

AN ANALYSIS OF CONIFER SEEDLING MORPHOLOGY AS INFLUENCED BY
TWO DIFFERENT SILVICULTURAL SYSTEMS.

By

TANIA ELISABETH PERZOFF

B.Sc., The University of British Columbia 1995

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Department of Botany)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

September 1997

© Tania Elisabeth Perzoff, 1997

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Botany

The University of British Columbia
Vancouver, Canada

Date September 30, 1997

Abstract

The growth responses of *Pseudotsuga menziesii* (Mirb.) Franco and *Abies grandis* (Dougl.) Lindl. seedlings planted near Squamish, British Columbia in the CWHdm biogeoclimatic zone were examined in order to describe the general growth patterns expressed and their relationships to light, temperature and soil moisture levels in two different forest environments, a small clearcut or clearing and a shelterwood.

Seedling growth patterns and general morphology were analyzed using a combination of multivariate and univariate statistics. Each revealed consistent spatial relationships between the measured plant parts which helped describe the overall morphology of the seedlings. The best descriptors of the seedlings were found to be the current height increment, the subtending lateral branches of the apical whorl and the buds produced along the current height increment. It was also demonstrated that while different morphologies were present among both seedling species (in terms of the presence or absence of proleptic free growth) the manner in which the plant parts were integrated to form the whole seedling was often the same.

The analyses of growth responses in relation to specific environmental variables resulted in the clear demonstration of site preference between each species. Grand fir seedlings grew best in the more shaded environment of the shelterwood, while Douglas fir grew best in the more open environment of the clearing. Seedlings of Douglas fir with proleptic free growth did not share this same response, however, and performed better in the shelterwood.

Results generated from these analyses are presented and discussed in relation to the current understanding of conifer growth patterns, as well as the general performance of Douglas fir and grand fir seedlings in the context of reforestation.

Table of Contents

Abstract	ii
List of Tables.....	v
List of Figures	vii
Acknowledgments	x
Chapter 1. General Introduction.....	1
Reforestation and Alternative Silviculture Systems.....	1
Seedling Morphology	3
Chapter 2. Comparative Analysis of Seedling Morphology	7
Introduction	7
Objectives.....	12
Materials and Methods	13
Site description	13
Plant material	16
Seedling measurements	19
Statistical analyses	21
Results	27
Discussion	57
Chapter 3. Seedling Growth in Relation to the Environment.....	69
Introduction	69
Materials and Methods.....	74
Climate of the Squamish area	74
On-site climatic measurements	79
Statistical analyses	83
Results	87
On-site climate	87
Relationships between the environment and seedling morphology.....	92
Discussion	99
When does the climate affect growth?.....	105
Chapter 4. Conclusions Regarding Reforestation, Alternative Silviculture Systems and Seedling Morphology	108
Reforestation and Alternative Silviculture Systems.....	108
Seedling Morphology	110
Reference List	113

List of Tables

Table 1. Component loadings, eigenvalues and percent of total variance explained by the first two axes extracted using PCA for the 1995 and 1996 variables analyzed together. Each site and species combination was determined using a separate PCA.	36
Table 2. Component loadings, eigenvalues and percent of total variance explained by the first two axes extracted using PCA for all 1995 and 1996 morphological variables. Each site, species and year combination was determined using a separate PCA.	39
Table 3. Component loadings, eigenvalues and percent of total variance explained for the first two axes extracted using PCA for 1996 morphological variables only. Each site, species and seedling-type combination was determined using a separate PCA.	47
Table 4. Adjusted least squares means and standard errors for categorical ANCOVA terms showing statistical significance for all seedlings in 1995 and 1996.	50
Table 5. Adjusted least squares means and standard errors for categorical ANCOVA terms showing statistical significance for all seedlings with a "normal" and "proleptic free growth" morphology.	52
Table 6. Eta squared values for variables used in analysis of covariance for all seedlings pooled in 1995 and 1996.	55
Table 7. Eta squared values for variables used in analysis of covariance for "normal" and "proleptic free growth" seedlings in 1996.	57
Table 8. Summary table of boxplot results demonstrating the effects of 1995 environmental variables on seedling morphology.	93
Table 9. Summary table of boxplot results demonstrating the effects of 1996 environmental variables on the morphology of all seedlings pooled together.	95
Table 10. Summary table of boxplot results demonstrating the effects of 1996 environmental variables on the morphology of "normal" seedlings.	96

Table 11. Summary table of boxplot results demonstrating the effects of 1996 environmental variables on the morphology of seedlings with proleptic free growth.	97
----------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

List of Figures

Figure 1. General branching pattern of conifers displaying articulate growth.	4
Figure 2. Location of the Ring Creek area.	14
Figure 3. Photograph of the shelterwood.	15
Figure 4. Photograph of the clearing.	16
Figure 5. Sketch of the planting layout in the shelterwood. The black line is the survival line for grand fir, while the white line is the survival line for Douglas fir. Dashed lines are roads.	18
Figure 6. Sketch of seedling measurements taken in 1995 and 1996.	20
Figure 7. Sketch of proleptic free growth characteristics commonly seen.	21
Figure 8. Means (dots) and standard deviations (vertical lines) of morphological features for all grand fir seedlings. "sw"=shelterwood, "cl"=clearing.	28
Figure 9. Means (dots) and standard deviations (vertical lines) of morphological features for all Douglas fir seedlings. "sw"=shelterwood, "cl"=clearing.	29
Figure 10. Means (dots) and standard deviations (vertical lines) of measured characteristics comparing seedlings of grand fir with a "normal" morphology to those with "proleptic free growth". "n"=normal, "f"=free growth, "sw"=shelterwood, "cl"=clearing.	30
Figure 11. Means (dots) and standard deviations (vertical lines) of measured characteristics comparing seedlings of Douglas fir with a "normal" morphology to those with "proleptic free growth". "n"=normal, "f"=free growth, "sw"=shelterwood, "cl"=clearing.	32
Figure 12. PCA scatterplot of factor scores with 95% confidence ellipses for grand fir and Douglas fir seedlings.	33
Figure 13. PCA vector ordinations of grand fir morphological variables for 1995 and 1996 combined.	34

Figure 14. PCA vector ordinations of Douglas fir morphological variables for 1995 and 1996 combined.	34
Figure 15. PCA vector ordinations of grand fir morphological variables in 1995 (a and b) and in 1996 (c and d).....	37
Figure 16. PCA vector ordinations of Douglas fir morphological variables in 1995 (a and b) and in 1996 (c and d).	41
Figure 17. PCA vector ordinations of all grand fir seedling types.	44
Figure 18. PCA vector ordinations of all Douglas fir seedling types.	46
Figure 19. Relationship between length of the current height increment and the number of lateral buds produced.	66
Figure 20. Average daily minimum, mean and maximum temperatures for Squamish Airport, generated from 1959 - 1996. Minimum temperatures are denoted by the lower portion of the curve, maximum temperatures by the upper portion. Mean temperatures are demonstrated by the yellow curve. Dashed vertical lines represent early and late spring and fall frost events. ...	75
Figure 21. Total and cumulative precipitation from 1959 - 1996 from Squamish Airport. Dashed vertical lines represent early and late spring and fall frost events.	76
Figure 22. Mean daily minimum, maximum and mean air temperatures for 1995 and 1996 from Squamish Airport. Minimum temperatures are denoted by the lower portion of the curve, maximum temperatures by the upper portion. Mean temperatures are demonstrated by the yellow curve.	77
Figure 23. Mean total and cumulative precipitation for 1995 and 1996 from Squamish Airport.	78
Figure 24. Photo of datalogger setup.....	81
Figure 25. Percent of total sunlight and percent of total PAR readings for 1995 and 1996 respectively. Measurements at both sites were recorded on a clear-sky day in the fall for both years. "sw" = shelterwood, "cl" = clearing. ...	89

Figure 26. Air temperature trends for the shelterwood and clearing sites in 1995 and 1996, measured on a clear-sky day in the fall of both years. "sw = shelterwood, "cl = clearing90

Figure 27. Humus and mineral soil water content for both the shelterwood and clearing sites in 1996. "sw" = shelterwood, "cl" = clearing.91

Acknowledgments

Many people helped develop and refine this thesis, for which I give my sincere thanks. Thanks goes out in particular to Mr. Rob Scagel and Dr. Jack Maze, who both listened for countless hours and were encouraging and helpful throughout the entire process. They were always very accommodating and understanding, which is greatly appreciated. Dr. Gary Bradfield also deserves thanks for his encouraging commentary and constant enthusiasm. I would also like to thank Dr.'s Bradfield and Maze for the efficient manner in which they sought out the third member of my committee, Dr. Roy Turkington. To Dr. Turkington in particular, thank you very much for agreeing on such short notice to become a part of my committee. It alleviated much of the worry which would have resulted, and is sincerely appreciated. Many thanks also go out to all those who helped with the data collection. Brooke Marshall, Jason Wetzel, Nina Piggott and Chris DeWreede were all great to work with in the field and made the ordeal that much easier. Jason Wetzel has also been indispensable from the beginning and deserves my deepest thanks. His calm, rational thought, continual encouragement and never ending support helped make this thesis a reality. To my family I also give thanks for their love and support.

Chapter 1.

General Introduction

Conifer ecology has become an increasingly important topic of research in British Columbia, due mainly to the extensive forests they form throughout the province and the large-scale forest industry they support. Research into the growth of coniferous species common to the province helps to ensure that informed decisions are being made regarding management strategies associated with reforestation. It also provides a larger understanding of the abilities and degree to which seedlings grown initially in a nursery environment can respond to their surroundings once planted into a new environment such as a harvested area.

Conifer seedling establishment and growth is important to a forest, as it determines the rate at which new trees will be produced. While nursery grown seedlings receive near optimal growing conditions, they must also be fully functional and capable of survival once planted in the field. By understanding the growth responses demonstrated by different conifer species to particular environments, the selection of species used in reforestation may become more clearly defined, and the species themselves more suited to the sites they are planted in.

Reforestation and Alternative Silviculture Systems

Natural regeneration has long been the method of reforestation used after logging operations have taken place in British Columbia. In the past, this had to be, as no prior thought was given as to how the trees would grow back once harvesting had been

completed. After many revisions of past laws, new legislation on logging requires that companies wishing to log an area submit a complete management plan prior to harvesting which includes a plan for reforestation (Knight 1990). This ensures that the production of a new forest will be set in motion almost immediately following harvesting.

Today, as much emphasis is being placed on regenerating the forest as well as harvesting it, which promotes research in the area of seedling production, which in turn creates a thriving nursery industry. Planting seedlings grown in nurseries as a method of reforestation has increased over the past few decades, with approximately 200 million seedlings being planted each year in British Columbia alone (Mitchell *et al.* 1990). Successful plantations renew a forest to its former productive self generally much faster than would natural regeneration (Mitchell *et al.* 1990; Weetman and Vyse 1990). Those plantations which fail, however, are driving the search for more sophisticated methods of predicting the overall field performance of the seedlings prior to them even being planted, the ultimate goal being the guarantee that the stock will survive well in the field (Rose *et al.* 1990; Mexal and Landis 1990; and all other symposium participants).

Producing better seedlings is only one way of ensuring that harvested areas will be sufficiently regenerated. Harvesting techniques geared towards encouraging natural regeneration are also being applied more widely around the province. Silviculture systems, such as seed tree and shelterwood harvests in particular, rely on the trees left behind following harvesting to provide the seed which will eventually produce the next forest (B.C. Ministry of Forests, 1993). These harvesting methods have not been used extensively on the coast of British Columbia, mainly because they have been "borrowed" from European silvicultural strategies and cannot be directly applied to the ecosystems

found here (Weetman, 1996). Instead, the relevant concepts of European harvesting and management techniques have been studied and uniquely tailored to meet the objectives and needs of specific sites, in an effort to ensure that once applied, these alternative silviculture systems will result in successful forest management with minimal negative repercussions (Weetman, 1996).

Combining the use of planted seedlings and alternative silvicultural systems, such as planting seedlings into the understory a shelterwood, as is the case in the study to be described, is not commonly done, as the purpose of this harvesting technique is to encourage natural regeneration. However, in some instances it is felt that the stocking requirements may not be met in proper accordance with the initial objectives set for the site, so measures must be taken to ensure this goal is achieved. This is just one example which demonstrates the level of flexibility necessary to achieve the larger goals of reforestation in British Columbia. Information gathered through the monitoring of established plantations in these and other harvested areas helps create a more complete picture of how well reforestation is progressing.

Seedling Morphology

Northern temperate tree species, such as conifers, grow according to a defined pattern which is determined primarily by their genetics (Tomlinson 1978). The pattern expressed, called "articulate" by Tomlinson and Gill (1973) or "rhythmic" or "episodic" by Hallé *et al.* (1978), is generally a repetitive reconstruction of the main axis (Tomlinson and Gill 1973) (Figure 1) and is typified by a period of rest or discontinuity in the growth cycle. The discontinuity in growth is usually caused by the onset of less

than favorable growing conditions, such as winter, and is signaled earlier in the season by the formation of buds.

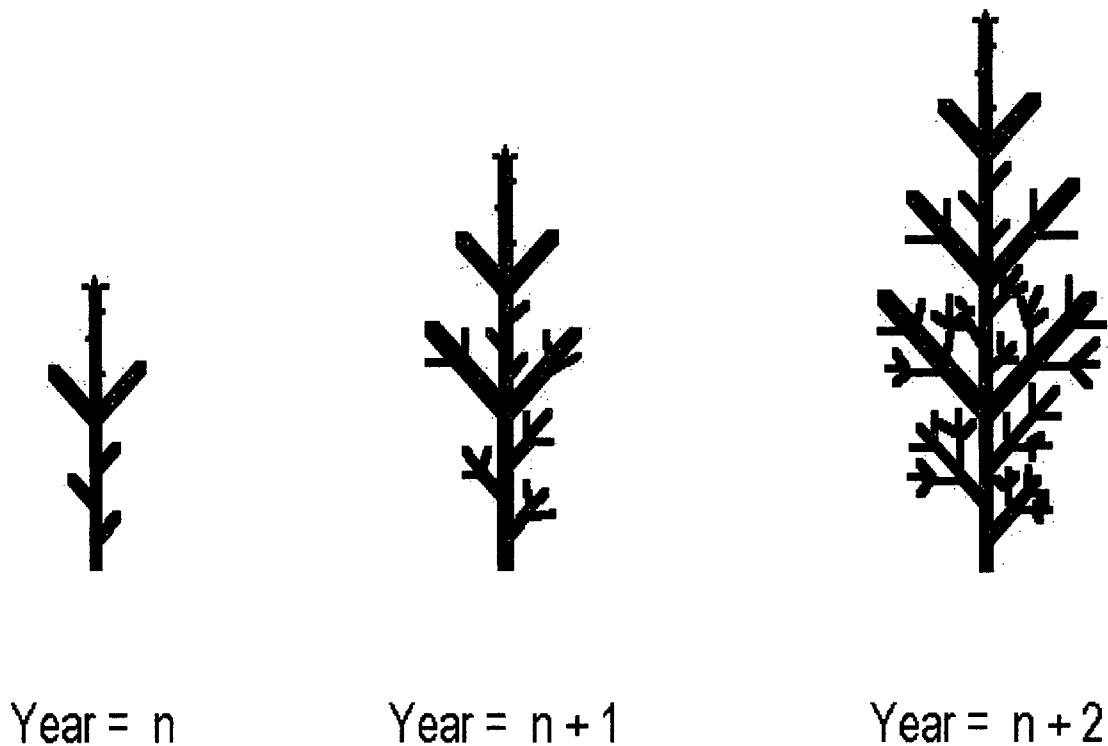


Figure 1. General branching pattern of conifers displaying articulate growth.

According to Tomlinson (1978), the normal expression of tree growth is influenced by two factors, its genetic make-up and its environment. When environmental conditions are optimal, such as in a nursery, the architecture or pattern displayed should reflect the true pattern encoded for by the genes of the tree. When the tree is growing in an environment not viewed as being “optimal”, as is usually the case in natural and unaltered settings, the pattern shown is one which is more constrained by the

environmental conditions, and not by the genetics of the tree itself. This is generally the case in more natural and unaltered settings (Tomlinson 1978). The pattern of growth expressed in these environments can be modified in direct response to the conditions which may present themselves. For example, the presence of high soil moisture levels following a period of drought late in the growing season sometimes promotes the premature flushing of buds, destined normally to overwinter and flush in the following spring (Carter and Klinka 1986). This phenomenon can lead to the production of additional whorl branches along the main stem, which does not generally conform to the idealized growth pattern or form displayed by most conifers (Carter and Klinka 1986). This process, however, is not seen as being in direct violation of the tree's overall growth pattern according to Tomlinson (1978). Instead, it demonstrates the high level of flexibility inherent in the tree's growth pattern, and is likened to a type of reaction mechanism used by both conifers and deciduous trees alike when damaged, stressed, or simply responding to the surrounding environmental conditions.

Recognizing the general growth patterns of conifers allows for a broader understanding of how different factors interact with the tree to produce a "normal" or "less than normal" growth form. Environmental factors, such as light, air temperature, soil temperature, and soil water availability, directly influence the growth patterns of trees and all other plants. Other factors, such as hormone levels, contribute to the shape of trees mainly through the role they play in the maintenance and loss of apical dominance (Salisbury and Ross 1992). Physical damage caused by animals or snow, for example, can also alter the growth patterns of trees (Carter and Klinka 1986) usually through the production of additional branches which help compensate for the damage

sustained (Tomlinson 1978). By knowing the general growth responses to expect from seedlings, a more accurate assessment of seedling performance can be predicted.

The study to be described involves monitoring the growth of two species of nursery grown seedlings planted into two different environments, both of which were created through forestry harvesting operations. It addresses aspects involving both regeneration and the general growth responses of trees to specific environmental variables, with the intent of determining whether or not the two species differ in the growth patterns and morphology expressed and responses to the environmental variables monitored, when analyzed using shared characteristics.

Chapter 2.

Comparative Analysis of Seedling Morphology

Introduction

The qualities of a future forest are determined primarily by the rates and growth patterns of the conifer seedlings growing in the understory. A growth pattern which does not conform to that which is considered "normal" can affect the productivity of the tree as well as its overall value if it is to be used as timber. For example, the production of multiple leaders, which does not normally conform to the general growth pattern expressed by conifers (Tomlinson and Gill, 1973; Tomlinson 1978; Hallé *et al.* 1978), can affect productivity by lowering the photosynthetic efficiency of the tree, as more energy will likely be put into fighting for apical dominance and the re-establishment of a single leader, than photosynthesis. The value of timber may be lowered by the presence of multiple leaders due to the production of more knots in the wood and a stem form which is forked (Carvell 1956, cited in Walters and Soos 1961). This section addresses the general processes involved in "growth" and how it relates to the overall morphology of conifers.

Plant growth, "normal" or otherwise, has been defined as "[the] increase in size by cell division and/or cell enlargement" (Esau 1977). These cell divisions, commonly localized within meristematic regions, are what leads to the production of the whole organism. In conifers, meristems are located at the shoot tips, which produce all of the aerial structures, root tips, which produce all of the below-ground structures, and

throughout the stem, which produces growth in width or girth of the stem itself (Romberger 1963).

The mid-1800's marked the beginning of exploration into the cellular organization of shoot apical meristems in particular, and their subsequent production of entire plants (Romberger 1963). While many theories were produced, none were formulated to address the apical meristems of gymnosperms specifically. It was not until much later, with the work of Foster (1938) in particular, that a comprehensive theory of shoot apical organization was produced for this plant group. Instead of following the fates of individual cells, as the earlier theories had directed, emphasis shifted to describing the characteristics and destinies of entire groups of cells (Romberger 1963). Based on this idea, Foster described the shoot apex of *Ginkgo biloba* using the concept of "cytological zonation" (cells can be distinguished from others according to their characteristics and position) (Romberger 1963; Esau 1977). The basic premise behind this theory is that the shoot apical meristem can be divided into four general groups of cells or zones, each of which gives rise to a particular part of the mature plant body.

Addressing specific cells and regions within meristems which work in conjunction with one another to produce the whole organism is only one way of describing the phenomenon known as "growth", however. The first definition of growth given earlier relates to distinct tissues, specifically meristems. A wider interpretation of growth lies in definitions which go beyond meristems. This is demonstrated in the definition of Hallé *et al.* (1978), who label growth specifically as "growth-habit", and define it as "the ultimate form of a plant as expressed in its physiognomy". The growth-habit is more clearly defined by the resulting appearance of the organism and not by the

mechanism through which this was achieved. This definition addresses a whole-plant perspective, and is only distantly related to the actions of meristems.

Because all conifers grow through the actions of meristems, it would seem logical that their morphologies should be similar as well. They are similar, in terms of the reiterative growth patterns they display, but the ability for meristems to produce different morphologies, such as seen between species, rises more from the variable levels of activity they can maintain. The apical meristem, in the sense used by Esau (1977), is only directly responsible for generating one component of the overall growth experienced by an organism, namely through cell division. The remaining component of growth comes from cell enlargement, an activity for which the apical meristem is not wholly responsible. A meristem which divides more slowly produces fewer cells, which can ultimately lead to a smaller overall size or the presence of fewer plant parts such as needles or branches. While cell enlargement can partially compensate for these apparent shortcomings, it has been found that the number of cells produced at the outset seems to impact more on the overall size of the structure in question than the subsequent enlargement of the cells of which it is formed (Lanner 1976, cited in Ford 1980). The combination of the activity of the meristem and the subsequent enlargement of the parts produced allows for the generation of variable, yet somewhat restricted growth morphologies between, as well as within species of conifers.

The growth patterns of conifers, as mentioned previously, are generally described as “articulate” (*sensu* Tomlinson and Gill 1973) or “rhythmic” or “episodic” (*sensu* Hallé *et al.* (1978)), with periods of active growth being interrupted by periods of dormancy. Prior to the full onset of dormancy, buds are formed which contain the condensed shoot

apical meristem and leaf primordia, destined to elongate in the following year. This pattern of growth is generally demonstrated throughout the life of the tree, with the exception of its first few years as a seedling. Newly germinated conifers in their first year of life form branches without the initial formation of a bud and the period of rest associated with it. These branches are termed "sylleptic" (Späth 1912, cited in Hallé *et al.* 1978) or neoformed (Hallé *et al.* 1978). As a seedling ages, the branches conform more and more to the general growth pattern of the tree, with buds containing the condensed shoots and a period of rest being produced prior to their extension. These branches formed from buds are termed "proleptic" (Hallé *et al.* 1978). The incidence of sylleptic branches generally decreases with age until all branches are produced exclusively through prolepsis (Remphrey and Powell 1984, 1985; Powell and Vescio 1986; McCurdy and Powell 1987 and references cited therein).

On occasion, the buds destined to become proleptic branches will burst prematurely, usually late in the growing season if climatic conditions and genetics allow. At one point, this phenomenon was called "proleptis" (Späth 1912, cited in Hallé *et al.* 1978), but it was later suggested by Tomlinson and Gill (1973) and further supported by Hallé *et al.* (1978), that because these "prematurely formed" shoots do not differ morphologically from those produced during the following growing season, all shoots produced from buds should be called proleptic regardless of when they had flushed. Researchers working in this area of study seem to accept this argument (Powell and Vescio 1986; Remphrey and Powell 1985), but have also suggested alternate terms to distinguish between branches formed from buds which flushed in the spring (when they "should") versus those which flushed prematurely in the fall. Terms which have been

used include “lammas” growth (Späth 1912, cited in Hallé *et al.* 1978), precocious growth (Hallé *et al.* 1978) or “free growth” (Jablanczy 1971; Pollard and Logan 1974, 1976). “Free growth” can be either neoformed, in which no period of rest occurs between the elongation of the predetermined shoot and new shoot growth, or “proleptic”, where bud scales are formed but the bud flushes before the plant itself becomes fully dormant prior to the coming of winter. von Wühlisch and Muhs (1986) have taken the term “free growth” and have further qualified it through the use of the terms “sylleptic” and “proleptic”. “Sylleptic free growth” becomes synonymous with neoformed shoot initiation which occurs after the elongation of the predetermined shoot, while “proleptic free growth” indicates that a temporary bud has been set (after the elongation of the predetermined shoot), and has flushed later in the same season. The terminology of von Wühlisch and Muhs (1986) will be adopted throughout the remainder of this thesis. An additional term, “lammas growth” (Rudolph 1964) will be used when referring specifically to the late-season flushing or proleptic free growth of the terminal bud.

There are mixed opinions regarding free growth and its effect on seedlings. Free growth has been viewed as damaging to the overall form of the tree, owing to the production of multiple leaders and acute branch angles (Kramer and Kozlowski 1960; Carter and Klinka 1986). These effects can be temporary however, and recovery to a more “normal” stem form is possible (Walters and Soos 1961; Carter and Klinka 1986). If multiple leaders persist, the wood quality can be reduced, especially for saw-log production, due to the undesirable shape of the stem (Carvell 1956, cited in Walters and Soos 1961).

The timing of these additional flushes are of concern, as it can damage the tree if unsuitable growing conditions followed soon after flushing. Because free growth usually occurs later in the growing season, the newly flushed shoots may be too succulent and not sufficiently frost resistant to survive early-fall frosts (Kramer and Kozlowski 1960; Rudolph 1964). If trees with free growth experience an early fall frost, it heightens their chances of being damaged.

Others believe free growth to be advantageous, giving seedlings the ability to supplement height growth if they have been subjected to herbivory or other forms of stem damage (Roth and Newton 1996). Because of this additional growth in height, suggestions have been made for the use of silvicultural treatments which encourage free growth, in an effort to accelerate reforestation, regardless of the potentially damaging effects of frost (Roth and Newton 1996).

The causes of proleptic free growth have been attributed mainly to the surrounding environmental conditions, although research has shown the presence of a genetic component as well (Rudolph, 1964). In general, soil water, nitrogen availability, and stem damage have been the most commonly noted causal factors (Walters and Soos 1961; Rudolph 1964; Carter and Klinka 1986; Roth and Newton 1996). These environmental variables and their influence on both "proleptic free" and "normal" growth will be examined in more detail in the next section.

Objectives

The main objective of this study was to explain the relationship which exists between the growth patterns of two conifers, Douglas fir (*Pseudotsuga menziesii* (Mirb.)

Franco) and grand fir (*Abies grandis* (Dougl.) Lindl.), and the morphology and patterns of integration which result. Morphological differences and patterns of integration were analyzed in three main areas for two conifer species: (i) between two measurement years; (ii) between two forest sites a shelterwood and small scale clearcut or clearing, and more specifically (iii) between two groups of seedlings which displayed obvious differences in morphology. The analyses were carried out using shared characteristics. The two groups of seedlings were those having a “normal” morphology and those with proleptic free growth.

Materials and Methods

Site description

The two sites involved in this study are located just outside the town of Squamish, B.C. (49°41' N, 123°10' W), in an area adjacent to Garibaldi Provincial Park called Ring Creek (Figure 2). Ring Creek is situated within the Coast-Interior Transition Zone, which is formally part of the Coastal Western Hemlock Dry Maritime (CWHdm) biogeoclimatic zone (Green and Klinka 1994). The dominant tree species of the CWHdm include coastal Douglas fir, western redcedar (*Thuja plicata* Donn) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Common understory vegetation include salal (*Gaultheria shallon* Pursh), red huckleberry (*Vaccinium parvifolium* Smith) and to a lesser extent, dull Oregon grape (*Mahonia nervosa* Pursh) (Green and Klinka 1994). Common mosses include step moss (*Hylocomium splendens*), and Oregon beaked moss (*Kindbergia oregana*). The sites themselves, a 15.7 hectare shelterwood and a smaller 40 m by 22 m “clearing” (to be later defined in more detail), were established using a cable-

yarding procedure conducted during the fall-winter season of 1994. Both sites are at an elevation of approximately 350m.

