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Modern and Late Holocene Climate-Tree-Ring Growth Relationships and Growth Patterns in Douglas-fir, Coastal British Columbia, Canada

by

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A Dissertation Submitted in Partial Fulfilment of the
Requirements for the Degree of

DOCTOR OF PHILOSOPHY

in the School of Earth and Ocean Sciences

We accept this dissertation as conforming
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ABSTRACT

This thesis investigates nonlinear climate-growth relationships and spatio-temporal variations in radial growth of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) in coastal British Columbia (BC), Canada. The technique of Artificial Neural Network (ANN) is used to model tree-ring growth response to climatic variables. Spatial variations in radial growth are examined by comparing ring-width chronologies from three sites on southeastern Vancouver Island and nine sites in Bella Coola area of central coast BC. Radial growth in late Holocene is analyzed by examining ring-width chronologies developed from subfossil Douglas-fir at the Heal Lake site on southern Vancouver Island.

A two-level linear aggregate model is proposed as an improved conceptual framework for study of tree-rings and environment. This model is useful for better understanding the interactions and transformations between different environmental factors and for unambiguous interpretation of the impact of disturbance on tree growth. The ANN technique is demonstrated to be superior to the traditional linear regression approach because of its ability to capture nonlinear and complex relationships between climatic variables and tree-ring growth. The ANN model can be used to predict tree-ring growth under given climatic conditions, and to understand climate-growth relationships by scenario analysis. Comparisons of tree-ring chronologies from three sites on southeastern Vancouver Island suggest that the climate-growth responses are generally similar. In the Bella Coola area of central coast BC, principal component analysis shows that there is common growth response throughout the nine sites of different elevations. However, there is also contrasting growth responses between sites of high and low elevations. The growing season precipitation is likely a major factor controlling radial growth of Douglas-fir on macro-regional scale in coastal BC. Five floating ring-width chronologies in the past 3rd and 4th millennia are developed using 79 subfossil Douglas-fir from the Heal Lake site on southern Vancouver Island. These chronologies show slight fluctuations and strong variations at different intervals. Notable growth anomalies occurred at about 4000 years before present, suggesting intense environmental changes, e.g., frost and droughts, at a time of suspected climate transition. The results of this study will be of use to forest management and climate studies in coastal BC.

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DEDICATION

This dissertation is dedicated to my colleagues studying tree-rings in China.

Chapter 1 Rationale

1.1 Background and Existing Problems

Today's forests are snapshots of a long and changing series of ecosystems shaped by many processes, the two most important of which are climate change and ecological disturbance (Glenn-Lewin et al., 1992; Hebda and Whitlock, 1997). Understanding the patterns and processes of these ecosystem changes are essential for developing plans of sustainable forestry and also critical to decoding past climate patterns.

Studies of the Holocene climate reveal that the earth's climate has experienced changes at various time scales, such as annual to decadal (LaMarche, 1974; Hughes and Diaz, 1994; Eronen et al., 1999), interdecadal to century (Stocker and Mysak, 1992; Mann et al., 1995; Minobe, 1997), and millennial (Bond et al., 1997; Oppo, 1997). These climatic variations have different causes (Denton and Karlen, 1973; Nesje and Johannessen, 1992; Broecker, 1997; Taylor, 1999) and different biological effects on forest ecosystems (Prentice, 1992; Campbell and McAndrews, 1993; Hebda, 1997, 1998; Millar and Woolfenden, 1999).

Natural disturbances are another prominent factor affecting forest dynamics. They are relatively distinct events that disrupt the structure of an ecological system by partial or total destruction of its biomass (Grime, 1977, 1979; Pickett et al., 1989). For example, canopy disturbance by defoliating insects reduces the radial growth of infested trees and increases the amounts of radiation available for the establishment of new individuals or for the growth of understory trees (Mott et al., 1957; Nowierski et al., 1999). In addition, the occurrence of some disturbances, such as fire and insect oubreaks, are linked to climate changes in a complex way (Gilbert and Raworth, 1996; Swetnam and Betancourt, 1998). If human-induced climate changes and disturbances (e.g., climate warming due to increase in anthropogenic "green-house" gases in the atmosphere, and disturbances due to management practices) alter the current growth conditions and natural disturbance regimes, it is likely that there will be changes in forest composition, structure and productivity (Kimmins and Lavender, 1987; Graumlich et al., 1989; Hebda, 1994, 1997; Williams and Liebhold, 1995). Whereas some of these changes might be beneficial for the long-term forest productivity and integrity of forest ecosystems, others might be harmful (Overpeck et al., 1990; Karl et al., 1997; Knutson, et al., 1998).

In British Columbia (BC), there are a variety of forest ecosystems (Meidinger and Pojar, 1991) which are supported by a diverse and complex landscape and will be subject to change under the influence of climate change and related disturbance (Hebda, 1997; Hebda and Brown, 1999). The potential climate warming of 2 to 5°C in BC in the middle of this century (McBean and Thomas, 1992; Hengeveld, 2000) has been raising concerns about potential changes in timber yields and forest ecosystems (Kimmins, 1997: Hebda, 1998). Such concerns include the ability to accommodate these uncertain effects in order to ensure a sustainable forestry (Wilson and Wang, 1998). The natural disturbances in forests of coastal BC include mainly wildfires, windstorms, droughts, and insect infestations (BC Ministry of Forests and BC Ministry of Environment, Lands, and Parks, 1995). These disturbances vary in their frequency, duration, intensity and extent, and have different effects on forest growth (Parminter, 1998). Given that we need to maintain a sustainable forest ecosystem in the context of potential climate warming and continued management practices, it is pertinent to ask how will BC forests respond to future climate and disturbances. Particularly critical is the question how will forests respond in a period of climatic change or severe stress. Studies of proxy climate indicators, such as tree-rings (Laroque, 1995, Zhang, 1996; Smith and Laroque, 1998; Gedalof, 1999), pollen (Allen, 1995; Hebda, 1995; Heinrichs, 1999; Brown, 2000), and glacier activity (Desloges and Ryder, 1990; Smith and Laroque, 1996) have shown that climate in the Holocene could change gradually or suddenly, and these changes affected the forest structure and productivity in many ways, such as changing the composition of forest species, moderating some factors that limit forest growth, and increasing site stress for tree growth (Hebda, 1994, 1997; Hebda and Whitlock, 1997; Hebda and Brown, 1999). Understanding the year-by-year growth response characteristics of forest trees to climatic change will help managers develop adaptive strategies to maintain sustainable forest ecosystems; it will also allow us to examine past climates and gain insight into the way they change.

Seeking answers to the climate-growth relationships through direct field experimentation is impractical because of the need for observation for a long time interval (decades to centuries) and over a large area (regional). Patterns of tree-ring growth response to climate and disturbances in the late Holocene can provide a framework for evaluating environmental changes and their effects on tree growth (Swetnam and Betancourt, 1998; Landres et al., 1999). Spatial variation of response patterns can be investigated by studying tree-ring growth responses in different areas.

Our current knowledge of the climate-growth relationships and of the impacts of disturbance on tree growth is limited for several reasons. First, traditional approaches for detecting climate-growth relationships are mainly based on linear regression techniques, whereas the biological processes of a tree's growth is likely non-linear and complex (Fritts, 1976; Graumlich and Brubaker, 1986; Keller et al., 1997). For example, the role of water in tree growth can vary depending upon the amount of water supply and the interactions with other growth controlling factors, e.g., greater effect when the supply is inadequate and temperature is too high (Fritts, 1976). Therefore, the linear techniques may not reveal the real nonlinear and complex climate-growth relationships, and may affect the way we interpret past environment and the way we predict growth response.

Second, the application of tree-ring data to studies of climate/growth patterns in regional scale requires understanding of the climate-growth responses at multiple sites of the region. In British Columbia, there is a diverse and complex landscape where steep climatic and ecological gradients occur (Cannings and Cannings, 1999). Therefore, the site-specific growth characteristics of a tree species cannot be expected to reflect the whole spectrum of the relationships between tree growth and environmental factors. Particularly, in the coastal mountain area, the effects of elevation-related climatic factors on tree-ring growth are not well understood.

Third, the observed record of climate and natural disturbances is relatively short, and longer proxy record usually contains a wider range of natural variability. Tree-rings, especially those from ancient trees produced in different climate and disturbance regimes in the late Holocene can help us examine past environmental changes and gain insights into the way they affect tree growth (LaMarche, 1974, 1978). Such information about ancient tree growth is rarely available due to the difficulties of obtaining well-preserved wood (Pilcher and Hughes, 1982). This lack of data makes it difficult to analyze the full spectrum of growth response to environmental variations.

1.2 Objectives and Organization of the Dissertation

This research project attempts to resolve the preceding three problems in the study of climate-growth response of Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) trees in coastal British Columbia. Douglas-fir is a pre-eminent species in coastal BC forests in terms of both scale and commercial importance, and has long served as the cornerstone of the provincial economy (Rajala, 1998). Tree-ring and pollen studies in this region reveal that climate change has historically affected the growth of individual Douglas-fir trees as well as the forest composition and structure (Allen, 1995; Hebda, 1995, 1997, 1998; Zhang, 1996; Hebda and Brown, 1999). The maintenance of a sustainable forestry in the context of future climate change mandates a need to understand the response characteristics of Douglas-fir trees to climate changes. To meet that need, the overall aim of this research has been to determine the relationships between climatic factors and the radial growth of Douglas-fir trees, and to apply such knowledge to understand the past range of variability in environments so as to provide a base line for evaluating the effects of current climate change and disturbance.

To do so, dendrochronological techniques[1] (Stokes and Smiley, 1968; Fritts, 1976) are used to develop tree-ring chronologies of Douglas-fir at different sites in coastal BC. The year-by-year variations in tree-rings are a result of changes in limiting environmental factors, and the growth response is modeled by traditional linear regression techniques (Fritts, 1976) and by recently developed nonlinear artificial neural network method (Guiot et al., 1995; Keller et al., 1997, 1998). The discovery of subfossil logs from the bottom of Heal Lake on southern Vancouver Island (Hebda, 1994) provides an exceptional opportunity to examine tree-ring growth characteristics under different climatic regimes at the same location. Tree-rings in the past, therefore, can serve as a biological time capsule that contains information of past environmental changes. Deciphering the information in these time capsules will provide great help in our effort to understanding the on-going ecological processes and anticipating the future (Morgan et al., 1994).

Specifically, the following objectives are pursued in the study.

1) to develop a climate-growth response model capable of predicting nonlinear effects of climatic variables on the radial growth of coastal Douglas-fir trees.

2) to establish the radial growth characteristics of Douglas-fir in regionally different climate regimes (southern Vancouver Island vs. Central Coast), and to explore the radial growth patterns in relation to elevational changes.

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[1] refers to the development of tree-ring chronology through crossdating and standardization which will be described in chapter 3.

3) to determine the radial growth patterns of Douglas-fir at the same site under different climate regimes in the late Holocene, and to identify disturbances that significantly affect tree-ring growth.

Understanding the biology and ecology of tree-ring formation is necessary in dendrochronological studies because the characteristics of tree-rings, e.g., ring-widths, earlywood, latewood and ring-density, and their relationships with the environment are the basis for interpretation of tree-ring variations. Chapter 2 describes the biological basis of tree-ring formation, and the ecological aspects of stresses and disturbances and their effects on tree-ring growth.

Chapter 3 covers the methodology of tree-ring analysis in environmental studies. A two-level linear aggregate model is proposed as an improved conceptual framework for tree-ring studies of environmental change. The methods of developing tree-ring chronologies are described, and the concept of Artificial Neural Networks (ANN) in modeling nonlinear and complex climate-growth relationships is introduced. The application of tree-ring chronologies and climate-growth relationships to environmental studies is discussed.

Chapter 4 deals with the development of growth response ANN models using tree-ring and climate data from Douglas-fir trees at the Heal Lake site of southern Vancouver Island. The applications of the ANN models in predicting growth response to a given set of climatic conditions and in understanding the climate-growth relationships are described. The ANN modeling of climate-growth responses is demonstrated to be superior to traditional linear regression techniques because of its potential to capture nonlinear relationships between tree-ring growth and climatic variables.

Chapter 5 examines the spatial patterns of Douglas-fir tree-ring growth in three sites on southeastern Vancouver Island and nine sites of different elevations in Bella Coola area of central coast BC. Principal component analysis is applied to summarize the various growth-response signals and extract the dominant modes of variability in Bella Coola area. The radial growth patterns along elevational gradients are analyzed, and the common growth patterns are related to climatic factors. The radial growth responses of Douglas-fir under regionally different climate regimes are compared to examine whether temperature or precipitation, or a combination thereof, is the predominant growth controlling factor operating on a macro-regional scale.

Chapter 6 analyzes the late Holocene growth variations in subfossil Douglas-fir discovered from the bottom of Heal Lake, southern Vancouver Island. Radiocarbon dates of selected samples and tree-ring crossdating techniques are used to date the subfossil logs in an interval of time. Five floating ring-width chronologies are developed for the past 3rd and 4th millennia using 79 crossdated log samples. Distinct patterns in the tree-ring chronologies are identified and described. A major focus is the 4000 year before present (BP) horizon, a time of known regional climatic change (Hebda, 1995; Heinrichs, 1999; Brown, 2000).

The final chapter summarizes the major findings and discusses their implications to forest management as well as for scientific research involving tree-rings and climate change. The chapter concludes with suggestions for further research.

Chapter 2 Tree-Ring Formation: Biological and Ecological Aspects

The radial growth of a tree is affected by a variety of environmental factors, which include water supply, temperature, fire, insect infestation, competition, and others (Fritts, 1976). This chapter describes the biological and ecological aspects of tree-ring formation, the knowledge of which is essential in tree-ring chronology development, interpretation and application in environmental studies.

2.1 The Biology of Tree-Ring Formation

The biology of tree-ring formation is described in many books on botany and tree physiology (e.g., Raven et al., 1986; Mauseth, 1991, Taiz and Zeiger, 1998). Since tree-ring formation is the integrated result of many biological processes (Fritts, 1982), it is helpful to review some of the basic botanical and physiological concepts of tree growth before tackling the ecological aspects of the relationships between environmental factors and tree-ring growth.

The growth of a tree starts from the germination of a seed, followed by both longitudinal and radial growth, also known as primary and secondary growth (Raven et al., 1986; Mauseth, 1991). Longitudinal growth is due to cell divisions in shoot and root apical meristems (tissues capable of producing new cells by cell division). Radial growth is due to cell division in the vascular cambium, a secondary meristematic tissue formed from differentiated cells. During the growing season, the vascular cambium, which is a cylindrical structure surrounding the stem wood, produces xylem cells inward to form new wood, and phloem cells outward to form new bark. It remains dormant in the non-growing seasons. For conifers growing in temperate zone, the xylem cells produced during spring and early summer are light-colored, large-sized and thin-walled, and are called earlywood (or spring wood), whereas the xylem cells produced in summer and before seasonal dormancy are usually dark-colored, small-sized and thick-walled, and are called latewood (or summer wood) (Figure 2.1). One year's growth of earlywood and latewood together forms one annual ring, and it can be distinguished from the previous year's ring by the sharp boundary between last year's latewood and current year's earlywood. The predominant cells in a conifer ring are tracheids, which have thick lignified walls and are vertically oriented and tube-liked in shape (Figure 2.1). Other components of a ring include thin-walled parenchyma cells, such as horizontally oriented ray cells, epithelial cells, and storage cells (Figure 2.1). Tracheid cells die when they mature and become functional, whereas parenchyma cells often remain alive for many years in the sapwood, the outer light-colored portion of the stem. Metabolic wastes move inward (toward the center of the stem) through the living rays and are deposited at the point where these cells are no longer living so that the wood inside the sheath of living rays turns darker and is referred to as heartwood. In some species (e.g., Douglas-fir), tree-rings contain resin ducts, which are tubular spaces sheathed by living parenchyma and are both horizontally and vertically oriented (Figure 2.1).

Although the anatomy of tree-rings is relatively well understood, the internal physical and physiological processes governing the characteristics of a ring, such as the total width of a ring, the proportion of earlywood and latewood, and the ring density, are not well understood (Haigler, 1994; Kozlowski and Pallardy, 1997). Tree-ring growth

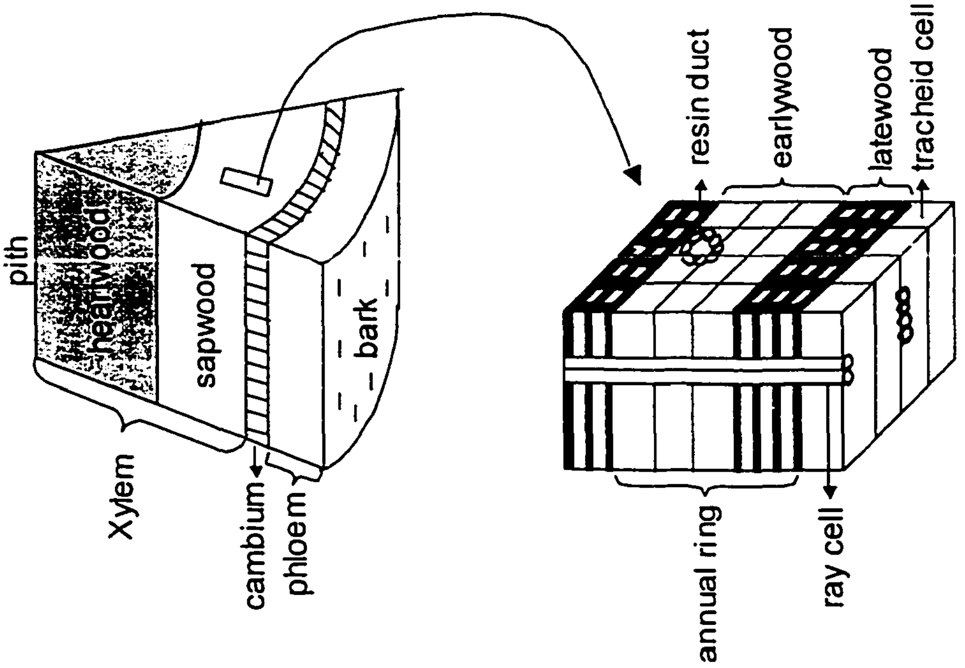

Figure 2.1 Stylized drawing of a block of wood showing the anatomical features of stem radial growth in Douglas-fir.

is the result of cambial cell division followed by cell enlargement and maturation. These three processes require adequate growth conditions and the availability of sufficient growth materials that must be transported to the cambium from other parts of the tree. The synthesis and transportation of the growth materials are part of a complex physical and physiological system in plants. In general, water and mineral nutrients are absorbed by roots from soils and transported upward through tracheids; whereas carbohydrate and hormonal growth regulators are produced by photosynthesis in leaves and transported downward through sieve cells in the phloem. Ray cells transport substances required for growth horizontally (Figure 2.2).

The growth rate of a tree is determined by three major physiological processes, namely, food synthesis, translocation, and cell assimilation (Fritts, 1976; Fritts et al., 1999). The food consists of organic molecules such as carbohydrates, fats, and proteins, which serve to provide the energy and organic materials required for the growth of a tree. It is synthesized through a variety of biochemical reactions, the most basic of which is the photosynthesis and respiration. The photosynthesis produces glucose from inorganic molecules and converts light energy into chemical energy, whereas the respiration releases chemical energy for plant use. Translocation refers to the transport of food and growth resources from source to sink areas where they are used by plant or accumulated and stored in parenchyma cells. Cell assimilation is the process by which food is utilized to produce the protoplasm, cell walls, and numerous other substances making up the structure of a cell. These physiological processes involve a variety of biochemical reactions and biophysical activities, which usually interact and are regulated directly or

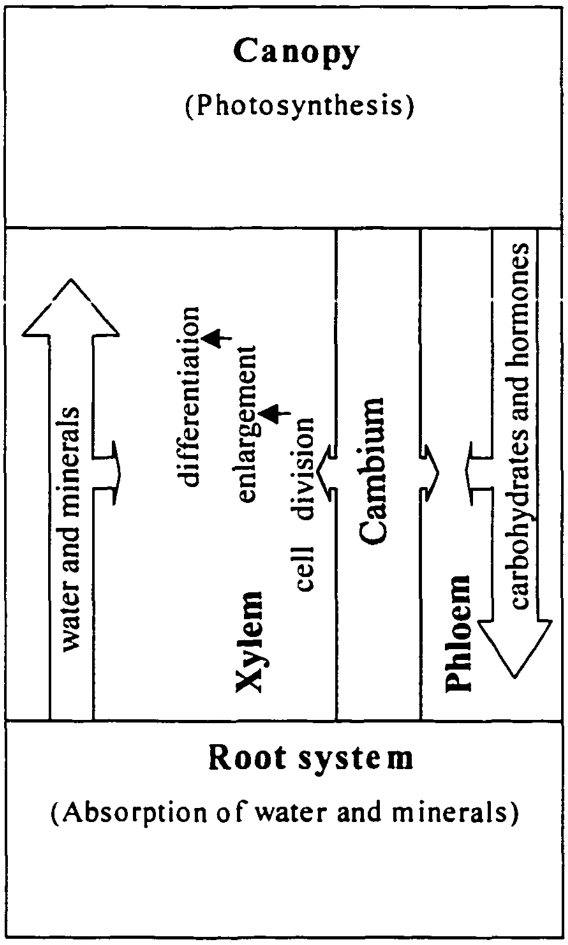

Figure 2.2 Schematic diagram showing the process of tree-ring growth, which involves cambial cell division, the subsequent cell enlargement and maturation, and the transportation of growth materials within a tree.

indirectly by many growth-controlling factors such as water supply, temperature, mineral nutrients, and others. The physiology of these processes has been a major research field (Larcher, 1995; Taiz and Zeiger, 1998), and will not be discussed in detail in this dissertation. The following description of the tree-ring growth focuses on the ecological perspective, with attention paid to the environmental factors limiting the radial growth of Douglas-fir in the Pacific Northwest.

