &= 1000 \text{ ml } ([1.0250 \text{ Mg m}^{-3} - 1] / [1 - 1 / 2.65 \text{ Mg m}^{-3}]) \\ &= 40.15 \text{ g of Silt and Clay} \end{aligned}$$

Weight of sand in the column:

$$\mathbf{WSand} = \text{weight of soil used} - W_s = 50\text{g} - 40.15\text{g} = 9.83 \text{ g of Sand}$$

After 5 hours it is assumed that only the clay remains in suspension thus W_s (5hrs) is used to compute the weight of Clay in the column.

$$\begin{aligned} \mathbf{WClay: W_s (5hrs)} &= 1000 \text{ ml } ([1.0080 \text{ Mg m}^{-3} - 1] / [1 - 1 / 2.65 \text{ Mg m}^{-3}]) \\ &= 12.85 \text{ g of Clay} \end{aligned}$$

Therefore the weight of silt in the column is:

$$W_s (40sec) - W_s (5hrs) = \mathbf{WSilt}$$

$$40.15 \text{ g (Si and C)} - 12.85\text{g (C)} = 27.30 \text{ grams of Silt.}$$

$$\begin{aligned} \% \mathbf{Sand} &= (9.83\text{g} / 50\text{g}) 100\% = 19.7\%; \quad \% \mathbf{Clay} = (12.85\text{g} / 50\text{g}) 100\% = 25.7 \text{ and } \% \mathbf{Silt} = \\ &(27.30\text{g} / 50\text{g}) 100\% = 54.6\% \end{aligned}$$