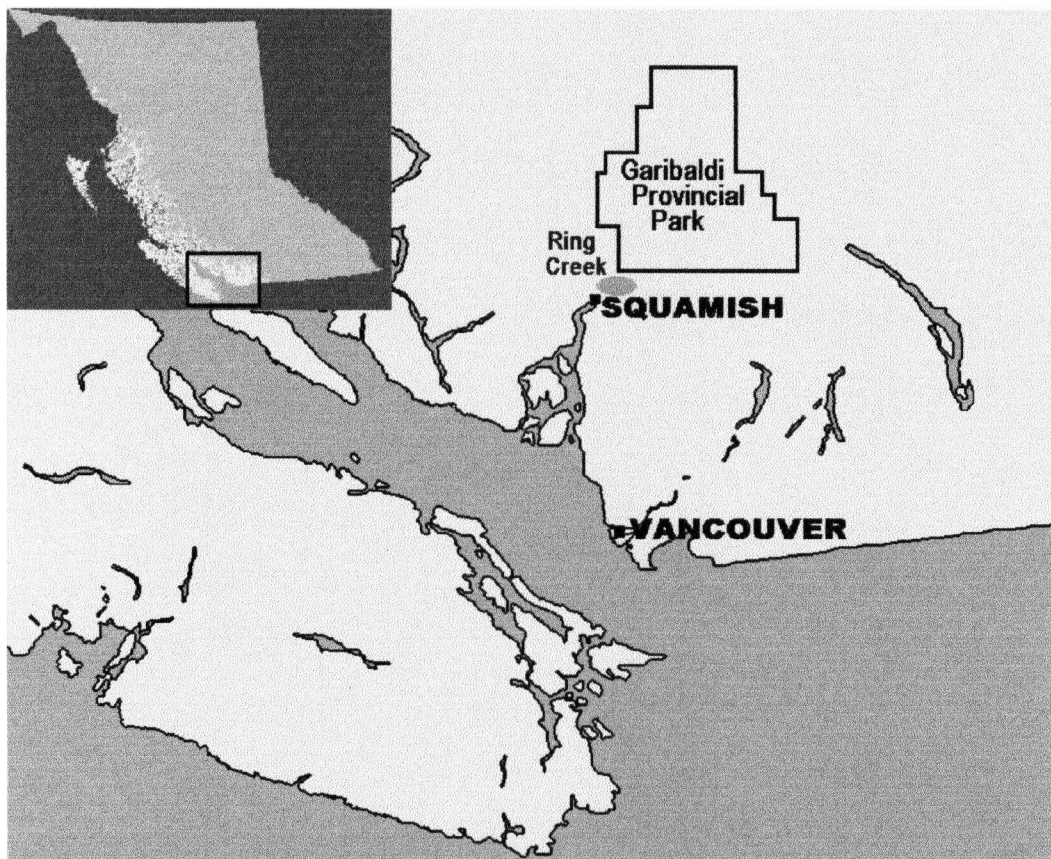


Figure 2. Location of the Ring Creek area.

The shelterwood site was established in a 70-year old second growth forest (Hedin 1996) which had regenerated naturally after a previous clearcut and slashburn operation. Prior to the 1994 harvest, the tree density was approximately 941 stems/ha (a basal area of roughly 122 m²/ha) and was a mixture of the three tree species typical of this biogeoclimatic zone. The residual stand is approximately 133 stems/ha (a basal area of roughly 30 m²/ha) and consists mainly of Douglas fir (Figure 3). The understory is a mixture of red huckleberry, sword fern (*Polystichum munitum*), three-leafed foamflower (*Tiarella trifoliata*), step moss and Oregon beaked moss. Soils include ferro-humic

podzols along the upper slopes and drier portions of the site and humo-ferric podzols in the flatter, more moist areas. The site faces a southwesterly direction and has slopes ranging from 5-45%, the average being 30% (Hedin 1996). In the spring of 1995, one-year old seedlings of Douglas fir, grand fir, and western redcedar were planted throughout the understory. Of these seedlings, 100 of each species were randomly flagged, forming a survival line.



Figure 3. Photograph of the shelterwood.

The clearing was created in the midst of a younger Douglas fir plantation which had not yet reached canopy closure (Figure 4). It is a relatively flat site and also faces to the southwest. Vegetation common to this site includes dull Oregon grape, red huckleberry, bracken fern (*Pteridium aquilinum*) and awned haircap moss (*Polytrichum*

piliferum). Soils are ferro-humic podzols. This site as well was planted with 100 seedlings each of Douglas fir, grand fir and western redcedar seedlings of the same seedlots and stocktype used in the shelterwood. As an aside, this site, by definition, is not considered to be a true clearcut simply because of its smaller size (hence the use of the term “clearing”). Its main purpose was to provide seedlings with an open-canopy environment so that comparisons could be made to seedlings growing in the more closed-canopy environment of the shelterwood.



Figure 4. Photograph of the clearing.

Plant material

Both the clearing and shelterwood sites were planted with Douglas fir, grand fir, and western redcedar seedlings in the spring of 1995. All seedlings were one year old at

planting and of a common stocktype (PSB 615A). Douglas fir seed used to grow the seedlings was collected from the Quinsam seed orchard, located 500m above sea level, at a latitude of $49^{\circ}08'$ and longitude of $124^{\circ}24'$. The seedlot is 6513. Grand fir seeds, seedlot 9832, were collected from the Cheakamus River area, located 70m above sea level, at a latitude of $49^{\circ}50'$ and longitude of $123^{\circ}03'$. Seeds of western redcedar, seedlot 6753, were from the Mt. Newton seed orchard. All three species were grown in styroblocks at Surrey Nursery, Surrey, B.C..

The planting arrangement of the seedlings in the shelterwood was random, resulting in the intermixing of individuals of each species throughout the site. Due to the abundance of understory vegetation and the greater spatial layout of the seedlings, Vexar sleeves as deterrents to herbivory were deemed unnecessary on this site (Richard Timm, pers. comm.). A subset of 100 seedlings of each species were then chosen using a random walk method to form the survival line to be used in future comparisons to those seedlings planted in the clearing. Each seedling received a numbered tag from 1 - 100 so that individual trees could be monitored over the years. The distributions of tagged individuals forming the survival lines are shown in Figure 5. In the fall of 1995, 97 Douglas fir seedlings were alive for measurement. This number dropped to 95 seedlings in 1996. All 100 grand fir seedlings were surviving after both years. The western redcedar seedlings were not very successful in this site during their first winter. Approximately 90% of the survival line was heavily browsed, thus rendering any future comparisons difficult due to the very small sample size remaining. Due to this event, western redcedar was dropped from the study.

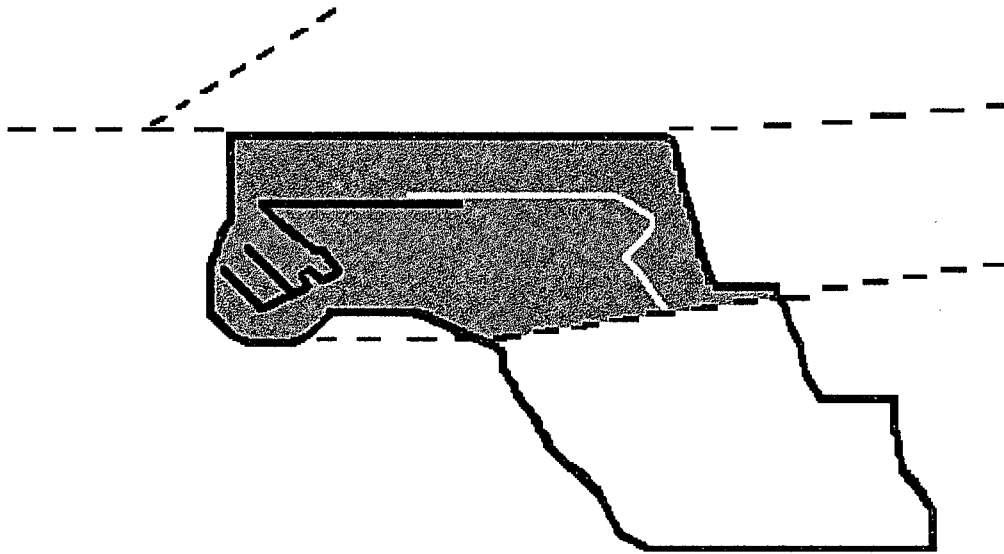


Figure 5. Sketch of the planting layout in the shelterwood. The black line is the survival line for grand fir, while the white line is the survival line for Douglas fir. Dashed lines are roads.

Seedlings in the clearing were planted in rows due to the smaller area. One hundred seedlings of each species were planted into 12 rows which alternate between species (see Figure 4). Because of their close spatial arrangement, all seedlings were placed in Vexar sleeves to deter herbivores from damaging the entire plot. These seedlings were also flagged with a number ranging from 1 to 100, making it possible to track the same individual trees from year to year. In the fall of 1995, 15 Douglas fir seedlings had died due to rodent damage or planting error, leaving 85 available for measurement. In the fall of 1996, 3 more Douglas fir seedlings had died, thus leaving a total of 82. All 100 grand fir seedlings lived, as did those of western redcedar, but the latter species was not studied any further due to the damage incurred in the shelterwood.

The site heterogeneity existing in both the shelterwood and clearing is a factor beyond the control of this study. Both sites were established before the study was

proposed and upon its development, the inherent heterogeneity both within and between the sites was realized and accepted. The larger goals of this study are twofold, both of which are met by these sites: (i) the practical goal of assessing some aspects of reforestation efforts and (ii) the theoretical goal of assessing conifer growth patterns. Because both site qualities met the larger goals, the benefits of proceeding outweighed the potential problems of site heterogeneity. As well, such a study addresses the goals of interest in a more pertinent manner due to the conditions under which the study was conducted.

Seedling measurements

Standard features of growth were measured in the fall of both years. They included total seedling height in both 1995 and 1996 (THT95 and THT96 respectively), length of the height increment in 1995 and 1996 (HI95 and HI96 respectively) and the basal stem diameter in 1995 and 1996 (D95 and D96). These measurements are viewed as being valid indicators of seedling growth performance and are both practical and repeatable if a study is carried out over a number of years. Additional variables illustrating the overall shape or form of the seedlings were also measured. They included the length of the dominant subtending lateral branches of the apical whorl formed in 1995 (L195) and 1996 (L296), as well as the length of branch produced in 1996 found at the end of the 1995 subtending lateral (L196) (see Figure 6). The number of buds formed on both the 1995 and 1996 height increments were also counted (B95 and B96 respectively). These variables were measured on the Douglas fir and grand fir seedlings planted in both the clearing and shelterwood sites (Figure 6).

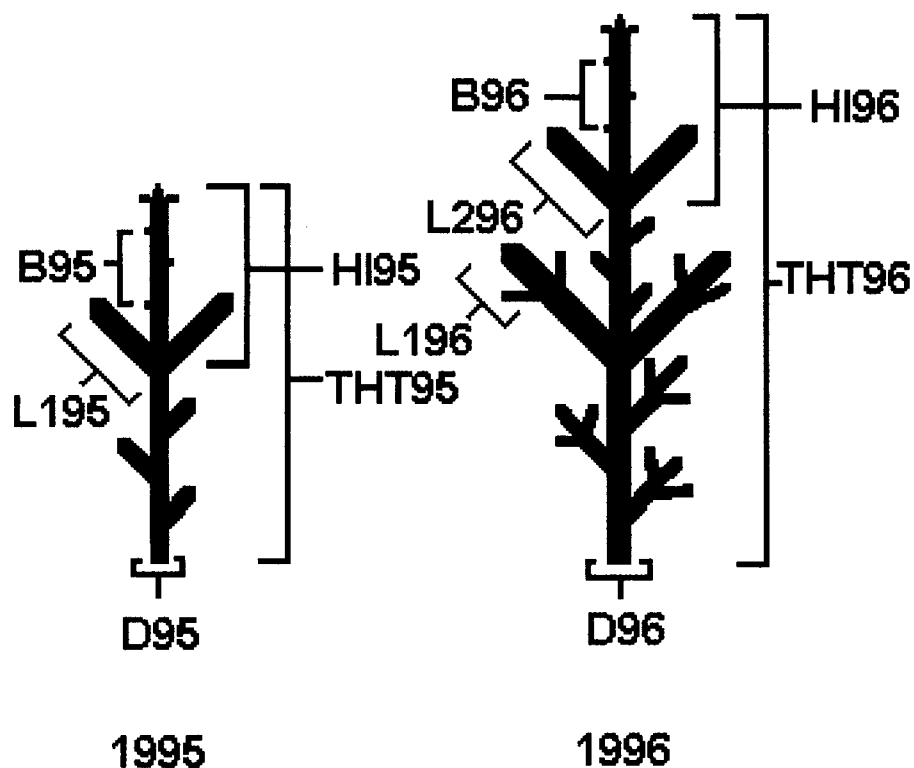


Figure 6. Sketch of seedling measurements taken in 1995 and 1996.

Proleptic free growth characteristics were also studied in 1996 particularly, because its presence was more evident in 1996 than 1995. An increase in the incidence of proleptic free growth from 8% to 33% and 0% to 19% was seen in grand fir seedlings in the shelterwood and clearing respectively in 1996. Similarly for Douglas fir seedlings, the presence of proleptic free growth increased from 7% to 39% in the shelterwood and 1% to 46% in the clearing.

Measurements of proleptic free growth characteristics included the length of the lammas shoot produced (FL96), which is specifically the length of the re-flush of the terminal bud. The length of the dominant proleptic free growth shoot of the apical whorl

(FPA96) and the length of the proleptic free growth shoots produced on other lateral branches not associated with the apical whorl (FP96) were also measured (Figure 7).

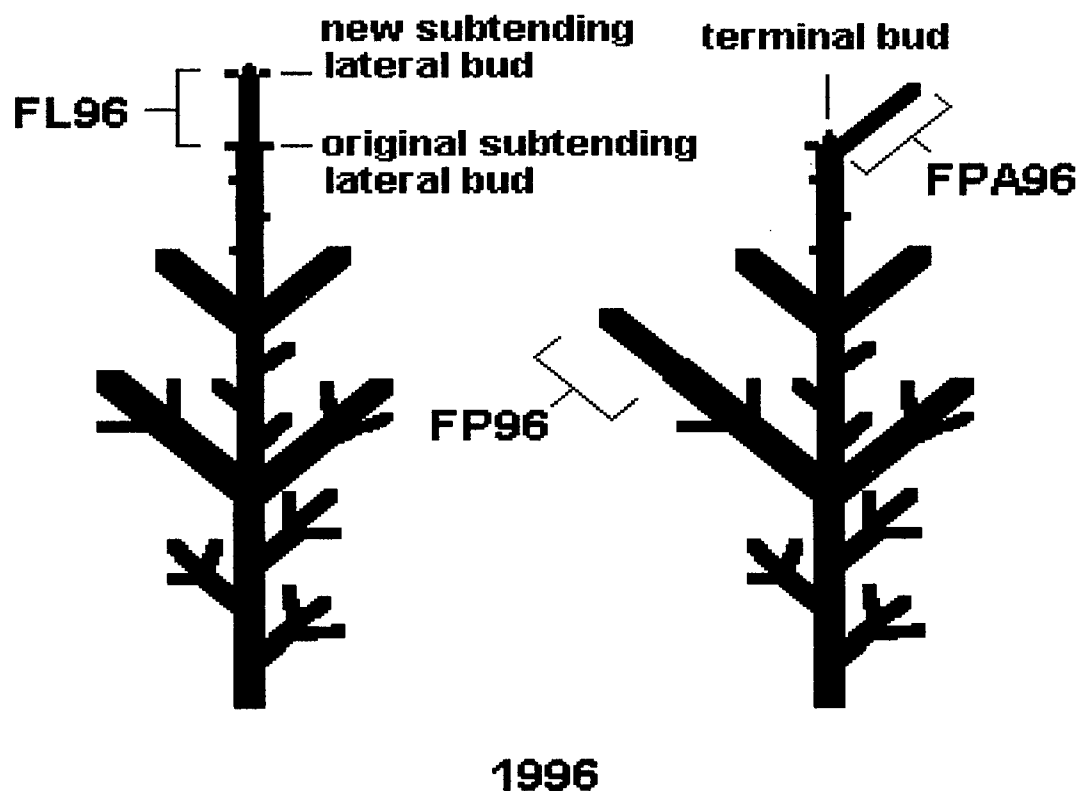


Figure 7. Sketch of proleptic free growth characteristics commonly seen.

Statistical analyses

Prior to the commencement of any formal data analysis, all morphological variables were graphed as probability plots to determine if they followed a normal distribution using SYSTAT 6.0 for Windows (Wilkinson 1996) (data not shown). As all variables appeared to be normally distributed, parametric statistical methods were used. Descriptive statistics including means and standard deviations were also performed on

each measured attribute to illustrate the general morphology produced by each year studied. Standard deviations were used as opposed to standard errors, as it was desired to show the actual dispersion of the data around the means.

Principal components analysis (PCA) was used to assess seedling organization and growth patterns and was carried out using SYSTAT 6.0 for Windows (Wilkinson 1996). PCA offers the analytical advantage of evaluating more than one variable at a time thus preserving the interrelationships which can exist among variables

Component scores, eigenvalues and eigenvectors are the main statistics generated during PCA. Component scores are new variables created by the PCA which, while orthogonal themselves, are strongly correlated with the variables making up the original data matrix. When graphed, they allow for the easier detection of spatial trends not readily visible in the raw data. Eigenvalues describe the amount of variation accounted for by each axis generated during the analysis. Larger eigenvalues represent stronger relationships to the PCA axes in particular, and thus account for more of the variation present in the data. Component loadings or eigenvectors illustrate the relationships between each variable and the PCA axes generated during the analysis. The larger the eigenvector of a particular variable, the smaller the angle between the vector formed by that variable and the corresponding PCA axis. This relationship indicates that a stronger correlation exists between that variable and the PCA axis, compared to variables with smaller eigenvector values. Eigenvectors of similar magnitude and identical sign reflect a form of variation attributed to size differences between samples, while eigenvectors of differing magnitude and opposite sign reflect both size and shape variation (Pimentel 1979). Assessing the angles between vectors lends insight into the relationship held

between the variables and the patterns they display through time in relation to one another. This allows for a whole-plant perspective to be formed by way of how each plant part relates to one another to form the whole organism. The smaller the angle between two variables, the more strongly correlated they are to each other and the more similar their responses are (Scagel *et al.* 1985). In the analyses conducted, groups of variables deemed “strongly” or “loosely” correlated to one another were assessed visually and are thus fairly subjective.

Twenty PCAs were performed overall, each on a site and species basis. The first four involved analyzing all of the measured variables for 1995 and 1996 at the same time. The next eight involved analyzing the 1995 and 1996 variables separately, to determine whether or not variable patterns differed between the measurement years. The final eight PCAs used the 1996 variables only and deliberately distinguished between the different growth morphologies being demonstrated by a number of the seedlings. These PCAs were conducted separately on groups of seedlings with a “normal” growth morphology as well as on those with proleptic free growth characteristics.

Adjusted least squares means (LS Means) and sums of squares (SS), both generated through analysis of covariance (ANCOVA) models performed in SYSTAT 6.0 for Windows (Wilkinson 1996), were used to address seedling growth response in relation to the experimental treatments and morphological features measured. Contrary to the multivariate method used earlier, ANCOVA estimates and tests differences between population means (Huitema 1980) and can be more a more effective tool used in the detection of differences between group means through the removal of unwanted variability due to one or more covariates (Wilkinson 1996). Two general models were

used, one for 1995 and one for 1996. Each followed a 2X2 factor ANCOVA format, where factor 1 was the species and factor 2, the site. Each factor contained two levels, grand fir and Douglas fir for factor 1 and the shelterwood and clearing for factor 2. The measured morphological characteristics served as both dependent variables and covariates in the models. When a given characteristic was being used as the dependent variable, it was excluded from the model as a covariate. Model [1] illustrates the format used in 1995 specifically, using the height increment in 1995 as a sample dependent variable:

$$[1] \text{ HI95} = \text{constant} + \text{SP} + \text{S} + (\text{SP} * \text{S}) + \text{H} + \text{D95} + \text{L195} + \text{B95} + e$$

where:

HI95 = dependent variable, height increment in 1995

SP = species

S = site

(SP*S) = the species by site interaction

H = height of the seedling at planting, a derived variable formed by subtracting the length of the 1995 growth increment from the total height of the seedling after the 1995 growing season

D95 = basal diameter in 1995

L195 = the length of subtending lateral branch #1 in 1995

B95 = the number of buds produced on the growth increment in 1995

e = the error term.

The 1996 model followed the same format as that of 1995, but included more morphological features, as more were produced by the plant in this year. It is as follows, using the height increment in 1996 as a sample dependent variable:

$$[2] \text{ HI96} = \text{constant} + \text{SP} + \text{S} + (\text{SP} * \text{S}) + \text{H} + \text{DI96} + \text{L196} + \text{L296} + \text{B96} + e$$

The terms common to [1] above are as before. New variables include:

HI96 = the height increment for 1996

DI96 = the diameter increment for 1996, calculated by subtracting the 1995 diameter measurement from that recorded in 1996

L196 = the growth of subtending lateral branch #1 which was produced in 1996

L296 = the length of subtending lateral branch #2, newly formed in 1996

B96 = the number of buds formed on the growth increment for 1996

Model [2] was used on all seedlings in 1996, as well as the two unique classes of seedling: those with a “normal” growth morphology and those with proleptic free growth.

Both models [1] and [2] include every measured characteristic as a covariate primarily for two reasons. The first was to ensure repeatability and avoid the logistical problem of trying to determine subjectively which variables should be included and omitted from each model given a certain dependent variable. In the manner used currently, every characteristic is included in the model thus alleviating a certain amount of the guesswork which comes with the decision of which covariates to include.

The second reason for including all of the measured characteristics in each model was to gain insight into which parts of the seedling best describe the dependent variable

in question. This was achieved through variance partitioning using the sums of squares generated during the analyses. Variance partitioning describes the proportion of the variability explained by the treatments once the effects of the covariates have been accounted for statistically (Huitema 1980). The statistic, eta squared (η^2), is calculated by:

$$\frac{(\text{Sums of Squares})_{\text{term}}}{(\text{Sums of Squares})_{\text{total}}}$$

SS_{term} is generated during the analysis, while SS_{total} is obtained through the summation of all SS terms. This statistic can be left as a decimal value or re-expressed as a percentage by multiplying by 100. The results shown in the tables below are left as decimal values.

ANCOVA results expressed as adjusted least squares means and standard errors describe the amount of influence the species (SP), site (S) and species by site interaction (SP*S) have on each dependent variable once the effects of the covariates have been removed. Adjusted least squares means are predicted values generated during the analyses and are perceived as being independent of all variables included as covariates in the models used (Huitema 1980).

To ensure that the data were not in violation of any of the assumptions required for an ANCOVA, residuals were plotted after each model was run to determine if they were heteroscedastic. Overall, the plots were evenly distributed about a residual value of zero (data not shown), and no obvious patterning or relationships were demonstrated, indicating that the variance across the residuals is constant (Wilkinson 1996). Levene's test for unequal variances was also run. A small proportion of the models displayed

significant F ratios but the data were not transformed to correct for this. Despite the fact that an ANCOVA requires equal variances to fully support the interpretations made from the results, the calculation of η^2 does not, as it is assumption-free (Scagel 1984, and references cited therein). Terms which were found to be significant by Levene's test have been singled out in Table 4 and Table 5 so that caution may be taken when looking at the results and subsequent interpretations.

Results

Descriptive statistics illustrating the overall trends and spread of the data performed on all seedlings in 1995 and 1996 are shown as means and standard deviations for grand fir (Figure 8) and Douglas fir (Figure 9). All of the trends described are done so in a purely qualitative nature, as no statistical significance has been determined through these analyses

Seedlings of grand fir seemed to grow best in the shelterwood environment in both years, with 1996 producing more growth overall compared to 1995. Larger standard deviations are seen in 1996 compared to 1995, indicating a larger amount of dispersion exists about the mean.

Larger seedlings were planted in the clearing initially, but the leader growth of seedlings in the shelterwood in 1995 resulted in taller seedlings overall at this site. This same growth response was seen again in 1996 as well. The shelterwood site also produced a larger stem diameter than the clearing. Lateral branch #1 grew more in 1995 than 1996, a trend best shown by seedlings in the shelterwood. This pattern is repeated in one other variable; the number of buds produced on the height increment.

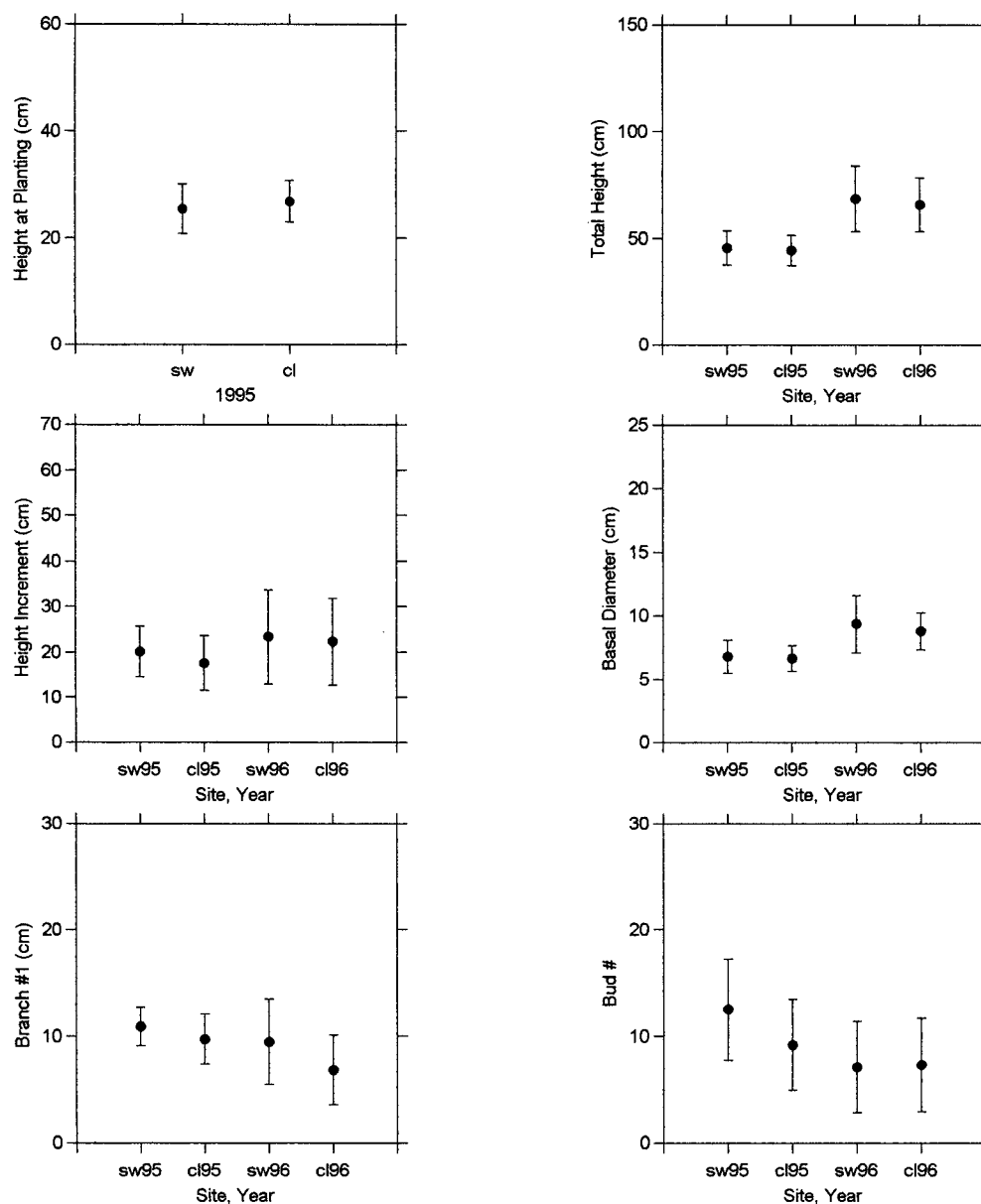


Figure 8. Means (dots) and standard deviations (vertical lines) of morphological features for all grand fir seedlings. "sw"=shelterwood, "cl"=clearing.