2.2 The Ecology of Tree-Ring Growth

The environmental factors affecting the growth of an individual tree can be classified into two categories: stress and disturbance (Grime, 1977). Stress occurs because of a shortage of resources or suboptimum of conditions that restrict the functioning capacity of plant tissues and, therefore, limit the growth rate of a tree (Grime, 1977; Bazzaz, 1996). Resources are consumable substances, such as nutrients and water, that are required for the growth of a tree; whereas, conditions are non-consumable factors, such as temperature, that influence the biological processes which use those resources (Begon et al., 1990; Ricklefs, 1990). Disturbance refers to external events that cause partial or total destruction of the tree and, therefore, limit the tree's ability for continued biomass production (Grime, 1977). Disturbances fall into two categories: 1) abiotic (from non-living agents), such as fire, windstorm and snow loading, and 2) biotic (from living agents), such as insect and disease infestations (White, 1979).

2.2.1 *Stress*

The growth of a tree requires both essential resources and appropriate conditions. However, in nature these are rarely all in an optimum state (Mooney et al., 1991; Larcher, 1995). Therefore, trees are often subject to a variety of stresses that tend to restrict their growth. In the Pacific Northwest, lack of water is a major stress factor limiting tree-ring growth in areas where there is insufficient precipitation (Lassoie and Salo, 1981; Robertson et al., 1990). Water is required for many biological processes, such as photosynthesis, translocation, and cell development (Taiz and Zeiger, 1998; Wullschleger et al., 1998), therefore, insufficient water supply can inhibit radial growth directly or indirectly by altering many biochemical and biophysical processes. For example, water deficit directly inhibits cell enlargement by reducing the pressure potential of a cell (Slatyer, 1976; Kozlowski and Pallardy, 1997), and indirectly inhibits cell division and differentiation by slowing down the rate of biochemical reactions involved in food synthesis, e.g., reducing the rate of photosynthesis through stomate closure in leaves (Bauerle et al., 1999; Bond and Kavanagh, 1999; Tezara et al., 1999). Water deficit in the growing season may also play a role in inducing early formation of latewood, and reducing the quantity of latewood production (Zahner, 1968; Brix, 1972).

Temperature is another major factor affecting tree-ring growth. Ecologically speaking, temperature plays its most significant role in cambial growth in two ways. First, it plays a role in determining the time of seasonal initiation and cessation of growth thus controlling the length of growing period (Kozlowski et al., 1991; Kozlowski and Pallardy, 1997). Once daily temperature rises to late spring and summer levels, it will show only a weak and indirect relation to the quantity of growth, and other factors usually become more limiting (Fritts, 1976). Second, extreme temperature affects the radial growth of a tree by influencing physiological processes. At low temperatures, biomembranes become more rigid, and the available energy often is inadequate for maintaining the biochemical processes essential for growth (Larcher, 1995). In contrast, high temperatures accelerate molecular activity, which may result in high rates of respiration that deplete carbohydrate pools (Brix, 1967; Larcher, 1995; Kozlowski and Pallardy, 1997). Inhibition of growth at high temperatures also may be associated with excessive evapotranspiration (Kozlowski and Pallardy, 1997) which often result in water stress for tree-ring growth.

Other factors that may produce stress in tree-ring growth mainly include low light and insufficient nutrients. Light is necessary for photosynthesis. When other factors are favorable, biomass production typically increases with the amount of intercepted light until a saturation level is reached (Landsberg, 1986). In Douglas-fir, high rate of photosynthesis occurs at a light intensity of about 600 μmol$\cdot$m$^{-2}\cdot$s^{-1} (Leverenz, 1981a). However, the actual amount of light intercepted by needles is usually insufficient for high rate of photosynthesis because of the three-dimensional nature of tree crowns and the mutual shading of needles between branches of a tree or among different trees (Lassoie, 1982; Lewis et al., 2000). Furthermore, low light levels also inhibit the formation of needle primordia (initial needles in a bud before differentiation) and the expansion of needles and thereby reduce their production of photosynthates, hence regulating stem growth (Kozlowski and Pallardy, 1997).

Nutrients participate in many essential functions in plants, especially as constituents of plant tissues, regulators of cell water potential, and activators or inhibitors of enzyme systems (Kozlowski and Pallardy, 1997). The most known and acknowledged nutrient deficiency in Douglas-fir is that of nitrogen (Radwan and Brix, 1986). Nitrogen fertilization has been shown to increase biomass production by increasing foliage quantity and the rate of photosynthesis (Brix, 1971, 1983; Barclay et al., 1982). A low mineral nutrient level in forest stands is usually chronic, so it causes little variation in stem growth (Fritts, 1976). Changes in the availability of nutrients, such as those caused by stand disturbances, often result in changes in stem growth (Matson and Boone, 1985; Miller et al., 1989; Billow, et al., 1994).

The state of each growth controlling factor can be described as being either in deficiency, at optimum, or toxic on a continuum from minimum requirement to maximum tolerance (Salisbury and Ross, 1992; Larcher, 1995). The biological principle of limiting factors, known as the Liebig's Law of Minimum, states that a biological process, such as tree-ring growth, is limited by the single factor that has the lowest supply relative to need (Blackman, 1905). In natural forests, the environment is unlikely to provide optimal supply for all resources, thus trees are often subject to one or more factors that limit their potential growth (Mooney et al., 1991). The multiple limitation is due to the seasonal variability of the environment that allows different factors to be limiting in different intervals (Fritts, 1976). The strategy of "optimal foraging" in plants (Bloom et al., 1985), which tends to avoid excess uptake of enriched resources and to maximize effort to acquire a limiting resource, can also result in multiple limitation, for which the increase in relatively abundant resources has only a small effect, whereas the increase in rare resources has a large effect (Gleeson and Tilman, 1992). The theory of growth control by limiting factors is important in the study of tree-rings and environmental changes because the temporal variation of the intensity of limiting factors results in changes in ring characteristics, which allow for the crossdating of tree-ring sequences among different trees by matching their ring patterns and, furthermore, for the extraction of past environmental information by correlating the ring characteristics with the limiting environmental factors (Fritts, 1976).

2.2.2 *Disturbance*

The concept of disturbance

The growth of forest trees is often disturbed by a variety of abiotic and biotic factors and agents, such as fire, windstorm, and insects. The role of disturbances in forest growth has received research attention in the past few decades (e.g., see reviews in Pickett and White, 1985; Rogers, 1996; Pickett et al., 2000). The concept of disturbance has evolved from an intuitive physical disruption of a community to a more generalized event that occurs in a variety of ecological systems (Pickett et al., 2000). The definition of disturbance, however, has appeared in different forms and has long been a topic of debate (van der Maarel, 1993). For the purpose of this dissertation, I use the concepts of "structure" given by Pickett et al. (1989) and of "destruction of biomass" given by Grime (1977) to define disturbance as *an event that disrupts the structure of an ecological system by partial or total destruction of its biomass*. The "structure" refers to the arrangement of entities and the interactions among them that result in their organized persistence (Pickett et al., 1989). The entity refers to an ecological object, such as leaves in a tree, with which some action will interfere. The concept of disturbance is scale-dependent and can be applied to a variety of ecological systems over a hierarchical spatial scale. For example, a windstorm that causes partial destruction of the crown of an individual tree is a disturbance to that tree, but not to the forest stand; an insect outbreak that causes canopy defoliation is a disturbance to the forest stand, but not necessarily to every individual tree. Therefore, before disturbance is evaluated, the target ecological system and its structure must be clearly described according to the objectives of the study (Pickett et al., 1989).

If the growth of an individual tree is the focus of examination, the system structure can then be viewed as consisting of three interacting entities: crown-stem-root. Any event, such as windstorm, frost or insect infestation, that disrupts this structure by partial or total destruction of its biomass is a disturbance which can directly affect tree growth by decreasing its functioning capacity. If there is competition for light, nutrients and other resources between one target tree and its neighbors, disturbance to the target tree, such as fire that injures or kills the tree, will indirectly affect its neighbors by altering their growth conditions and increasing their availability of resources (Bazzaz, 1996).

If the collective behavior of tree growth in a forest stand is the focus of research, the system structure can then be viewed as consisting of three interacting entities: canopy-understory-root system. Again, any event, such as fire or insect outbreak that disrupts this structure by partial or total destruction of its biomass is a disturbance. Forest disturbances were previously considered as a destructive force and as a secondary factor to long-term forest succession (Wu and Loucks, 1995). Currently, however, accumulating evidence suggests that disturbances are an important component of the ecological processes that contribute to creating stand heterogeneity, increasing the availability of resources to surviving trees, and sustaining the long-term healthy functioning of forests (Pickett and White, 1985; Forman, 1987; Wu and Loucks, 1995). For instance, canopy disturbance by insect outbreaks in closed forests helps light penetrate into understory layers, and hence facilitates the establishment and growth of light-demanding species (Mott et al., 1957; Ballaré, 1994; Nowierski et al., 1999). The following section emphasizes the effects of disturbances on tree-ring growth, the knowledge of which is useful for interpretation of forest dynamics and tree-ring variations.

Effects of disturbances on tree-ring growth

Disturbances that affect a forest stand may leave evidence in the annual growth rings of many trees. This evidence includes morphological symptoms (e.g., fire scar and reaction wood), growth reduction or mortality in disturbed trees, and growth release in undisturbed trees during and after the disturbance event. Disturbances can be studied by examination of their effects on tree-rings. However, except for a few diagnostic features such as fire scar as an indication of burning, a clear distinction among the different kinds of disturbances is difficult to achieve if merely based on a particular tree-ring response. This problem arises because the growth response of a tree to a particular disturbance may vary considerably, depending upon the tree's age, health state, as well as the intensity and duration of the disturbance (Oliver, 1981).

Insights into the tree-ring response to different disturbances can be gained by understanding the disturbance regimes of the study area and by comparing the response characteristics resulting from observed disturbances. Natural disturbances important to Douglas-fir trees in British Columbia include: fire, windstorm, droughts, and insect outbreaks (BC Ministry of Forests and BC Ministry of Environment, Land and Parks, 1995). The disturbance-induced morphological symptoms (e.g., fire scar and reaction wood) and the manifestation of tree-ring patterns (e.g., abrupt growth reduction) may vary according to the nature of the disturbance. Such different response characteristics provide an opportunity to identify the causal agents. Information from species other than Douglas-fir is considered as relevant knowledge because it relates to principles basic to the understanding of tree-ring response to disturbances. The following description focuses the major characteristics of tree-ring response to intense disturbances by different agents. The effects of less intense disturbances are usually not apparently different from each other and from climate variations and, thus, are difficult to distinguish merely from tree-ring patterns (Bormann and Likens, 1979). Unhealthy trees that have been injured but survived the disturbances generally show a declining growth trend (Manion, 1981; Pedersen, 1998), and will not be discussed in the following comparisons.

Wildfire is an infrequent stand initiating disturbance in Coastal Douglas-fir biogeoclimatic zone (CDF) (BC Ministry of Forests and BC Ministry of Environment, Land and Parks, 1995). Large fires usually occur after periods of extended drought, and the average return interval is about 200 years (Fahnestock and Agee, 1983; BC Ministry of Forests and BC Ministry of Environment, Land and Parks, 1995). Douglas-fir, which has thick fire-resistant bark, has been dominant in the CDF zone because of disturbance by fire and the species' adaptation to fire (Agee, 1991). Pollen records establish that Douglas-fir dominance in the past millennia often coincided with charcoal peaks in the pollen profile (Brubaker, 1991; Brown, 2000). Studies on Douglas-fir (Stewart, 1986; Agee, 1991; Brown et al., 1999), redwood (*Sequoia sempervirens* (D.Don.) Endl.) (Brown and Swetnam, 1994; Brown et al., 1999), and giant sequoia (*Sequoiadendron gigantem* (Lindl.) Buchh.) (Brown et al., 1992; Hughes and Brown, 1992) indicate that tree-rings in the year of fire usually do not show growth suppression. However, abrupt and strong growth release lasting several years to several decades or even up to a century, depending on the intensity of the fire, is a typical response in tree-rings following the fire. This pattern occurs because fire not only reduces competition by killing the surrounding trees, but also increases the availability of some nutrients by processes such as enhanced rates of decomposition and mineralization (Wright and Bailey, 1982; Zhang, 1993, 1994). Fire may also leave some visible morphological features on tree-rings such as a fire scar, double latewood (a brief return to the production of earlywood-type cells during the period of latewood formation), locally missing rings, and resin ducts (bands of traumatic resin ducts formed parallel to ring boundaries) (Brown and Swetnam, 1994).

Windstorms can cause damage to trees by toppling and uprooting trees, breaking branches and stems, and removing leaves. Such damage can cause abrupt radial growth reduction, if not death, by increasing dehydration of the leaves and decreasing total photosynthesis (Kozlowski and Pallardy, 1997). Wind-thrown trees not only create a relatively open canopy, but also provide an agent of soil mixing by producing pit and mound micro-relief (Stephens, 1956; Armson and Fessenden, 1973; Schaetzl et al., 1989). In the years following the windstorm, the surviving trees usually show an abrupt and medium to strong growth release lasting several years to a few decades (Peters, 1998). Frequent and strong winds greatly modify tree size and form, and result in asymmetric crown (Telewski, 1995). Tree-ring growth in such situations is usually greater on the leeward side than the windward side of the stem (Bannan and Bindra, 1970). The effects of windstorms on tree-ring growth vary with meteorological conditions (e.g., wind speed and storm duration), topographic characteristics (e.g., wind exposure and direction), stand and tree characteristics (e.g., stand height and density and rooting strength) (Stathers et al., 1994; Parminter, 1998). Information about the temporal patterns of windstorms is limited because of the difficulty in obtaining long time-series of windstorm records.

Severe drought is considered to be a stand disturbance because it can cause structural changes of the stand by initiating stress-induced mortality to individual plants (Elliott and Swank, 1994; Villalba and Veblen, 1997; Swetnam and Betancourt, 1998). The occurrence of regional drought is related to the mode of atmospheric circulation which has a Pacific/North America (PNA) teleconnection pattern (Wallace and Gutzler, 1981, Cayan et al., 1998). Compared to wildfire and windstorm, the radial growth suppression due to drought is characterized by being less abrupt, lasting longer (usually several years to a few decades), and appearing in all trees in the stand (Barden, 1988;

Elliott and Swank, 1994; Savage, 1994). The growth release resulting from the death of neighbor trees is usually not apparent compared to those from wildfire and windstorm (Case and MacDonald, 1995).

Insect infestations are a major biotic disturbance that affects tree growth by causing defoliation, removal of growing materials in sapwood, and death of cambium (Williams, 1967; Nowierski et al., 1999; Zhang et al., 1999). The Douglas-fir tussock moth (*Orgyia pseudotsugata* (McDunough)) and western spruce budworm (*Choristoneura occidentalis* Freeman) are the two most important defoliating insects attacking Douglas-fir trees. In the CDF biogeoclimatic zone, however, the outbreaks of these two insects are infrequent (Russell et al., 1986).

Compared to abiotic disturbances, the effects of insect outbreaks on tree's radial growth have been well studied. The separation of signals from insect attacks and other factors (e.g., climate) is carried out by comparing growth responses in insect host and non-host tree species, i.e., growth suppressions due to outbreaks only occur in host trees, whereas those due to adverse climate occur in both host and non-host trees (Alfaro et al., 1982; Swetnam et al., 1985; Swetnam and Lynch, 1993). In general, the radial growth in Douglas-fir trees decreases during outbreaks of tussock moth and western spruce budworm, and such growth reduction usually lags 1-3 years following outbreaks (Brubaker, 1978; Wickman et al., 1980; Alfaro et al., 1982; Mason et al., 1997). In some cases tree-rings prior to the first year of significant defoliation show a positive growth response, which might be related to the elimination of inefficient crown foliage (Graham and Knight, 1965; Alfaro and Shepherd, 1991; Mason et al., 1997). Variations in response patterns are due to defoliation history, tree size, nutritional resources, physiological condition, and inherent susceptibility to damage (Kulman, 1971, Wickman et al., 1980; Alfaro et al., 1985; Nichols, 1988; Wickman et al., 1992; Mason et al., 1997). Such variations make it difficult to distinguish the effects of insect attacks and those of abiotic disturbances.

Although both tussock moth and budworm cause growth reduction in Douglas-fir trees by consuming foliage, there are differences in their behavior and, therefore, in their effects on ring growth, which permit the two defoliators to be distinguished (Brubaker and Greene, 1979). Tussock moth outbreaks start rapidly and are usually only 3 to 4 years long, whereas budworm outbreaks typically build gradually and last 10 or more years (Wickman et al., 1973; Brubaker and Greene, 1979). As a result, tussock moth usually causes a rapid growth reduction and greater loss during the short infestation years; in contrast, the radial growth reduction due to budworm is gradual and lasts longer before recovery (Brubaker and Greene, 1979).

The radial growth of forest trees in stands subjected to insect outbreaks usually shows periodic growth suppressions and releases due to recurrence of insect infestations, which are controlled by intrinsic population dynamics (e.g., density-dependent regulation) and/or extrinsic factors (e.g., climate fluctuations) (Royama, 1984; Huffaker et al., 1999). Studies of radial increments in Douglas-fir trees in central BC show that budworm outbreaks recurred around the late 1910s-early 1920s, 1950s, and late 1970s (Shepherd et al., 1977; Alfaro et al., 1982; Harris et al., 1985). Studies of other insects and tree species, such as the two-year cycle spruce budworm (*Choristoneura biennis* (Freeman)) in spruce-fir forests of central BC (Figure 2.3) (Zhang and Alfaro, 2000), also indicate that insect outbreaks are pseudo-periodic and tree-ring response to outbreaks is stronger than that to climatic fluctuations (Blais, 1965, 1983; Jardon et al., 1994). The stronger response to outbreaks is due to: 1) the destruction of considerable quantities of leaves, which leads to a great reduction in photosynthesis; and, 2) the removal of mature and overmature host trees, which prevents the perpetuation of decadent stands and brings about a rejuvenation of the forest (Wickman et al., 1980; Blais, 1983; Alfaro and Shepherd, 1991).

In summary, the disturbance regime of the CDF zone is characterized by small-scale, low-intensity, and infrequent disturbances that are dispersed in time and space and that occur through a diversity of processes (Lertzman et al., 1996). To identify the causal disturbance factor merely from tree-ring patterns remains a difficult problem. In most cases the tree-ring record should be used only as supportive evidence of a specific disturbance when corroborative evidence is available from other sources. Understanding the biology and ecology of tree growth is essential for interpretation of tree-ring variations.