Douglas fir seedlings seemed to grow best in the clearing overall, with growth in 1996 exceeding that of 1995 (Figure 9). The amount of variation increased with time as well, with 1996 having a larger standard deviation than 1995. As was seen in grand fir, taller seedlings were planted in the clearing, however growth was maintained at a higher

level here compared to the shelterwood. Larger stem diameters were produced in the shelterwood in 1996, a trend not consistent with the majority of the growth responses demonstrated. Lateral branch #1 grew best in the clearing in both years, again with 1996 producing the most growth. The number of buds produced on the height increment was similar in both years and across both sites (Figure 10).

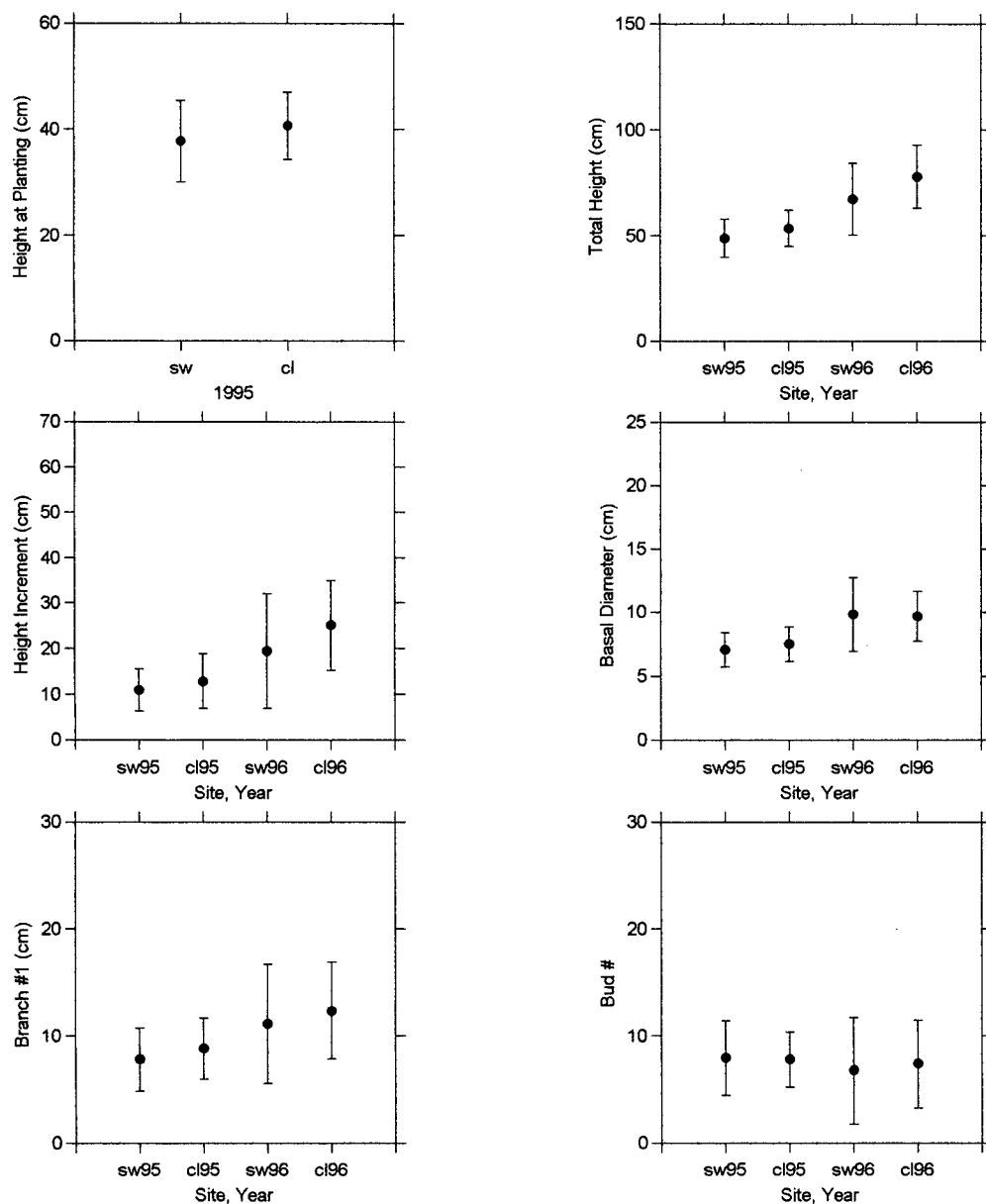


Figure 9. Means (dots) and standard deviations (vertical lines) of morphological features for all Douglas fir seedlings. “sw”=shelterwood, “cl”=clearing.

Results of the descriptive statistics comparing the two morphological types of seedling (“normal” and “proleptic free growth”) are shown as means and standard deviations for grand fir (Figure 10) and Douglas fir (Figure 11).

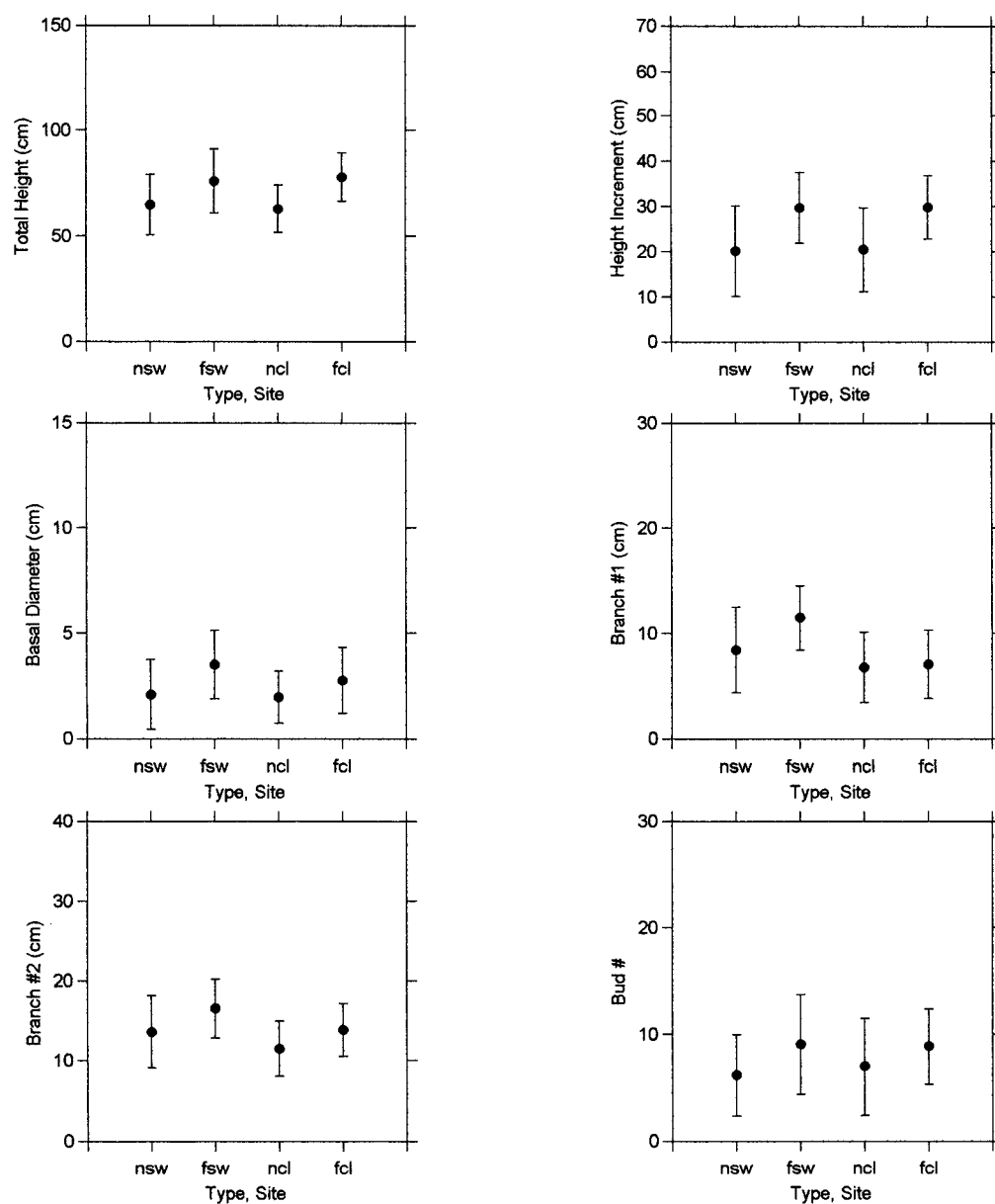


Figure 10. Means (dots) and standard deviations (vertical lines) of measured characteristics comparing seedlings of grand fir with a “normal” morphology to those with “proleptic free growth”. “n”=normal, “f”=free growth, “sw”=shelterwood, “cl”=clearing.

Seedlings of grand fir having proleptic free growth demonstrated the most growth overall, regardless of site. Growth of the basal stem diameter, lateral branches (both #1 and #2) and the number of buds produced on the height increment were all best in the shelterwood for these seedlings.

Growth in total height and height increment of grand fir did not differ noticeably between sites in seedlings with proleptic free growth. "Normal" seedlings did not demonstrate a convincing response to any one site, with perhaps the exception of lateral branches #1 and #2, which grew more in the shelterwood (Figure 10).

Similar trends to those seen in the grand fir seedlings are demonstrated in the Douglas fir seedlings as well, in that the presence of proleptic free growth produced larger seedlings overall (Figure 11). A distinct site preference was shown in the growth of the basal diameter. Seedlings with a "normal" morphology produced the most growth in the clearing for all of the variables measured, with the exception of the basal diameter which grew slightly larger in the shelterwood (Figure 11).

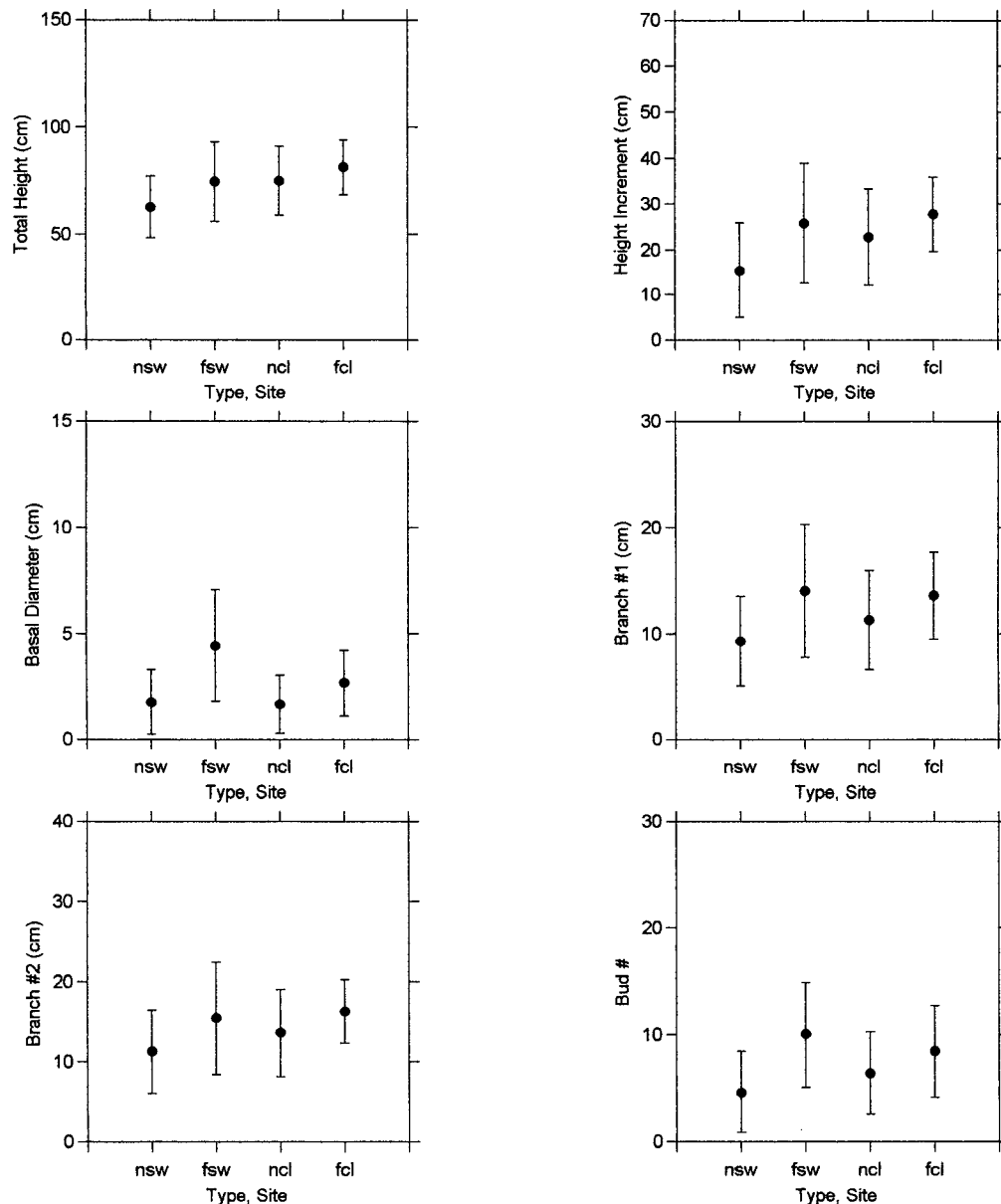


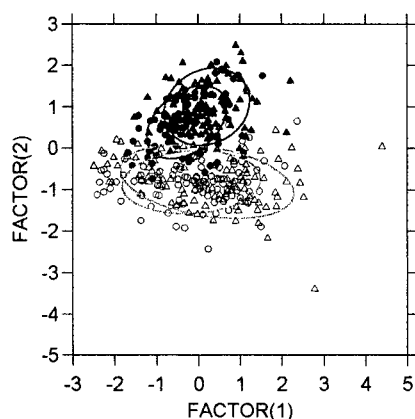
Figure 11. Means (dots) and standard deviations (vertical lines) of measured characteristics comparing seedlings of Douglas fir with a “normal” morphology to those with “proleptic free growth”. “n”=normal, “f”=free growth, “sw”=shelterwood, “cl”=clearing.

PCA scatterplots of factor scores with 95% confidence ellipses generated during the analysis of all morphological characteristics measured over the 2 year period are given for grand fir (Figure 12a) and Douglas fir (Figure 12b). The sites themselves are

virtually indistinguishable, but the years form two relatively distinct clusters of points.

While this suggests there may be no apparent effect of site on seedling morphology, the differences between them may be too subtle to be detected using PCA. Site differences may also be masked by the stronger yearly trends.

(a) Grand fir



(b) Douglas fir

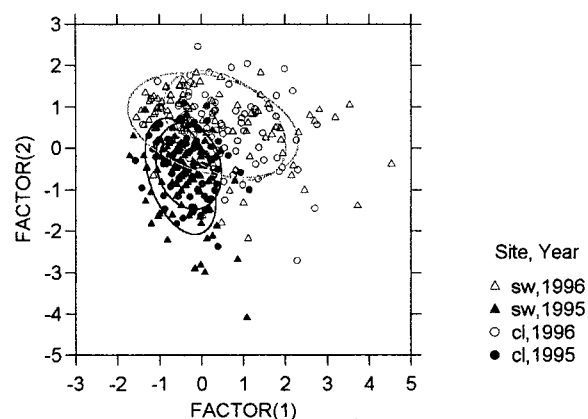
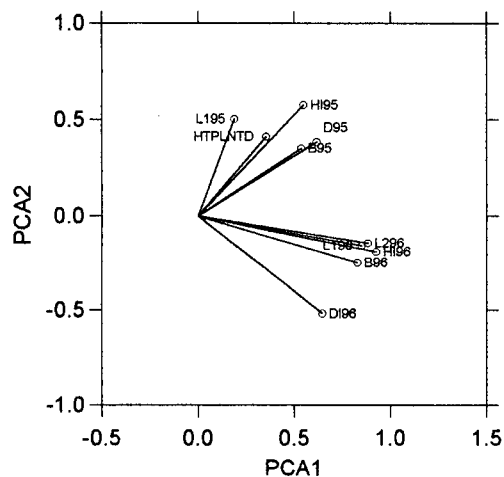


Figure 12. PCA scatterplot of factor scores with 95% confidence ellipses for grand fir and Douglas fir seedlings. “sw” = shelterwood, “cl” = clearing.

The PCA vector ordination diagrams which combine both the 1995 and 1996 morphological variables reinforce the patterns seen in the scatterplots (Figure 13, a and b, for grand fir and Figure 14, a and b for Douglas fir). A distinct separation is seen between the variables measured in each year, outlining the possibility that a change in these variables is occurring with time. All of the variables measured in the same year form stronger relationships with one another rather than with those variables measured in the opposing year.

(a) Grand fir, Shelterwood



(b) Grand fir, Clearing

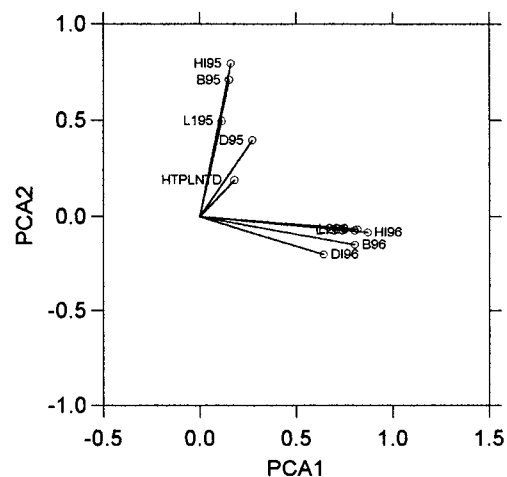
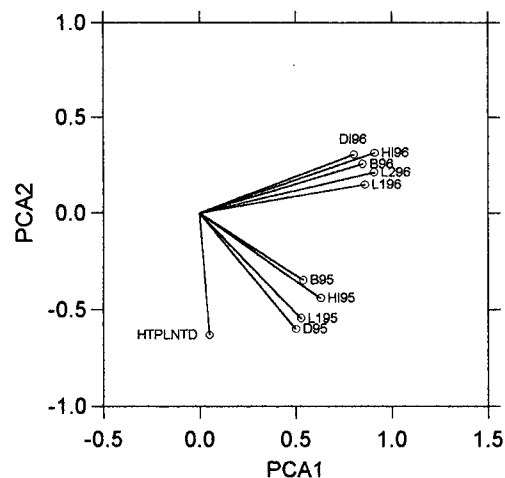


Figure 13. PCA vector ordinations of grand fir morphological variables for 1995 and 1996 combined.

(a) Douglas fir, Shelterwood



(b) Douglas fir, Clearing

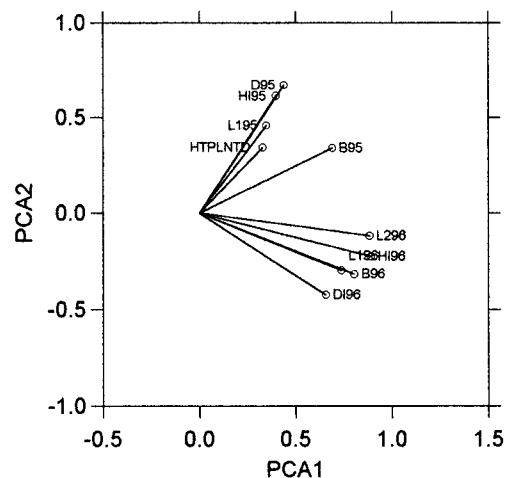


Figure 14. PCA vector ordinations of Douglas fir morphological variables for 1995 and 1996 combined.

The amount of variation accounted for by the first two PCA axes generated during the analyses of all 1995 and 1996 variables of grand fir and Douglas fir are shown in Table 1. In general, a majority of the variation present in the data can be explained by

the first two axes extracted during the analyses. The minimum amount of variation accounted for, 49%, was seen in grand fir seedling planted in the clearing. The highest amount of variation accounted for by both axes was 67%, reached by Douglas fir seedlings in the shelterwood (Table 1). Those seedling combinations remaining (grand fir in the shelterwood and Douglas fir in the clearing) had virtually the same amount of variation accounted for, 60% and 59%, respectively.

Vector ordination diagrams were graphed for the first two PCA axes extracted during the analyses of grand fir seedlings (Figure 15, a-d). Each PCA was conducted on the measured morphological variables of 1995 and 1996 separately. Two yearly trends were demonstrated across the sites. The first was demonstrated by the height increment and the number of buds produced along the height increment. These variables formed a close association with each other at both sites for all seedlings in 1995 and 1996, although this relationship is somewhat weaker in 1996, as shown by the larger angle between these two variables (Figure 15, a-d).

The second yearly trend was demonstrated by the basal stem diameter. At all sites, this variable formed a group noticeably removed from the remaining variables. It was coupled with the height of the seedling at planting in 1995, and alone in 1996 (Figure 15, a-d). As the height of the seedling at planting was excluded from the analyses in 1996, it is uncertain whether or not the stem diameter would have remained in close association with it in 1996. The pattern of the stem diameter forming a group on its own apart from the remaining variables was still maintained in this year however.

Table 1. Component loadings, eigenvalues and percent of total variance explained by the first two axes extracted using PCA for the 1995 and 1996 variables analyzed together. Each site and species combination was determined using a separate PCA.

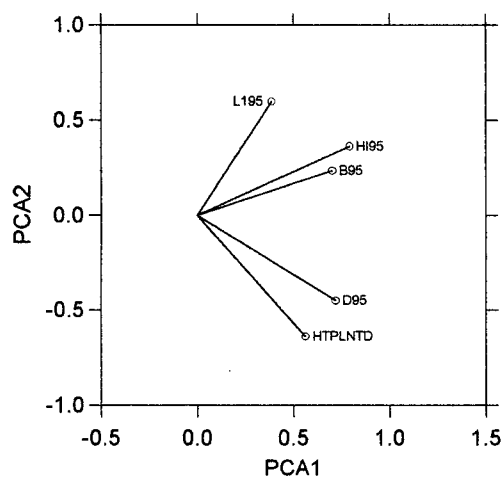
Site	Variable	Grand fir		Douglas fir	
		Loading		Loading	
		PCA1	PCA2	PCA1	PCA2
Shelterwood	HTPLTND	0.352	0.411	0.051	-0.630
	HI95	0.548	0.575	0.629	-0.438
	L195	0.188	0.504	0.527	-0.543
	D95	0.616	0.383	0.501	-0.600
	B95	0.536	0.350	0.539	-0.345
	HI96	0.925	-0.191	0.910	0.317
	L196	0.850	-0.158	0.860	0.149
	L296	0.882	-0.144	0.907	0.215
	DI96	0.644	-0.518	0.803	0.309
	B96	0.827	-0.249	0.848	0.260
	Eigenvalue	4.581	0.434	4.790	1.695
	%Variance	45.814	14.344	49.700	16.946
Clearing	HTPLTND	0.179	0.190	0.328	0.344
	HI95	0.162	0.795	0.397	0.613
	L195	0.114	0.497	0.347	0.459
	D95	0.272	0.396	0.439	0.670
	B95	0.152	0.710	0.689	0.343
	HI96	0.869	-0.083	0.889	-0.221
	L196	0.801	-0.073	0.736	-0.294
	L296	0.816	-0.067	0.883	-0.116
	DI96	0.642	-0.202	0.656	-0.423
	B96	0.803	-0.149	0.803	-0.315
	Eigenvalue	3.287	1.655	4.240	1.699
	%Variance	32.870	16.550	42.399	16.986

Trends maintained within each site across the years were only seen in the previously mentioned relationship between the stem diameter and the remaining variables. No other striking trends attributable to a particular site were seen.

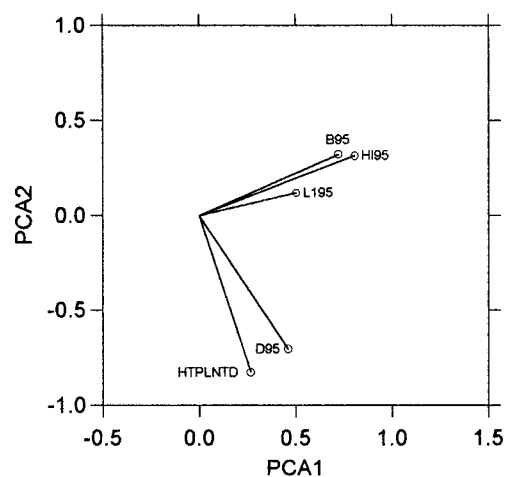
One relationship which was not shown consistently across any one site or year was that of lateral branch #1 (L195 and L196). In 1995, this characteristic formed a

group by itself in the shelterwood, a trend which only repeated itself in seedlings of the clearing in 1996 (Figure 15a and d).