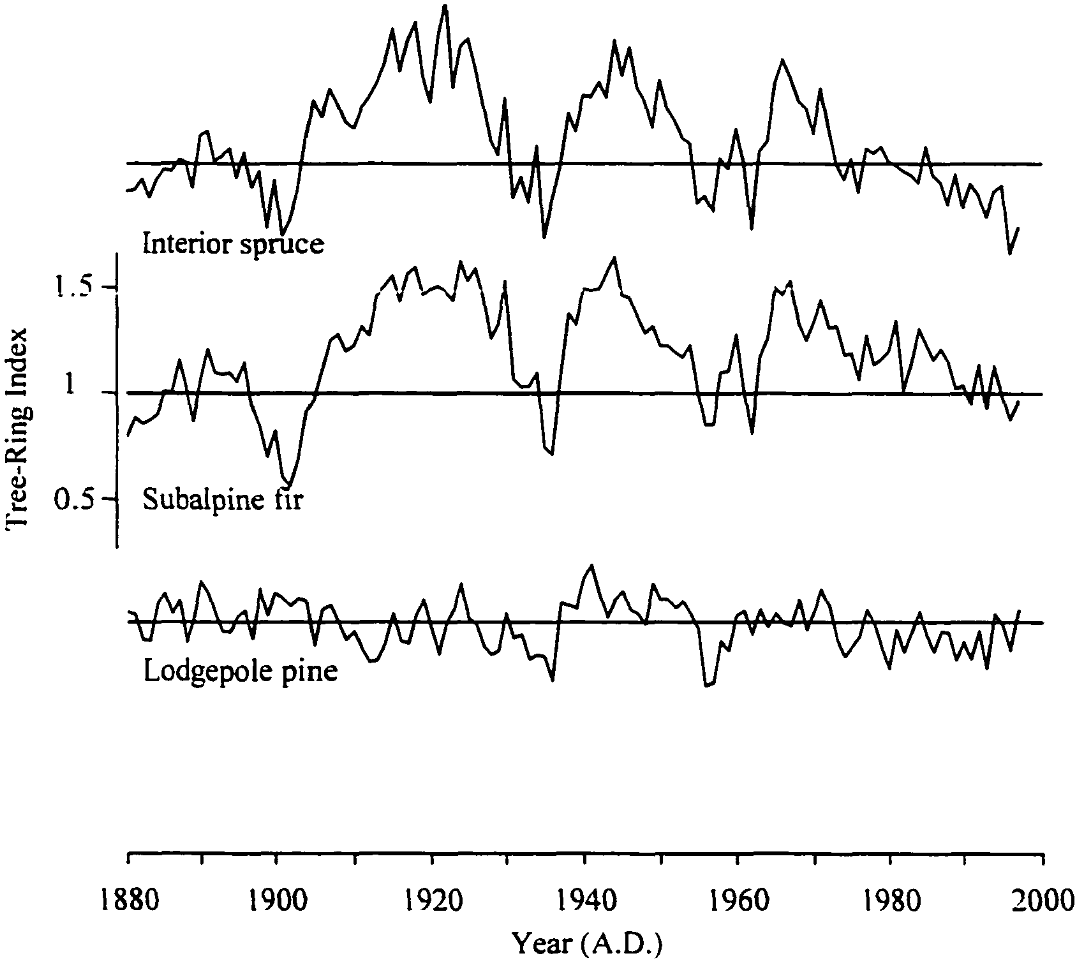

Figure 2.3 Periodic suppressions and releases of growth in interior spruce and subalpine fir, host tree species to the two-year cycle spruce budworm, in Fort St. James area, central British Columbia. The ring-width chronology of lodgepole pine, a nonhost tree species, is used to separate the effects of climate on tree growth (from Zhang and Alfaro, 2000).

Chapter 3 Methodology

The method of using tree-rings to study environmental changes has been developed and improved rapidly since its foundation by A.E. Douglass in the early 1900s, and has formed the unique discipline called dendrochronology (*dendro* refers to tree in Greek, and *chronology* to the study of time) (Fritts, 1976). This chapter describes the dendrochronological methods that have been used in this study. Section 3.1 discusses the conceptual framework of tree-rings and environments. Section 3.2 examines the techniques of developing tree-ring chronologies. Section 3.3 discusses the use of tree-ring chronologies for environmental studies.

3.1 Tree-Rings and Environment: a Conceptual Framework

Tree growth is affected by variations in environment, and the yearly sequence of favorable and unfavorable environmental conditions can be faithfully recorded by the sequences of wide and narrow rings in a large number of trees (Fritts, 1976). This relationship forms the basis for using tree-rings to study environmental changes. The interpretation of tree-rings, however, is not an easy task because of the complex relationships between tree growth and environment. Furthermore, each tree within a forest stand may record different amounts and/or types of environmental signal due to the influence of microsite conditions and disturbances occurring at different spatial scales. Considering the complex nature of the relationships, a simplified conceptual framework is useful to better understand and interpret tree growth-environment interactions. This section examines the linear aggregate model of tree-ring analysis (Cook, 1987), and suggests a two-level linear aggregate model as an improved conceptual framework for tree-ring studies.

3.1.1 *The Linear Aggregate Model and Its Limitations*

The range of concepts and principles behind using tree-rings to study environmental changes have been described in several publications (Fritts, 1976; Fritts and Swetnam, 1989). Cook (1987) proposed a linear aggregate model as a simplified conceptual framework for studying tree-rings and environment. In this model, one year's radial growth, denoted as R_t, is considered as a linear aggregate of five discrete classes of signals.

$$R_t = A_t + C_t + dD1_t + dD2_t + E_t$$

Where, A_t is the age-related growth trend which reflects, in part, the geometrical constraint of adding a volume of wood to a stem of increasing radius; C_t is the climate-related environmental signal; d is a binary indicator for presence (d=1) or absence (d=0) of the disturbance specific to the tree ($D1_t$) or generally to all the trees in a stand ($D2_t$); and E_t is the unexplained year-to-year variability not related to the other signals, e.g., microsite differences within a stand and gradients in soil characteristics.

This linear aggregate model divides environmental factors into four discrete types and estimates the signal from each type separately by using different techniques, the details of which will be discussed in the next section.

Although this model is helpful for understanding the framework of tree-ring analysis, the way it considers environmental factors is not fully satisfactory for the following reasons. First, a target ecological system and its structure must be clearly defined for the study of disturbance (Pickett et al., 1989). The formulation of the linear aggregate model is primarily concerned with the growth of an individual tree, but the classes of signals used in the formulation operate at different scales and relate to different targets, e.g., the individual tree under study (A_t, and in some cases $D1_t$), its neighboring trees (some cases of $D1_t$), and the standwide forest (C_t and $D2_t$). This lack of definition and consistency of target system may cause confusion in the interpretation of tree-ring data and result in difficulties when communicating observations among researchers of different disciplines. For example, should climatic events, such as severe drought, be considered as a climatic signal (C_t) or a standwide disturbance ($D2_t$)? To what intensity/extent can a destructive event be considered as a stand disturbance?

Second, the radial growth of a tree is determined by environmental stresses and disturbances (Grime, 1977). In the linear aggregate model, the signal A_t is separated from other environmental signals and is termed as the age-related growth trend. However, this growth trend, when practically used as a detrending curve in the development of a stand tree-ring chronology, may include a variety of signals depending on the purpose of the study and it may not be related only to the tree's age. For example, when the standwide climate is of primary interest, as in dendroclimatic studies, the radial growth trend that needs to be removed when producing stand tree-ring chronology usually includes, as much as possible, the signals resulted from the effects of standwide disturbances as well as local factors, e.g., substrate conditions and local disturbances to the tree under study or to its neighbouring trees. Therefore, this growth trend is not a simple one that relates to the age of the tree, but it also relates to the effects of different environmental factors.

3.1.2 *Two-level Linear Aggregate Model as an Improved Conceptual Framework*

With the advance in the research of forest ecology, there has been growing recognition that climate changes and ecological disturbances are two important factors affecting the dynamics of forest growth (Wu and Loucks, 1995; Millar and Woolfenden, 1999). Studies of the effects of climate and disturbance on forest trees have shown that tree growth is affected by multiple limiting factors and by disturbances of different scales (see section 2.2). Based on these new concepts, it would seem that a two-level linear aggregate model may provide a more appropriate conceptual framework for tree-ring studies of environmental changes.

The new conceptual framework recognizes two levels of the ecological system: the individual trees and the forest stand (Figure 3.1). At the level of the individual tree, each tree is viewed as a complex structure consisting of three interacting entities, i.e., crown-stem-root. The external factors affecting a tree's growth fall into two categories: stress and disturbance. At the forest stand level, a stand is viewed as a complex structure consisting of three vertically layered and interacting entities, i.e., canopy-understory-root zone. The external factors affecting forest growth include two categories: climate and disturbance. The reason to define two systems at different levels is based on the nature of tree-ring analysis which involves examination of factors affecting both the individual trees and the standwide forest, and on the current concept of disturbance which requires the system of concern to be explicitly defined (Pickett et al., 1989).

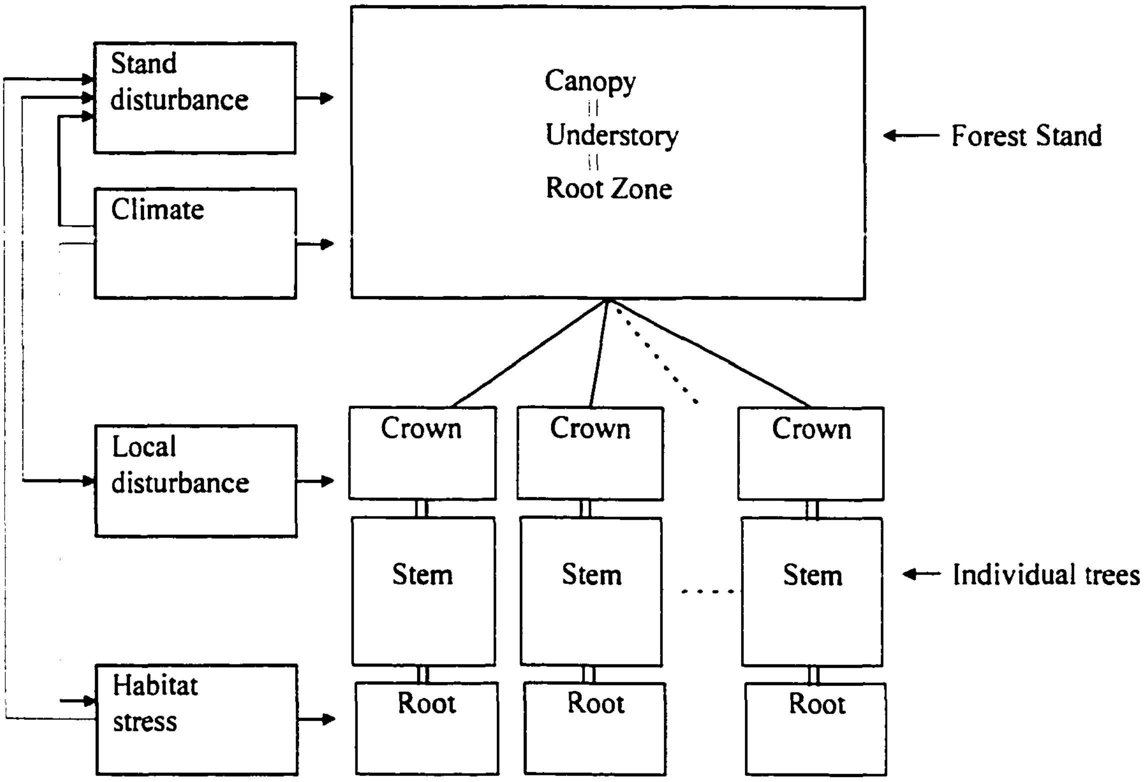

Figure 3.1 A two-level linear aggregate model for tree-ring analysis of environmental changes. The external factors affecting the growth of an individual tree include habitat stress and local disturbance; whereas, at the forest stand level, the external factors affecting forest growth include standwide climate and disturbance. There are interactions between environmental factors within a level and between the two levels.

In dendrochronological analysis, standwide climate and disturbances are usually of interest. The information concerning these factors is obtained from stand level tree-ring chronologies developed from a number of individual sampled trees. Therefore, the development and interpretation of tree-ring chronologies involve two levels of the system, i.e., the individual tree and the stand.

At the level of individual tree, one year's tree-ring growth is considered as a linear aggregate of signals from stresses and disturbances. The stress can be decomposed into three sources, i.e., substrate, competition, and climate-related factors. The substrate stress refers to growth constraint by insufficient resources or sub-optimal conditions in the local substrate, and it may gradually increase or decrease with the change in growth demand as the tree ages. The competition stress, which is caused by resource competition by neighbouring trees, gradually changes with the change in competition environment of an aging tree (Bazzaz, 1996) and abruptly changes with the disturbances to its neighbours (Blasing et al., 1983). Climate stress refers to growth constraints resulting from climate-related factors, such as water stress due to low precipitation, and it changes with the variation in standwide climate. Disturbances limit the tree's growth by partial or total destruction of its biomass.

At the forest stand level, climate variation and stand disturbance are the main causes for collective growth-behavior of forest trees. Climate changes alter the growth conditions and resource supply to virtually all the trees in the stand, although the degree of response in different trees may vary due to the effects of local factors. For example, trees growing on slopes covered in coarse shallow soil are more sensitive to precipitation changes than those growing on level ground in deeper, less coarse soil (Fritts, 1976). Stand disturbances, e.g., surface fire and insect outbreaks, affect the growth of a large number of trees (if not all) by altering their growth conditions and availability of resources. Although stand disturbances are discrete events in time, their consequences on forest trees may last a long time because disturbances, such as spruce beetle outbreaks, may have a thinning effect by causing death of some trees and facilitate the growth of surviving trees for many years (Glenn-Lewin and van der Marrel, 1992; Zhang et al., 1999).

There are interactions between the environmental factors within each level and between two levels (Figure 3.1). The degree of stress to an individual tree is affected by disturbances to its neighbouring trees and by the standwide climate. Disturbances to an individual tree may also be a part of the stand disturbances. Climatic events, such as severe droughts, can be transformed into a disturbance if the climate-induced stress results in mortality of many trees and changes the structure of the forest stand (Swetnam and Betancourt, 1998; Pickett et al., 2000). Climate changes may also affect the susceptibility of a forest to disturbances. For example, climate warming favors increased rates of forest fire, as a result of increased probability of drought, wind and natural ignition sources (Overpeck et al., 1990). One disturbance may predispose the stand to another disturbance. For example, windthrow plays a role in triggering spruce beetle outbreaks in spruce subalpine forests (Veblen et al., 1991).

The extraction of standwide climate and/or disturbance signals from tree-ring samples is accomplished by separation and exclusion of those signals that are not of interest through dendrochronological techniques. The result of the extracted signals is expressed as a stand tree-ring chronology. The next section describes the methods of developing tree-ring chronologies.

3.2 Methods of Developing Ring-Width Chronologies

The development of stand ring-width chronologies involves three basic procedures: 1) sample collection, preparation, and measurement, 2) crossdating, and 3) standardization and chronology formation. The following description and review of these procedures is not exhaustive. More detailed information on the method of developing ring-width chronologies can be found in a variety of publications (Stokes and Smiley, 1968; Fritts, 1976; Hughes et al., 1982; Fritts and Swetnam, 1989; Cook and Kairiukstis, 1990).

3.2.1 *Sample Collection, Preparation, and Measurement*

Tree-ring samples are usually collected in the form of increment cores or discs. Field sampling strategy is designed to reflect the environmental factors of particular concern. In this study, the increment core samples are collected selectively, with consideration of the sensitivity of trees to climatic variations so as to reduce the signals of nonclimatic factors (e.g., competition between trees, crown conditions, etc.). The sensitivity of ring-widths is measured by the relative changes in neighbouring rings using the following formulas (Fritts, 1976):

$$\text{Sensitivity} = \frac{2 \times |r_1 - r_2|}{|r_1 + r_2|}$$

Where, r_1 and r_2 are ring-widths of two successive rings. Fritts (1976) discussed the sensitivity of tree-rings in relation to site habitat. For example, precipitation-sensitive trees are usually found in a slope habitat with coarse soil.

The preparation of increment core samples includes mounting the cores into slotted wooden boards, and polishing the sample surface with sand papers of progressively finer grit up to 600. Detailed description of the preparation technique can be found in several publications (e.g., Stokes and Smiley, 1968; Swetnam et al., 1985). A major care in preparation is to mount samples with their cross-section facing up in the wooden board so as to obtain the clearest characteristics of the rings (Stokes and Smiley, 1968). For disc samples, a radius of interest is selected based on the wood quality and the ring's sensitivity to the environmental factor(s) under study. The selected radius is then prepared by either polishing with sand papers or grooving with a sharp carving gouge to make the ring features clearly readable.

Measurement of ring-widths can be carried out using a variety of systems, in which the measuring stage, such as a traveling microscope or a scanner, is electronically interfaced with a computer that serves as the data recorder and editor (Pilcher, 1990). The traditional systems are characterized by moving a microscope over the ring series or moving a sample under a fixed microscope and recording ring-widths by hand-clicking a digital micrometer on each ring boundary. Examples of these systems include the MEASU-CHRON Digital Micrometer (Micro-Measurement Technology, Bangor, Maine, USA) which has a moving microscope, the Digimic tree-ring incremental measuring system (Holman Digimicrometer, New Brunswick, Canada) which has a moving sample stage, and others (Cook and Kairiukstis, 1990).

In recent years, image analysis has emerged as an important technique in ring-width measurement, an example of which is the Windendro™ Image System (Régent Instruments Inc., Québec, QC, Canada), which consists of a scanner and a computer. This system automatically detects ring boundaries on the scanned image of tree-ring samples according to colour changes between one ring (ending with dark latewood) and the next (beginning with bright earlywood). A line tangent to ring boundary is assigned to each ring and the ring-widths can be measured and recorded (Régent Instrument Inc., 1997). The Windendro™ Image System allows users to adjust the positions and orientations of the machined-assigned ring boundary lines to correct possible mistakes in ring detection. The system is able to measure ten ring parameters including widths of total ring, earlywood and latewood, percentages of earlywood and latewood in a total ring, brightness (i.e., intensity of reflected light) of total ring, earlywood and latewood, minimum brightness of earlywood, and maximum brightness of latewood. Among these variables, the annual ring-widths have proven to be a useful indicator of environmental changes (Fritts, 1976), and the brightness variables have been demonstrated to be an alternative to density for dendroclimatic studies (Thetford et al., 1991; Sheppard et al., 1996).

The precision of ring-width measurement using the above systems is 0.01mm. Errors of measurement, such as missing one or more rings or counting more rings within one ring, can usually be detected by crossdating which will be described in the next section.

3.2.2 *Crossdating*

A single tree-ring sequence might contain some missing rings or false rings (rings not measured for some years or more than one ring measured within a single year) because of failure of biological activities in some years, or environmental changes within a growing season, or simply due to mistakes in the measurement (Fritts, 1976). Crossdating is the procedure of matching tree-ring variations among different trees in the study area, in order to identify missing or false rings and assign each ring with an exact year either relative to or absolute of formation (Figure 3.2). This procedure is based on the recognition that trees growing in the same period and under the same controlling factors exhibit similar variation in the year-to-year ring sequences (Ferguson, 1968; Fritts, 1976)[2]. The techniques of crossdating include the skeleton plot, graphic comparison of ring sequences, correlation test by computer programs, and visual comparison of ring characteristics (Fritts, 1976; Swetnam et al., 1985).

A skeleton plot is a graphical means of representing tree-ring widths (Strokes and Smiley, 1968; Swetnam et al., 1985). It is constructed for each sample by plotting the

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[2] Trees that do not have distinct rings, such as those growing in tropical areas where there are not distinct seasonal variations, are difficult to crossdate and are not considered in this discussion.

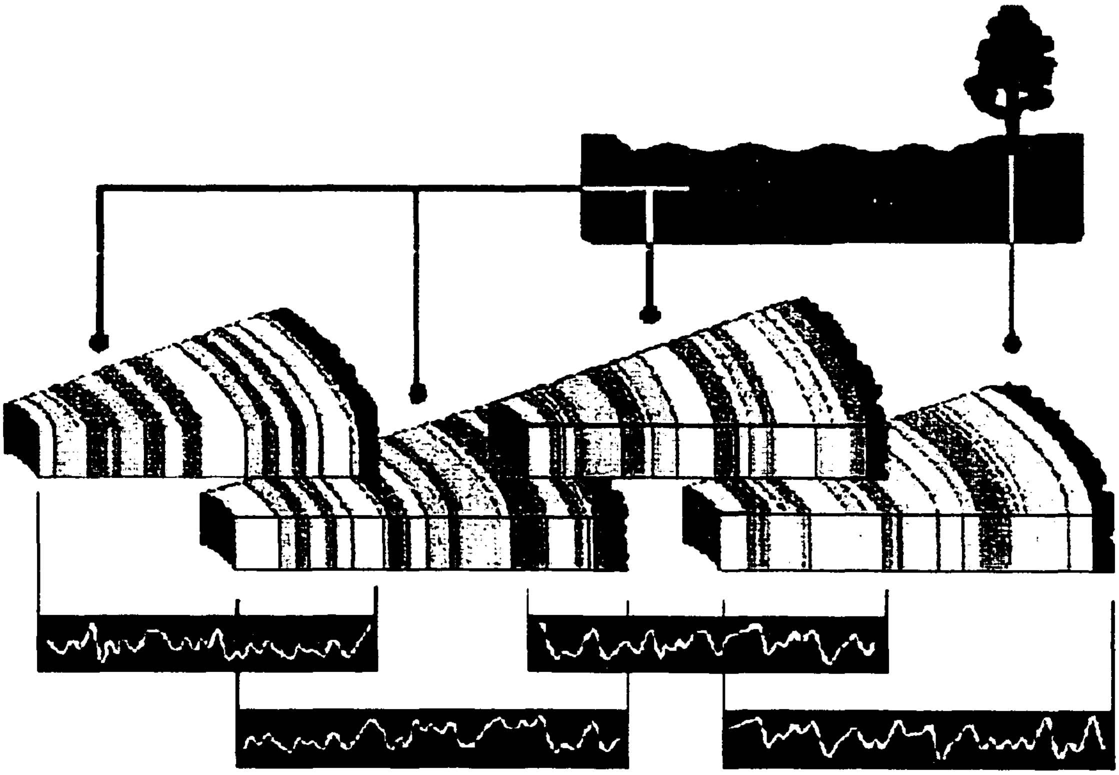


Figure 3.2 Illustration of crossdating tree-ring samples. The ring patterns, such as wide and narrow ring sequences, are compared across different trees to check the missing or false rings.

exceptionally narrow rings as a series of discrete vertical bars (therefore the skeletons)on a strip of graph paper of which each vertical line represents one ring and a longer vertical bar represents a narrower ring. Tree-ring sequences can then be crossdated by matching the skeleton plots of different samples. This technique is useful in regions where tree-ring variation is affected mainly by standwide environmental changes. In those regions where microsite conditions and competition among different trees significantly affect tree growth, crossdating by skeleton plot is difficult to implement because the narrow rings may appear in different degrees for the same year or appear inconsistently among different trees over time.

Measured ring sequences can be plotted and compared on a light table to help crossdating. By overlaying the zig-zag ring sequences and visually checking how well they match, workers can reach a sense of crossdating positions and obtain information concerning potentially missing rings or false rings.

Correlation coefficients among tree-ring sequences can be calculated by computers and used as an aid to crossdating. The better the ring sequences are correlated, the greater the likelihood of crossdating. The computer programs are usually designed to mimic the action of sliding one graph of ring-series past another to look for a position of best match (e.g., Cropper, 1979; Holmes, 1983). The program COFECHA (Holmes, 1983) is used in this study to quality-check the crossdating. This program is characterized by its ability to divide a ring-series into successive segments with partial overlaps (e.g., 50-year long segments with 25-year overlap) and to calculate the correlation coefficients for these successive segments to other tree-ring series. Examining the values of the correlation coefficients and the consistency of segment positions at sequential matches helps assess the quality of crossdating (Holmes, 1983).

Although both the graphic and computer methods assist in crossdating, they only use limited information from tree-ring features and cannot be treated as conclusive methods. Visual comparison of ring characteristics is the most informative and conclusive method for crossdating, because it provides the full image of ring characteristics that includes not only the widths of the annual ring but also the widths of earlywood and latewood, darkness of latewood, and other ring anomalies (Fritts, 1976). Some pointer years, in which the rings are extremely narrow or have narrow latewood in a large number of samples, are usually used as a diagnostic feature for crossdating (Cook and Kairiukstis, 1990; Lavoie and Payette, 1997). However, extensive visual comparison among all the samples, usually under a microscope, is time-consuming.

The techniques of crossdating can usually be well implemented for samples with a known period of life time, such as those collected from living trees. For samples of unknown ages (referred to floating samples in the following sections), such as subfossil logs recovered from lake sediments, the crossdating is usually not an easy task, especially when the samples do not represent long life spans and are distributed over a wide range of time. A floating ring sequence may have more than one possible match position when comparing with other ring sequences. Radiocarbon dating of these samples helps delimit the range of time intervals for possible crossdating. The problems of crossdating these floating samples will be further discussed in chapter 6.

3.2.3 *Standardization and Averaging*

The measured ring-width sequences from individual trees cannot be used directly to represent the variation in the standwide environment because the growth of individual trees is also affected by many local factors such as substrate stress, competition stress, and disturbance of individual trees. The signals of these local factors in tree-ring series should be minimized when preparing the stand tree-ring chronology.

There are two ways to minimize the signals of local factors in tree-rings. One is standardization which uses curve-fitting techniques to remove the unwanted growth trends of individual trees, and the other is the averaging of standardized tree-rings of a number of trees to reduce the random signals from local factors. The unwanted growth trend, which refers to potential growth in situations without any changes in climate and occurrences of any stand disturbances, appears as a smooth curve that can be expressed as a function of the tree's age. This pattern occurs because the effects of substrate and competition stress on the growth of a tree gradually change with the developmental stages of the tree (Bazzaz, 1996). In reality, the observed tree-ring pattern is a result of the combined effects of various stresses and disturbances. Consequently, the ideal growth trend is usually distorted by the effects of a variety of factors including the standwide climate variation and disturbance. Therefore, there is no simple equation that can describe such a growth trend (Fritts, 1976). The growth trend is usually estimated by fitting different curves to the measured ring-width series depending on the nature of tree growth and the purpose of the study.

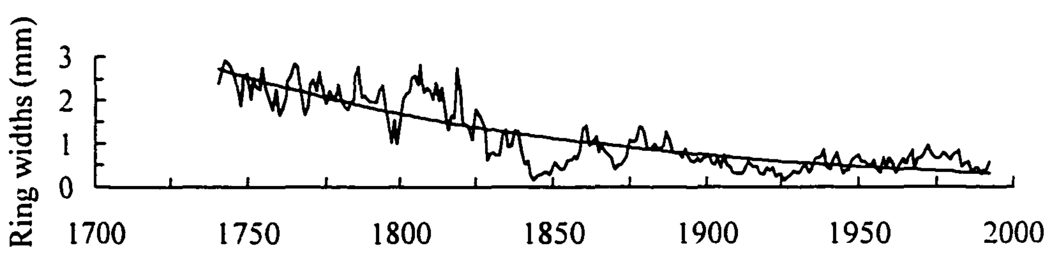
In this study, the computer program ARSTAN (Holmes et al., 1986) is used to standardize tree-ring series and to average them into tree-ring chronologies. Because the growth response to standwide climate is of primary interest, the detrending curves are chosen to retain as much climate signal as possible during the process of standardization. If a tree-ring series exhibits gradual decreasing ring-widths combined with long-term variation, then a negative exponential curve or a straight line with negative slope is used to approximate the overall growth trend (Figure 3.3). Sometimes, a measured tree-ring series does not show a clear decreasing growth trend because the trend is obscured by combined effects of all stresses and disturbances. In such a case, a straight line through the mean of tree-ring series is used as a conservative estimation of the growth trend (Figure 3.3).

Once the growth trend is estimated, the measured ring-widths are then converted into dimensionless ring-width indices (I_t) by dividing each ring-width (R_t) for year t by the value of the curve-fitted growth trend (A_t) as follows:

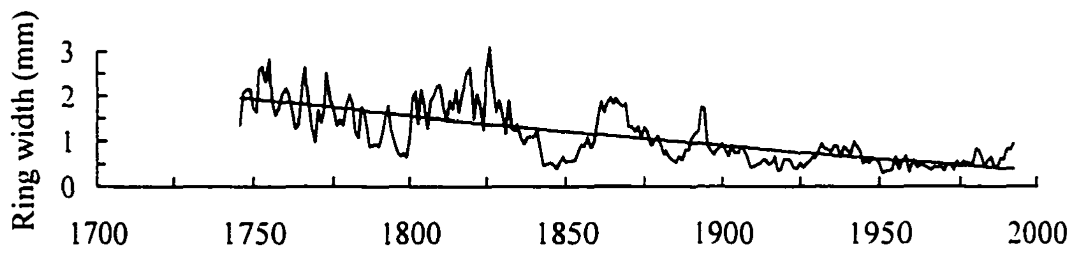
$$I_t = R_t/A_t$$

Division by the growth trend curve not only removes the growth trend itself but also scales the ring-width variance so that the variance of wide rings in fast growing periods does not overwhelm that of the narrow rings in slow growing periods (Fritts, 1976). The resultant tree-ring indices have a constant mean of 1 and homogeneous variance. The autocorrelation within tree-ring indices is not removed by prewhitening techniques (e.g., autoregressive moving average) because it may contain useful information of low-frequency variation in climate.

(a) The negative exponential curve fitted on sample HLIC029



(b) The linear regression line fitted on sample HLIC039



(c) The horizontal line fitted on sample HLIC004

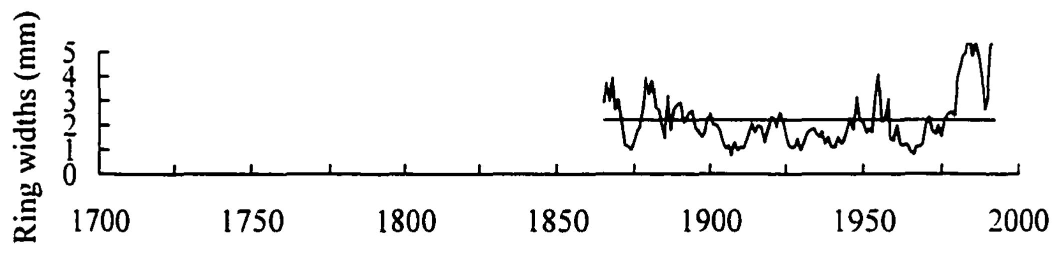


Figure 3.3 Examples of detrending using (a) negative exponential curve, (b) linear regression line of negative slope, and (c) horizontal line through the mean (from Zhang, 1996).

A stand ring-width chronology is formed by averaging standardized ring-width index series across several sequences for each year. This process of averaging produces a time series that enhances the common signals within different trees (e.g., climate and stand disturbances) and averages out random signals (e.g., microsite disturbances to the tree or to its neighbors). Differentiation of climatic signals (C_t) from standwide disturbances ($D2_t$) is not an easy task (Fritts and Swetnam, 1989) and will be discussed in the next section.

3.3 Using Tree-Ring Chronologies for Environmental Studies

Stand tree-ring chronologies for one or more species can be used in a variety of environmental studies, such as evaluation of growth responses to climate and disturbances (Swetnam and Betancourt, 1998), reconstruction of past climate (Briffa et al., 1983; Hughes et al., 1999), assessment of the severity and recurrence patterns of insect disturbances (Swetnam and Lynch, 1993), and dating of glacial advances (Luckman, 1995; Smith and Laroque, 1996), earthquakes and volcanic eruptions (Jacoby et al. 1992; Yamaguchi et al., 1997). These studies usually involve two procedures: 1) establishment of the relationships between environmental factors and tree-ring growth; and 2) application of such relationships to tree-rings from intervals of unknown environment and using tree-rings as an indicator of environmental changes.

3.3.1 *Establishment of the Environment-Growth Relationships*

The relationships between environmental factors and tree-ring growth are established through experimental or empirical analysis under known environmental conditions (Fritts, 1976; Horáč ek, 1995). The experimental analysis provides clues for biological mechanisms of how environmental factors affect tree growth. However, experiments on large trees in field conditions and over long time (e.g., more than decades) are hard to implement, and thus most of the insights on growth responses are gained from experiments using young trees in controlled lab conditions. The empirical analysis uses observed environmental data and statistical and/or analytical methods to establish environment-growth relationships. Statistical methods (e.g., calculation of correlation coefficients between observed climate series and tree-ring series) are usually used when the environmental data are sufficient in length, whereas the analytical methods are often used to establish the association between disturbances and tree-ring growth (e.g., correspondence of observed insect defoliation to narrow rings [Zhang et al., 1999]) based on empirically determined correlation between tree-ring and environmental characteristics.

In this study, the climate-growth relationships are examined empirically using response function analysis (Fritts et al., 1971) and artificial neural networks (Haykin, 1994; Zhang, 1998). The following is a description of these two methods.

Response function analysis

Response function analysis is designed to detect the association between the variation of tree-ring growth and the climatic variables (Fritts et al., 1971). The climatic variables investigated include monthly mean temperature and total monthly precipitation. Because there usually exist intercorrelations among the climatic variables (Cropper, 1984), direct regression of tree-ring variable with climatic variables may cause rejection of important climatic variables and, consequently, produce misleading results (Cropper, 1984). To overcome this problem, principal components of monthly climatic data are extracted and used in a regression analysis with the tree-ring data. The regression coefficients are then multiplied by the PCs of climate to obtain a new set of regression coefficients related to the original monthly climatic variables (Fritts et al., 1971). The result is expressed in the form of a response function and the significance of the response coefficients is tested using a bootstrap method (Guiot, 1991) so as to avoid the problem arisen from the autocorrelation within tree-ring chronologies.

The computer program PRECON (Fritts, 1994) developed on the basis of the above concept is used in this study to produce the response function. Although the response function analysis is widely used in dendroclimatology and has been demonstrated to be a useful tool for identifying limiting factors for tree growth, its uses in predicting tree growth and understanding the climate-growth response are limited (Hughes and Milsom, 1982; Cropper, 1984; Fritts and Wu, 1986). The limitation occurs because the response function analysis is basically a linear regression technique, whereas the biological processes governing the radial growth of a tree usually include nonlinear characteristics (Guiot et al., 1982; Graumlich, 1991). Consequently, some parts of the climate-growth information may be lost while other parts may not be well represented by the response function.

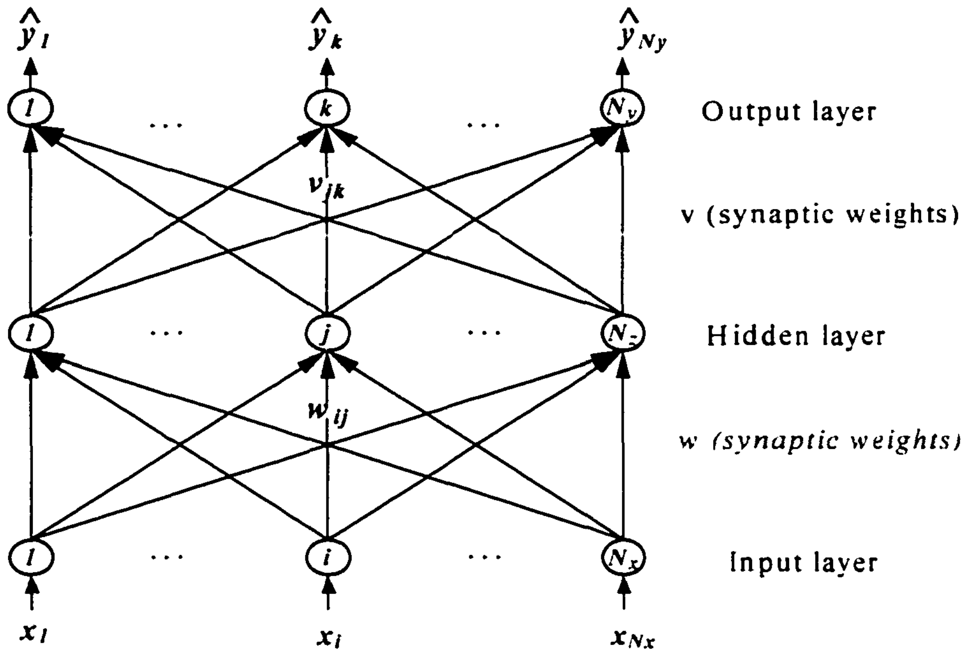
Artificial neural networks (ANN)

With the rapid development of high-speed digital computers and recent advances in the technology of Artificial Neural Network (ANN) (Haykin, 1994; Zhang and Gupta, 2000), it is now feasible to develop ANN models to examine nonlinear and complex climate-growth relationships.

An artificial neural network (ANN), or neural network in short, is an information-processing system inspired by the ability of the human brain to learn from observations and to generalize by abstraction (Zhang and Gupta, 2000). It consists of many simple processors (called neurons) and many weighted interconnections among them. There are many kinds of ANN models designed for different tasks (Fausett, 1994; Haykin, 1994). In dendroclimatic applications, the relationships between climatic variables and tree-ring variables can be modeled by a common type of neural network, namely, multilayer feedforward ANN such as a three-layer feedforward ANN (Figure 3.4) (Keller et al., 1997; Woodhouse, 1999).

The ANN shown in Figure 3.4a has N_x input neurons, N_z hidden neurons and N_y output neurons organized in three layers with full connections among neurons of adjacent layers. The connections, which are analogous to *synapses* in biological neural systems, function as signal mediators between neurons. Each connection has a synaptic weight (w_{ij} or v_{jk}) that can modify the magnitude of signal transmission. The signal transmitted from one neuron to the next is multiplied by the synaptic weight, thus can get excited (if the weight is positive) or inhibited (if the weight is negative) on the receptive neuron. Inside an artificial neuron (Figure 3.4b), the incoming signals are received and added, and

(a) a fully-connected three-layer feedforward neural network



(b) the internal structure of a neuron

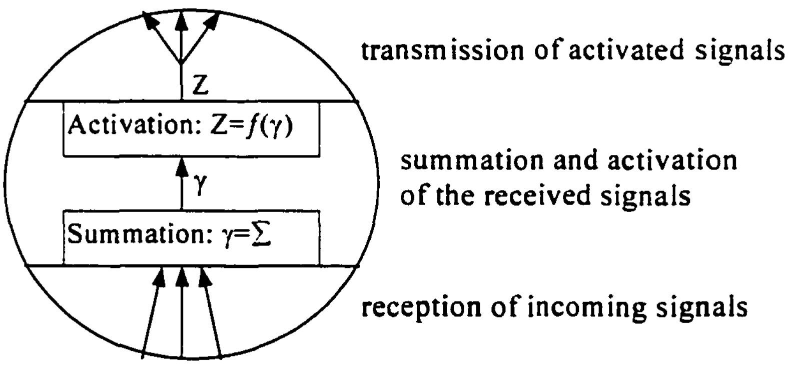


Figure 3.4 Illustration of a fully connected three-layer feedforward neural network (a), and the internal structure of a neuron (b). For each neuron in the input layer, there is only one incoming signal (from the corresponding input variable). For each neuron in the output layer, there is only one outgoing signal (representing the model predicted response).

the sum is transformed into an axonal signal by an activation function[3] which performs in a manner similar to the action of firing in the soma of a biological neuron cell. The axonal signal is then transmitted to the next layer of neurons through the synaptic connections.

For example, let **X** be a N_x-vector describing climatic variables (e.g., monthly mean temperature and total monthly precipitation), and **Y** be a N_y-vector describing tree-ring growth variables (e.g., ring-widths and ring-densities). For a given case of input climatic conditions, $x_i\,(i=1,\ldots,N_x)$, the signals propagate forward (layer-by-layer) through the network, during which the signals are processed inside each neuron and modified on each connection path. The signals eventually sent out by the output neurons, $\hat{y}_k$ ($k=1, \ldots, N_y$), represent the ANN predicted tree-ring responses to the input climatic conditions.

In mathematical terms, the response at output neuron k can be described as:

$$\hat{y}_k = \left(\sum_{j=1}^{N_z} v_{jk} z_j \right) - v_{0k} \qquad (1)$$

$$z_j = f(\gamma_j) = \frac{1}{1 + \exp\left(-\gamma_j - w_{0j}\right)} \qquad (2)$$

$$\gamma_j = \sum_{i=1}^{N_x} w_{ij} x_i \qquad (3)$$

---

[3] The commonly used activation functions include identity function [$f(x) = x$] for input neurons, logistic sigmoid function [$f(x)=(1+\exp(-x))^{-1}$] for hidden neurons, and linear function [$f(x) = b \cdot x$, where b is a constant] for output neurons.

where w_{ij} and v_{jk} are synaptic weights associated with the connection paths of *i-j* neurons and *j-k* neurons respectively; w_{0j} and v_{0k} are threshold parameters associated with neurons *j* and *k* respectively, and can be treated as special synaptic weights that adjust the summed incoming signals; and *f*(.) is an activation function in the hidden neurons.