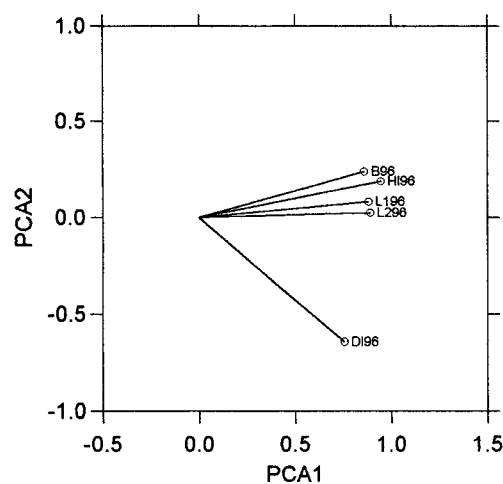
(a) Grand fir, Shelterwood, 1995



(b) Grand fir, Clearing, 1995



(c) Grand fir, Shelterwood, 1996



(d) Grand fir, Clearing, 1996

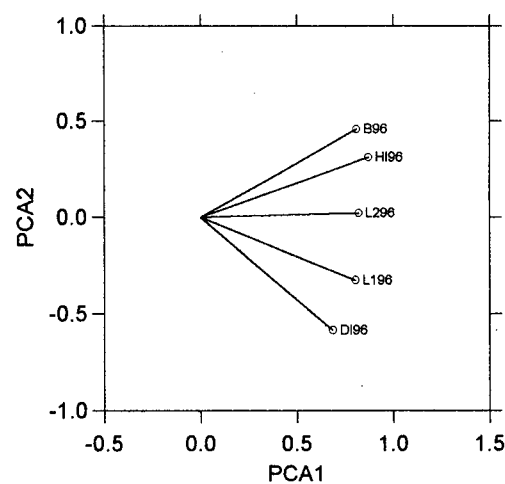


Figure 15. PCA vector ordinations of grand fir morphological variables in 1995 (a and b) and in 1996 (c and d).

The PCA for grand fir seedlings indicate that a larger amount of the total variation is accounted for by the 1996 measurements compared to those taken in 1995 (Table 2).

This trend is particularly evident in the principal axis of 1996 (PCA1), which accounts for a substantially larger proportion of the total variation compared to this same axis generated from the 1995 data (Table 2). The reverse is seen with the secondary axis however, with 1995 accounting for much more of the variation than this same axis in 1996. This is presumably due to the fact that there is more variation left unaccounted for by the principal axis in this year, thus allowing more to be accounted for by the second axis.

Vector ordination diagrams for Douglas fir seedlings conducted on the morphological variables of 1995 and 1996 separately are given in Figure 16 (a-d). Yearly trends are demonstrated in several of the variables. The height increment and length of the subtending lateral branches (either L195, L196 or L296) all form close associations with one another which remain fairly constant in 1995 and 1996 (Figure 16, a-d). The basal stem diameter forms a group on its own in the shelterwood in 1995, a trend which is only repeated in the clearing site in 1996 (Figure 16, a and d). In the shelterwood for 1996, and the clearing for 1995, this variable forms a group with the number of buds found along the height increment (Figure 16, b and c).

Table 2. Component loadings, eigenvalues and percent of total variance explained by the first two axes extracted using PCA for all 1995 and 1996 morphological variables. Each site, species and year combination was determined using a separate PCA.

Site	Variable	Grand fir		Douglas fir	
		Loading		Loading	
		PCA1	PCA2	PCA1	PCA2
Shelterwood 1995	HTPLTND	0.561	-0.638	0.374	-0.865
	HI95	0.791	0.363	0.807	0.370
	L195	0.387	0.598	0.785	0.219
	D95	0.718	-0.450	0.741	-0.350
	B95	0.701	0.234	0.672	0.167
	Eigenvalue	2.098	1.154	2.408	1.083
	%Variance	41.956	23.071	48.150	21.654
Clearing 1995	HTPLTND	0.265	-0.826	0.549	0.643
	HI95	0.805	0.313	0.667	-0.600
	L195	0.503	0.119	0.552	-0.575
	D95	0.460	-0.704	0.784	0.238
	B95	0.721	0.321	0.760	0.235
	Eigenvalue	1.704	1.393	2.242	1.216
	%Variance	34.079	27.860	44.850	24.313
Shelterwood 1996	HI96	0.946	0.192	0.961	0.143
	L196	0.882	0.084	0.885	0.274
	L296	0.890	0.025	0.930	0.224
	DI96	0.755	-0.643	0.863	-0.427
	B96	0.859	0.241	0.896	-0.246
	Eigenvalue	3.771	0.517	4.119	0.388
	%Variance	75.423	10.332	82.387	7.768
Clearing 1996	HI96	0.870	0.314	0.926	0.172
	L196	0.803	-0.324	0.788	0.078
	L296	0.819	0.022	0.888	0.243
	DI96	0.687	-0.585	0.744	-0.662
	B96	0.809	0.458	0.860	0.066
	Eigenvalue	3.199	0.755	3.561	0.537
	%Variance	63.971	15.104	71.216	10.733

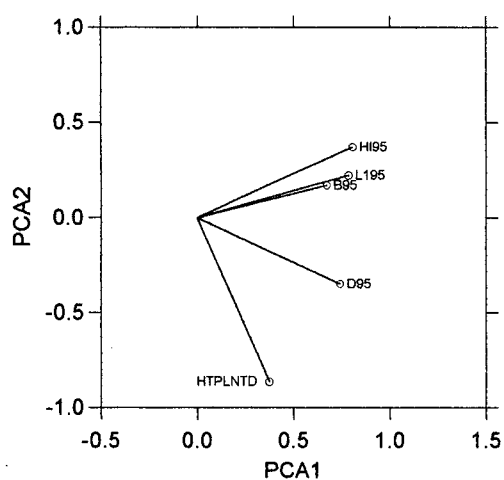
Consistent trends held within the sites across each year are seen only in the relationship described previously involving the height increment and the subtending lateral branches (Figure 16, a-d).

Similar within-site variable relationships are demonstrated by both grand fir and Douglas fir seedlings. The relationship between the height increment in 1995 (HI95) and the number of buds produced upon it in that same year (B95) was maintained in the shelterwood site for grand fir (Figure 15a) and Douglas fir (Figure 16a), the only difference being that seedlings of Douglas fir have subtending lateral #1 (L195) forming a part of this grouping as well. Seedlings of both grand fir and Douglas fir in the clearing in 1995 formed similar relationships between their height increments (HI95) and subtending lateral branch #1 (L195) as well (Figure 15b and Figure 16b, respectively). The number of buds produced along the height increment (B95) also forms a part of the variable grouping demonstrated by grand fir seedlings, a trend not seen in Douglas fir. This same relationship is shown in 1996 as well for both species, only this time in the shelterwood (Figure 15c and Figure 16c, respectively). Here as well, additional plant parts were included in these variable groupings, with lateral branch #2 (L296) being included across both species, and B96 being included in grand fir seedlings only. Finally, the diameter increment (DI96) maintains a similar relationship across each seedling species in the clearing in 1996 (Figure 15d and Figure 16d).

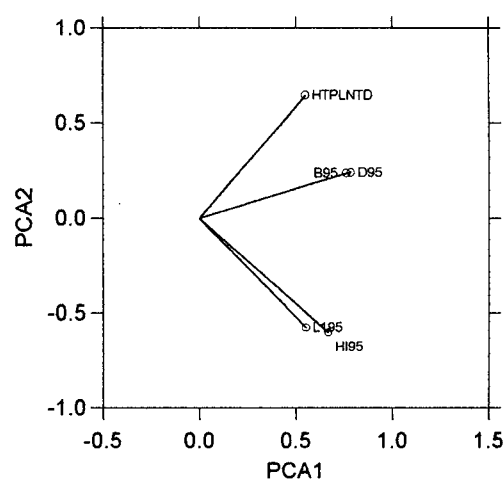
Additional PCA results for Douglas fir seedlings are shown in Table 2. As was shown for grand fir, a larger amount of the total variation is accounted for by the 1996 measurements than those taken in 1995. The principal axis of 1996 again accounts for more of the total variation than does this same axis in 1995. However, both the principal

and secondary axes of Douglas fir, when combined, account for more of the total variation in both years than do those of grand fir.

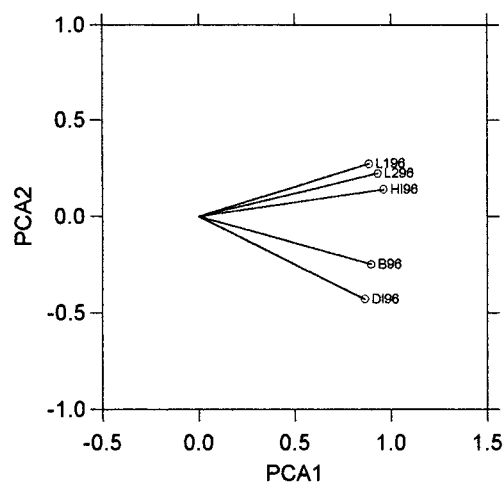
(a) Douglas fir, Shelterwood, 1995



(b) Douglas fir, Clearing, 1995



(c) Douglas fir, Shelterwood, 1996



(d) Douglas fir, Clearing, 1996

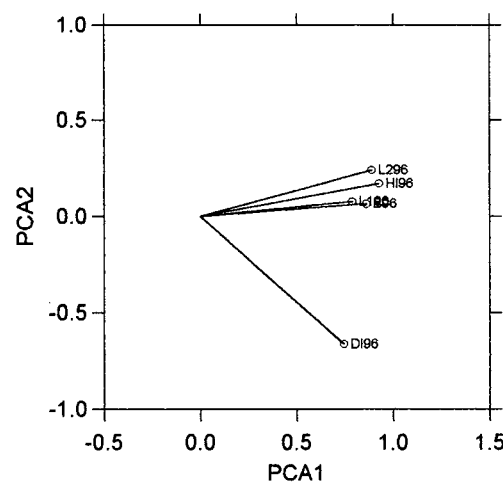


Figure 16. PCA vector ordinations of Douglas fir morphological variables in 1995 (a and b) and in 1996 (c and d).

PCA vector ordinations resulting from the analyses of the 1996 morphological variables of “normal” and “proleptic free growth” seedlings at each site are given in

Figure 17 for grand fir and Figure 18 for Douglas fir. Variable relationships in “normal” seedlings of grand fir were formed between the height increment (HI96) and the number of buds formed upon the height increment (B96) (Figure 17, a and b), a trend seen previously when all grand fir seedlings were analyzed together. Both lateral branches #1 and #2 formed a part of the grouping involving the height increment and the number of buds in grand fir seedlings in the shelterwood. However, the lateral branches formed a stronger relationship with one another than with the two other variables found in this group (Figure 17a). Similarly, the height increment and number of buds both were more closely related to each other than to either of the lateral branches (Figure 17a).

“Normal” seedlings also demonstrated similar trends to those of the pooled seedlings in their diameter increment, which forms a group apart from the rest of the variables (Figure 17, a and b).

Seedlings with proleptic free growth also demonstrated the same trend in their diameter increment. This variable again forms a group in which it is the only member, and is separated from the remaining variables (Figure 17, c and d). Another trend similar to that of the diameter increment is seen in subtending lateral branch #1 (L196) of seedlings with proleptic free growth. This variable also forms a group on its own apart from the other variables (Figure 17, c and d). Proleptic free growth seedlings also formed similar relationships between the height increment (HI96), bud number (B96) and lateral branch #2 (L296) across the sites (Figure 17 c and d). The height increment and bud number of seedlings in the shelterwood formed a closer relationship with one another compared to the third member of the group, lateral branch #2 (Figure 17c), while the

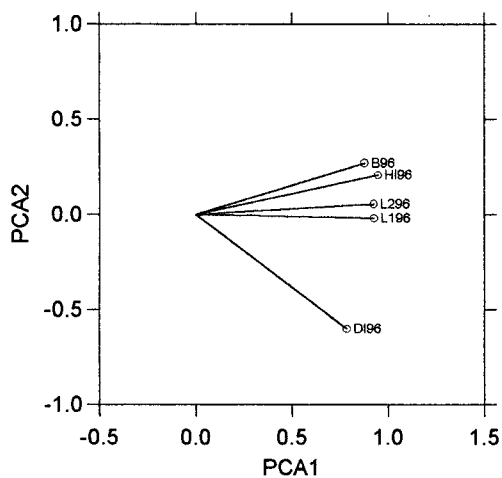
reverse was shown by seedlings in the clearing. At this site, the height increment formed a stronger relationship with lateral branch #2, compared to the bud number (Figure 17d).

Several of the trends mentioned above are not unique to a particular seedling type however. For example, the trend demonstrated by lateral branch #1 (L196) in seedlings with proleptic free growth is also seen in seedlings with a “normal” morphology in the clearing site (Figure 17 b-d). Similarly, the relationship seen between the height increment (HI96) and the number of buds produced upon the height increment (B96) demonstrated by “normal” seedlings is seen again in all seedlings with proleptic free growth (Figure 17 a-d).

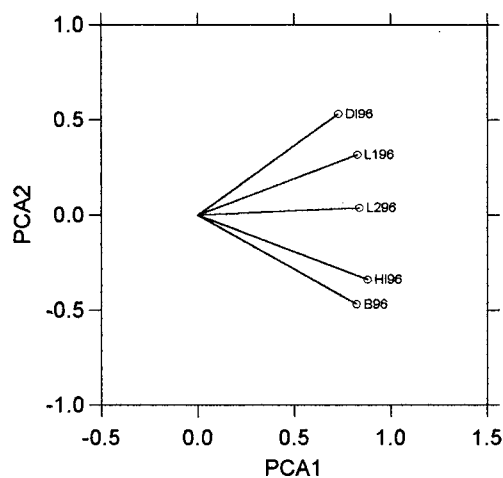
A larger amount of the total variation is accounted for when the distinction between “normal” and “proleptic free growth” seedlings is made (Table 3), compared to the previous analyses involving the 1995 and 1996 variables analyzed both together and separately (Table 1 and Table 2). This is not demonstrated by seedlings with proleptic free growth however, which show a smaller amount of the total variation being accounted for when compared to both “normal” seedlings and all seedlings combined in 1996 (Table 2 and Table 3).

The variable relationships formed by Douglas fir seedlings with a “normal” or proleptic free growth morphology differed from each other (Figure 18). Seedlings with a “normal” morphology at each site demonstrated similar variable groupings in the diameter increment, which formed a group on its own (Figure 18, a and b). Close inter-variable relationships existed between lateral branch #2 (L296), the height increment (HI96) and the number of buds produced along the height increment (B96) in these seedlings as well (Figure 18, a and b).

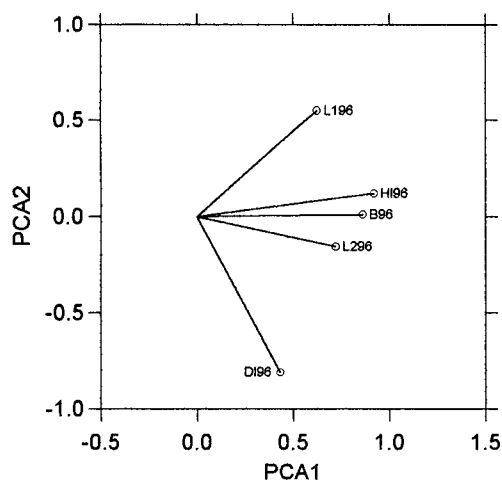
(a) "Normal" Grand fir, Shelterwood



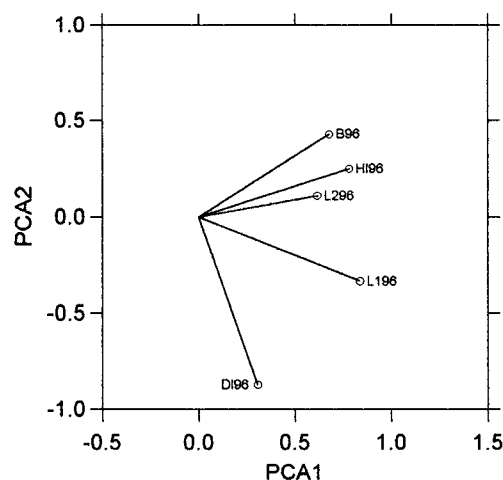
(b) "Normal" Grand fir, Clearing



(c) "Proleptic free growth" Grand fir, Shelterwood



(d) "Proleptic free growth" Grand fir, Clearing

**Figure 17. PCA vector ordinations of all grand fir seedling types.**

Seedlings with proleptic free growth demonstrated similar variable groupings in lateral branch #1 (L196), which forms a group on its own (Figure 18, c and d), and between the diameter increment (DI96) and the number of buds produced along the

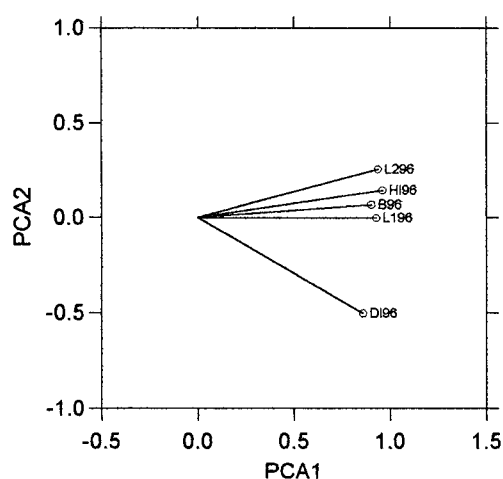
height increment (B96). Seedlings of this type in the clearing specifically also have the height increment (HI96) falling within this group, and its relationship with the diameter increment is much closer than that seen between it (HI96) and the number of buds (Figure 18d).

Relationships seen across seedling types are demonstrated in L196 alone and HI96 together with L296. The relationship demonstrated by lateral branch #1 of proleptic free growth seedlings is also seen in “normal” seedlings planted in the clearing (Figure 18b). The height increment (HI96) and lateral branch #2 (L296) of seedlings with proleptic free growth in the shelterwood share a relationship similar to that seen across all “normal” seedlings (Figure 18 a, b, and c). Seedlings with proleptic free growth in the clearing also demonstrated a similar relationship between the height increment (HI96) and the number of buds along the height increment (B96) to that seen in “normal” seedlings, but the relationship is not as strong, judging by the larger angle between these two variables (Figure 18 a, b, and d).

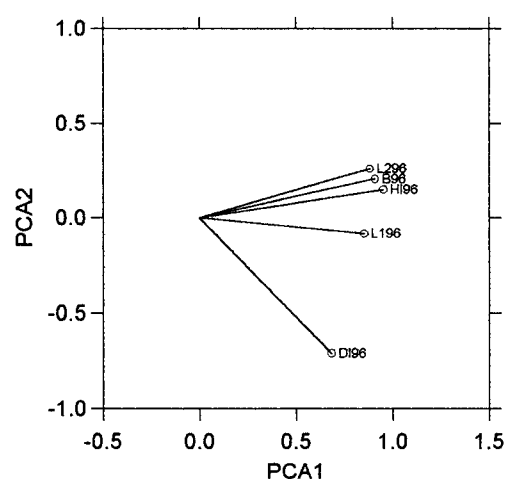
Similar between species relationships are demonstrated by each seedling type. In “normal” seedlings of the shelterwood for both grand fir and Douglas fir, virtually identical variable relationships are seen between all plant parts (Figure 17a for grand fir and Figure 18a for Douglas fir). For “normal” seedlings in the clearing, similar relationships are demonstrated by the diameter increment (DI96) and lateral branch #1 (L196), both of which form a separate variable group (Figure 17b for grand fir and Figure 18b for Douglas fir). Seedlings of grand fir and Douglas fir with proleptic free growth show similar responses in lateral branch #1 (L196) at both sites, with this variable forming a group on its own (Figure 17 c and d for grand fir, and Figure 18 c and d for

Douglas fir). A trend held across virtually every seedling type and site is that shown between the height increment (HI96) and the number of buds produced upon it (B96). All seedling types, with the exception of Douglas fir seedlings in the shelterwood with proleptic free growth, demonstrated a consistently close relationship between these two variables (Figure 17 a-d and Figure 18 a, b, and d).

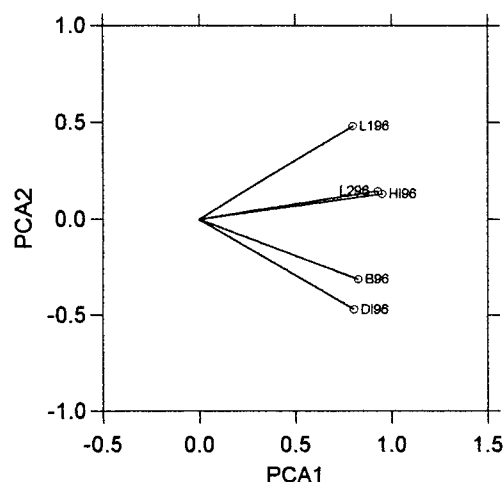
(a) "Normal" Douglas fir, Shelterwood



(b) "Normal" Douglas fir, Clearing



(c) "Proleptic free growth" Douglas fir, Shelterwood



(d) "Proleptic free growth" Douglas fir, Clearing

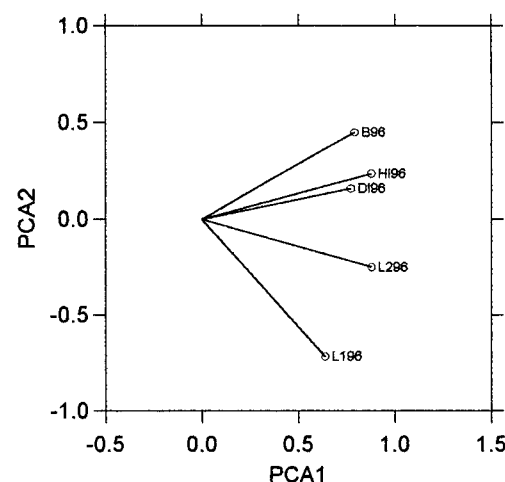


Figure 18. PCA vector ordinations of all Douglas fir seedling types.

Table 3. Component loadings, eigenvalues and percent of total variance explained for the first two axes extracted using PCA for 1996 morphological variables only. Each site, species and seedling-type combination was determined using a separate PCA.

Combination	Variable	Grand fir		Douglas fir	
		Loading		Loading	
		PCA1	PCA2	PCA1	PCA2
Normal, Shelterwood	HI96	0.947	0.209	0.960	0.143
	L196	0.927	-0.019	0.927	-0.002
	L296	0.925	0.057	0.936	0.253
	DI96	0.785	-0.600	0.858	-0.503
	B96	0.877	0.271	0.902	0.067
	Eigenvalue	3.995	0.480	4.206	0.341
	%Variance	79.897	9.606	84.128	6.825
Proleptic free growth, Shelterwood	HI96	0.919	0.119	0.951	0.126
	L196	0.622	0.552	0.799	0.480
	L296	0.720	-0.155	0.929	0.142
	DI96	0.433	-0.811	0.804	-0.471
	B96	0.861	0.012	0.826	-0.313
	Eigenvalue	2.679	1.000	3.735	0.587
	%Variance	53.589	20.005	74.699	11.731
Normal, Clearing	HI96	0.879	-0.338	0.951	0.148
	L196	0.826	0.316	0.852	-0.082
	L296	0.837	0.040	0.881	0.258
	DI96	0.729	0.532	0.682	-0.710
	B96	0.823	-0.468	0.909	0.204
	Eigenvalue	3.365	0.718	3.698	0.642
	%Variance	67.293	14.365	73.956	12.833
Proleptic free growth, Clearing	HI96	0.780	0.247	0.876	0.232
	L196	0.837	-0.335	0.639	-0.716
	L296	0.615	0.108	0.877	-0.251
	DI96	0.307	-0.875	0.771	0.156
	B96	0.677	0.427	0.790	0.448
	Eigenvalue	2.241	1.132	3.164	0.854
	%Variance	44.810	22.642	63.273	17.089

Least squares means (LS MEAN) and standard errors (SE) for the site (S), species (SP) and site by species (S*SP) factors found to be significant at the 0.05 level in the

models run are given in Table 4 for all seedlings pooled in 1995 and 1996, and Table 5 for seedlings in 1996 having a "normal" and "proleptic free growth" morphology.

In 1995 and 1996 for all seedlings pooled, a varied growth response was seen in terms of the effects of species, site, and species by site interactions (Table 4). In general, the site had a greater impact on seedling growth in 1996 compared to 1995, as shown by the increase in the number of dependent variables demonstrating a significant site term. In 1995, larger seedlings were planted in the clearing (as shown by the significant site term for "H", the height at planting in Table 4) and more buds were produced on the height increment in the shelterwood, shown by the significant site term for B95. In 1996, virtually every dependent variable demonstrated a significant response to the site term, but no clear preference for any one site was established (Table 4).

Species effects on all pooled seedlings seemed to decrease in 1996 compared to 1995 (Table 4). In 1995, every dependent variable displayed a significant response to the species term, with grand fir seedlings growing more overall than Douglas fir seedlings, with the exception of the height at planting (H). In 1996, the effect of species remained only for the total height achieved in 1996 (THT96), in which grand fir seedlings grew the tallest, and the amount of growth produced by lateral branch #1 in 1996 (L196), in which Douglas fir seedlings were superior (Table 4).

Species by site interactions were few in 1995, but increased in 1996 across all seedlings (Table 4). In 1995 two dependent variables displayed a significant interaction term, the length of lateral branch #1 (L195) and the number of buds produced on the height increment for this year (B95). In both cases, grand fir seedlings in the shelterwood outperformed the remaining combinations (Table 4). In 1996, every dependent variable,

with the exception of the height increment (HI96) demonstrated a significant interaction term (Table 4). No particular combination of species and site took precedence however, as the responses varied between grand fir and Douglas fir seedlings found in the shelterwood and grand fir seedlings in the clearing. Grand fir seedlings in the shelterwood grew best in total height for this year (THT96) and produced the most growth for lateral branch #2 (L296) (Table 4). Douglas fir seedlings in the shelterwood grew best in diameter (DI96) and produced the most growth for lateral branch #1 (L196) (Table 4). Finally, grand fir seedlings in the clearing produced the largest number of buds on the height increment (B96) (Table 4).

The effects of species, site, and species by site interactions were again variable when addressing seedlings with a “normal” morphology and those with proleptic free growth (Table 5). The number of dependent variables responding significantly to the site term was similar between the two seedling types, with the total height (THT96) and height increment (HI96) responding in both “normal” and “free growth” seedlings, lateral branch #2 (L296) responding in “normal” seedlings only, and diameter increment (DI96) and lateral branch #1 (L196) responding in “free growth” seedlings only (Table 5). No distinct site preferences were shown however, as the responses varied regularly between both sites.

The number of dependent variables demonstrating a significant response to the species term was equal between “normal” and “free growth” seedlings, each having four dependent variables responding (Table 5).

Table 4. Adjusted least squares means and standard errors for factors used in the ANCOVA models showing statistical significance for all seedlings in 1995 and 1996.

All Seedlings, 1995				All Seedlings, 1996			
Dep. Var.	Factor	LS Mean	SE	Dep. Var.	Factor	LS Mean	SE
H	S			THT96	S		
	CI	33.531	0.375		CI	70.306	0.563
	Sw	31.827	0.359		Sw	68.363	0.533
	SP ^L				SP		
	Bg	26.979	0.396		Bg	72.669	0.675
	Fd	38.378	0.431		Fd	66.001	0.737
THT95	SP				SP*S		
	Bg	48.978	0.401		BgCI	72.418	0.873
	Fd	46.297	0.443		BgSw	72.920	0.865
HI95	SP				FdCI	68.195	1.018
	Bg	16.783	0.401		FdSw	63.806	0.857
	Fd	14.102	0.443	HI96	S ^L		
L195	SP				CI	23.811	0.337
	Bg	9.866	0.204		Sw	21.043	0.319
	Fd	8.740	0.227	DI96	S		
	SP*S				CI	2.127	0.098
	BgCI	9.463	0.241		Sw	2.582	0.094
	BgSw	10.270	0.276		SP*S		
	FdCI	9.034	0.299		BgCI	2.514	0.151
	FdSw	8.446	0.262		BgSw	2.500	0.149
B95	S				FdCI	1.740	0.173
	CI	8.443	0.256		FdSw	2.664	0.151
	Sw	10.265	0.243	L196	S		
	SP				CI	9.406	0.201
	Bg	10.253	0.324		Sw	10.279	0.189
	Fd	8.455	0.356		SP		
	SP*S				Bg	8.572	0.227
	BgCI	8.963	0.381		Fd	11.114	0.253
	BgSw	11.542	0.430		SP*S		
	FdCI	7.923	0.464		BgCI	7.797	0.291
	FdSw	8.987	0.418		BgSw	9.346	0.301
					FdCI	11.015	0.357
					FdSw	11.212	0.300
				L296	S		
					CI	13.235	0.190
					Sw	13.891	0.181
					SP*S ^L		
					BgCI	12.810	0.290
					BgSw	14.461	0.286
					FdCI	13.659	0.343
					FdSw	13.320	0.291
				B96	SP*S		
					BgCI	7.478	0.288
					BgSw	6.881	0.287
					FdCI	6.367	0.334
					FdSw	7.153	0.287

L indicates term was significant according to Levene's test.

“Normal” seedlings of grand fir grew more overall in terms of total height (THT96) and diameter (DI96), and produced a larger number of buds on the height increment (B96) compared to Douglas fir seedlings of this same type (Table 5).

“Normal” Douglas fir seedlings outgrew grand fir of the same type in lateral branch #1 (L196). No particular species showed a superior response where “free growth” seedlings were concerned. Grand fir seedlings with proleptic free growth grew the tallest, both in terms of the total height achieved (THT96) and the height increment produced (HI96) and Douglas fir seedlings produced the longest lateral branches in both position #1 and #2 (L196 and L296) (Table 5).

“Normal” seedlings had a larger number of dependent variables responding significantly to the interaction term (four) compared to those with proleptic free growth, which had only two (Table 5). Again, no one species by site combination proved to be superior. Grand fir seedlings in the shelterwood grew the tallest overall (THT96) and produced the longest lateral branches for lateral branch #2 (L296) (Table 5). Grand fir seedlings in the clearing grew most in diameter (DI96) while Douglas fir seedlings in the clearing produced the longest lateral branches for lateral branch #1 (L196) (Table 5). Douglas fir seedlings having proleptic free growth produced the only significant responses to the interaction term, with those seedlings in the shelterwood growing best in diameter (DI96) and those found in the clearing producing the longest lateral branches for lateral branch #2 (L296) (Table 5).

Table 5. Adjusted least squares means and standard errors for factors used in the ANCOVA models showing statistical significance for all seedlings with a “normal” and “proleptic free growth” morphology.

“Normal” Seedlings, 1996				Proleptic Free Growth Seedlings, 1996			
Dep. Var.	Factor	LS Mean	SE	Dep. Var.	Factor	LS Mean	SE
THT96	S			THT96	S		
	Cl	66.439	0.676		Cl	80.695	1.249
	Sw	64.076	0.632		Sw	76.835	1.077
	SP				SP		
	Bg	67.509	0.748		Bg	84.897	1.512
	Fd	63.006	0.997		Fd	72.634	1.131
	SP*S				S		
	BgCl	67.425	0.931		Cl	30.118	0.698
	BgSw	67.592	0.997		Sw	27.117	0.601
	FdCl	65.453	1.342		SP		
HI96	FdSw	60.560	1.101		Bg	31.110	0.844
	S ^L				Fd	26.125	0.631
	Cl	21.002	0.395	DI96	S		
	Sw	18.382	0.369		Cl	2.922	0.231
	SP				Sw	3.756	0.194
	Bg	2.146	0.114		SP*S		
	Fd	1.489	0.151		BgCl	3.309	0.424
	SP*S				BgSw	3.558	0.316
	BgCl	2.247	0.142		FdCl	2.536	0.296
	BgSw	2.045	0.155		FdSw	3.954	0.286
	FdCl	1.158	0.203	L196	S		
	FdSw	1.819	0.170		Cl	10.442	0.469
L196	SP				Sw	13.050	0.412
	Bg	7.569	0.229		SP		
	Fd	10.203	0.304		Bg	10.336	0.593
	SP*S				Fd	13.156	0.451
	BgCl	7.008	0.279	L296	SP		
	BgSw	8.130	0.319		Bg	14.676	0.511
	FdCl	10.396	0.422		Fd	16.348	0.382
	FdSw	10.010	0.340		SP*S		
	S				BgCl	14.134	0.747
	Cl	11.928	0.230		BgSw	15.218	0.570
	Sw	12.873	0.213		FdCl	16.990	0.539
	SP*S				FdSw	15.706	0.517
	BgCl	11.942	0.311				
	BgSw	13.786	0.325				
L296	FdCl	11.915	0.457				
	FdSw	11.960	0.368				
	S						
	Cl	11.928	0.230				
	Sw	12.873	0.213				
	SP*S						
	BgCl	11.942	0.311				
	BgSw	13.786	0.325				
	FdCl	11.915	0.457				
	FdSw	11.960	0.368				
B96	SP						
	Bg	6.468	0.230				
	Fd	5.337	0.304				
	S						
	Cl	11.928	0.230				
	Sw	12.873	0.213				
	SP*S						
	BgCl	11.942	0.311				
	BgSw	13.786	0.325				
	FdCl	11.915	0.457				

L indicates term was significant according to Levene's test.

Variation partitioning using η^2 values viewed covariates which accounted for more than 10% (0.100 in the tables) of the variation of the dependent variables as adequate descriptors of these plant parts. While many of the covariates were found to be statistically significant at the 0.05 level by the ANCOVA models, only a select few accounted for a noticeable amount of the total variation (Table 6 and Table 7).

In every model, with the exception of that where the total height achieved in 1995 (THT95) is the dependent variable, the error term accounts for the most variation. This indicates that for the remaining models, the large majority of variation is unaccounted for by the factors and covariates used to construct the model, and the seedlings being dealt with are highly heterogeneous.

Table 6 addresses the yearly trends displayed by all seedlings pooled in 1995 and 1996. Trends demonstrated in 1995 which are maintained in 1996 reflect the relationships of certain plant parts to the overall production of the seedling's growth form or architecture. Specifically, the height increment in 1995 (HI95), when used as a dependent variable, is best described by lateral branch #1 (L195) and the number of buds produced along the height increment (B95) (Table 6). This same relationship is repeated in 1996 when that year's current height increment (HI96) is also best described by the new subtending lateral, lateral branch #2 (L296), and the number of buds produced along the height increment (B96). The relationship between these variables is reciprocated only by the height increment when either the subtending lateral branches (L195 or L296) or the number of buds produced along the height increment (B95 or B96) are the dependent variables. In each case, the height increment is the covariate which accounts for the most variation. The remaining variables (B95/B96 or L195/L296) do not account

for a substantial amount of the variation when one or the other is the dependent variable (for example, when L195 is the dependent variable, B95 accounts for only 0.6% of the total variation and when B95 is the dependent variable, L1 accounts for only 0.1% of the total variation (Table 6)). In fact, each of these variables were not even found to be of any significance statistically and are thus not notable descriptors of these dependent variables (Table 6).

Different relationships were demonstrated in stem diameter for 1995 and 1996 when it was the dependent variable. This variable in 1995 found its best descriptor to be the height of the seedling at planting (H), which accounted for 18.9% of the total variation (Table 6). In 1996 however, no covariate adequately described the stem diameter and the amount of the total variation left unaccounted for increased by approximately 7% (Table 6).

The height of the seedling at planting (H) also best described the total height of the seedling at the end of the growing season (THT) in both 1995 and 1996 (Table 6). This is a logical relationship, as plants which are big (for example) to begin with, should be big at the time of measurement as well, unless they did not grow at all. As well, for seedlings in 1996, the subtending whorl lateral (L296 in this case) also accounts for a substantial amount of the total variation (Table 6).

Finally, in 1996, no adequate descriptors were found for lateral branch #1 when it is the dependent variable. The error term for this variable decreased from 1995 however, presumably due to the slightly larger increases in the overall amount of variation accounted for by all of the covariates in the model (Table 6).

Table 6. Eta squared values for variables used in analysis of covariance for all seedlings pooled in 1995 and 1996.

Factors/ Covariates	1995 dependent variables						1996 dependent variables					
	H	THT95	HI95	D95	L195	B95	THT96	HI96	DI96	L196	L296	B96
S	0.013*	0.002	0.003	0.002	0.000	0.054*	0.008*	0.045*	0.024*	0.018*	0.010*	0.000
SP	0.382*	0.014*	0.024*	0.002	0.019*	0.019*	0.039*	0.002	0.005	0.076*	0.000	0.002
H	-	0.443*	0.014*	0.189*	0.006*	0.004	0.213*	0.008*	0.001	0.021*	0.000	0.004
HI	0.014*	-	-	0.040*	0.191*	0.146*	-	-	0.001	0.058*	0.258*	0.293*
D/DI	0.124*	0.014*	0.025*	-	0.001	0.010*	0.001	0.003	-	0.069*	0.013*	0.024*
L1	0.005*	0.082*	0.145*	0.000	-	0.001	0.000	0.030*	0.068*	-	0.057*	0.000
L2	-	-	-	-	-	-	0.182*	0.195*	0.007	0.054*	-	0.001
B	0.002	0.076*	0.135*	0.012*	0.006	-	0.086*	0.228*	0.034*	0.000	0.002	-
S*SP	0.000	0.000	0.001	0.002	0.019*	0.009*	0.011*	0.001	0.027*	0.011*	0.024*	0.013*
E	0.460	0.369	0.653	0.754	0.756	0.756	0.459	0.487	0.833	0.693	0.636	0.664

* indicates significance at the 0.05 level.

Differences between “normal” and “proleptic free growth” seedlings are shown in Table 7. Many of the trends seen when the seedlings were analyzed as a pooled group in 1996 are maintained here as well. Most noticeably, the relationships between the current height increment (HI96), subtending whorl lateral (L296) and number of buds produced upon the height increment (B96) are identical to those seen in 1995 and 1996 (Table 6 and Table 7). An interesting feature of seedlings with proleptic free growth however is the amount of variation accounted for by L296 and B96 when HI96 is the dependent variable. In these seedlings only, the amount of variation accounted for by lateral branch #2 is more than that accounted for by the number of buds produced upon the height increment (Table 7). This trend tends to stand out mainly because in “normal” seedlings, as well as all seedlings pooled in 1996, this relationship is reversed, with the number of buds along the height increment accounting for more variation than lateral branch #2. This particular trend seen in seedlings with proleptic free growth was demonstrated in

1995, but the differences in the amount of variation accounted for between these two variables were not as prominent as was seen in 1996 (Table 6).

Lateral branch #2 and the number of buds produced upon the height increment were again best described by the height increment in both “normal” and “proleptic free growth” seedlings, a trend consistent with that shown in 1995 and all seedling pooled in 1996 (Table 6 and Table 7). The η^2 value of the error term for lateral branch #2 in particular, while it decreased from 1995, was largest in “normal” seedlings by approximately 13% compared to “free growth” seedlings (Table 7). Conversely, the η^2 value of the error term for the number of buds produced upon the height increment was approximately 13% larger in seedlings with proleptic free growth than those with a “normal” morphology (Table 7).

A trend unique to “normal” seedlings only is seen when the diameter increment (DI96) is the dependent variable. Lateral branch #1 accounted for the majority of the variation in this seedling type, while, consistent with the trend seen when all seedlings were pooled in 1996, no adequate descriptor was found for this component in seedlings with proleptic free growth (Table 7). The error term for the diameter increment maintained the large increase seen from 1995 to 1996 (Table 6) when the distinction between “normal” and “proleptic free growth” seedlings was made (Table 7).

Consistent with the trends seen in all pooled seedlings in 1996, lateral branch #1 still remains without a notable descriptor when “normal” and “proleptic free growth” seedlings are analyzed separately (Table 7). The error term is slightly lower when the distinction between these two seedling types is made, mostly in seedlings with proleptic free growth.

In addition to the height of the seedling at planting (H) and subtending whorl lateral (L296) accounting for the most variation when total height is the dependent variable, seedlings with proleptic free growth are also best described by the species term (Table 7). The error term for this particular seedling type is also lower than that demonstrated by "normal" seedlings, which may be attributable to the fact that they do not exhibit a large amount of variation accounted for by the species term (or any other term not yet mentioned).

Table 7. Eta squared values for variables used in analysis of covariance for "normal" and "proleptic free growth" seedlings in 1996.

Factors/ Covariates	"Normal" dependent variables						"Proleptic free growth" dependent variables					
	THT96	HI96	DI96	L196	L296	B96	THT96	HI96	DI96	L196	L296	B96
S	0.013*	0.046*	0.008	0.004	0.025*	0.000	0.019*	0.036*	0.048*	0.087*	0.000	0.003
SP	0.018*	0.002	0.028*	0.094*	0.010	0.015*	0.121*	0.064*	0.001	0.057*	0.023*	0.007
H	0.191*	0.025*	0.000	0.008	0.010	0.011*	0.208*	0.001	0.001	0.065*	0.035*	0.001
HI	-	-	0.001	0.069*	0.203*	0.362*	-	-	0.001	0.032*	0.279*	0.179*
DI	0.000	0.001	-	0.083*	0.007	0.004	0.007	0.003	-	0.012	0.025*	0.060*
L1	0.000	0.045*	0.108*	-	0.045*	0.000	0.004	0.011	0.015	-	0.068*	0.000
L2	0.204*	0.133*	0.008	0.055*	-	0.000	0.121*	0.277*	0.017	0.095*	-	0.003
B	0.074*	0.269*	0.004	0.000	0.000	-	0.075*	0.161*	0.059*	0.005	0.005	-
S*SP	0.014*	0.001	0.030*	0.018*	0.023*	0.010	0.000	0.001	0.029*	0.009	0.024*	0.011
E	0.486	0.478	0.812	0.668	0.678	0.597	0.445	0.445	0.829	0.638	0.541	0.734

* indicates significance at the 0.05 level.

Discussion

The results generated through both PCA and ANCOVA uncovered similar patterns of growth and consistent variable relationships, which ultimately helped describe the general morphology of the seedlings. The apex of the seedlings seemed to hold all the features necessary to describe the whole organism (the height increment, subtending lateral branch and number of buds produced upon the height increment). These three features both held fairly constant variable relationships with each other as shown by

PCA, and also accounted for a substantial amount of the variation when eta squared values were addressed.

The diameter increment generally formed no close variable relationships with any of the other plant parts, and also had few, to no plant parts adequately describing it.

Yearly variation, as demonstrated through PCA by the change in variable intercorrelations or groupings, is seen in both grand fir and Douglas fir seedlings. The variables which maintained similar relationships to one another over the two year measurement period were the height increment and number of buds produced upon the height increment, a logical relationship as the buds are found along the entire length of the height increment. This association was found to be most consistent in grand fir seedlings, but was evident in Douglas fir as well. On occasion, the subtending lateral branches (either L195, L196 or L296) were found in association with these variables as well, or alone with the height increment. This association was not as regular as the grouping between bud number and the height increment however, and demonstrated no specific species, site, or yearly pattern.

Another consistent variable grouping which was demonstrated across species, site and seedling type was that involving the stem diameter. This variable more often than not formed a group on its own with no close association with any of the other variables and was seen predominantly in 1996.

The remaining variables had a tendency to shift their associations, forming a variety of different groupings, depending on the site and year. This shift in growth pattern may be attributed to the different growing conditions experienced each year by the seedlings. In the 1995 growing season, all buds which flushed during this time had

been formed in a nursery environment. In 1996 however, all buds were formed (in 1995) and flushed (in 1996) in the field. The contrasting growing conditions experienced by the seedlings both during the time of bud formation and elongation could account for the shift in the pattern of integration demonstrated between both years (integration in the sense of how each individual plant part relates back to the morphology of the seedling as a whole).

The PCAs of the 1996 morphological traits specifically seem to address the responses shown by the meristematic regions within the seedlings. All characteristics produced by the apical meristem (height increment, lateral branches and lateral buds along the height increment) form associations which generally do not include the diameter increment, which is produced by the vascular cambium. Different growth phenomena are reflected in integration. The height increment, lateral branches and lateral buds along the height increment when formed by the apical meristem are the result of primary growth, or growth in length. The stem diameter is produced through secondary growth, or growth in width or girth. The combination of these two different types of growth work in unison to produce the whole organism.

Distinguishing between seedlings with proleptic free growth and those with a more "normal" morphology did not lead to the automatic conclusion that these two seedling types possess different patterns of integration simply because they display different morphologies. The larger number of variable groupings formed specifically by grand fir seedlings in the clearing compared to the shelterwood suggests that these seedlings, regardless of their morphology, are more complex, as it would take a larger amount of information to describe them, compared to those seedlings having fewer

groups (Scagel *et al.* 1985; Maze *et al.* 1987). The production of a wide number of variable groupings in Douglas fir seedlings however, suggests that no specific site or morphological type is consistently seen as being the most complex. While “proleptic free growth” seedlings of Douglas fir in the clearing have the largest number of variable groupings, and can thus be seen as being the most complex (according to the above stated arguments for grand fir), both “proleptic free growth” seedlings of the shelterwood, and “normal” seedlings of the clearing possess the same number of variable groupings, thus obscuring the real effects of either site or growth morphology on the assignment of complexity.

While morphologically many of these seedlings differ from one another, the one unifying property they possess is the way their parts are integrated to form a complete organism. Seedlings demonstrating proleptic free growth specifically, while they grow more vigorously than those with a “normal” morphology, and also simply “look” different because of the extra plant parts they possess, are not seen as distinct from other seedlings when analyses are conducted using shared characteristics. When patterns of integration are addressed through the analyses of common characteristics held between the two seedling types, the boundaries separating “normal” seedlings from those with proleptic free growth are dissolved.

Speculation as to the relative complexity of seedlings with proleptic free growth can be validated using the reasoning of Scagel *et al.* (1985), which suggests that an increase in the variation of a system (i.e.: a small amount of the total variation is accounted for, as detected with PCA) is analogous to an increase in complexity. Through the various PCAs, it was shown that those seedlings with proleptic free growth

characteristics had a smaller amount of the total variation accounted for by the first two PCA axes, compared to “normal” seedlings and all seedlings pooled in 1996. Seedlings with proleptic free growth could thus be viewed as being more complex, as they have more variation left unaccounted for.

On a more qualitative but less theoretical level, this same conclusion may be drawn if the additional characteristics unique to these seedlings were included in the analyses. Overall, “proleptic free growth” seedlings could be viewed as being more complex than “normal” seedlings simply because they possess additional plant parts (i.e. lammas and “proleptic” shoots), and thus occupy additional and differing developmental states or forms (*sensu* Banerjee *et al.* 1990) than those of seedlings with a “normal” morphology. According to Banerjee *et al.* (1990), “organisms do not realize all potential forms for a variety of reasons, the most important of which are historical and physical constraints”. The historical constraints can be akin to general developmental pathways maintained through the aid of genes, in which an evolutionary shift is needed to induce a change. Physical constraints involve factors which “impact on survival”, such as the plant’s immediate environmental surroundings (Banerjee *et al.* 1990). Following this logic, it can be hypothesized that all grand fir and Douglas fir seedlings used in this study are subject to similar historical constraints, as they are of the same species (respectively) and thus must follow similar general patterns of development dictated by their genes. The morphological differences held between “normal” and “proleptic free growth” seedlings could thus be due to physical constraints, with those seedlings having “proleptic free growth” being less physically constrained by the environment. This flexibility allows them to take advantage of the conditions which permit for the re-

flushing of their buds which were formed earlier in the growing season. The ability to perform such a function allows these seedlings to occupy more of the potential growth states (forms) normally unattainable due to the presence of these constraints. It can perhaps be assumed then that all seedlings have the potential for proleptic free growth, but are unable to take advantage of this due to environmental constraints and seedling microsite differences. The nature of these differences will be further discussed in the following chapter.

This suggests that at one point during the course of growth in "proleptic free growth" seedlings, more information was translated and subsequently expressed as these additional plant parts, and thus contributed to the more detailed patterns of integration and morphological complexity possessed by these seedlings.

The results shown by the Least Squares Means indicate that regardless of the factor addressed (site, species or the interaction between the two), each plant part used as a dependent variable responds differently, in a manner which obscures the determination of site preference and overall species performance. By demonstrating such varied responses, each part of the seedling seems to be differentially influenced by the site conditions as well as by its own genetic make-up.

That site effects increase in 1996 from 1995 is not very surprising, owing to the fact that the seedlings had had over one year to adjust to their new environments by 1996. Any differences seen between seedlings both within and between each site would be more pronounced one year after planting compared to a few months after planting, as was the case in 1995. No site in particular generated consistent plant responses however. Using "normal" seedlings of 1996 as an example, it was demonstrated that the height

increment of these seedlings, regardless of species, grew better in the clearing, but lateral branch #2 grew best in the shelterwood. Varied responses such as these suggest that no one site contains all the qualities considered “ideal” by every part of the seedling. While certain environmental factors in the clearing (for example) may promote the best growth of one particular plant part, it may be a hindrance to another part, which as a result, demonstrates less than superior growth in this same site. Perhaps each site promotes the differential allocation of resources to select plant parts, depending on which environmental factors are present or absent.

Species effects vary as well. Using “normal” seedlings of 1996 again as an example, it was shown that grand fir seedlings grew better with respect to diameter, while Douglas fir grew better with respect to lateral branch #1. These differences suggest that no one species demonstrates consistent, superior growth over the other. While these differences in growth could be attributed to site, neither of these components produced a significant site term.

The significant species by site interaction terms indicate that the effect of site is not the same for the two species involved (Bernier-Cardou and Genest 1992). Here again, no specific species/site combination affects any seedling grouping consistently. When similar responses are shown (for example, both lateral branch #2 and diameter increment show a significant site by species interaction term in “normal” and “proleptic free growth” seedlings), the actual species/site combination producing the response differs. “Normal” seedlings of grand fir in the shelterwood produce the longest #2 lateral branches, while this same plant part grows longest in Douglas fir seedlings with proleptic free growth planted in the clearing. Similarly for the diameter increment, “normal”

grand fir seedlings in the clearing produce the most stem growth, while Douglas fir seedlings with proleptic free growth in the shelterwood grow more in basal stem diameter.

The analyses involving η^2 values indicate which variables are the best descriptors of the plant i.e. which parts influence the overall form of the plant, and which parts have the greatest influence on other plant parts being examined. Different responses are again demonstrated between years. That the amount of variation left unaccounted for declines for the most part as seedlings progress from 1995 to 1996 indicates that more of the component parts of the plant are accounting for more of the variation. This can be due in part to the fact that more plant parts are being added to the seedling each year, and these help account for more of the overall variation.

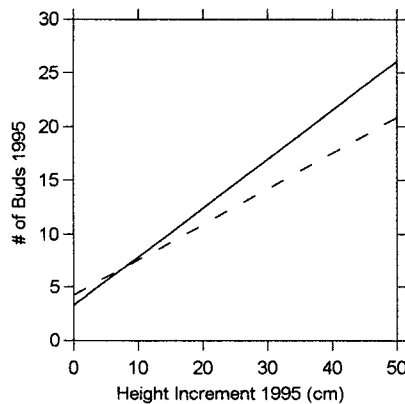
Many of the relationships held between the best descriptors of a particular plant part and the part itself tend to be of a spatial nature, and are consistent with the variable groupings generated by PCA already discussed. Using height increment as an example, this component is best described in both 1995 and 1996 by a subtending lateral branch of the apical whorl and the number of buds produced upon the height increment itself. Both of these parts are in the closest proximity to the height increment compared to the other plant parts available as descriptors. These components are found at the tip of the tree and are ultimately controlled by the apical meristem. The overall architecture of a tree results from the activity of primary meristems, of which the apical meristem is included (Hallé *et al.* 1978). The current height increment, its subtending laterals and the buds produced along the height increment were all formed by the apical meristem (Foster 1938;

Romberger 1963; Esau 1977) and these features are essentially all that is necessary to form a tree, as they are repeated over and over again as the tree grows (see Figure 1).

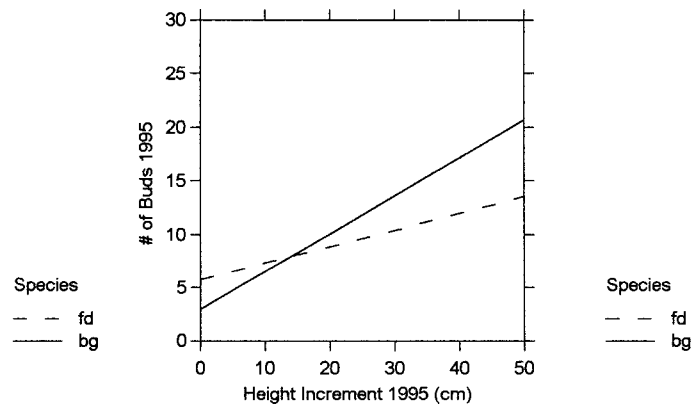
A similar relationship is also demonstrated when the number of buds is the dependent variable being examined. Here, the height increment is found to be the best descriptor. This makes practical sense, as the buds lie directly upon the height increment, and more than likely their numbers are determined by the length of the height increment itself. Figure 19 illustrates this point. Shorter height increments do not allow for large numbers of buds to be produced, perhaps due to a lack of space, while the reverse relationship is demonstrated with longer height increments.

Results similar to these were reported by Cannell (1974), Cannell *et al.* (1976) and Cannell and Bowler (1978), on various species of *Picea*. This relationship seems to be of more relevance than the previous (that bud number determines the length of the height increment), as lateral buds are formed on the juvenile stem when it is still enclosed within the terminal bud (Romberger 1963). Powell (1974); Cannell and Bowler (1978) and J. N. Owens (pers. comm., cited in Worrall 1984) added that these buds are formed just prior to the flushing of the terminal bud, usually around mid-April, early-May. Because the shoot itself needs to be produced prior to the placement of lateral buds upon it, this would argue for the idea that the length of the shoot determines the number of buds that are able to be placed upon it, rather than the reverse. The more stem units produced within the terminal bud, the more space available along the shoot itself for the placement of lateral buds. The reason, perhaps, for the large amount of variation accounted for by the number of buds when the height increment is the variable of interest, is because the buds themselves are physically attached to this part of the stem.

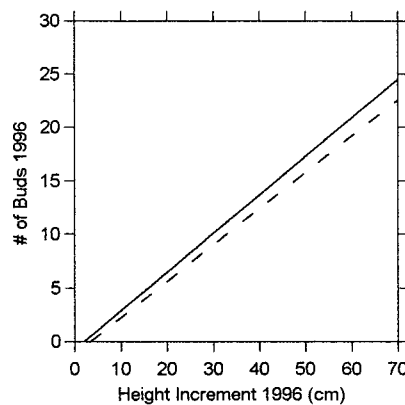
(a) Shelterwood, 1995



(b) Clearing, 1995



(c) Shelterwood, 1996



(d) Clearing, 1996

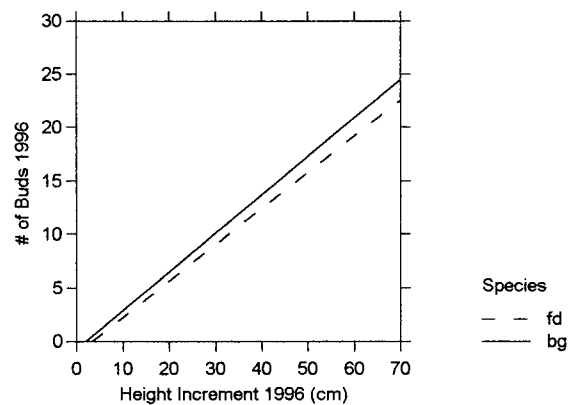


Figure 19. Relationship between length of the current height increment and the number of lateral buds produced. “fd” = Douglas fir, “bg” = grand fir.