The number of input and output neurons is equal to the number of input and output variables, N_x and N_y, respectively. The number of hidden neurons, N_z, is chosen according to the expected complexity of the climate-growth response, i.e., the more complex of the climate-growth response, the greater the number of hidden neurons. The neural network's synaptic weights, w_{ij}, v_{jk}, w_{oj} and v_{ok}, are free parameters used for storing the essential relationships (called knowledge) between climate and growth. These free parameters can be gradually adjusted from initially random (usually in the range [-1, 1]) to eventually optimal values through a training process using observed **X-Y** data pairs (called training examples, and collectively a training set). During the training process, the network is fed with input signals from training examples, and the responses from output neurons ($\hat{y}$) are compared with the actual responses (y). The sum of squared errors, denoted as ξ, over an entire training set is used as a measure of the network's performance.

$$\xi = \sum_{m=1}^{M} \sum_{k=1}^{N_y} \left(y_{mk} - \hat{y}_{mk}\right)^2 \qquad (4)$$

Where M is the number of training examples in the entire training set. The objective of the training is to adjust the weights so as to minimize ξ. To do so, the value of ξ is backpropagated through the network, and a weight correction Δw (or Δv) is obtained for each weight.

$$\Delta w = -\eta \frac{\partial \xi}{\partial w} \qquad (5)$$

where the minus sign accounts for the opposite direction of weight correction with respect to the gradient of function ξ; and η is a constant that determines the rate of weight adjustments and is called a learning-rate parameter. A detailed error-backpropagation training algorithm for computation of Δw can be found in introductory books on neural networks (e.g. Fausett, 1994; Haykin, 1994).

After all the weight correction terms have been determined, the weights are updated simultaneously. The updated network is then trained again by another iteration of the training set, leading to a newly updated network. This training process is repeated for many iterations of the training set, and the synaptic weights are gradually adjusted to optimal values. Once the cost function (3) reaches the minimum point, the training process is finished.

After a well-trained neural network is obtained, it is validated using an independent set of **X-Y** data pairs (called a testing set). A satisfactory neural model should be able to memorize the learned **X-Y** patterns, and to use the knowledge for generalization. The memorization refers to the ability of a neural network to reproduce the input-output patterns learned in the training examples; whereas the generalization refers to the ability of a network to generate reasonably accurate responses to novel inputs never seen during the training.

Neural networks can be used to establish empirical relationships between **X** and **Y**, where specific details of the underlying relationships are not well understood. Given enough hidden neurons, a three-layer fully connected feed-forward neural network (Figure 3.4a) is able to approximate any continuous function to a specified accuracy (Hornik et al., 1989). The nonlinear and complex relationships between X and Y are realized by the nonlinear activation functions in the hidden neurons and by the presence of hidden neurons that provide an extra dimension of interactions between input and output neurons.

3.3.2 *Tree-Rings as Indicators of Past Environmental Changes*

The relationships between environmental factors and tree-ring growth can be applied to tree-rings produced from intervals of unknown environment to interpret the observed variations in tree-ring series. However, to assign the specific environmental factors based solely on tree-rings is usually a difficult task because numerous factors, e.g., climate and abiotic and biotic disturbances, have effects on tree-ring growth (Glock, 1955). A further complication is that these causal agents may interact and it is their combined effects that determine the tree-ring growth (Fritts, 1976). Nevertheless, some environmental factors can be identified as likely causal factors of particular tree-ring responses.

The determination of causal factors for tree-ring changes involves the following several methods: examining irregular ring features and intra-ring characteristics, and comparing rings of different tree species and with independent records. First, tree-rings may have recognizable morphological characteristics or irregular ring patterns that indicate specific causal factors. For example, fire scars in cross-section of a tree bole are caused by cambium injury from fire (Swetnam, 1993); reaction wood (asymmetric ring growth in the stem) is caused by tilting of tree due to slope movement (Shroder, 1976, 1980) or by asymmetric crown due to frequent wind (Bannan and Bindra, 1970); and abrupt growth suppression followed by long-term growth release is most likely caused by stand disturbances such as insect outbreaks (see section 2.2.2). Second, intra-ring (earlywood and latewood) characteristics may contain specific environmental information. For example, variations in light rings (i.e., rings with narrow latewood) or dark rings (i.e., rings with wide latewood) may suggest growth season temperature changes (Filion et al., 1986). Third, different tree species vary in their growth response to environmental changes and, thus their growth patterns can be compared for the purpose of differentiating the causal factors. For example, comparison of tree-ring chronologies from insect host and nonhost tree species helps to identify the occurrence of insect outbreaks (Swetnam and Lynch, 1993). Fourth, environmental records from independent sources, such as pollen analysis, ocean sediments, and ice cores, can be used to identify the possible causal factors for tree-ring changes (Baumgartner et al., 1989; Hughes and Diaz, 1994).

It should be noted that in dendrochronological analysis of unknown environments, the cause (a change in environment) is measured and studied by its effects (a response in tree-rings). Stand tree-ring chronologies represent the growth response to a combination of macro-environmental factors. Despite the several methods described in the last paragraph, the assignment of specific causal factors to ring-width changes is a challenging task, and all possible factors must be considered in the analysis of tree-rings.

Chapter 4 Modeling Tree-Ring Growth Responses to Climatic Variables Using Artificial Neural Networks[4]

Modeling tree-ring growth responses to climatic variables is important for predicting the growth rate under future climatic changes, for understanding the effects of climatic variables on tree growth, and for reconstructing past climate from tree-ring chronologies. Conventional linear regression techniques confront the problem of modeling nonlinear and complex relationships between climatic variables and tree-ring growth (Fritts, 1976; Keller et al., 1997). The technique of artificial neural network (ANN), which has the ability to capture nonlinear patterns, has been demonstrated to be applicable to tree-ring studies by the pioneering work from Guiot et al. (1995), Keller et al. (1997, 1998), and Woodhouse (1999). The problem of "overlearning" (which will be discussed in section 4.2.3) in the development of ANN models is a major obstacle to the practical application of this technique. This chapter describes the ANN modeling of climate-growth responses for Douglas-fir at the Heal Lake site of southern Vancouver Island. Procedures to avoid the problem of "overlearning", and the application of ANN models in predicting tree-ring growth and understanding climate-growth relationships are described.

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[4] The material in this chapter have been published in the journal *Forest Science* (Zhang et al., 2000). The article is co-authored with Drs. R. Hebda, Q.-J. Zhang, and R.I. Alfaro, who provided valuable discussions on the topic.

4.1 Tree-Ring and Climate Data

The tree-ring data used in this ANN modeling include a segment of a ring-width chronology spanning A.D. 1891-1992 (Figure 4.1), taken from a two-millennium long chronology of Douglas-fir developed from living trees and subfossil logs at the Heal Lake site (48°32'N Lat., 123°28'W Long.), near Victoria, southern Vancouver Island, British Columbia (BC), Canada (Zhang, 1996). This recent chronology was constructed from 24 increment cores (one core per tree), which were prepared, measured, cross-dated, standardized, and averaged into a stand ring-width chronology according to the standard procedures (Fritts, 1976) described in the section 3.2 of chapter 3. Each increment core covers the period A.D. 1891-1992, and the mean sensitivity of ring-width series is 0.23. The yearly ring-width indices represent the tree's radial growth under the influence of macro-environmental factors, mainly climatic variables. More characteristics of the Heal Lake tree-ring chronology will be introduced and compared to that of other sites in the same region in section 5.1 of chapter 5.

The climatic data, obtained from the Ministry of Forests, Province of B.C., Canada, include monthly mean temperature and total monthly precipitation from A.D. 1891-1992. The data were derived from observed records at four meteorological stations (located at the Victoria International Airport, Dominion Astrophysical Observatory, Gonzales Hill and Esquimalt) (see Figure 4.2) near Victoria by averaging after evaluation of the coherency and the ratio of climatic variables among the stations (Spittlehouse, 1994, personal communication, Ministry of Forests, Victoria, BC., Canada). The four meteorological stations and the Heal Lake site are located in similar topographical

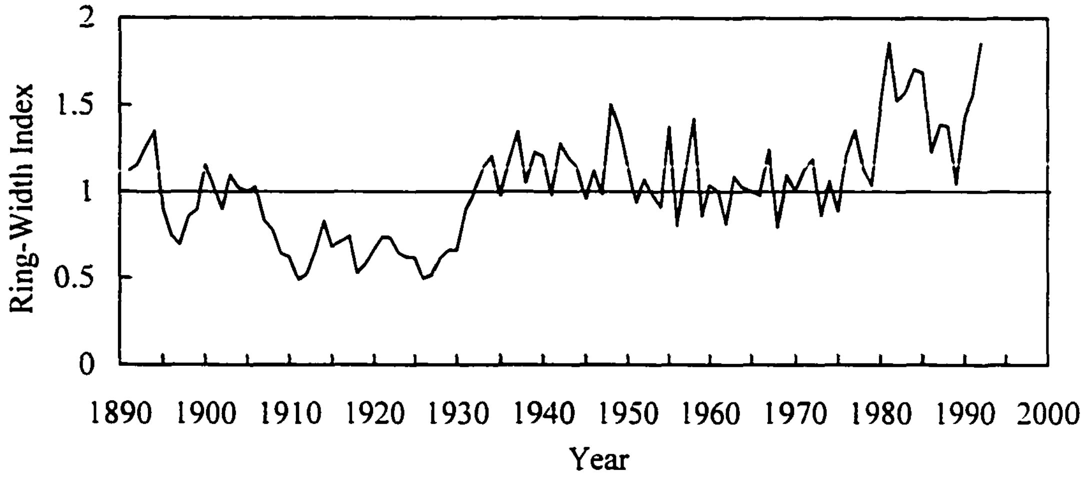


Figure 4.1 Ring-width indices of Douglas-fir at the Heal Lake site, southern Vancouver Island, B.C., Canada for the period A.D. 1891-1992. The sample depth (the replication of tree-ring samples for each year) for the chronology is 24.

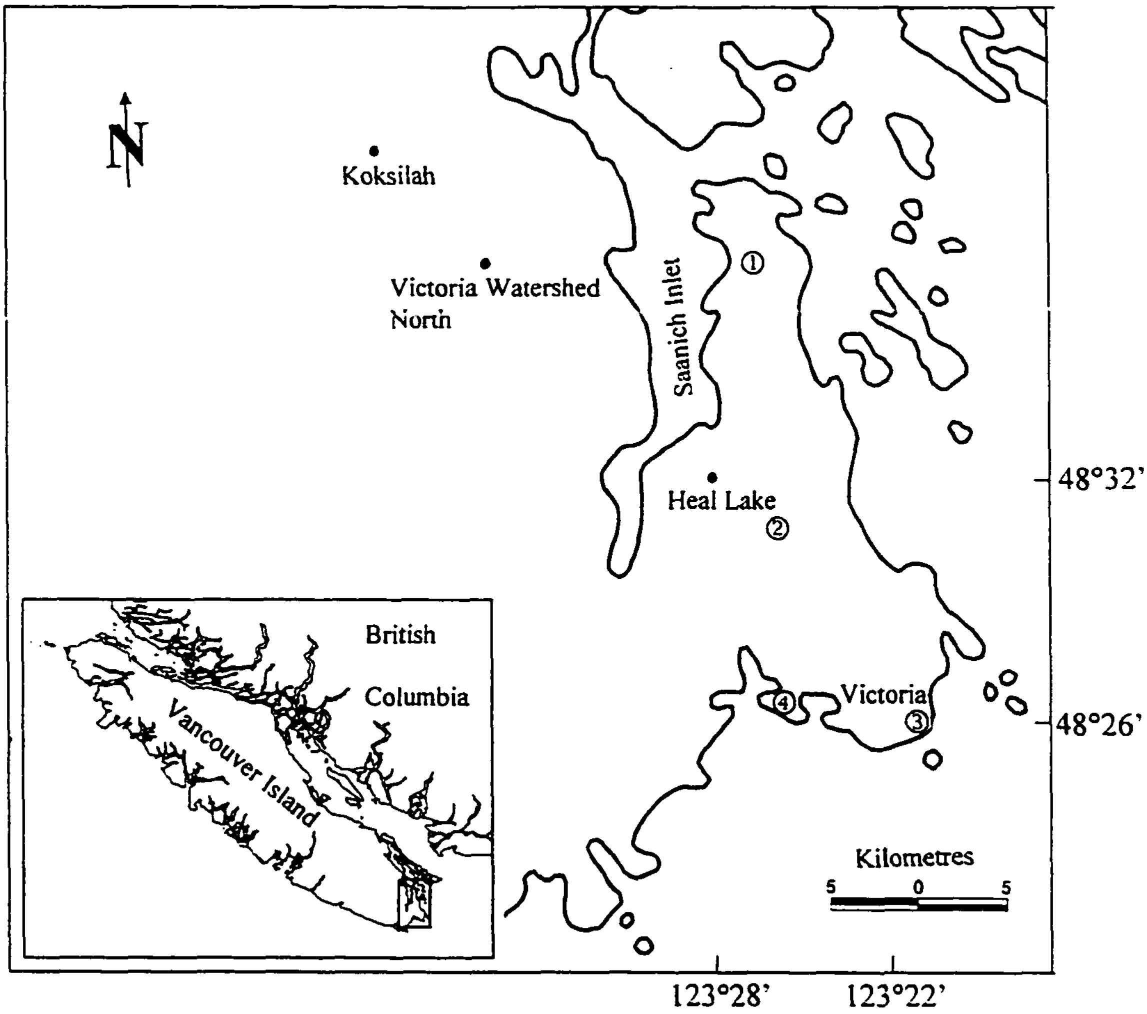


Figure 4.2 Map showing the location of tree-ring study sites at Heal Lake, Koksilah, Victoria Watershed North, and four weather stations on southern Vancouver Island, British Columbia. ①: Victoria International Airport, ②: Dominion Astrophysical Observatory, ③: Gonzales Point, ④: Esquimalt.

situations in lowland terrain (Yorath and Nasmith, 1995), and there is little difference in orographic effect among these localities. These sites lie in the Coastal Douglas-fir (CDF) biogeoclimatic zone (Meidinger and Pojar, 1991), and the climate is characterized by warm, dry summers and mild, wet winters (Figure 4.3). The mean annual air temperature for the period A.D. 1891-1992 ranged from 7.9°C to 11.5°C, with mean January temperature of 2.9°C and mean July temperature of 17.8°C.

4.2 Development of Growth-Response Models Using the ANN Technique

The performance of a neural network depends on the quantity and quality of the training data (Zhang and Gupta, 2000). In dendroclimatic studies, however, the length of climatic records is insufficient to include every aspect of climatic variability, and the growth of tree-rings is usually affected by many other factors not included in the climatic data set. This insufficiency and impurity of the climate-growth database usually cause difficulties in constructing well-performing growth response ANN models. This section tackles these difficulties by selecting input variables, splitting sample data, controlling the training processes, and designing the architecture of the neural network. The computer software used in the study is NeuroModeler (Zhang, 1998), which incorporates recent advances in the field of ANN research. Although this software was originally developed for electrical engineering design, it is user-friendly and can be readily applied in dendroclimatic studies.

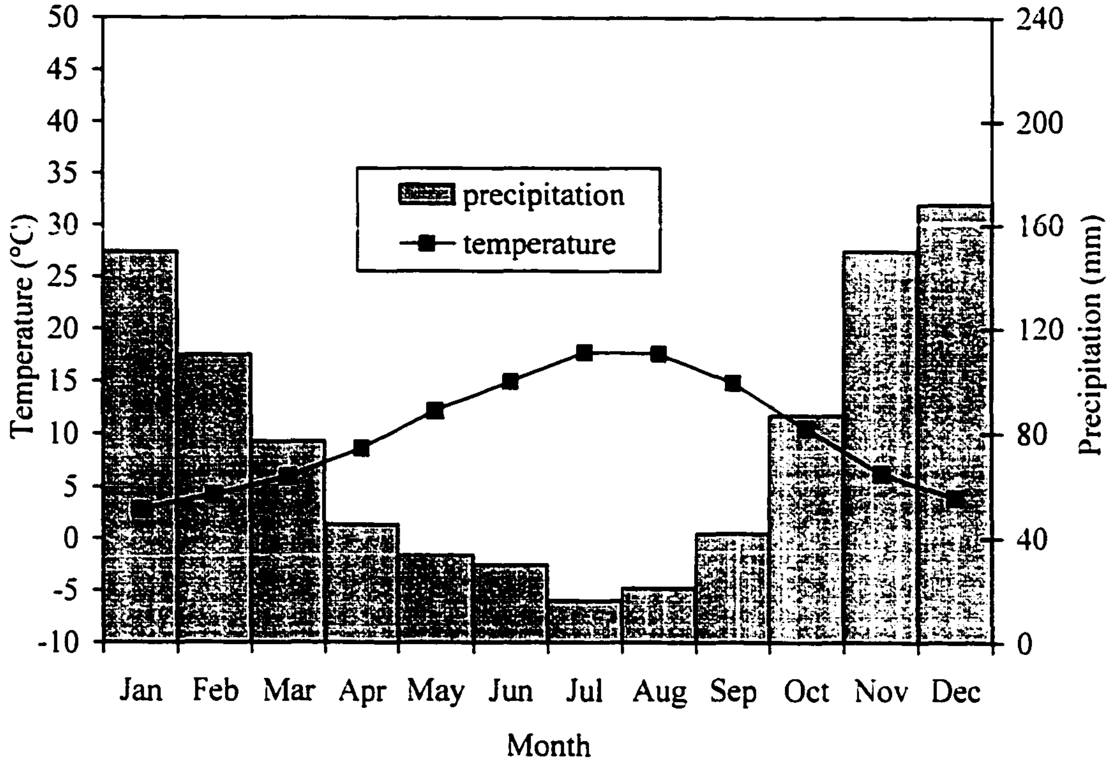


Figure 4.3 Representative diagram of the climate for Heal Lake site of Coastal Douglas-fir Biogeoclimatic zone on southern Vancouver Island (averaged for A.D. 1891-1992 using records at four meteorological stations near Victoria [see Figure 4.2]; data obtained from Spittlehouse, Ministry of Forests, Victoria, BC).

4.2.1 *Selection of the Input Variables*

In dendroclimatic analysis of climate-growth relationships, the climatic variables investigated as possible candidates for affecting tree growth usually include monthly mean temperature and total monthly precipitation over the span of 12 months or more (Fritts, 1976). Therefore, the total number of possible input variables for a neural network is usually at least 24. Among these 24 or more variables, there usually exist irrelevant and redundant variables that play little role in limiting the growth of tree-rings (Fritts, 1976). In neural network modeling, these irrelevant and redundant input variables not only lead to more computational requirements (i.e., greater number of synaptic weight parameters), but often they can create confusion in learning these features, thereby causing degradation in network's generalization capability (Pal and Eluri, 1998). This so-called "curse of dimensionality" can be avoided by reducing the number of input variables, while preserving the distinguishing characteristics of the original data, through extraction of major features from the original higher dimensional input variables using several ways such as selecting relevant variables, grouping of homogeneous inputs, and extracting principal components (Setiono and Liu, 1997; Pal and Eluri, 1998; Yuan and Fine, 1998).

In this study, the response function analysis (Fritts et al., 1971) and the software PRECON (Fritts, 1994) were used to select the relevant factors affecting tree-ring growth. The monthly climatic data over a 14-month period, from the previous year's August to September of the growth year, and the prior ring growth (acting as a proxy of the tree's health state) were used as independent variables to determine their significance in affecting the concurrent ring growth. The results show that ring growth was significantly related to six monthly total precipitations, three monthly mean temperatures, and the prior ring growth (Figure 4.4). Those variables that were not identified as significant by the response function analysis were considered as having minimal effects on tree growth and, therefore, were not used as input variables for the neural network. To further reduce the number of input variables, the April, May, June and July total precipitation were summed into one variable, reflecting the growing season precipitation. As a result, the inputs used for the ANN models were reduced to seven variables, i.e., mean temperature in the preceding September, November, and in August of the growth year, total precipitation in the preceding August, in January and April-July of the growth year, and the width of prior ring growth.

The April-July total precipitation and August mean temperatures affect growth activity as growing season factors. The rest of the variables likely play a role by preconditioning the tree's growth potential for the next year. Determining how tree growth responds to these factors is one of the key aims of developing the ANN models in this study.