A similar spatial argument can be made for the lateral branches (#1 in 1995 and #2 in 1996) as well. In both years (and all seedling types in 1996), the height increment was found to be the best descriptor of these features, it too being the component in the closest vicinity to the lateral branches in question. Baxter and Cannell (1978) discovered that both the height increment and subtending laterals grew more in relation to lower order branches, presumably because these upper branches were supplied with more nutrients.

That the stem diameter was best described in 1995 by the height of the seedling at planting suggests that this may be a nursery carry-over effect. The optimal growing conditions received by the seedlings in the nursery had subsequently been carried over into the field after planting. As nurseries generally select seedlings which are suitable for planting on the basis of total height and stem diameter (Rose *et al.* 1990), this lends an explanation to this relationship not being repeated in the following measurement year.

The above argument is reinforced by the lack of adequate descriptors for the diameter increment in 1996. This plant part also demonstrates an increase in the overall amount of variation left unaccounted for in 1996. It would seem that the measurement of the basal diameter does not adequately summarize the functional morphology of the stem, at least in terms of how it is linked to the rest of the plant. Providing this trend of increasing variation continues through the years as the seedling ages, and is not just a random yearly fluctuation, a more detailed look at both the internal and external features of the stem would perhaps uncover which morphological or anatomical features best describe this system. These conclusions are also supported by the variable groupings found through the PCAs mentioned above. That this variable consistently formed a distinct group separate from the other variables in 1996 reinforces the idea that it is a unique characteristic which requires more input in order to adequately describe it and its relationship to the other plant parts, as well as to the plant as a whole.

Lateral branch #1, another plant part which had no convincing descriptors in 1996, does not demonstrate an increase in the overall amount of variation left unaccounted for in 1996. Instead, more of the plant parts account for slightly more variation, even though no part in particular best describes this characteristic. This part

“lost” its spatial relationship with the current height increment when new growth began in the spring and has now become a less pronounced feature of the plant as a whole.

In general, both the diameter increment and lateral branch #1 in 1996 may be better described by plant parts not included in the current analyses, or else they simply cannot be described by any single plant part.

Chapter 3.

Seedling Growth in Relation to the Environment

Introduction

Trees, like any other plant, are influenced by their environment during all stages of their growth and development. While there is no single environmental variable which promotes growth, three of the more widely studied variables are light, temperature and water. Appropriate levels of these variables are necessary in the maintenance of daily functioning in plants. Light, both in terms of the quantity and quality received by a plant evokes a number of different growth responses. Light intensity (quantity) drives the most obvious physiological function of plants; photosynthesis (Tinus and McDonald 1979; Lavender 1984; Salisbury and Ross 1992 for example), and can also influence the general development and morphology of leaves (Tucker and Emmingham 1977; Tucker *et al.* 1987; Klinka *et al.* 1992; Mitchell and Arnott 1995; Chen *et al.* 1995). Light quality promotes such growth responses as stem elongation, lateral branching, shoot and leaf orientation, leaf pigmentation (Moe and Heins 1990; Salisbury and Ross 1992) and seed germination (Salisbury and Ross 1992). The length of the photoperiod is also important in the promotion of bud set and dormancy, when days become shorter (Downs and Hellmers 1975; Tinus and McDonald 1979; Lavender 1984; Kozlowski *et al.* 1991; MacDonald and Owens 1993a, 1993b) as well as signaling the coming of the growing season, when days become longer again (Kozlowski *et al.* 1991).

Several of the growth responses labeled as being light induced have been found to be temperature induced as well, irrespective of the light environment. These include stem elongation (Downs and Hellmers 1975; Ford 1980; Moe and Heins 1990; Kozlowski *et al.* 1991; Salisbury and Ross 1992), lateral branching (Moe and Heins 1990), seed germination and photosynthesis (Salisbury and Ross 1992). Bud break, flower formation (Kozlowski *et al.* 1991; Salisbury and Ross 1992) and bud set (Downs and Hellmers 1975; Kozlowski *et al.* 1991; MacDonald and Owens 1993b), as well as the physiological processes of diffusion, transpiration, and virtually any physical and biochemical process which make up the plant's physiology (Downs and Hellmers 1975; Tinus and McDonald 1979; Lavender 1984) also respond to temperature.

Water is the environmental variable which has the capability of affecting nearly every plant process (Downs and Hellmers 1975). Water helps plant growth through the maintenance of turgor pressure (Downs and Hellmers 1975; Kozlowski *et al.* 1991), acts as a solvent for the multitude of biochemical reactions which take place within plants, and acts as a solvent for gases and nutrients (Downs and Hellmers 1975). It also plays a role in the initiation of dormancy (Lavender 1984).

These same variables, and others, are also responsible for the production of more unique growth responses not demonstrated in all plants. Proleptic free growth, for example has been largely attributed to growing season environmental conditions (Walters and Soos 1961; Rudolph 1964; Carter and Klinka 1986; Roth and Newton 1996). The most common environmental variables thought to promote the occurrence of this characteristic are soil moisture (Rudolph 1964; Walters and Soos 1961; Carter and Klinka 1986; Roth and Newton 1996), nitrogen availability (Carter and Klinka 1986; Roth and

Newton 1996), and various forms of stem damage sustained during the growing season (Rudolph 1964; Walters and Soos 1961; Carter and Klinka 1986; Roth and Newton 1996). An increase in soil moisture later in the growing season following, in particular, an earlier period of summer drought is a scenario commonly associated with an increase in the presence of proleptic free growth (Walters and Soos 1961; Rudolph 1964; Carter and Klinka 1986). This concurs with the finding that droughty conditions promote the formation of bud scales which serve to offset the desiccation of the apical meristem (MacDonald and Owens 1993a). A subsequent increase in soil moisture (providing all other environmental variables are still conducive for growth) may be enough to stimulate the apical meristem to initiate activity, thus prompting the resumption of growth.

Heredity most certainly contributes to proleptic free growth as well, but research to date shows mixed results, with either a strong genetic influence being argued for (Rudolph 1964 and references cited therein; Carter and Klinka 1986) or one that is negligible (Walters and Soos 1961; Roth and Newton 1996).

From these brief descriptions, it is apparent that similar growth responses can be stimulated by different factors. Stem elongation, for example, can be promoted by light quality, temperature or water supply. This level of interaction between environmental variables makes the study of the causes of plant growth very difficult, especially in the field, owing to the intercorrelated nature of separate factors.

The continuous improvement of growth chambers after World War II (Kramer 1978), promoted more studies of plant responses to environmental variables in a controlled environment. This helped minimize the complexity which exists in a natural setting, by decreasing the number of interactions which may affect the response of the

plant (Helms 1976). The standard procedure was to manipulate one or several environmental variables at a time, while keeping the remainder at constant levels, so they would not confound the results (Sweet and Wareing 1966; Kramer 1978; Tinus and McDonald 1979).

Physiological research conducted in the field has been approached in several ways. One is through the use of equipment which monitors processes such as photosynthesis and transpiration in an effort to determine which environmental conditions produce the "best" result (Helms 1965; Hodges 1967; Hodges and Scott 1968; Leverenz 1981; Norman *et al.* 1974; Harrington *et al.* 1994). Another commonly used format studies the ecology and overall growth of the plants under a naturally occurring gradient of the environmental variable being addressed (Aztet and Waring 1970; Emmingham and Waring 1973; Carter and Klinka 1992; Klinka *et al.* 1992; Wang *et al.* 1994; Mitchell and Arnott 1995). These studies are effective in determining the varying growth responses of plants when encountering different levels of a given variable. Studies such as those by Aztet and Waring (1970), Carter and Klinka (1992), Klinka *et al.* (1992) and Wang *et al.* (1994) while specifically addressing the effects of varying light levels on conifer growth responses also considered other environmental variables, such as soil moisture or temperature, through the comparison of different sites. The outcome of such studies, while they may be more difficult to interpret and control, allow for the derivation of a more balanced picture of the complex system within which plants operate.

Another method of studying the effects of the environment on plant growth responses is through the monitoring of the surrounding climate. Large-scale or macroclimate (atmospheric conditions at a scale ranging between 10 - 1000 kilometers

(Spittlehouse and Stathers, 1990)) data can be obtained from weather stations installed throughout the province, (for example), for the purpose of monitoring the surrounding areas for weather trends. The use of large-scale climate data to describe the conditions occurring at a particular site relies more on extrapolation, but still allows for a qualitative view of the growing environment to be formed, as the smaller-scale, on-site climate conditions are governed by macroclimatic events (Spittlehouse and Stathers, 1990). Finer-scale climate conditions, such as those occurring at a particular site, can be monitored using dataloggers and instruments set up directly in the site of interest. This data allows for a more accurate description of the site, as well as the growing conditions at the level of the plants. Both large-scale weather stations and small, on-site weather stations have been used successfully in a number of studies (for example, Holbo *et al.* 1985; Holbo and Childs 1987; Childs and Flint 1987; Spittlehouse and Stathers 1990; Stathers and Spittlehouse 1990; Chen *et al.* 1995; Scagel *et al.* 1997).

The study conducted here was an observational one, and attempted to determine the relationships existing between specific environmental variables and conifer growth. The main objectives were to compare the responses of measured characteristics of conifer seedlings to (i) specific environmental variables alone, and (ii) combinations of two environmental variables at a time (combining more than two variables was not feasible due to the insufficient number of samples which resulted). Environmental data were gathered throughout the growing seasons of 1995 and 1996, and morphological data were gathered after the growing seasons of each year had ended.

Variation in growth responses were examined both within and between: (i) the measurement years; (ii) the two conifer seedling species; (iii) the different environmental

conditions monitored within two different sites, (a clearing and a shelterwood); and (iv) the two morphological types of seedling present in both species, (those with a “normal” growth morphology and those with proleptic free growth).

Materials and Methods

Climate of the Squamish area

Thirty-seven years of climate data for the Squamish area were obtained from an Atmosphere and Environment Services Canada weather station located at the Squamish Airport approximately ten kilometers away from the sites. Both longterm normal trends as well as yearly trends for 1995 and 1996 were obtained for temperature and precipitation. No data on solar radiation or vapor pressure deficit (or relative humidity) were available from this weather station.

Longterm normal minimum, mean, and maximum temperatures are given in Figure 20. Mean daily temperatures remain just above freezing for the entire winter, falling slightly below this point in late-December. Mean temperatures reach their highest (18.5°C) in late-July, early-August, after a steady and gradual increase in temperature is seen throughout the winter, spring and summer months. A more rapid decline in temperature from this high point begins in mid-September.

The lowest average minimum temperatures occur in late-December, reaching approximately -2.5°C while the highest average maximums reach 24.7°C during late-July and early-August. Overall, these temperatures produce mild growing conditions during the spring and summer months, and colder winters.

Late-spring frosts, which can occur in early-May, tend to coincide with the same general time as bud burst, posing a potentially damaging threat to the newly flushing tissues. The earliest fall frosts can occur during the first week in October, which allow for the extension of the growing season well into this time and provide a frost-free growing period of approximately five months.

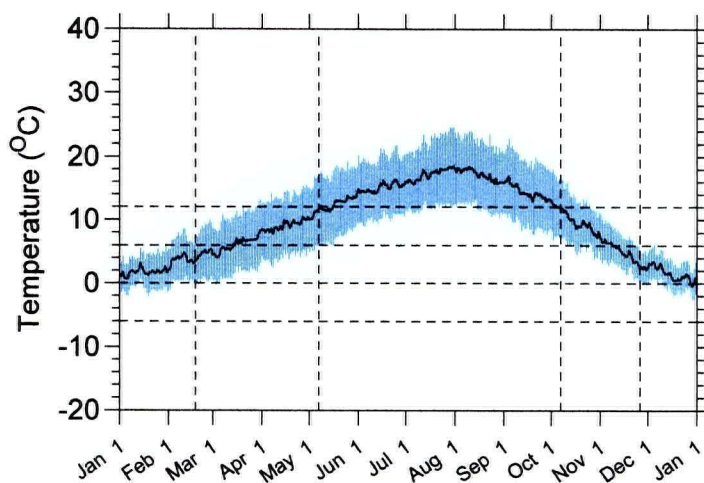
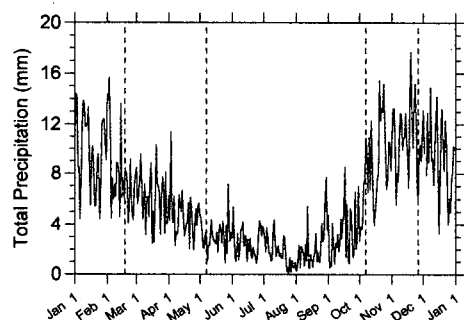


Figure 20. Average daily minimum, mean and maximum temperatures for Squamish Airport, generated from 1959 - 1996. Minimum temperatures are denoted by the lower portion of the curve, maximum temperatures by the upper portion. Mean temperatures are demonstrated by the black curve. Dashed vertical lines represent early and late spring and fall frost events.

Total precipitation (Figure 21a) is highest during the late-fall and winter. A gradual decline in precipitation events is seen as the growing season progresses, with the lowest levels of rain being received in late-July and early-August.

The average amount of precipitation falls gradually over the course of a year and reaches a yearly total of 2072mm (Figure 21b). The rate of precipitation is highest in the fall and winter months (Figure 21b).

(a) Total Precipitation



(b) Cumulative Precipitation

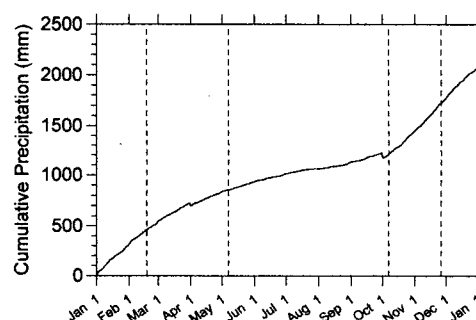


Figure 21. Total and cumulative precipitation from 1959 - 1996 from Squamish Airport. Dashed vertical lines represent early and late spring and fall frost events.

The patterns of minimum, mean and maximum temperatures for 1995 and 1996 differ (Figure 22). Both years rose above 0°C for the first time around early-March and gradually increased in temperature as the seasons progressed. The highest overall mean temperature recorded was 24°C for both years, but the month in which it was achieved differed substantially (mid-July in 1995 compared to late-August in 1996). As the temperatures declined towards freezing in the fall, a difference was again seen in the time at which 0°C was reached (early-December in 1995 compared to mid-November in 1996).

Average minimum temperatures were lowest between early-December and mid-February in 1995, reaching -7.7°C . 1996 was much colder around this same time, reaching a low of -12.2°C .

Average maximum temperatures reached a high of 34°C in July of both years. The summer months of 1995 demonstrated a longer period of warm temperatures compared to 1996, which tended to peak later in the season, more sharply, and for a

shorter length of time. Temperatures dropped in August of 1995, but recovered slightly in late-September before declining once more along with the seasonal change. A similar drop in temperature was seen in August of 1996, but this was much less pronounced, and of a shorter duration than that seen in 1995.

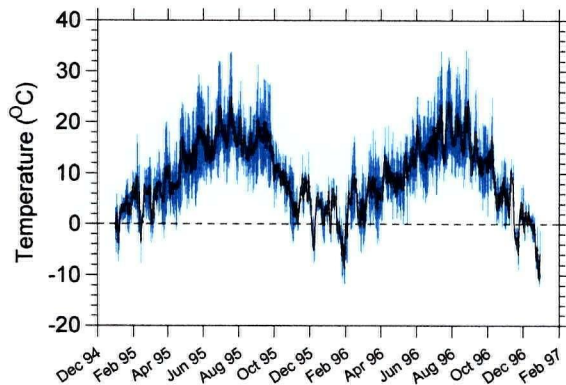


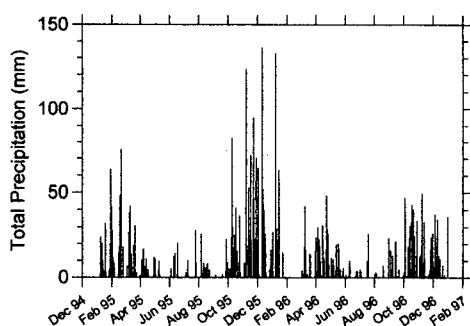
Figure 22. Mean daily minimum, maximum and mean air temperatures for 1995 and 1996 from Squamish Airport. Minimum temperatures are denoted by the lower portion of the curve, maximum temperatures by the upper portion. Mean temperatures are demonstrated by the black curve.

Mean total and cumulative precipitation are given in Figure 23 (a and b).

Precipitation occurred consistently throughout the two years, with occasional periods of dry weather. Maximum precipitation occurred during the winter months, the most notable events taking place in October, 1995 and lasting well into late-January, 1996. The months of the growing season received periodic inputs of rain. The early months of the season (April - June) received more rain in 1996 than 1995. The gap in precipitation events for February, 1996, is due to the lack of data retrieved from the climate station at the Squamish Airport.

1995 had a much higher accumulation of precipitation by the end of the year than 1996, reaching a total of 2813mm. 1996 had 744mm less rain, reaching a total of only 2069mm (minus the rainfall data from February). Rain fell steadily until late-April in 1995, after which it began to taper off during the summer months. This same pattern was seen in 1996, but the duration of the period of rainfall lasted a full month longer, showing signs of tapering off in late-May. During the summer months, rain was infrequent, and only a slight and gradual accumulation was seen. Rain began to fall more consistently by October for both 1995 and 1996, and a steady, rapid rate of accumulation was maintained until the end of the year. This trend is more pronounced in 1995.

(a) Total Precipitation



(b) Cumulative Precipitation

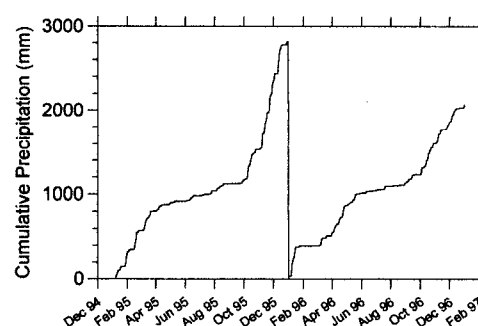


Figure 23. Mean total and cumulative precipitation for 1995 and 1996 from Squamish Airport.

Both 1995 and 1996 differ from the longterm normal trends. Both years have displayed a wider range of temperatures, in all of the attributes considered (means, minima and maxima). 1995 and 1996 were both approximately 6°C warmer on average during the growing season compared to the longterm trends. This range widened to 10°C when average maximum temperatures were addressed. Winters in both years were also

comparatively much colder. The greatest example of this is shown in 1996, when a difference of 10°C separated this year from the longterm trends.

Precipitation trends demonstrated in 1995 deviated from those of 1996 and the longterm normals. A higher amount of precipitation fell during this year, with approximately 741mm more rain falling altogether. As well, the month of September was considerably drier than both the longterm normals and 1996.

1996 differed from 1995 and the longterm normals in the duration of the winter-spring rainy period, which lasted approximately one month longer than what is normally expected. Also, the month of August received approximately half the usual amount of precipitation seen in this area, with levels approaching what is normally expected in September.

On-site climatic measurements

Several smaller-scale environmental variables were monitored during the growing seasons of both 1995 and 1996 in both the clearing and shelterwood sites. The intensity of the survey was of an exploratory nature and was not designed to provide a full description of the microclimate surrounding each planted seedling. It served merely to quantify the environmental variables seen as being the most relevant to the growth of the seedlings, so that comparisons of environmental conditions experienced by each of the seedlings could be made in terms of the overall growth expressed.

In 1995, two environmental variables, total solar radiation and air temperature, were measured. These same variables were measured again in 1996 along with two additional variables, PAR (photosynthetically active radiation) and soil moisture. All

environmental measurements, with the exception of soil moisture, were conducted on clear-sky days in an effort to lower the variation attributable to passing clouds. Soil samples were gathered only on days when it was not raining, and a minimum of two days after a period of rain, to avoid the potential of obtaining biased samples due to a recent rainfall.

Total solar radiation and air temperature data were gathered in the clearing in 1995 using a solar panel and thermocouple connected to a Campbell CR21X datalogger (Campbell Scientific Co., Logan, Utah). Both the solar panel and thermocouple were elevated to a height similar to that of a seedling, with the panel in particular placed on a flat, horizontal surface free from any shadows. The same procedure was repeated in 1996. PAR readings, taken in the clearing in 1996, were made using a LI-COR LI-190SA quantum sensor (LI-COR Inc., Lincoln, Nebr.) connected to the datalogger and elevated to "seedling height" as well. It too was kept horizontal. Figure 24 illustrates the setup of the datalogger in the clearing. Data were gathered at 30 second intervals and averaged over 2 minutes by the datalogger. The time at which the readings were taken was also recorded.

Total solar radiation readings measured in the shelterwood site in both 1995 and 1996 were collected using an identical solar panel to that used in the clearing, connected to a hand held voltmeter. The panel was held in a horizontal position directly above the seedling (approximately 1m above the ground, depending on seedling height) and always faced in a southerly direction.



Figure 24. Photo of datalogger setup.

This was to avoid shading any part of the panel and to ensure that the placement of the panel was consistent and repeatable between trees and sampling times. The amount of PAR recorded in the shelterwood in 1996 was measured using another LI-COR LI-190SA quantum sensor (LI-COR Inc., Lincoln, Nebr.) connected to a voltmeter. The placement of the sensor was identical to that of the solar panel, and readings were taken at the same time as those of total solar radiation.

Air temperature readings from the shelterwood were taken simultaneously with the other measurements in both 1995 and 1996. A hand held thermocouple was used in

1995 and was connected to an ohmmeter. Its placement was identical to that of the other instruments used for the solar radiation measurements. In 1996, a thermometer replaced the thermocouple, but its placement with respect to the seedlings remained the same as in 1995. As each reading was taken in the shelterwood for all the environmental variables involved, the time of day was recorded so that a corresponding reading could be obtained from the datalogger in the clearing and a site comparison could thus be achieved.

All of the environmental data were collected between the hours of 10:00am and 2:00pm in an effort to minimize the effects of a changing solar angle. All measurements were taken periodically throughout the growing seasons of 1995 and 1996. Solar radiation in 1995 and 1996 and PAR in 1996 was expressed as a percentage of full sunlight (or full PAR), with the values obtained in the clearing representing full sunlight (or full PAR).

Soil samples to determine moisture content were taken from both the humus and mineral fractions throughout the 1996 growing season. Samples of mineral soil and humus were placed in separate 4oz tins, weighed, dried in an oven for approximately two to three days at a temperature of 75°C, and then reweighed.

Percent water by weight of soil was then determined for each sample using the equation from McKeague (1978):

$$\% \text{water} / \text{dry wt of soil} = (100 * ((\text{wet weight} / \text{dry weight}) - 1))$$

Sampling was conducted at approximately every third tree in the shelterwood and every fifth tree in the clearing, a sampling scheme determined primarily by the amount of tins available. The wider spacing of samples taken in the clearing was also due to the closer proximity of each seedling to one another and the smaller overall area of this site in particular. These sampling arrangements allowed for a general characterization of soil moisture status within each site to be achieved, as well as permitted a between site comparison of growth in relation to soil moisture for select seedlings to be made.

Statistical analyses

The goal behind the collection of the on-site climate data was to quantify the effects of the surrounding environment on seedling growth. Initially, environmental effects were to be determined using ANCOVA models similar to those employed in the analysis of morphological traits, with the environmental variables being added as covariates. However, problems in the acquisition of data and non-normal sampling distributions made it necessary to resort to non-parametric tests.

The data collected represented different sampling days and it was to be expected that the raw values taken on each day differed. It was thus necessary to standardize each sampling day on a scale ranging between 0 - 1, so that each value could be directly

compared on the same scale. By standardizing the data, the differences between the raw values obtained on the different sampling days were eliminated, but the ranking of the values relative to each other were maintained. To illustrate more clearly, say for example on two separate sampling days, the maximum temperatures recorded were 18°C and 15°C respectively. By standardizing in the way described above, these two different values would both receive a value of 1.0 on the scale ranging between 0 and 1. While their raw values differed, their standardized ones are identical and can thus be directly compared.

Means and standard deviations were then calculated across all sampling days for each standardized environmental variable, thus forming summary variables which were deemed representative of the average climatic conditions experienced by the seedlings at each site. The standard deviations of these environmental variables were graphed as probability plots to determine whether or not they were normally distributed, in order to determine their suitability for parametric analyses. All proved to be positively skewed and thus required transforming. Both a square root and log transformation (performed separately) could not correct the skewed distribution, thus indicating that a parametric analysis may be unsuitable.

As an alternative to using parametric methods on the environmental data, notched boxplots were employed instead to examine the variation in seedling growth response within and between sites. The notches represent 95% confidence intervals and thus allow for more breadth in interpreting the graphs, as statistical significance at the 0.05 level can be attached to those boxplots whose notches do not overlap. The determination of

overlap was very conservative, and only those boxplots whose notches clearly did not overlap were deemed significantly different from each other.

To simplify the use of the boxplots, the standardized environmental variables were re-expressed as categorical variables representing “low”, “medium” and “high” levels of light, PAR, temperature and soil moisture. The cutpoints used to create these groups were the lower and upper hinges of each environmental variable found using stem-and-leaf plots. All values found to be less than that of the lower hinge were classified as “low”. All values found between the lower and upper hinges were classified as “medium”, and all values larger than the upper hinge value were classified as “high”. This procedure was carried out for all of the environmental variables of the clearing and shelterwood separately.

To compare the effects “low”, “medium” and “high” levels of each environmental variable had on seedling growth, each morphological variable was used as the Y-variable of a notched boxplot and was thus graphed against the categorical environmental variables for each site. The morphological variables used in 1995 included the length of the 1995 height increment (HI95), basal diameter (D95), length of the first subtending lateral branch formed in 1995 (L195) and the number of buds formed on the 1995 height increment (B95). The only environmental variables available for analysis in this year were total solar radiation and air temperature.

For 1996, the variables included the height increment for 1996 (HI96), the diameter increment for 1996 (DI96), the length of growth formed in 1996 on lateral branch #1 (L196), the length of subtending lateral branch #2, newly formed in 1996 (L296) and the number of buds formed on the 1996 height increment (B96). The

environmental variables analyzed included total solar radiation for the shelterwood only, air temperature, PAR and both humus and mineral soil water content. All boxplots deemed significantly different from one another had a minimum sample size of 7.

To assess the more interconnected nature of the environmental variables considered, combinations of each environmental variable were formed and graphed as un-notched boxplots using the same morphological variables as previous. Un-notched boxplots were used here as opposed to the notched boxplots used previously due to the small sample sizes which resulted from the combining of the environmental variables. Too small a sample size renders the interpretation if a notched boxplot suspect. The intention of this analysis is thus more qualitative and simply to demonstrate the trends visible between each environmental combination. The new environmental variable classifications combined light and temperature measured in 1995, PAR and temperature measured in 1996 (the sunlight data was incomplete to do so) and humus and mineral soil water content. Three-way combinations, as well as addressing these patterns in terms of “normal” and “free growth” seedlings were not attempted as there were not enough samples to perform this exercise in a practical manner. Again, all boxplot results reported have a minimum sample size of 7.

While the collection of the on-site climate data took place approximately once a month during both the 1995 and 1996 growing seasons, the amount of useable data collected was less than expected, especially in the clearing. The main causal factors were attributable to equipment failure involving either the datalogger or the solar panel. The datalogger overheated on several occasions thus erasing the stored data, while the solar panel contained an electrical short. Due to these problems, only two days worth of

data were recorded successfully for the clearing, one in September and another in November. In 1996, these equipment failures repeated themselves once more, regardless of the precautions taken to control them. Thus, only a few days worth of data were again retrieved, again in September.

The environmental data gathered should still adequately describe the growth trends which occurred during the growing season. While collected after the growing season had ended, the raw values themselves are simply lower than those which occurred during this time. The environments surrounding each planted seedling at each site should hold the same relative relationships between each other regardless of the time of year. Because it was the relationship between seedling environments which was being sought, and not so much the actual values recorded within each environment, these relationships should be reflected in the data collected, regardless of the time at which it was gathered.

Other studies which used similar sampling techniques to those employed here also gathered environmental data well into September and October as well (Klinka *et al.* 1992 and Carter and Klinka 1992, respectively).

All statistical analyses were carried out using SYSTAT 6.0 for Windows (Wilkinson 1996).

Results

On-site climate

Trends of both total solar radiation in 1995 and PAR in 1996 are demonstrated in Figure 25. The plateaus in these graphs represent gaps in the sampling times, dictated by the time taken to measure the variables at each seedling in the shelterwood.

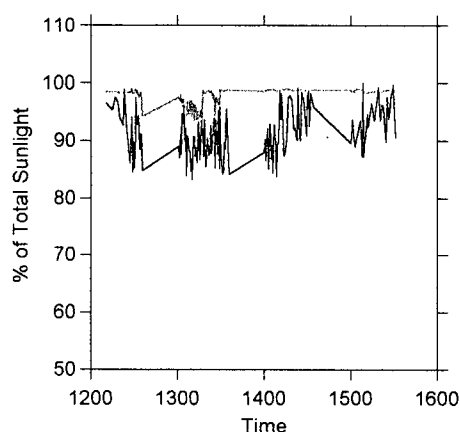
Overall, the light levels of the shelterwood site measured along the survival line for 1995, as expressed as a percent of full sunlight ranged between 83 and 100%. In 1996, the light levels along the survival line were exactly alike, ranging between 83 and 100%. That these ranges are identical illustrates the repeatability of the panel placement, as well as the more restricted range over which total solar radiation is integrated along the panel. This indicates that the range of data values obtained is more narrow, thus increasing the probability of achieving a closer approximation of the data recorded previously.

The light levels recorded within the shelterwood with the quantum sensor were noticeably lower than those recorded with the solar panel. Again, as expressed as a percentage of full sunlight (or full PAR in this case), the PAR levels ranged between 53 - 100%. This demonstrates the wider range, and higher sensitivity of the PAR sensor compared to the solar panel.

The larger amount of fluctuation seen in the shelterwood compared to the clearing reflects the effect of the residual canopy which creates a more variable environment.

Air temperature trends for both the clearing and shelterwood sites for 1995 and 1996 are shown in Figure 26; the plateaus in these graphs are gaps between sampling times. The shelterwood demonstrates a lower overall temperature, but more variation, owing to the larger area and more varied conditions created by the overstory.

(a) Total Sunlight 1995



(b) PAR 1996

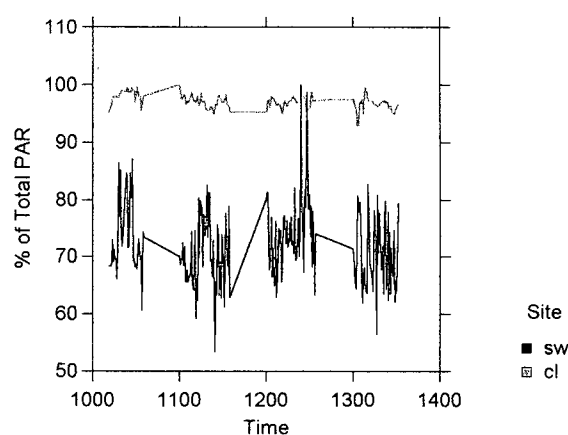
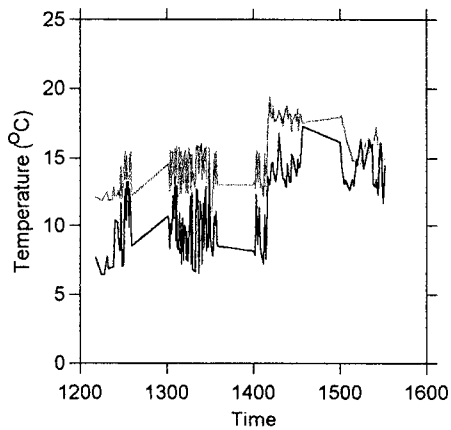


Figure 25. Percent of total sunlight and percent of total PAR readings for 1995 and 1996 respectively. Measurements at both sites were recorded on a clear-sky day in the fall for both years. “sw” = shelterwood, “cl” = clearing.

Temperatures in 1995 range between 6.4°C and 18.8°C in the shelterwood and between 10.8°C and 19.4°C in the clearing (Figure 26a), while in 1996 it ranged between 5°C and 11.7°C in the shelterwood and between 8.6°C and 13.9°C in the clearing (Figure 26b). All of these ranges fall within the ranges found in the fall months of data graphed for these same years from the Squamish Airport (Figure 22). In 1995, between the months of September and November, the average temperature dropped to as low as 0.5°C and reached as high as 20.5°C. Similar trends are seen in 1996, where average temperatures from Squamish Airport for these same months were as low as -5.9°C and as high as 18.2°C (Figure 22).

(a) Air Temperature, 1995



(b) Air Temperature, 1996

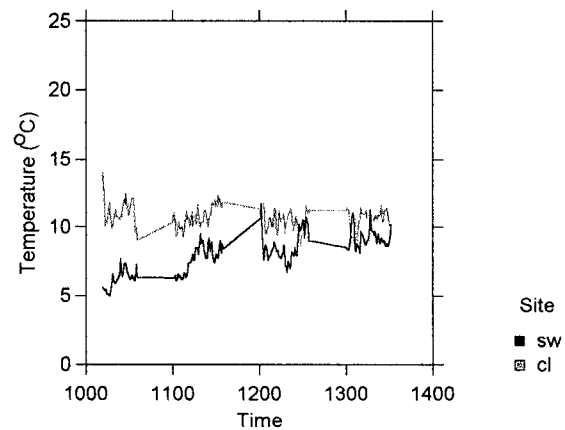
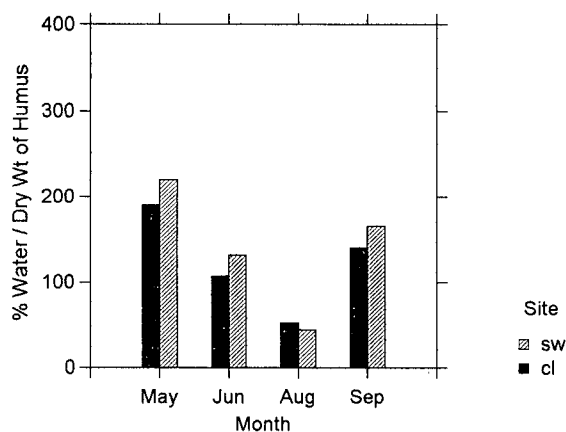


Figure 26. Air temperature trends for the shelterwood and clearing sites in 1995 and 1996, measured on a clear-sky day in the fall of both years. “sw = shelterwood, “cl = clearing.

Plots of the water content of humus and mineral soil fractions throughout the growing season are given in Figure 27. A general decline in water content is demonstrated as the growing season progresses, with the lowest point being reached in August. Water content begins to increase again in September. These trends are much more obvious in the humus fractions, where direct contact with the surrounding air and the properties of this soil fraction cause these stronger fluctuations. A larger percentage of water is contained within the humus layers compared to those of the mineral soil, and in the shelterwood site compared to the clearing.

(a) Humus Fraction Water Content



(b) Mineral Fraction Water Content

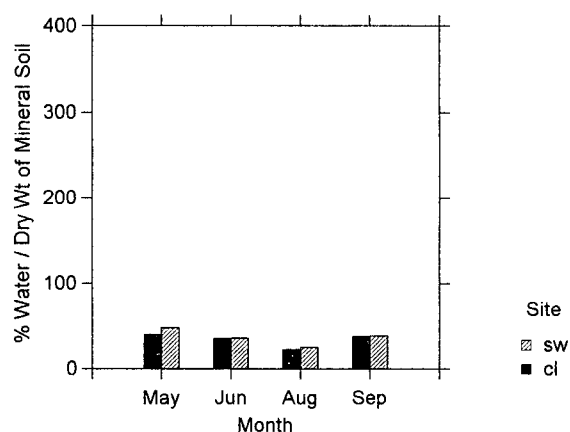


Figure 27. Humus and mineral soil water content for both the shelterwood and clearing sites in 1996. "sw" = shelterwood, "cl" = clearing.

Several random walks within the shelterwood site were carried out during the growing season, using a Sunfleck Ceptometer (model SF-80, Decagon Devices Inc., Pullman, Wash.) integrating radiometer. These were performed prior to the acquisition of the LI-COR PAR sensors mentioned earlier, and served merely to further qualify the light environment of the shelterwood. From these random walks, under clear sky conditions, it was found that the amount of PAR approximately 1m off the ground ranged from $98 - 1668 \mu\text{molm}^{-2}\text{s}^{-1}$ (between 10 - 100% full sunlight), averaging approximately $685 \mu\text{molm}^{-2}\text{s}^{-1}$ (41% full sunlight). These levels vary substantially from those obtained from both the solar panel and LI-COR quantum sensor, and illustrates the seemingly wider sensitivity of this sensor to the others used. This difference can also be attributed to the fact that the random walk was not along the survival lines, all of which seem to fall within more open areas and alongside the yarding corridors. The random walk method

reveals the spatial heterogeneity of the shelterwood site more effectively than the measurements gathered along the survival lines.

Relationships between the environment and seedling morphology

The relationships between the morphology of measured plant characteristics and their surroundings are of a correlative nature. As no experimental manipulation was carried out on any of the environmental variables, no causal relationships linking specific microclimates with growth were established. The correlations shown, however, have the potential of reflecting possible causal mechanisms behind the growth which did result. In both 1995 and 1996, the growth of grand fir seedlings was most positively correlated with the environmental conditions of the shelterwood site, while the growth of Douglas fir seedlings was more strongly correlated with conditions found within the clearing (Table 8 to Table 11).

In 1995, virtually every measured part of the grand fir seedlings showed a positive correlation between the growth produced and the environmental variables measured in the shelterwood (Table 8). Exceptions to these trends are seen in basal stem diameter (D), which were larger in high temperature environments in the clearing compared to medium temperature environments in the shelterwood and low temperature environments in the clearing. A significant correlation which differed from the norm was also seen in the light levels of the clearing, in which larger stem diameters (D) were found within low light levels at this site compared to high levels.

The only significant difference between the levels of environmental variables and growth of Douglas fir seedlings was by the basal stem diameter (D). This part was

largest in low temperatures in the clearing compared to medium temperatures in the shelterwood (Table 8).

Table 8. Summary of boxplot results demonstrating the correlations between the 1995 environmental variables and the resulting seedling morphology.

Grand fir	Total Sunlight	Temperature
HI	sm>cm ch	-
D	sl sm>ch cl>ch	sl>sm cl cm ch>sm cl
L1	sh>sm cm	sl>cl cm
B	sl sh>cl sm>cl cm ch	sl sm sh>cl
Douglas fir		
HI	-	-
D	-	cl>sm
L1	-	-
B	-	-

sl, sm, sh = shelterwood, "low", "medium" and "high" levels respectively
cl, cm, ch = clearing, "low", "medium", and "high" levels respectively

The growth of grand fir seedlings in relation to the environmental variables measured in 1996 was strongly correlated with those variables of the shelterwood site (Table 9). The newly added variable, mineral soil water content was positively correlated with growth in every measured plant part. The remaining variables, with the exception of total sunlight, were all positively correlated with the lengths of lateral branch #1 (L1) and lateral branch #2 (L2). The amount of water contained in the humus fraction was also highly correlated with the amount of growth in stem diameter (DI). In general, the medium and high levels of each variable in the shelterwood had the largest stems, while significant, positive correlations to low levels of these variables were only demonstrated by lateral branch #2 (L2) to PAR (Table 9).

The growth of Douglas fir seedlings in relation to the variables measured in 1996 were strongly correlated with those of the clearing site (Table 9). The growth of two

measured parts in particular was positively correlated with the variables in the shelterwood however. The first was the diameter increment (DI), which was largest in the low temperature levels at this site compared to medium levels at this same site (a response which does not indicate a preference to site, as it does not demonstrate a preference to shelterwood levels over those seen in the clearing). This part was truly correlated with the shelterwood site when PAR levels were measured however, growing largest in medium PAR levels in the shelterwood compared to high PAR levels produced in the clearing.

The second part more strongly correlated with the environmental variables of the shelterwood was the number of buds produced on the height increment (B). It was positively correlated with medium temperature levels at this site compared to all temperature levels of the clearing (Table 9).

Grand fir seedlings with a "normal" growth morphology demonstrated similar relationships with the environmental variables as they had when all types were pooled (Table 10). While fewer parts overall demonstrated significantly different growth in terms of the environmental variables, those which did were more strongly correlated with the variables measured in the shelterwood site. Mineral soil water content and temperature were the only variables which showed positive correlations with growth. Again, as was seen previously in Table 9, the medium and high levels of each variable in the shelterwood contained the largest seedlings.

Table 9. Summary of boxplot results demonstrating the correlations between the 1996 environmental variables and the resulting morphology of all seedlings pooled together.

Grand fir	Total Sunlight	Temperature	PAR	Humus water	Mineral water
H1	-	-	-	-	sh>sm sl cm
D1	-	-	-	sm>cm ch	sm sh>sl cl cm ch
L1	-	sm>ch sh>cl cm ch	sm>cl cm ch sh>ch	sh>cm ch	sh>sl cl cm ch sm>cl ch
L2	-	sm sh>cl cm ch	sl sm sh>cl cm	sh>cl cm ch	sh>sl cl cm ch sm>cm
B	-	-	-	-	sh>sl sm cl
Douglas fir					
H1	-	cl cm ch>sm	ch>sl sm sh	cm>sm	ch>sl sm sh
D1	-	sl>sm	cl>ch sm>ch	-	-
L1	-	ch>cm	-	cl>sm	cm>sm
L2	-	cl cm>sm	ch>sh	cl cm>sm sh	ch>sl sm sh
B	-	sm>cl cm ch	-	-	ch>sm

sl, sm, sh = shelterwood, "low", "medium" and "high" levels respectively

cl, cm, ch = clearing, "low", "medium", and "high" levels respectively

Douglas fir seedlings with a "normal" morphology demonstrated very strong correlations with the clearing site (Table 10). Most plant parts demonstrated positive correlations in the different temperature classes, while the only other relationships seen were by the number of buds produced along the height increment to PAR and the height increment to the amount of water contained in the humus fraction (Table 10).

Table 10. Summary of boxplot results demonstrating the correlations between the 1996 environmental variables and the resulting morphology of "normal" seedlings.

Grand fir	Total sunlight	Temperature	PAR	Humus water	Mineral water
HI	-	-	-	-	sm cm>sl
DI	-	-	-	-	sm>sl cl cm ch
L1	-	-	-	-	-
L2	-	sh>cl ch	-	-	-
B	-	-	-	-	sm>sl
Douglas fir					
HI	-	cl>sm cm>sl sm	-	cm>sm	-
DI	-	-	-	-	-
L1	-	-	-	-	-
L2	-	cm>sm	-	-	-
B	-	cm sl>sm	cm ch>sl	-	-

sl, sm, sh = shelterwood, "low", "medium" and "high" levels respectively

cl, cm, ch = clearing, "low", "medium", and "high" levels respectively

Seedlings with proleptic free growth were most strongly correlated with the shelterwood site, regardless of species (Table 11). However, grand fir seedlings, which had been fairly consistent in their relationships with the shelterwood environmental variables, had a larger height increment (HI) in high levels of PAR in the clearing compared to low PAR levels of the shelterwood. Mineral soil water content, which had consistent and significant correlations in all seedlings pooled in 1996 and "normal" seedlings (Table 9 and Table 10 respectively), demonstrated no significant relationships in seedlings with proleptic free growth (Table 11).

Douglas fir seedlings with proleptic free growth only demonstrated a positive correlation with the clearing site in the length of lateral branch #2 (Table 11). This part was largest in medium levels of water contained within the humus fraction in the clearing compared to medium levels in the shelterwood. All of the other significant relationships

were more strongly correlated with the shelterwood site, a trend most pronounced in this particular seedling group than any seen beforehand.

Table 11. Summary of boxplot results demonstrating the correlations between the 1996 environmental variables and the resulting morphology of seedlings with proleptic free growth.

Grand fir	Total sunlight	Temperature	PAR	Humus water	Mineral water
HI	-	-	ch>sl	-	-
DI	-	-	-	-	-
L1	-	sm>cm	sl sm sh ch>cm	-	-
L2	-	-	sl sm>cm	-	-
B	-	-	-	-	-
Douglas fir					
HI	-	-	-	-	-
DI	-	sm>cm	sm sh>ch	-	-
L1	-	-	-	-	-
L2	-	-	-	cm>sm	-
B	-	sm>sl cm ch	-	-	-

sl, sm, sh = shelterwood, "low", "medium" and "high" levels respectively
cl, cm, ch = clearing, "low", "medium", and "high" levels respectively

The relationships demonstrated between the morphological variables and the different combinations of environmental variables were unlike those trends found thus far when single environmental variables were addressed on their own (data not shown). Growth of grand fir seedlings, for all morphological variables except the number of buds produced on the height increment in 1996, was most strongly correlated with the shelterwood environment, results which are consistent with those demonstrated already. In 1995, the height increment and lateral branch #1 were largest in environments of high light and moderate temperatures. Diameter growth and bud production in this same year was largest in moderate light and low temperatures.

In 1996 for grand fir, the same relationships were repeated in the height increment and lateral branch #1, with the most growth being demonstrated by seedlings found within high PAR levels and moderate temperatures prevailed (data not shown).

Conversely, the diameter increment and lateral branch #2 was largest under medium PAR levels and high temperatures.

The correlation of growth in grand fir to soil moisture suggests that all seedlings in the shelterwood with high levels of both humus and mineral soil water have a the potential to grow the most. This trend, as mentioned previously, is not demonstrated in the number of buds produced in 1996, however. More buds were found on seedlings growing in the low and medium levels produced in the clearing.

Douglas fir seedlings showed a varied response to the combined environmental variables compared to those analyzed singly (data not shown). In 1995, the majority of the measured characteristics were strongly correlated with the variables of the clearing environment, as was shown through the analysis of these same variables separately. The growth produced by all of the measured plant parts, with the exception of lateral branch #1, was strongly correlated with low light levels and medium temperatures of the clearing.

This trend changed in 1996 however, with the best growth of Douglas fir being strongly correlated with the various microclimate combinations found within the shelterwood site (data not shown). All of the measured characteristics except the height increment, were found in high levels of PAR and medium temperatures within this site. In addition, the growth of both lateral branches, #1 and #2, was more correlated with low levels of both PAR and temperature.

A similar relationship between soil moisture and growth, seen initially in grand fir, was demonstrated in Douglas fir seedlings as well. Most of the growth demonstrated

in the morphological characteristics was best correlated with high humus and high mineral soil water levels of the shelterwood.

Discussion

The strong correlations between the growth of grand fir seedlings and the environmental variables produced within the shelterwood site are consistent with their autecological classification. Grand fir is classified as being tolerant of shade (Fowells 1965; Krajina 1969; Minore 1979; Krajina *et al.* 1982), but does not demonstrate as high a tolerance for low light levels as other *Abies* species (Krajina 1969). It prefers slightly cooler temperatures with well drained soils (Fowells 1965; Krajina 1969; Minore 1979; Krajina *et al.* 1982). All of these trends are upheld in the relationships demonstrated by this species.

Microclimate studies of partial cuts, particularly shelterwood sites throughout the Pacific Northwest, have shown that these sites generally provide a milder climate for growth when compared to adjacent clearcuts, mainly due to the partial retention of the canopy (Holbo *et al.* 1985; Holbo and Childs 1987; Childs and Flint 1987; Spittlehouse and Childs 1990; Stathers and Spittlehouse 1990). The remaining overstory buffers the effects of incoming solar radiation, thus dampening extreme levels of light and temperature primarily. The shelterwood at Ring Creek seems to conform to these descriptions as well, as shown by the temperature differences and soil moisture regimes between this site and the clearing (Figure 26 and Figure 27). While drastic temperature differences were not demonstrated between the two sites, perhaps due to the fall sampling time and the modifying effects on the clearing from the surrounding plantation,

the principle is still clearly shown: the clearing is generally warmer than the shelterwood. This trend is demonstrated with soil moisture as well. The shelterwood had higher levels of soil moisture compared to the clearing, results similar to those of Holbo and Childs (1987), Childs and Flint (1987), and Spittlehouse and Childs (1990). While the conditions in the clearing may not be extreme enough to adversely affect the growth of grand fir (as shown by survival, which remained at 100% after both seasons), the shelterwood seemed to promote more growth, as indicated by the larger seedlings and seedling characteristics produced by this site (see plots of descriptive statistics, Figure 8 and Figure 11). Better growth produced in partially shaded sites by grand fir was also shown by Norman *et al.* (1974).

Both total solar radiation in 1995 and PAR in 1996 were positively correlated with the amount of growth demonstrated in all grand fir seedlings pooled together in 1995 and 1996 and those with proleptic free growth in 1996. Studies of natural light gradients, involving species with a similar shade tolerance to that of grand fir, have shown that growth of these trees (usually natural or planted seedlings and saplings) is best under 100% full sunlight (PAR specifically) (Emmingham and Waring 1973; Carter and Klinka 1992; Klinka *et al.* 1992; Wang *et al.* 1994). While the results from this particular study show the contrary, Carter and Klinka (1992) indicate that the effects of light as a limiting factor on growth are most important at levels below 30% of full sunlight, and that growth of seedlings in light regimes of 60% and higher of full sunlight are likely to be more influenced by other microsite conditions. Following that criterion, the total solar radiation measurements for 1995 (83 - 100% of full sunlight) and PAR measurements for 1996 (53 - 100% of full PAR), are not likely to be growth limiting.

That these light levels are sufficient for the promotion of a "better" growth response in grand fir in the shelterwood compared to the clearing may only be a fraction of the larger system at work however. While the environmental conditions within the clearing did not affect the overall survival of grand fir seedlings, it is possible that other factors not addressed in 1995 limited their growth, or that the levels of the factors examined were too extreme (seeing that both light levels and temperatures were higher in the clearing). This second supposition cannot be commented upon, unfortunately, owing to the lack of data collected during the growing season and the observational nature of the study.

The growth of grand fir seedlings, both collectively and those with a "normal" growth morphology, showed strong correlations with soil moisture levels of the mineral horizons in the shelterwood in 1996. The higher levels of soil moisture found within the shelterwood site overall (Figure 27), lends support to previous assertions that grand fir seedlings perform best on sites with well drained but slightly moist soils (Fowells 1965; Krajina 1969 Krajina *et al.* 1982; Norman *et al.* 1974).

Douglas fir seedlings in both measurement years also demonstrated a strong correlation in growth with a particular site, this being the clearing. This generally coincides with its autecological classification as well, except that certain aspects are not as conclusive as compared to what was shown with grand fir. Douglas fir is considered intermediate in its shade tolerance, requiring more light than grand fir (Fowells 1965; Krajina 1969; Minore 1979; Krajina *et al.* 1982). Depending upon the moisture content of the soil however, this classification can change. Krajina (1969) and Krajina *et al.* (1982) indicate that when found on wetter sites, this species is largely intolerant of any

shade, and needs higher light intensities to survive. At Ring Creek, the higher levels of soil moisture found within the shelterwood site compared to the clearing could help to explain why Douglas fir grew better in the latter site.

The tolerance of Douglas fir to temperature is also classified as being “moderate” based on its ability to withstand higher temperatures than grand fir (Fowells 1965; Krajina 1969; Minore 1979; Krajina *et al.* 1982). Temperature was the most influential environmental variable detected in 1995 and 1996, correlating strongly with the growth displayed by all Douglas fir seedlings combined, and those with a “normal” or “proleptic free growth” morphology. The lack of research addressing naturally established temperature gradients makes direct comparisons between these results and other studies difficult. Supporting evidence, however, can be derived from those studies which addressed light gradients. As light and temperature are highly correlated throughout the year, positive changes in light generally result in positive changes in temperature, and vice versa (Ford 1980; Holbo and Childs 1987; Carter and Klinka 1992; Chen *et al.* 1995). In view of this assumption, the more pronounced responses to temperature could be indirectly related to light. That Douglas fir seedlings, in particular, show positive correlations with the temperature regimes in the clearing is not surprising. Aztet and Waring (1970) and Emmingham and Waring (1973) found that the best growth of Douglas fir seedlings was demonstrated at levels of full irradiance, which are more than likely associated with higher temperatures. This is also shown by Carter and Klinka (1992), Klinka *et al.* (1992), and Wang *et al.* (1994), in studies of tree species with a higher shade tolerance than that of Douglas fir. As mentioned previously, both tree

species examined here grew best at levels of full irradiance and thus may be experiencing higher, more favorable temperatures as well.

An exception to the consistently strong correlations found between the growth of Douglas fir seedlings and the environmental variables of the clearing is shown by those seedlings with proleptic free growth. While the growth of these seedlings is still strongly linked with temperature, it is the lower temperatures of the shelterwood environment correlating more with growth than those levels of the clearing. The diameter increment and number of buds produced on the height increment of Douglas fir seedlings with proleptic free growth correlated strongly with medium-ranged temperatures in the shelterwood environment. Even though the incidence of proleptic free growth was higher in the clearing for this species (46% compared to 39% in the shelterwood), the seedlings in the shelterwood produced much more growth. The components correlating with the shelterwood site (the diameter increment and the number of buds produced on the height increment) are much larger at this site than in the clearing.

When the environmental variables were combined, a variety of relationships were seen in both species. For 1995, the combination of total solar radiation and temperature produces similar correlations to those seen when variables were analyzed separately. Douglas fir growth was best correlated with the combinations formed within the clearing, while growth in grand fir seedlings was better correlated with the shelterwood. 1996, in which combinations of PAR and temperature as well as humus and mineral soil moisture content were formed, produced different correlations in Douglas fir growth in particular, whose growth was now better correlated with the shelterwood environment, alongside grand fir. These relationships represent the general trends which present themselves once

the combinations are formed and do not have any statistical significance attached to them. A larger sample size would be necessary for the determination of whether or not these trends can be justified in a more quantitative manner.