4.2.2 *Splitting of Samples into Training and Testing Sets*

The selected seven input variables and the tree-ring output variable from the period A.D. 1891-1992 formed the database for developing neural network models. This 101 input-output data pairs (the ring of the earliest year, 1891, was not used as output because of lack of input data for prior year's climate) were split into 51- and 50-year data sets for training and testing respectively. Six different groups of training and testing sets were created by splitting the data in different ways (Figure 4.5). The method of splitting

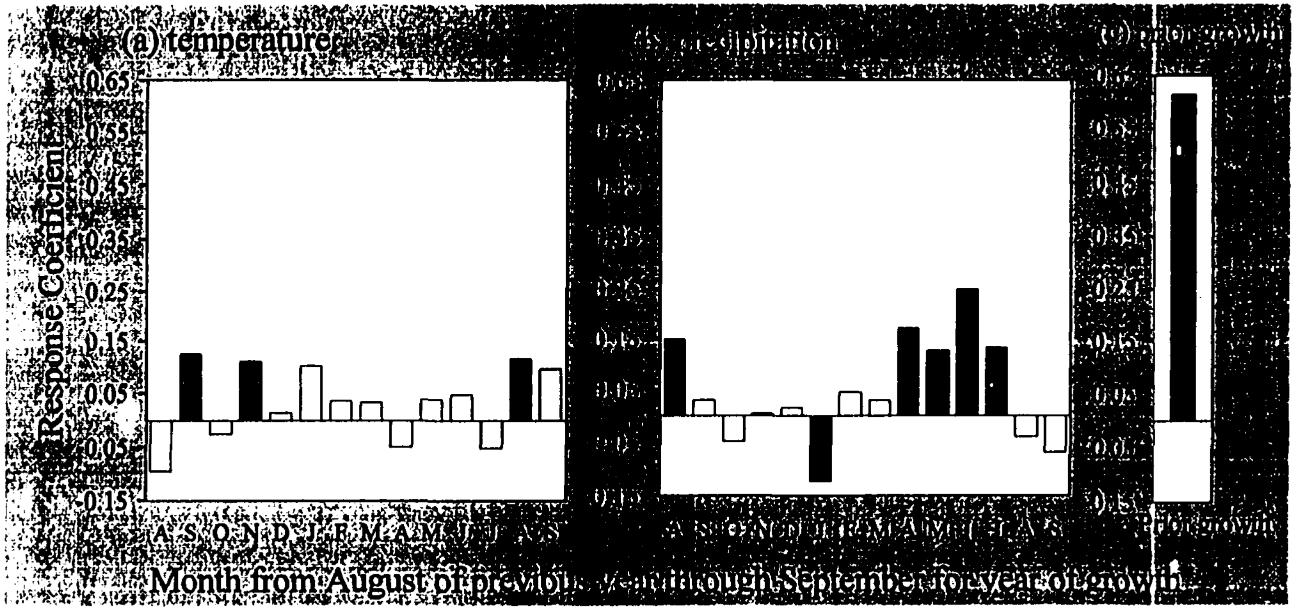


Figure 4.4 Response function coefficients for the ring-width chronology of Douglas-fir at Heal Lake, southern Vancouver Island, B.C., Canada. The significant factors (95% level based on bootstrapping tests) influencing ring growth are shaded in dark.

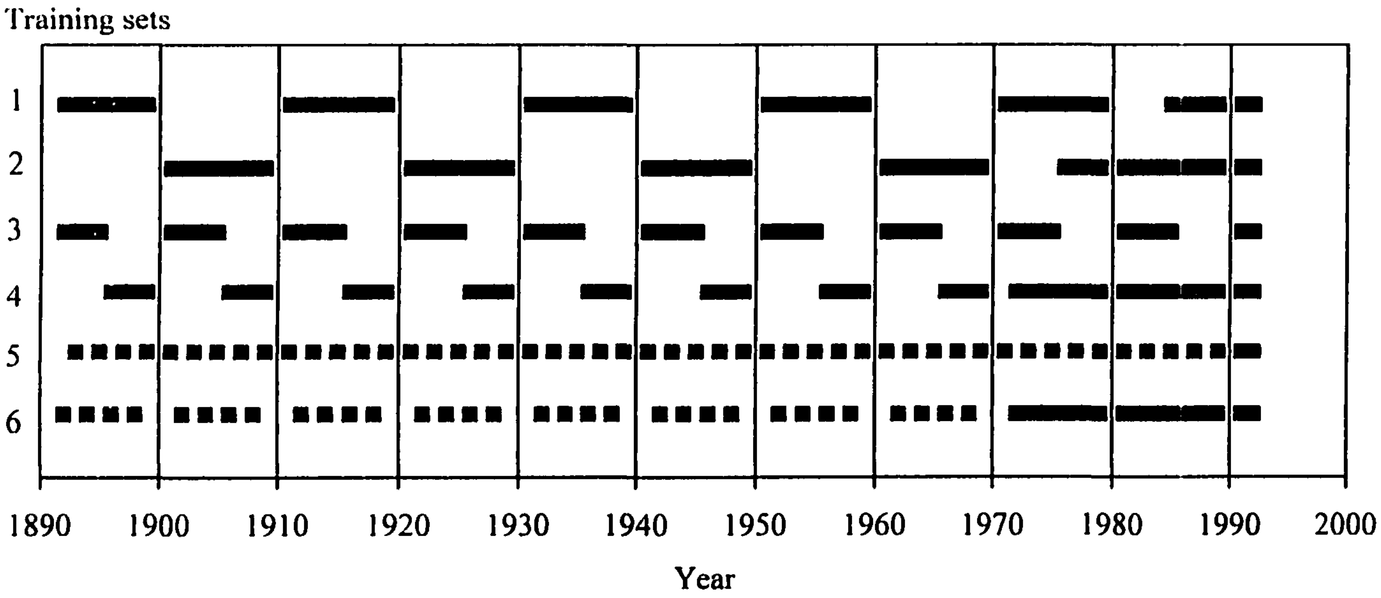


Figure 4.5 Six different groupings of 51-year subsamples (represented by the horizontal bars) used as training sets for developing ANN models. The rest of the samples in each group were used as a testing set. The ten first years of each decade (e.g., 1900, 1910, 1920, etc.) served as common testing years. Each bar in the 5th and 6th training sets represents a sample from a single year.

included 1) splitting the whole data in three different ways into segments of decades, five years, and one year respectively; 2) grouping the alternating segments derived from each splitting to form six data sets; and 3) withdrawing the first year of each decade (i.e., the years of 1900, 1910, 1920, etc.) from the six data sets and recruiting each of the six data sets with the most recent data to make them contain 51 years of data. Each of these 51-year data sets was used as a training set, whereas the remaining 50-year data set was used as a testing set. These six groups of training/testing sets would be used later to construct and validate neural networks. The idea behind this kind of splitting is that using scattered data over the entire period may help neural network learn a wide spectrum of climate-growth information, and using different training/testing sets may provide a way to evaluate the variations of neural networks across data splits, thus avoiding the prediction pitfalls specific to a single training/testing set.

4.2.3 *Early-Stopping to Avoid Overlearning*

The variations in ring-width indices are affected by many factors such as macro-scale ecological and climatic factors. The actual climatic factors that affect tree growth may not be well represented by monthly mean temperature and total monthly or seasonal precipitation. There may also exist measurement errors in both the tree-ring and climate variables. Therefore, the variance in ring-width indices cannot be fully explained by the seven selected input variables. In other words, there are some additional factors contributing to the unexplained variance in tree-ring growth. These factors might have no relation with the seven selected input variables, e.g., measurement errors and ecological shocks (such as insect outbreaks), or might be related to the input variables but not be fully represented (such as the effects of diurnal climate regimes). In any case, these unrepresented factors are usually hard to define, and they act as "noise", masking the underlying relationships between the climatic variables used in the modeling and the tree-ring series. By using a large number of training examples, the effects of this "noise" on climate-growth response can be minimized by recognizing the majority of growth responses. However, if the number of training examples is insufficient, the effect of this "noise" can hardly be minimized to an insignificant level during the training process, instead, the "noise" may be learned by the neural network as deterministic information between the input and output variables. This learning from the "noise" is called overlearning (also called overtraining or overfitting) (Haykin, 1994), which leads the neural network to memorize too many specific climate-growth features in the training examples, and makes the network less able to generate accurate output growth values for novel input climatic conditions never experienced during the training process.

Overlearning is an inevitable consequence of insufficient and noisy training examples. One method used in this study to avoid overlearning is early-stopping, i.e., stopping the training process before the neural network fully acquires the input-output information in training examples (Haykin, 1994). The termination of the training process is determined by the time at which the errors in the testing set are no longer decreasing but starting to increase. This increase of errors in the testing set suggests that the neural network is memorizing specific input-output features in the training examples, and losing the ability to generalize for novel inputs. If the errors for the testing set are still high in an unsatisfactory level (e.g., errors greater than those from linear regression models) at the stopping time, then the network might have been set with improper initial weights, which make it difficult to reach a balance between good memorization and generalization using the limited training examples (Haykin, 1994). This network of poor generalization cannot be used, and the internal weights of the network need to be reset for a new round of training and testing. Sometimes many trial-and-error experiments might be needed before an "expert" (well-performing in both memorization and generalization) neural network can be found. This method of early-stopping implies that the performance of the neural network should be monitored by the testing set during the training process. Other methods used in this study to avoid the overlearning problem include adding prior knowledge into the architecture of a neural network, such as using partially connected architectures to make effective use of the weights and connections. These methods are described in the following section.

4.2.4 *ANN Architecture Design*

The arrangement of neurons into layers and the connection pattern between neurons is called the network architecture (Fausett, 1994). Networks with different architectures learn the information embedded in training examples in different manners according to their specific pathways of signal transmission. When the training examples are insufficient in number and noisy due to unrepresented factors, carefully designed architectures may help neural networks guide the direction of signal flows and alleviate the problem of overlearning (Haykin, 1994, Zhang and Gupta, 2000).

In this study, a three-layer neural network was used to develop the growth response model. The first layer contains seven input neurons, of which the first five (χ_1,

.... χ_5) receive signals from the preconditioning variables (i.e., total precipitation in preceding August and January of the growing year, mean temperature in preceding September and November, and the width of prior ring growth), and the last two (χ_6 and χ_7) receive signals from the two growing season variables (i.e., April-July total precipitation and mean August temperature). The third layer contains only one output neuron producing the modeled growth response. The performance of fully connected neural networks using different numbers of neurons in the hidden layer was explored. The results show that these networks could not achieve satisfying generalization capability although they could get good memorization for training examples. The reason for this could be, in part, that the fully connected neural networks have too many free parameters (i.e., the weights) but small training set size. For example, a fully connected neural network with four hidden neurons will have 4x(7+1)+(4+1)=37 weight parameters, but there are only 51 data pairs available in the training data set. In such a case, the neural networks tend to overlearn the input-output patterns in the training set and have poor generalization performance for unseen input data (Yuan and Fine, 1998).

To avoid the overlearning problem, neural networks with a partially connected architecture and a small number of hidden neurons were designed with biological plausibility in consideration. This design of network architecture is equivalent to implanting prior knowledge of the input-output relationships into the network so that the network can learn more efficiently during the training process. The results show that the architecture with four hidden neurons, of which two were locally connected to the tree's preconditioning variables and the other two were locally connected to the growing season climatic variables (23 weight parameters altogether) (Figure 4.6a), performed the best. This demonstrated that using a small number of hidden neurons and locally connected architecture based on prior information about the temporal and functional characteristics of the input signals (e.g., the tree's preconditioning signals come earlier and function differently than the growing season climatic signals) can reduce the chance of a network learning undesirable specific features in the training examples and enhance the generalization performance of the network.

For comparison of nonlinear and linear models, two-layer neural network (Figure 4.6b) for each training set was also developed. Given input **X**, the output $\hat{y}$ is computed by:

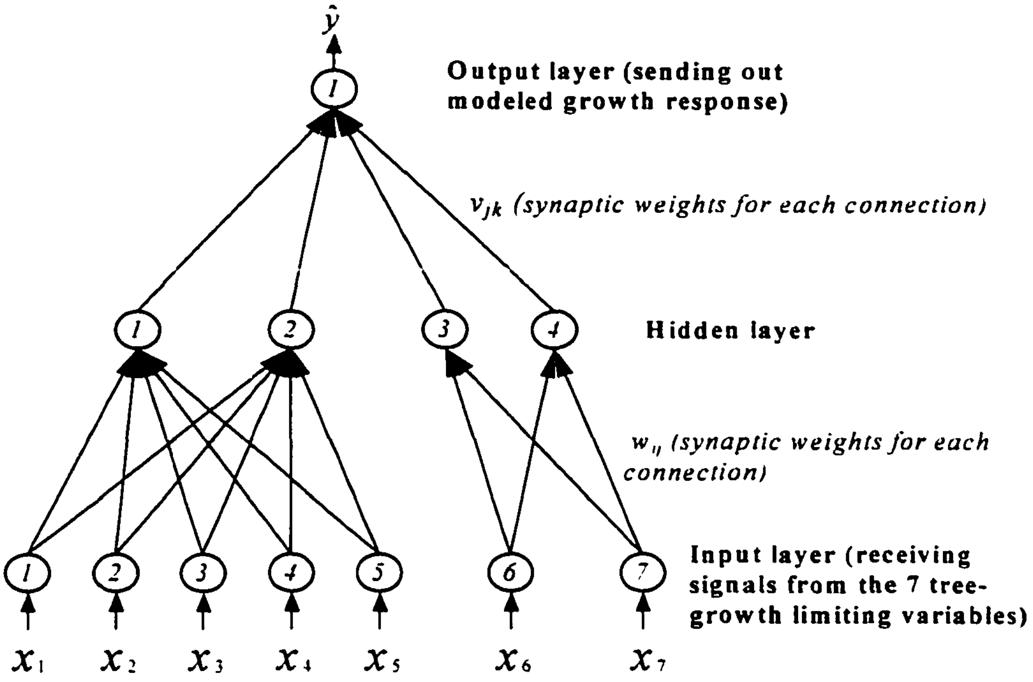
$$\hat{y} = \left(\sum_{i=1}^{N_r} w_i x_i \right) - w_0$$

Without the hidden layer neural interactions, the two-layer neural networks perform equivalently to linear multiple regressions. Early-stopping is not needed for the development of these two-layer neural networks, because the linear networks with the least square errors are the optimal representatives of the input-output relationships (Haykin, 1994). Therefore, the development of linear networks is much easier than that of three-layer nonlinear networks.

4.3 Applications of the Growth-Response ANN Models

Using the three-layer architecture (Figure 4.6a) and different training sets (Figure 4.5), six nonlinear ANN models were developed. These models, specifically the optimized synaptic weights and the architectures, were saved in computer files and could

(a) Three layer partially connected neural network (nonlinear model)



(b) Two-layer neural network (linear model)

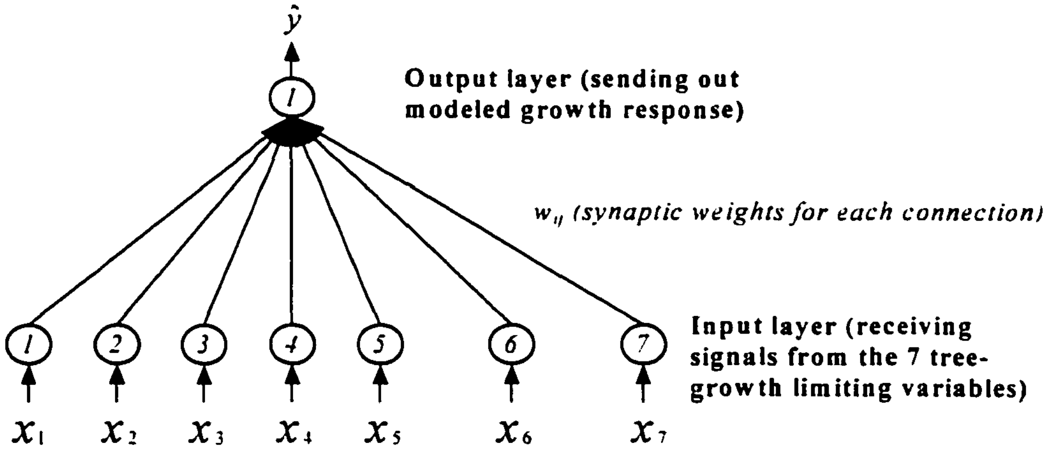


Figure 4.6 The three-layer partially connected neural network (a) used in this study for modeling the nonlinear and complex climate-growth response. The two-layer linear neural network (b) was used for comparison with the performance of the nonlinear models.

be retrieved for use. For comparison, six linear ANN models were also developed using the two-layer architecture (Figure 4.6b) and the same training sets (Figure 4.5).

4.3.1 *Predicting Tree-Ring Growth Using ANN Models*

The ANN models are capable of predicting tree-ring growth for given climatic conditions, and the accuracy of the predictions can be evaluated from the error (the absolute difference between the modeled ring growth and the actual growth) distribution on the testing set. The results of the ANN modeling show that with similar memorization ability in the training sets, all the nonlinear neural networks had better generalization capability than the linear models as measured by percentage error distribution and the amount of explained variance in the tree-ring series (Figure 4.7 and Table 4.1). The errors in nonlinear models, compared to those of linear models, were more concentrated in the small error ranges, and the likelihood of large errors was less. For the 300 testing ring-width indices, the nonlinear models explained 66.8% of the variance, whereas the linear models explained only 51.3% of the variance, i.e., an improvement of 15.5% by the nonlinear models. The ability to explain variance by nonlinear models degraded 15.6% from training sets to testing sets, whereas the linear models degraded 31.4%. The larger degradation in the linear models suggests that the prediction ability of the linear models in training sets tends to be more overly optimistic than that of the nonlinear models.

For the ten common testing years withheld from each sample split (Figure 4.5), the nonlinear models predicted growth responses more accurately than the linear models (Figure 4.8). The nonlinear models, developed by using different training sets, produced

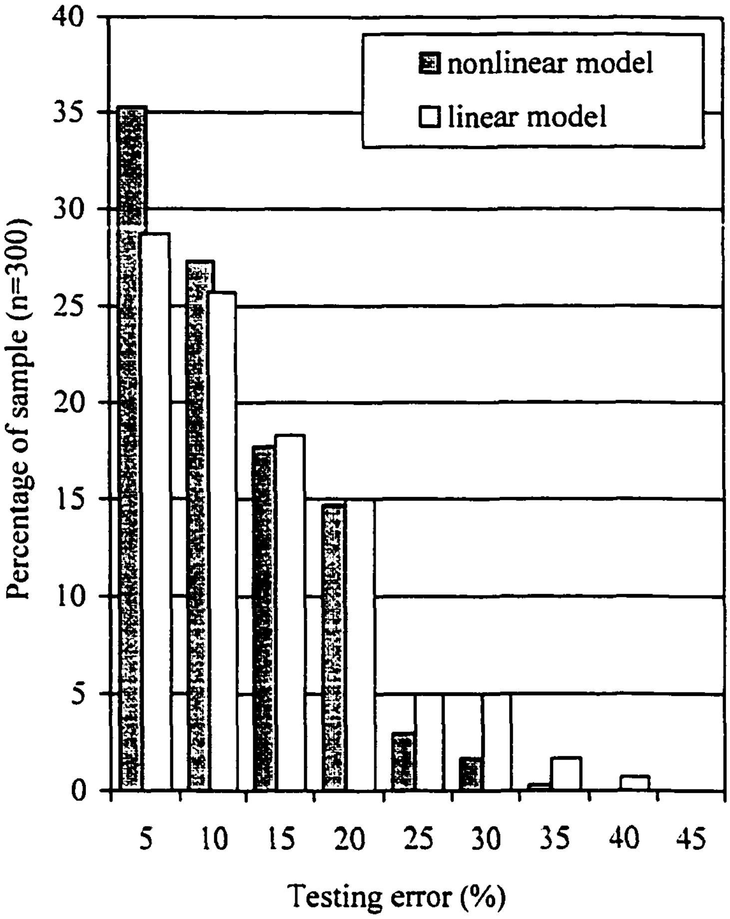


Figure 4.7 Comparison of the testing error distribution for nonlinear and linear growth response ANN models. The testing error refers to the absolute difference between the modeled ring growth and the actual growth for the data in testing set. and is expressed here as a percentage value of the range between maximum and minimum ring-indices.

Table 4.1 Tree-ring variance explained by nonlinear and linear ANN models developed over six different splits of samples.

No. of Training set (see Fig. 4.5)	Model type	Variance explained (%) Training set (n=51)	Testing set (n=50)	Difference
1	nonlinear	79.2	77.2	2.0
	linear	77.6	68.9	8.7
	difference	1.6	8.3	
2	nonlinear	83.4	64.0	19.4
	linear	83.7	49.2	34.5
	difference	-0.3	14.8	
3	nonlinear	85.4	69.8	15.6
	linear	85.4	57.5	27.9
	difference	0	12.3	
4	nonlinear	82.6	59.2	23.4
	linear	84.6	27.0	57.6
	difference	-2.0	32.2	
5	nonlinear	79.3	73.7	5.6
	linear	79.3	64.8	14.5
	difference	0	8.9	
6	nonlinear	84.5	57.1	27.4
	linear	85.6	40.6	45.0
	difference	-1.1	16.5	
		(n=306)	(n=300)	
Total	nonlinear	82.4	66.8	15.6
	linear	82.7	51.3	31.4
	difference	-0.30	15.5	

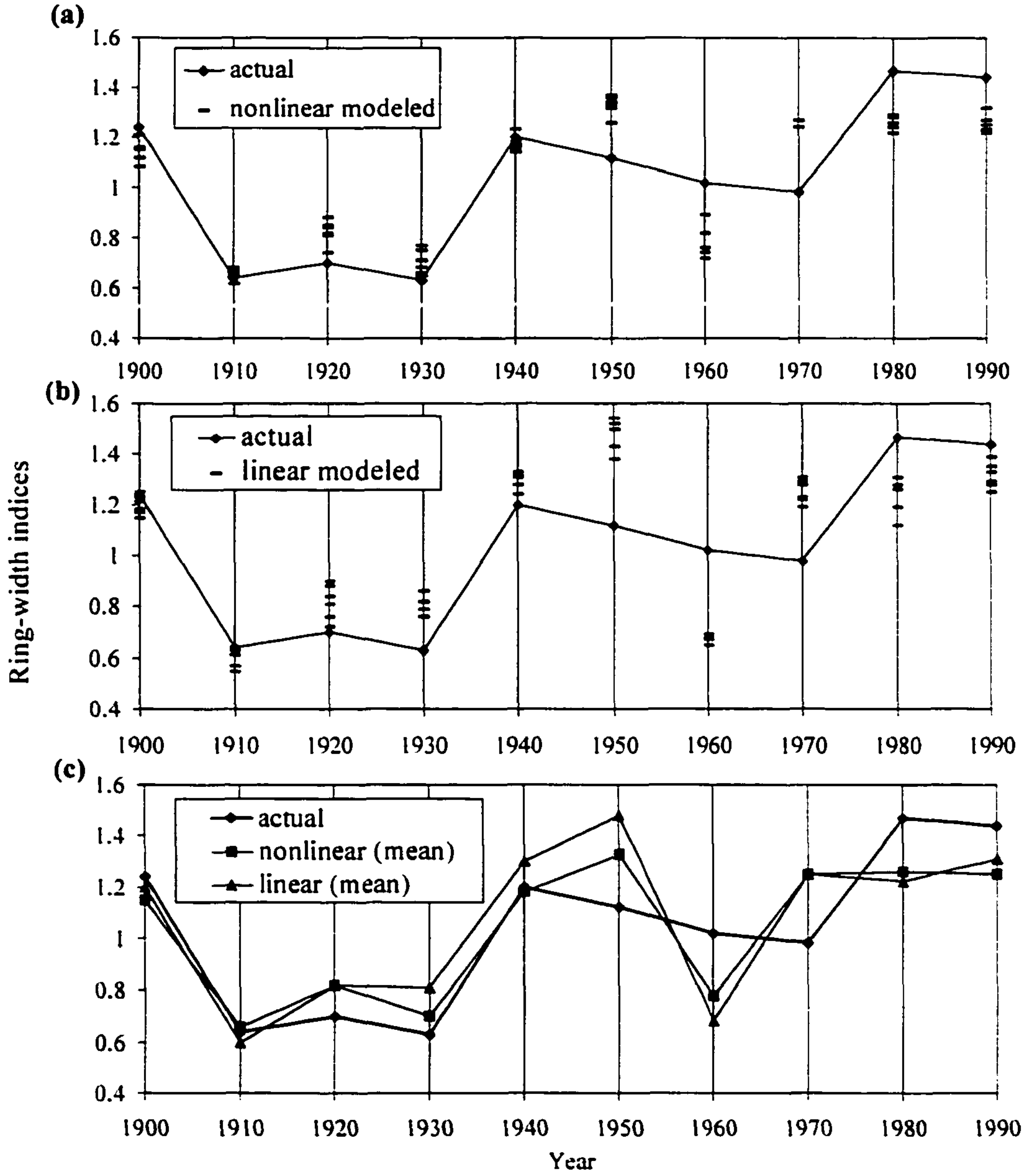


Figure 4.8 Comparison of the performance of nonlinear (a) and linear (b) ANN models for predicting growth responses to climatic conditions over the ten common testing years. Six nonlinear and linear models, developed using different training sets, were used for prediction respectively. The mean of the six modeled growth responses is plotted in (c).

different predictions although the variation was not great. This observation suggests the existence of noise distributed differently in the six training/testing sets which affects the performance of the neural networks. In spite of this, the neural networks developed by using different sample splits all learned the essential climate-growth response to an "expert" level (e.g., better performance than linear regression models) during the training stage. Therefore, when there is no prior information about the noise distribution, it would seem better to use an "expert panel" for prediction rather than a single best "expert" obtained over one specific splitting of the samples.

It is also noted that the predictions for the last five common testing years (i.e., 1950, 60, 70, 80, and 90) had relatively larger errors than the first five years (i.e., 1900, 10, 20, 30, and 40). This suggests that there may be other unrecognized factors influencing tree growth in the later half of the century than the first half. For example, are these unrecognized factors related to the increase in atmospheric CO_2 concentration, the climatic extremes in recent decades, or the occurrence of other disturbances (Briffa et al., 1998)? Collection of data for these variables and incorporation of them into neural networks will help understand their effects on tree-ring growth.

4.3.2 *Understanding Climate-Growth Relationships*

Beside its use for growth predictions, the ANN models can also be used for understanding the relationships between climate and tree growth. Unlike the traditional multiple regression techniques, which use the regression coefficients to interpret the relationships between input and output variables, the ANN models evaluate such relationships by presenting a series of input scenarios to the neural network and examining the response patterns produced by output neurons. The difficulty of directly interpreting the free parameters in the ANN models will be discussed in section 7.1.2 of chapter seven.

Using the ANN model developed on the first training set (which is the grouping of data by alternate decades, see Figure 4.5), the growth-response patterns for some scenarios of input climatic conditions are presented in Figure 4.9. In each scenario, the effect of one or two input variables on tree-ring growth were examined, and the non-examined input variables were set at their means for the period A.D. 1892-1992. The results show that the August total precipitation of the previous year had a positive association with concurrent tree growth only when the tree was in a state of above-average growth in the previous year (relative to the year of concurrent growth) (Figure 4.9a). The prior September mean temperature also had a positive association with tree growth, but this association could only be realized when the temperature was high and January precipitation was low (Figure 4.9b). Tree growth increased slightly with the increase in current year's August temperature only when April-July precipitation was low (Figure 4.9c). The prior November temperature showed no association with tree growth, when the other input variables were in their mean conditions (Figure 4.9d). These growth-response patterns suggest that the tree's radial growth responds nonlinearly to variables related to climate and prior growth, and that there are interactions among the effects of these input variables. Consequently, the growth-response pattern to a particular variable may change under different combinations of input climatic conditions, and the new patterns can be examined in the same way (i.e., the scenario analysis) using the

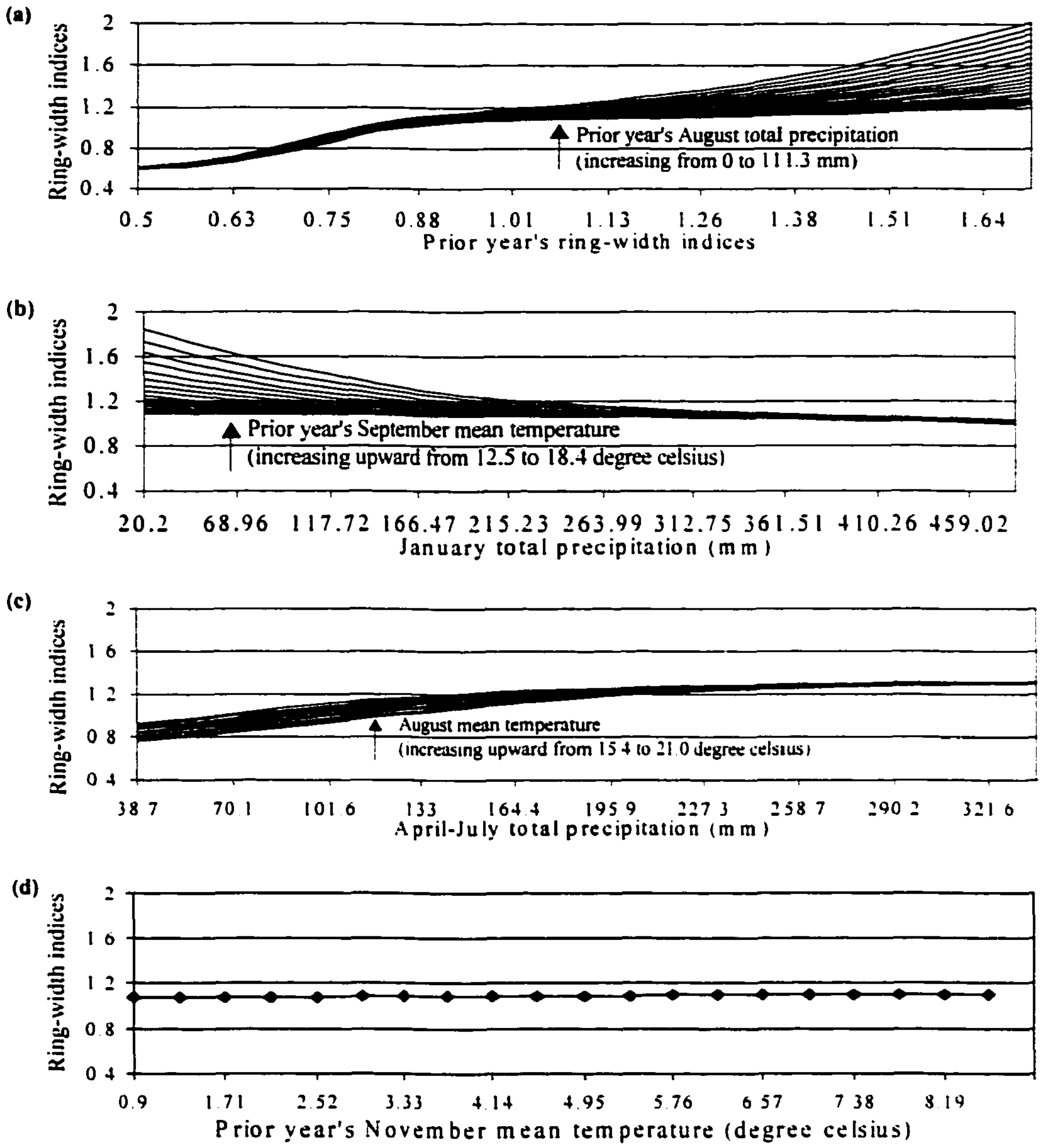


Figure 4.9 Examples of the ANN revealed nonlinear growth responses to prior ring growth and prior August precipitation (a), January precipitation and prior September temperature (b), April-July precipitation and August temperature (c), and prior November temperature (d). In each case, the non-examined variables were set at their means for the period A.D. 1892-1992.

established ANN models.

It should be noted that these growth-response patterns were obtained from empirical modeling, thus they cannot be used directly to demonstrate as causal relationships. However, these response patterns can help us understand climate-growth relationships when the species' biological characteristics are taken into account. For example, the patterns of growth response to prior August precipitation, to the previous year's growth, and to prior September temperature and January precipitation, as obtained from the ANN model, might reflect the biological processes that affect the preconditioning of tree growth. Douglas-fir has preformed needles (needles initialized within the bud but not elongated until after winter dormancy) (Allen and Owens, 1972), so stress conditions such as drought (as indicated by low precipitation in August) and poor state of health (as indicated by low radial growth) in the year prior to tree-ring growth can reduce the production of needle primordia (the initial needles within the bud), thereby reduce the tree's growth potential for the following year (Lassoie, 1982; Rensing and Owens, 1994). Douglas-fir has optimal photosynthesis at temperature around 15°C and can be photosynthetically active in temperatures ranging from 2 to 25°C (Doehlert and Walker, 1981; Leverenz, 1981a, 1981b), so low temperature and cloudy conditions during the autumn and winter may reduce photosynthesis, carbohydrate production, and carbohydrate storage to be used for subsequent stemwood production (Waring and Franklin, 1979; Little et al., 1995; Livingston, 1999 personal communication, Biology Dept. Univ. of Victoria, Victoria, Canada). The pattern of growth response to prior November temperature may suggest that it is likely the interaction of temperature, precipitation, and the state of tree's health that preconditions the radial growth of Douglas-fir. The pattern of growth-response to April-July precipitation obtained from the ANN model reflect the limiting effect of low moisture during the growing season and the decreasing effect of precipitation when approaching saturation (Waring and Running, 1978; Lassoie and Salo, 1981).

The reliability of these growth-response patterns depends on the quality and quantity of the original data used for training and testing the ANN models. Since the climate and tree-ring data sets are usually insufficient and noisy, caution should be used when interpreting the growth-response patterns. Normally, the ANN model can generalize well for input climatic conditions that are similar (but not identical) to those in the training set. However, when the input climatic conditions differ considerably from those in the training set, the ANN model may not generate a reliable response due to lack of experience with the new inputs. Furthermore, there usually exists inter-correlation among the climatic variables (Cropper, 1984). The response patterns extrapolated for unrealistic input scenarios, i.e., combination of climatic conditions unlikely to appear together due to the inter-correlation phenomena, can be disregarded. Although the performance of ANN model is highly dependent on the training/testing data, it does provide an opportunity to examine the nonlinear and complex growth-response patterns that cannot be recognized by the traditional multiple regression approaches.

Chapter 5 Spatial Variation in Douglas-fir Radial Growth

The climate-growth relationships established at the Heal Lake site of southern Vancouver Island represent, strictly speaking, a single site growth response pattern. Tree-ring chronologies at multiple locations of similar climate regimes can be compared to provide multi-scale spatial perspectives (Swetnam and Betancourt, 1998). Examination of the growth response of the same species under different climate regimes helps establish a wider spectrum of climate-growth relationships and reveal underlying mechanisms for growth responses. Section 5.1 compares the radial growth characteristics of Douglas-fir for three sites of similar climate regimes on south-eastern Vancouver Island. Section 5.2 examines the growth response of Douglas-fir in central coast BC where the climate is much colder than that on southern Vancouver Island. Section 5.3 compares the growth responses of Douglas-fir under regionally different climate regimes (i.e., southern Vancouver Island vs. Central Coast).

5.1 South-Eastern Vancouver Island

The availability of tree-ring samples of Douglas-fir at Koksilah and Victoria Watershed North on south-eastern Vancouver Island (Figure 5.1) from a study of forest chronosequence by J.A. Trofymow at the Pacific Forest Centre (PFC), Canadian Forest Service (Pollard and Trofymow, 1993; Trofymow and Porter, 1998) provides an opportunity to compare the radial growth characteristics of Douglas-fir from different sites of similar climate (Dai et al., 1997). These two sites are located approximately 30 km northwest of the Heal Lake site, and are in Douglas-fir dominated stands in very dry maritime of the Coastal Western Hemlock (CWHxm) biogeoclimatic zone (Meidinger and Poljar, 1991). The regional climate of the south-eastern Vancouver Island is regulated by the proximity of the Pacific Ocean and the rain shadow effect of the Olympic Peninsula and Vancouver Island Mountains (Meidinger and Poljar, 1991). It has warm, dry summers and mild, wet winters. If the climate-growth relationships are sufficiently strong, there should be similar annual growth patterns among stands that are influenced by the same regional weather systems (Brubaker, 1980). The comparison of tree-ring chronologies of Douglas-fir from multiple sites with a regionally similar climate regime can provide information about the spatial perspectives in radial growth characteristics.

5.1.1 *Tree-Ring Chronologies*

Sixty-five increment cores collected from living Douglas-fir trees (at breast height) from three sites, i.e., Koksilah, Victoria Watershed North, and Heal Lake, on south-eastern Vancouver Island (Figure 4.2) were used to develop ring-width chronologies. The samples from the first two sites were measured in the tree-ring laboratory at Pacific Forestry Centre using a Digimic tree-ring incremental measuring system. The samples from Heal Lake site were measured at the University of Victoria Tree-Ring Laboratory (UVTRL) using a Windendro™ image-analysis system. The measured ring-width series for each site were cross-dated, standardized, and averaged to form site ring-width chronologies according to the standard procedures introduced in section 3.2.

The chronology length used for comparison among different sites includes the interval with a minimum of ten samples per year. The tree-rings are sensitive to environmental factors as indicated by the mean sensitivity, which measures the ring-width variability between successive years (Table 5.1) (Fritts and Shatz, 1975; Brubaker, 1982). The mean series correlation, which is the average of correlation coefficients between each sampled ring-series and the mean of the remaining ring-series, is around 0.60 (Table 5.1). It describes the amount of common signal among trees within a chronology (Wigley et al., 1984). The first order autocorrelation, which measures the correlation between successive increments, ranges from 0.80 to 0.88, suggesting that tree-ring growth is highly influenced by the growth state (as a proxy of the tree's health state) in preceding growth year.

5.1.2 *Spatial Variation in Radial Growth*

Comparisons of the tree-ring chronologies from the three sites show that these chronologies are significantly correlated with each other (Table 5.2), and the periods of reduced and enhanced growth in Douglas-fir trees are generally synchronous among these sites (Figure 5.1). Major suppressed growth occurred during the mid 1770s-mid 1800s, early 1840s-1850s, late 1890s, and late 1900s-early 1910s. Major enhanced growth occurred during the 1860s, 1930s-1940s, and late 1970s-early 1990s. The consistent patterns of ring-width variation suggest that the radial growth of Douglas-fir in this region responds similarly to variation in large-scale climatic factors because it is unlikely for

Table 5.1 Dendrochronological characteristics of Douglas-fir ring-width chronologies at three sites on south-eastern Vancouver Island, British Columbia.

Site Code	**Site Name**	**Chronology length**	**Number of trees**	**Mean sensitivity**	**Series Correlation**	**First-order autocorrelation**
KSL	Koksilah	294 years (AD 1702-1995)	22	0.24	0.61	0.80
VWN	Victoria Watershed North	306 years (AD 1690-1995)	19	0.22	0.59	0.88
HLL	Heal Lake	252 years (AD 1741-1992)	24	0.23	0.59	0.86

Note: Chronology length is counted for the interval with at least ten sample replications. Mean sensitivity is a measure of high frequency between-ring variability and high values are characteristic of sensitive rings. Series correlation describes the signal strength of a chronology by averaging the internal correlations of all the series in the samples. First-order autocorrelation measures the correlation between successive increments, and positive values suggest that growth is conditioned by factors in the preceding growth year.

Table 5.2 Correlation matrix for the interval AD. 1741-1992 (252 years) illustrating the relationships between pairs of Douglas-fir chronologies from the three sites on south-eastern Vancouver Island, British Columbia.

Site Code Site Code	KSL	VWN	HLL
KSL	1.00		
VWN	0.87	1.00	
HLL	0.59	0.64	1.00

Note: The degree of freedom used for significance test is reduced because of the existence of autocorrelation within each tree-ring chronology (Livezey and Chen, 1983; Legendre and Legendre, 1998). The significance of the correlation coefficients can be evaluated by using reduced degree of freedom, such as 200, 100, 50 and 25, and examining their corresponding correlation coefficients significant at $p \leq 0.01$, i.e., 0.18, 0.25, 0.35, and 0.49, respectively (Clarke and Cooke, 1983).