While most of the plant parts in both species were correlated to one or several environmental variables, the result of "no correlation" does not suggest that the variable or variable combinations had no relationship with the plant. What it indicates is that the arbitrary classifications of "low", "medium" and "high" were not different enough from each other to promote a statistically significant relationship from the seedlings grouped within them.

While studying more than one environmental variable at a time poses to be a difficult task, due to their interconnected nature, the relevance of doing so needs to be stressed. Environmental variables in a natural setting do not work independently, and so joining them in all possible combinations, as was done here, seems to be one of the more straightforward ways of dealing with this complex issue. The need for more research addressing the effects of multiple environmental variables on plant responses has been expressed (Chapin III *et al.* 1987), but still much research needs to be done.

In general, both 1995 and 1996 bore witness to climatic conditions which produced a less stressful environment for seedling growth. Both the large and small scale environmental conditions in 1995 were mild enough to reduce the presence of transplanting stress (Rietveld 1989) experienced by many nursery-grown seedlings planted into a new environment, and the persistence of these mild growing conditions into 1996 continued the trend of positive growth. While 1996 had, on average, similar temperatures and rainfall accumulation compared to the longterm normals, a noticeable

period of hotter, dry weather occurred in August, which was followed by a cool, wet period in September. This series of events has accounted for the increased amount of proleptic free growth seen during that year. The hot, dry weather in August may have triggered bud scales to form, in order to minimize water loss from the apical meristem (MacDonald and Owens 1993a). The coming of temperatures which were cooler but still conducive to growth, as well as wet weather in September may have caused these buds to flush, and rapidly produce more stem units before the climate changed again to stimulate dormancy in a more convincing way.

When does the climate affect growth?

Analyzing growth responses to specific climatic variables is an area which needs more rigorously defined boundaries. When should environmental data be monitored and related back to the overall growth responses of the plant? The general consensus seen throughout many of the studies cited in Chapter 3 is to monitor the environment during the summer months, which tends to coincide with the period of shoot expansion. Several, however, monitor conditions well into the fall (Carter and Klinka 1992; Klinka *et al.* 1992; Chen *et al.* 1995).

The ambiguity of this procedure appears in the determination of when climatic measurements should be taken in relation to given parts of the plant. For example, it has been argued that the number of stem units formed in the bud the year prior to its extension plays a larger role in determining the overall length of the shoot, than does the actual extension of the stem units themselves in the following spring (Kozlowski, Torrie and Marshall 1973, cited in Ford 1980). This idea is also supported by claims that the

amount of shoot growth produced in a particular year is more strongly correlated with the temperatures demonstrated during the year of bud formation rather than during that of bud expansion (Kozlowski *et al.* 1991). Does this mean that in order to accurately understand the environmental influences on stem expression, the climate conditions one year prior to the extension of the stem must be monitored? Not entirely, as the climate conditions experienced by the stem while it is expanding are also of importance in determining the degree to which the stem units will expand (Garrett and Zahner 1973). If conditions are less than favorable during stem extension, the stem will be shorter, regardless of the number of stem units produced, simply because maximum extension of the stem units was not achieved (Garrett and Zahner 1973).

Another example which adds to this conundrum involves relating climate conditions to the formation of the interwhorl branches, found along the height increment. According to Romberger (1963); Powell (1974); Cannell and Bowler (1978); J. N. Owens (pers. comm., cited in Worrall 1984) and Scagel (1996), as mentioned in Chapter 2, these branches are formed up to two years before their extension. Thus, in order to fully understand the range of environmental influence upon these particular plant parts, the climatic conditions two years prior to their extension should be monitored.

Addressing the issue of when to measure environmental variables helps widen the interpretation of what the "growing season" of conifers actually is referring to. Generally, the summer months during which shoot extension growth occurs are viewed as being the growing season (see references cited in Chapter 3). However, once the buds are formed does this signal the end of the growing season even if the various meristems may still be active? The vascular cambium apparently remains active much longer than

the apical meristem, while the meristems of roots seem to outlast the activity of both (Kozlowski *et al.* 1991). It was found by Fielder and Owens (1989), in studying the shoot development of interior and coastal Douglas fir seedlings, that leaf primordia were formed within the bud up until as late as December for the coastal varieties of Douglas fir, indicating that dormancy did not occur until then (dormancy in this experiment was determined using the mitotic index as an indicator - see Fielder and Owens (1989) and the references cited therein). The cell divisions of the apical meristem ceased after this time, but then resumed activity in as early as mid-February (Fielder and Owens 1989). Should the concept of the growing season be extended to include the fall and following late-winter months as well? The answer has to remain unknown until further studies addressing these concepts are carried out.

Generally speaking, no simple solution exists for these situations. As mentioned previously, the norm for monitoring environmental variables in relation to plant growth response seems to lie with gathering data from the current growing season. This, however, seems to uncover only a portion of the full picture. Scagel (1996) suggested that the establishment of a two-year management period may be one way of adequately describing the full range of growth responses conifers display with respect to environmental factors. While this suggestion may seem to be somewhat excessive, it may be the only way of fully understanding how each stage of conifer growth is affected by the environmental variables which surround them. Until this management strategy is considered, or another suggestion made, the full picture on conifer growth in response to their environment will remain unknown.

Chapter 4.

Conclusions Regarding Reforestation, Alternative Silviculture Systems and Seedling Morphology

Reforestation and Alternative Silviculture Systems

From the results generated, was it found that these seedlings were performing well enough within each site to become a productive forest in the future? The answer is not as clearly defined as one would like. The selection of Douglas fir seedlings seemed appropriate as this species was present in the original forest and fared well in both the clearing and shelterwood sites. The overall survival demonstrated by this species reinforces this, even though some mortality was seen. While the survival was higher in the shelterwood by approximately 13%, it is believed that these results were obscured by the initial planting error which occurred in the clearing. This incident obviously impacted the survival of Douglas fir more so than any other environmental cause, as only 3 seedlings died in 1996, compared to 15 in 1995 in this site specifically. The environments produced within each site do not seem to be limiting to growth, as demonstrated by the environmental analyses conducted. Douglas fir growth seems to be more positively correlated with the clearing environment, but its growth is not limited in the shelterwood either.

Grand fir is not often used in reforestation, but does tend to fare well on sites with characteristics similar to those seen at Ring Creek (Klinka *et al.* 1990). This too was reflected by the complete survival and continued growth of the seedlings in both the

clearing and shelterwood sites. Conversely to what was seen with Douglas fir, the growth of these seedlings seems to be more positively correlated with the conditions of the shelterwood site. Again, however, the growth of grand fir in the clearing is not adversely affected, as is shown by their continued growth and survival within this site.

Determining whether or not the seedlings will continue to be successful in the future becomes obscured when addressing the issue of proleptic free growth. Its presence in grand fir was highest in the shelterwood at 33%, and reached 46% in the clearing for Douglas fir. Carter and Klinka (1986) indicated that in stands where distorted growth is present, only between 5 and 10% of the stand is usually affected. The proportions of trees found with distorted growth due to proleptic free growth at Ring Creek are much higher than the general assessments of Carter and Klinka (1986) and could be viewed as a potential problem. If this type of growth carries on when the trees reach a more merchantable size, (proleptic free growth is usually considered a trait of juvenile trees, lasting up to approximately seven to ten years of age (von Wuhlisch and Muhs 1986; Scagel 1996)) it could lead to the permanent deformation of the main stem, thus lowering the value of the wood in the future (Walters and Soos 1961; Carter and Klinka 1986) as well as increase the risk of sustaining stem and branch damage from surrounding environmental conditions due to the lateness of the flush..

However, if proleptic free growth is viewed simply as being an amplified expression of the overall growth pattern of seedlings, (*sensu* Tomlinson 1978) its presence should not be seen as a problem. Instead, the benefits associated with the presence of proleptic free growth, such as an increase in seedling height and overall shoot vigor as well as the ability to compensate for browsed or damaged plant parts, may in fact

accelerate reforestation (Roth and Newton, 1996). While it is uncertain whether or not the presence of proleptic free growth at Ring Creek was in response to intense herbivory, it most certainly did increase the shoot vigor and overall height of the seedlings, which were consistently larger than seedlings with a "normal" growth morphology, regardless of the species.

The results generated from this study may serve as an example of species and site combinations which are growing well in the field. The high incidence of proleptic free growth may be of interest to nurseries or other researchers who wish to explore the causes of this phenomenon in more detail. The seedlots used may be more conducive to this type of growth response than others, and thus may be beneficial if used in genetic studies.

Seedling Morphology

In general, the majority of the seedlings of both species exhibited a growth pattern which conformed to the norm. The spatial relationships demonstrated between specific plant parts, such as the height increment, number of buds produced upon the height increment and subtending whorl lateral branches, reinforce the idea that the precise pattern of growth usually followed by conifers is a repeated sequence of the parent shoot (Tomlinson and Gill 1973; Halle and Oldeman 1970), the parent shoot consisting mainly of these three components. This spatial relationship was generally maintained across the species and sites, illustrating the strength of the genetic component in directing the growth form in all conifers (Tomlinson 1978).

The lack of close inter-variable relationships formed by the stem diameter, as well as the scarcity of adequate descriptors for this particular plant part suggests that this particular part of the plant is not readily described by the most conspicuous features of the plant overall. The stem diameter gives an indication of the amount of tissue being added to the stem, and thus lends insight into the activity of the vascular cambium. Judging by the results obtained, the stem diameter may not be best described by the features most commonly acknowledged as being the foundations of conifer growth form, that being stems, branches and leaves (Halle and Oldeman 1970; Tomlinson and Gill 1973; Hallé *et al.* 1978; Tomlinson 1978, and others). All of these features in particular are produced by the apical meristem, and represent growth in length, while the stem diameter is basically an indication of the growth in girth produced by a different meristem altogether (Romberger 1963). Thus, perhaps, as suggested previously, features relating more to the anatomy of the stem, and thus the vascular cambium, such as measurements pertaining to the amount of xylem or cortex produced, may better describe the stem itself in comparison to those features seen externally. This may provide more insight into the role played by the basal stem diameter and its relationship to the other plant parts, all of which work together to produce the overall morphology of the tree.

The presence of proleptic free growth was the only phenomenon which did not conform outright to the regular branching patterns displayed by conifers. Its presence, however, did not seem to be promoted by any site in particular. This growth form seemed to be highest in the site each species was more suited to, the clearing for Douglas fir and the shelterwood for grand fir. This response may be the result of the seedlings being more adept at responding to environmental cues in an area where they are more

suited to grow in. Seedlings of Douglas fir growing in the shelterwood, or grand fir in the clearing may be more restricted in their overall ability to respond to these surroundings, simply because these habitats do not provide the type of growing conditions they respond to best.

Reference List

- Aztet, T., and R. H. Waring. 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. *Canadian Journal of Botany* 48: 2163-67.
- B.C. Ministry of Forests. 1993. Silvicultural systems in British Columbia: Clearcutting, seed tree, shelterwood and selection. Silviculture Branch Report, Victoria, B.C. 5pp.
- Banerjee, S., P. R. Sibbald, and J. Maze. 1990. Quantifying the dynamics of order and organization in biological systems. *Journal of Theoretical Biology* 143: 91-111.
- Baxter, S. M., and M. G. R. Cannell. 1978. Branch development on leaders of *Picea sitchensis*. *Canadian Journal of Forest Research* 8: 121-28.
- Bernier-Cardou, M., and C. Genest. 1992. Factors influencing root growth capacity of spruce seedlings: report on a statistical analysis. *Canadian Journal of Statistics* 20: 488-500.
- Cannell, M. G. R. 1974. Production of branches and foliage by young trees of *Pinus contorta* and *Picea sitchensis*: provenance differences and their simulation. *Journal of Applied Ecology* 11: 1091-115.
- Cannell, M. G. R., and K. C. Bowler. 1978. Spatial arrangement of lateral buds at the time that they form on leaders of *Picea* and *Larix*. *Canadian Journal of Forest Research* 8: 129-37.
- Cannell, M. G. R., S. Thompson, and R. Lines. 1976. An Analysis of Inherent Differences in Shoot Growth Within Some North Temperate Conifers. *In* Tree Physiology and Yield Improvement. M. G. R. Cannell, and F. T. Last editors. Academic Press, London. 567pp.
- Carter, R. E., and K. Klinka. 1986. Symptoms and Causes of Distorted Growth in Immature Forest Stands in Coastal British Columbia. Land Management Report No. 39. Ministry of Forests, Victoria, B.C. 61pp.
- . 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. *Forest Ecology and Management* 55: 87-105.
- Chapin III, F. S., A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. *BioScience*. 37: 49-57.

- Chen, J., J. F. Franklin, and T. A. Spies. 1995. Growing-season microclimatic gradients form clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* 5: 74-86.
- Childs, S. W., and L. E. Flint. 1987. Effect of shadeboards, shelterwoods and clearcuts on temperature and moisture environments. *Forest Ecology and Management* 18: 205-17.
- Downs, R. J., and H. Hellmers. 1975. *Environment and the Experimental Control of Plant Growth*. Academic Press, London. 145pp.
- Emmingham, W. H., and R. H. Waring. 1973. Conifer growth under different light environments in the Siskiyou Mountains of Southwestern Oregon. *Northwest Science* 47: 88-99.
- Esau, K. 1977. *Anatomy of Seed Plants*. 2nd ed. John Wiley and Sons, New York. 550pp.
- Fielder, P., and J. N. Owens. 1989. A comparative study of shoot and root development of interior and coastal Douglas-fir seedlings. *Canadian Journal of Forest Research* 19: 539-49.
- Ford, E. D. 1980. Impact of environment on the shoot elongation of conifers: short term effects. *In* Control of shoot growth in trees: IUFRO Proceedings on xylem physiology and shoot growth physiology. C. H. A. Little editor. Maritimes Forest Research Centre, Fredericton, New Brunswick. Pp. 107-26.
- Foster, A. S. 1938. Structure and growth of the shoot apex in *Ginkgo biloba*. *Bulletin of the Torrey Botanical Club* 65: 531-56.
- Fowells, H. A. 1965. *Silvics of forest trees of the United States*. USDA Forest Service. Agriculture Handbook No. 271. Washington. 553pp.
- Garrett, P. W., and R. Zahner. 1973. Fascicle density and needle growth responses of red pine to water supply over two seasons. *Ecology* 54: 1328-34.
- Green R. N., and K. Klinka. 1994. A field guide for site identification and interpretation for the Vancouver forest region. *Land Management Handbook No. 28*. Ministry of Forests, Victoria, B.C. 285pp.
- Hallé, F., R. A. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical Trees and Forests. An Architectural Analysis*. Springer-Verlag, Berlin. 441pp.
- Halle, F., and R. A. A. Oldeman. 1970. *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson, Paris.

- Harrington, T. B., R. J. Pabst, and J. C. Tappeiner II. 1994. Seasonal physiology of Douglas-fir saplings: response to microclimate in stands of tanoak or Pacific Madrone. *Forest Science* 40: 59-82.
- Hedin, I. B. 1996. Shelterwood harvesting with a Skyline system in a coastal second-growth forest. Forest Engineering Research Institute of Canada Wood Harvesting Technical Note TN-243. Vancouver, B.C. 8pp.
- Helms, J. A. 1965. Diurnal and seasonal patterns of net assimilation in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, as influenced by environment. *Ecology* 46: 698-708.
- . 1976. Factors Influencing Net Photosynthesis in Trees: An Ecological Viewpoint. *In* Tree Physiology and Yield Improvement. M. G. R. Cannell, and F. T. Last editors. Academic Press, London. 567pp.
- Hodges, J. D. 1967. Patterns of photosynthesis under natural environmental conditions. *Ecology* 48: 234-42.
- Hodges, J. D., and D. R. M. Scott. 1968. Photosynthesis in seedlings of six conifer species under natural environmental conditions. *Ecology* 49: 973-81.
- Holbo, H. R., and S. W. Childs. 1987. Summertime radiation balances of clearcut and shelterwood slopes in Southwest Oregon. *Forest Science* 33: 504-16.
- Holbo, H. R., S. W. Childs, and D. H. McNabb. 1985. Solar radiation at seedling sites below partial canopies. *Forest Ecology and Management* 10: 115-24.
- Huitema, B. E. 1980. The Analysis of Covariance and Alternatives. John Wiley and Sons, New York. 445pp.
- Jablanczy, A. 1971. Changes due to age in apical development in spruce and fir. Canadian Forestry Service Bi-Monthly Research Notes No. 27. Department of Fisheries and Forestry, Ottawa. Pp.10.
- Klinka, K., M. C. Feller, R. N. Green, D. V. Meidinger, J. Pojar, and J. Worrall. 1990. Ecological Principles: Applications. *In* Regenerating British Columbia's Forests. D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston editors. UBC Press, Vancouver, British Columbia. 372pp.
- Klinka, K., Q. Wang, G. J. Kayahara, R. E. Carter, and B. A. Blackwell. 1992. Light-growth response relationships in Pacific silver fir (*Abies amabilis*) and subalpine fir (*Abies lasiocarpa*). *Canadian Journal of Botany* 70: 1919-30.

- Knight, E. 1990. Reforestation in British Columbia: A Brief History. *In* Regenerating British Columbia's Forests. D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston editors. UBC Press, Vancouver, British Columbia. 372pp.
- Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The Physiological Ecology of Woody Plants. Academic Press, San Diego. 657pp.
- Krajina, V. J. 1969. Ecology of forest trees in B. C., Ecology of Western North America. Vol. 2. Department of Botany, University of British Columbia, Vancouver, B.C. Pp. 1-147.
- Krajina, V. J., K. Klinka, and J. Worrall. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, University of British Columbia, Vancouver, B.C. 131pp.
- Kramer, P. J. 1978. The use of controlled environments in research. *Hortscience*. 13: 447-51.
- Kramer, P. J., and T. T. Kozlowski. 1960. Physiology of Trees. McGraw-Hill, New York. 642pp.
- Lavender, D. P. 1984. Plant Physiology and Nursery Environment: Interactions Affecting Seedling Growth. *In* Forest Nursery Manual: Production of Bareroot Seedlings. M. L. Duryea, and T. D. Landis editors. Martinus Nijhoff/Dr. W. Junk Publishers, The Hague/Boston/Lancaster. 386pp.
- Leverenz, J. W. 1981. Photosynthesis and transpiration in large forest-grown Douglas-fir: diurnal variation. *Canadian Journal of Botany* 59: 349-56.
- MacDonald, J. E., and J. N. Owens. 1993a. Bud development in coastal Douglas-fir seedlings in response to different dormancy-induction treatments. *Canadian Journal of Botany* 71: 1280-1290.
- . 1993b. Bud development in coastal Douglas-fir seedlings under controlled-environment conditions. *Canadian Journal of Forest Research* 23: 1203-12.
- Maze, J., R. K. Scagel, and L. R. Bohm. 1987. Quantitative studies in ovule development. III. An estimate of shape changes in *Phyllostachys aurea*. *Canadian Journal of Botany* 65: 1531-38.
- McCurdy, W. D., and G. R. Powell. 1987. Syllepsis in *Larix laricina*: association of sylleptic branching with cross-sectional stem growth and stem form of saplings. *Canadian Journal of Forest Research* 17: 1609-19.
- McKeague, J. A. 1978. Manual on soil sampling and methods of analysis. 2nd ed. Canadian Society of Soil Science. Ottawa, Ont. 212pp.

- Mexal, J. G., and T. D. Landis. 1990. Target Seedling Concepts: Height and Diameter. *In* Target Seedling Symposium: Proceedings, Combined Meeting of the Western Forest Nursery Associations. R. Rose, S. J. Campbell, and T. D. Landis editors. USDA Forest Service. General Technical Report RM-200. Ft. Collins, CO. 286pp.
- Minore, D. 1979. Comparative autecological characteristics of Northwestern tree species. A literature review. USDA Forest Service. General Technical Report PNW-87. Washington.
- Mitchell, A. K., and J. T. Arnott. 1995. Effects of shade on the morphology and physiology of amabilis fir and western hemlock seedlings. *New Forests* 10: 79-98.
- Mitchell, W. K., G. Dunsworth, D. G. Simpson, and A. Vyse. 1990. Planting and Seedling. *In* Regenerating British Columbia's Forests. D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston editors. UBC Press, Vancouver, British Columbia. 372pp.
- Moe, R., and R. Heins. 1990. Control of plant morphogenesis and flowering by light quality and temperature. *Acta Horticulture* No. 272. Pp.81-89.
- Norman, C. M., H. Loewenstein, and F. H. Pitkin. 1974. Effects of light intensity on survival and growth of grand fir seedlings. Forest Wildlife and Range Experiment Station. Station Paper 17. 12pp.
- Pimentel, R. 1979. Morphometrics. The Multivariate Analysis of Biological Data. Kendall/Hunt Publishing Co., Dubuque, IA. 276pp.
- Pollard, D. F. W., and K. T. Logan. 1976. Inherent Variation in "Free" Growth in Relation to Numbers of Needles Produced by Provenances of *Picea mariana*. *In* Tree Physiology and Yield Improvement. M. G. R. Cannell, and F. T. Last editors. Academic Press, London. 567pp.
- . 1974. The role of free growth in the differentiation of provenances of black spruce *Picea mariana* (Mill.) B.S.P. *Canadian Journal of Forest Research* 4: 308-11.
- Powell, G. R. 1974. Initiation and development of lateral buds in *Abies balsamea*. *Canadian Journal of Forest Research* 4: 458-69.
- Powell, G. R., and S. A. Vescio. 1986. Syllepsis in *Larix laricina*: occurrence and distribution of sylleptic long shoots and their relationships with age and vigour in young plantation-grown trees. *Canadian Journal of Forest Research* 16: 597-607.

- Remphrey, W. R., and G. R. Powell. 1984. Crown architecture of *Larix laricina* saplings: shoot preformation and neoformation and their relationships to shoot vigour. *Canadian Journal of Botany* 62: 2181-92.
- . 1985. Crown architecture of *Larix laricina* saplings: sylleptic branching on the main stem. *Canadian Journal of Botany* 63: 1296-302.
- Rietveld, W. J. 1989. Transplanting stress in bareroot conifer seedlings: its development and progression to establishment. *Northern Journal of Applied Forestry* 6: 99-107.
- Romberger, J. A. 1963. Meristems, growth, and development in woody plants. An analytical review of anatomical, physiological, and morphogenic aspects. USDA Forest Service. Technical Bulletin No. 1293. 214pp.
- Rose, R., W. C. Carlson, and P. Morgan. 1990. The Target Seedling Concept. *In* Target Seedling Symposium: Proceedings, Combined Meeting of the Western Forest Nursery Associations. R. Rose, S. J. Campbell, and T. D. Landis editors. USDA Forest Service. General Technical Report RM-200. Ft. Collins, CO. 286pp.
- Roth, B. E., and M. Newton. 1996. Role of lammas growth in recovery of Douglas-fir seedlings from deer browsing, as influenced by weed control, fertilization, and seed source. *Canadian Journal of Forest Research* 26: 936-44.
- Rudolph, T. D. 1964. Lammas growth and prolepsis in Jack pine in the Lake States. *Forest Science Monograph* No. 6. 70pp.
- Salisbury, F. B., and C. W. Ross. 1992. *Plant Physiology*. 4th ed. Wadsworth Publishing Company, Belmont, CA. 682pp.
- Scagel, R. K. 1996. Bednesti Site - Testing the Biological Effectiveness of Mechanical Site Preparation Equipment (Preliminary Results). Ministry of Forests. FRDA II - Silviculture Report. Victoria, B.C..
- . 1984. Morphological and Anatomical Variation of *Picea* in Southwestern British Columbia. MSc. Thesis, Department of Botany, University of British Columbia. Vancouver, B.C.. 313pp.
- Scagel, R. K., J. Maze, R. Bohm, and N. L. Vogt. 1985. Quantitative studies in early ovule development. I. Intraindividual variation in *Nothofagus antarctica*. *Canadian Journal of Botany* 63: 1769-78.
- Scagel, R. K., J. Wetzel, and J. Charles. 1997. Climate Analysis and Modeling Silvicultural Interpretations. Unpublished report prepared by Pacific Phytometric Consultants. 36pp.

- Spittlehouse, D. L., and R. J. Stathers. 1990. Seedling Microclimate. Land Management Report No. 65. Ministry of Forests, Victoria, B.C. 28pp.
- Stathers, R. J., and D. L. Spittlehouse. 1990. Forest Soil Temperature Manual. FRDA Report No. 130. Forestry Canada and B.C. Ministry of Forests, Victoria, B.C. 47pp.
- Sweet, G. B., and P. F. Wareing. 1966. Role of plant growth in regulating photosynthesis. *Nature* 210: 77-79.
- Tinus, R. W., and S. E. McDonald. 1979. How to Grow Tree Seedlings in Containers in Greenhouses. USDA Forest Service. General Technical Report RM-60. Ft. Collins, CO. 256pp.
- Tomlinson, P. B. 1978. Branching and axis differentiation in tropical trees. *In* Tropical trees as living systems. P. B. Tomlinson, and M. H. Zimmermann editors. Cambridge University Press, Cambridge. Pp. 187-207.
- Tomlinson, P. B., and A. M. Gill. 1973. Growth Habits of Tropical Trees: Some Guiding Principles. *In* Tropical Forest Ecosystems in Africa and South America: A Comparative Review. B. J. Meggers, E. S. Ayensu, and W.D. Duckworth editors. Smithsonian Institution Press, Washington. 350pp.
- Tucker, G. F., and W. H. Emmingham. 1977. Morphological changes in leaves of residual western hemlock after clear and shelterwood cutting. *Forest Science* 23: 195-203.
- Tucker, G. F., T. M. Hinckley, J. Leverenz, and S. Jiang. 1987. Adjustments of foliar morphology in the acclimation of understory pacific silver fir following clearcutting. *Forest Ecology and Management* 21: 249-68.
- von Wühlisch, G., and H. J. Muhs. 1986. Influence of age on sylleptic and proleptic free growth of Norway spruce seedlings. *Silvae Genetica* 35: 42-48.
- Walters, J., and J. Soos. 1961. Some observations on the relationship of lammas shoots to the form and growth of Douglas-fir seedlings. University of British Columbia, Faculty of Forestry Research Paper No. 40. 8pp.
- Wang, G. G., H. Qian, and K. Klinka. 1994. Growth of *Thuja plicata* seedlings along a light gradient. *Canadian Journal of Botany* 72: 1749-57.
- Weetman, G. F. 1996. Are European Silvicultural Systems and Precedents Useful for British Columbia Silviculture Prescriptions? FRDA Report No. 239. Forestry Canada and B.C. Ministry of Forests, Victoria, B.C. 31pp.

- Weetman, G., and A. Vyse. 1990. Natural Regeneration. *In* Regenerating British Columbia's Forests. D.P. Lavender, R. Parish, C.M. Johnson, G. Montgomery, A. Vyse, R.A. Willis, and D. Winston editors. UBC Press, Vancouver, British Columbia. 372pp.
- Wilkinson, L. 1996. SYSTAT 6.0 for Windows: Statistics. SPSS Inc., Chicago, IL. 751pp.
- Worrall, J. 1984. Predetermination of lateral shoot characteristics in grand fir. *Canadian Journal of Botany* 62: 1309-15.