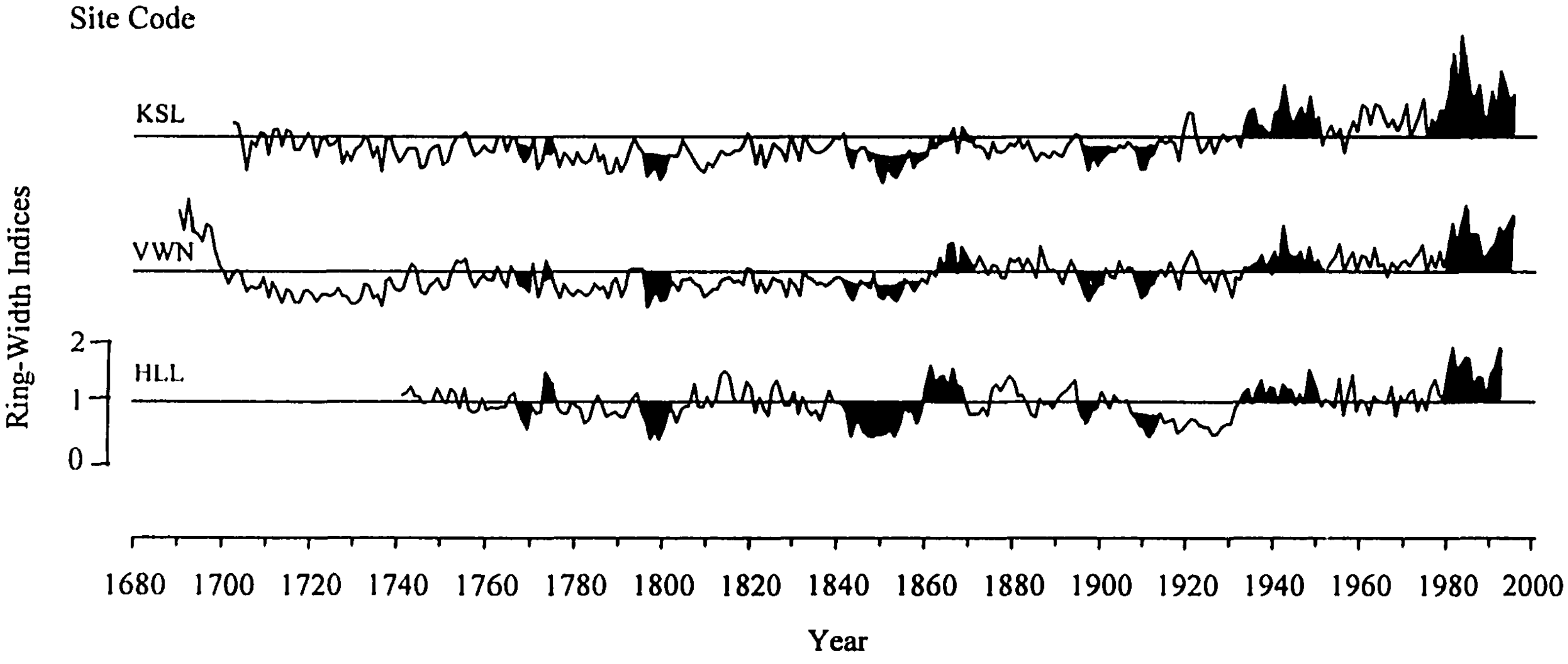


Figure 5.1 Ring-width chronologies of Douglas-fir at three sites on southeastern Vancouver Island, British Columbia. The major synchronous growth patterns are shaded in dark. The sample depth of the chronologies is at least ten for each year.

other factors to operate consistently both in large spatial scale and over a long temporal period.

Despite the similarity of growth patterns among the different site chronologies, there are differences in the magnitude of variation and in the short-term (annual) growth response. For instance, the signal of enhanced growth during the 1860s was weak in the chronology at the Koksilah site, but stronger in those at the Victoria Watershed North and Heal Lake sites (Figure 5.1). Also, the tree-ring indices at the Koksilah and Victoria Watershed North sites during the 18th-early 20th centuries are generally below the average growth. The differences among these chronologies are assumed to be a consequence of local site factors. For instance, the elevation at the Koksilah and Victoria Watershed North sites are about 630 m and 380 m asl, whereas the Heal Lake site is only 126 m asl. Perhaps the high elevation-related site factors such as decreased temperature and short growing season contribute, in part, to the differences in growth responses. The lack of climatic records at the Koksilah and Victoria Watershed North sites precludes the development of site-specific climate-growth relationships. Although local factors such as elevation, aspect, and disturbances influence the tree growth, the apparent synchroneity of enhanced and reduced growth among the three sites demonstrates that large-scale, regional climatic variations play a dominant role in determining the variation of Douglas-fir tree-ring growth within individual stands.

5.2 Central Coast of British Columbia

The coastal Douglas-fir can live in a wide ecological range from extremely dry, low elevation sites to moist montane sites (Poljar and Mackinnon, 1994) in the coastal areas of British Columbia (BC), Washington, Oregon, and northern California generally west of the crest of the Cascade and Sierra Nevada ranges (Oliver et al., 1986). The Bella Coola area of central coast BC is close to the northwestern limit of Douglas-fir's natural distribution. The climate in the central coast of BC is different from that in the southeastern Vancouver Island (Meidinger and Pojar, 1991). Study of the radial growth characteristics of Douglas-fir under regionally different climates provides critical comparative insight into the role of climate in tree growth, in particular, it helps establish whether temperature or precipitation, or a combination thereof, is the predominant radial growth controlling factor operating on a macro-regional scale.

The climate in the central coast of BC is colder than that of the south-eastern Vancouver Island. According to the climatic record from the weather station at Stuie-Tweedsmuir of Bella Coola (Figure 5.2), mean annual temperature ranges from 4.6°C to 9.1°C, with mean January temperature of -2.1°C and mean July temperature of 16.3°C (Figure 5.3). Douglas-fir trees are distributed in a wide range of elevations in the mountainous terrain of the Bella Coola area. As a result, tree-ring growth at different elevations may reflect the influence of climatic conditions associated with elevational gradients. This section deals with the tree-ring studies of Douglas-fir in the Bella Coola area.

5.2.1 *Tree-Ring Chronologies*

Two hundred and thirty-five increment cores were collected from 202 living Douglas-fir trees (at breast height) at 9 sites of different elevations, from 250 m asl to 1060 m asl, in the Bella Coola area of central coast BC (Figure 5.2, Table 5.3). All the

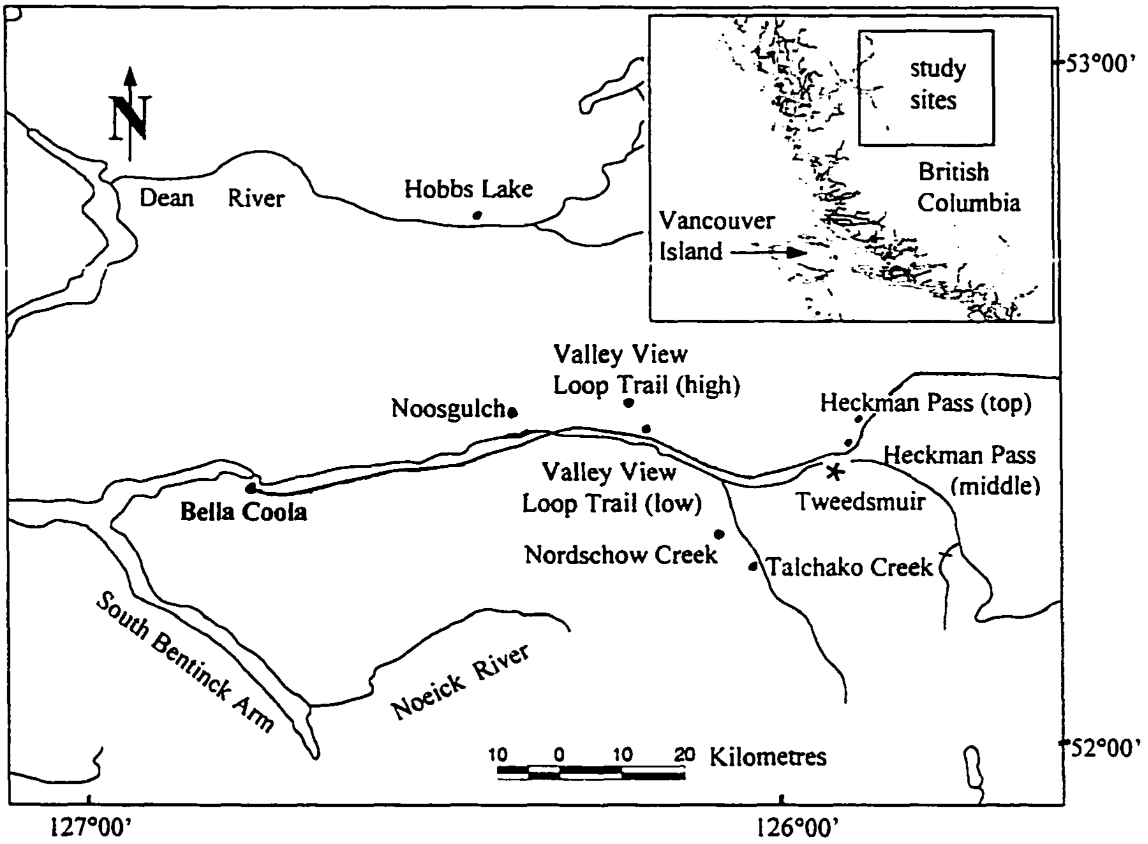


Figure 5.2 Location of the nine tree-ring study sites and the weather station at Stuie Tweedsmuir (★) in the Bella Coola area of central coast British Columbia.

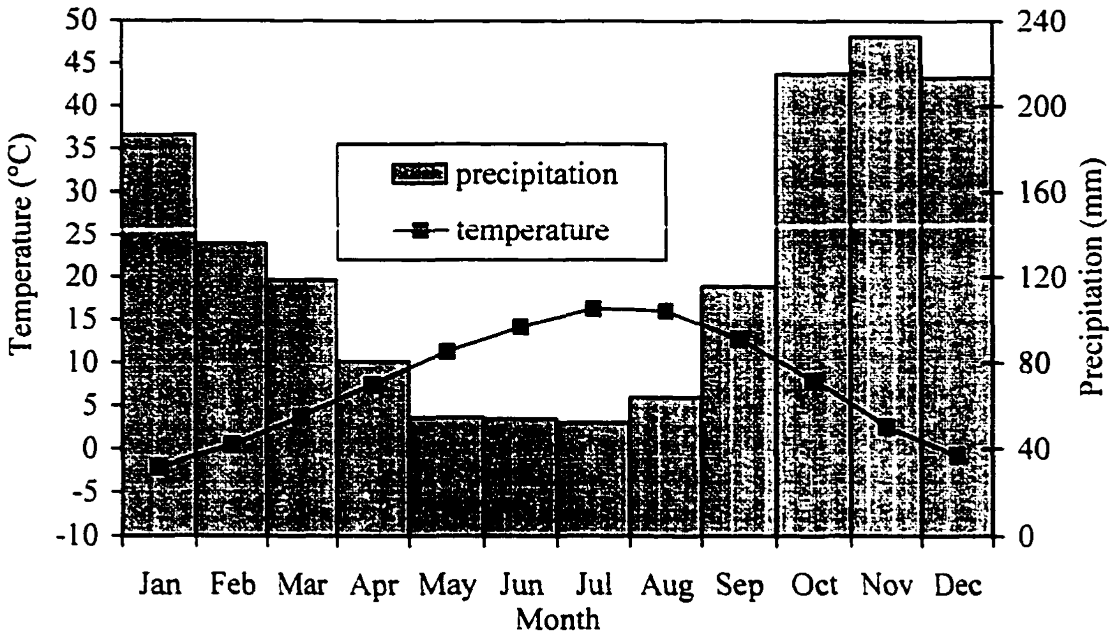


Figure 5.3 Representative diagram of the climate for the Bella Coola area of central coast British Columbia (averaged for A.D. 1907-1995 using records at the Stuie-Tweedsmuir weather station).

Table 5.3 Sample collections of Douglas-fir in the Bella Coola area of central coast British Columbia.

Site Code	**Site Name**	**Elevation (m asl)**	**Latitude (N) Longitude (W)**	**NTS Map Sheet**	**Number of Samples**
HP1	Heckman Pass (top)	1060	52°26'48" 125°52'00"	93 C/5	19 trees 19 cores
HBL	Hobbs Lake	850	52°46'00" 126°26'00"	93 D/16	16 trees 16 cores
HP2	Heckman Pass (middle)	820	52°25'12" 125°52'30"	93 C/5	20 trees 20 cores
NDS	Nordschow Creek	650	52°17'42" 126°05'30"	93 D/8	30 trees 38 cores
VV1	Valley View Loop Trail (high)	650	52°27'30" 126°13'00"	93 D/8	31 trees 56 cores
TCH	Talchako Creek	300	52°15'12" 126°01'42"	93 D/8	21 trees 21 cores
TWS	Tweedsmuir	260	52°24'24" 125°55'00"	93 C/5	22 trees 22 cores
VV2	Valley View Loop Trail (low)	250	52°26'12" 126°11'30"	93 D/8	24 trees 24 cores
NSG	Noosgulch	250	52°26'36" 126°22'48"	93 D/8	19 trees 19 cores

samples were prepared (mounted and surface-sanded) and measured at the UVTRL using a Windendro™ image-analysis system. The measured ring parameters included widths and brightness of total ring, earlywood and latewood. Ring-width chronologies were developed for each site following the established procedures of crossdating and standardization (see section 3.2 of chapter 3) (Table 5.4, Figure 5.4).

The values of mean sensitivity and series correlation of the tree-ring chronologies (Table 5.4) suggest that the radial growth of Douglas-fir in this region is sensitive to environmental changes (Fritts and Shatz, 1975; Brubaker, 1982), and that the individual trees in each site contain common environmental signals in their ring patterns. The high values of the first-order autocorrelation suggest that, as is the case for tree growth in southeastern Vancouver Island (section 5.1), the prior year's growth plays a significant role in controlling the current year's growth.

5.2.2 *Spatial Variation in Radial Growth*

The growth of Douglas-fir trees at each of the nine sites in the Bella Coola area is influenced by environmental factors at both local and regional scales. The relationships between local climate and tree growth cannot be developed for each site due to the lack of climatic record. The spatial variation in radial growth can be examined using principal component analysis (PCA) (LaMarche and Fritts, 1971; Blasing and Fritts, 1976; Brubaker, 1980). The PCA method has the ability to summarize, in a few dimensions, most of the dynamics of the observed system. It also shows the relationships among original variables in the reduced dimensions (Legendre and Legendre, 1998; von Storch and Zwiers, 1998). Such information provides insights into the role of climatic factors in

Table 5.4 Dendrochronological characteristics of Douglas-fir ring-width chronologies at nine sites in the Bella Coola area of central coast British Columbia.

Site Code	**Chronology Length**	**Number of Trees**	**Mean Sensitivity**	**Series Correlation**	**First-Order Autocorrelation**
HP1	111 years (1886-1996)	17	0.22	0.54	0.74
HBL	156 years (1841-1996)	15	0.21	0.58	0.77
HP2	125 years (1872-1996)	17	0.21	0.61	0.77
NDS	322 years (1675-1996)	29	0.19	0.51	0.86
VV1	217 years (1780-1996)	22	0.23	0.56	0.76
TCH	309 years (1688-1996)	20	0.19	0.57	0.77
TWS	251 years (1746-1996)	16	0.20	0.47	0.80
VV2	287 years (1710-1996)	17	0.26	0.60	0.75
NSG	216 years (1781-1996)	16	0.23	0.58	0.86

NOTE: The quality of the increment core samples was examined in the lab, and only the high quality samples (with sensitive rings and few broken pieces) were selected and used in the construction of chronology. As a result, the number of trees in the chronologies is equal to or less than the number of samples collected.

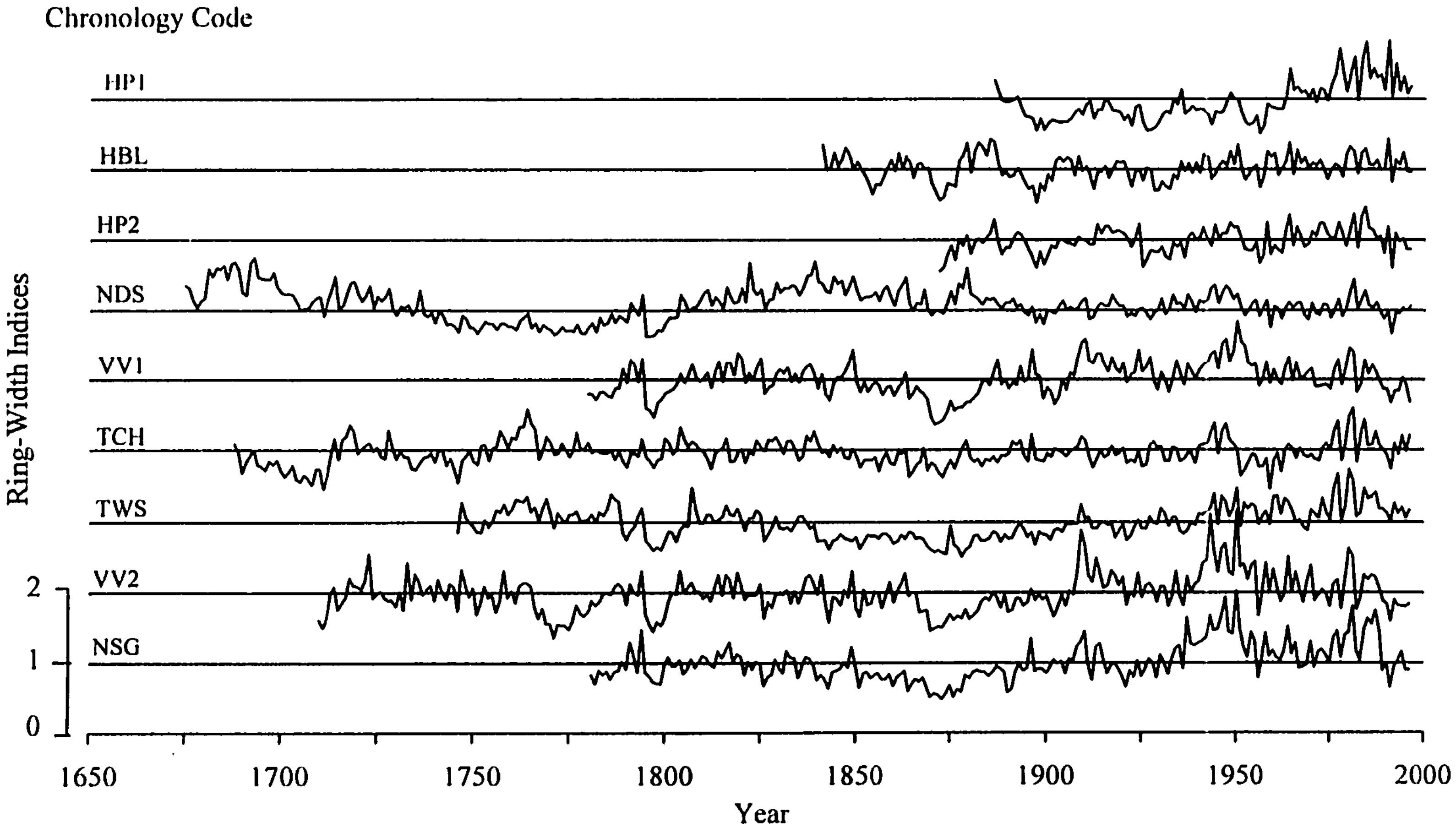


Figure 5.4 Ring-width chronologies of Douglas-fir from nine sites in the Bella Coola area of central coast British Columbia.

determining tree growth.

Principal component analysis (PCA) of the nine site chronologies

The tree-ring chronologies at the nine sites in Bella Coola area contain a variety of both local and regional environmental signals. Principal component analysis was used to summarize the dominant radial growth patterns, carried by the nine chronologies, into a smaller number of principal components (PCs). By this method, the first PC accounts for the greatest proportion of the total variance of the nine chronologies, and the second PC accounts for the largest fraction of the remaining total variance, and so on. Each PC is orthogonal (unrelated) to the other and involves a linear combination of the nine site chronologies. The weight associated with each chronology conveys information about characteristic growth relationship between this site and the principal component, i.e., the higher the value of the weight, the closer the relationship.

The Dendrochronology Program Library (DPL) software PCA (Holmes, 1994) was used to extract the PCs of the nine chronologies for the common interval A.D. 1886-1996. The result shows that the first two PCs accounts for 48.7% and 24.0% of the total variance, respectively (Table 5.6). Other PCs that account for less than 10% of the total variance describe small-scale variability and are considered to be insignificant (Table 5.6). The first two PCs were then used in the following analysis to examine the spatial patterns of Douglas-fir tree-ring growth.

The weights associated with each chronology were plotted against the site elevations to display the spatial growth patterns represented by the first two PCs (Figure 5.5). For the first PC, the weights of the nine site chronologies all have positive values

Table 5.5 Principal components of the nine site Douglas-fir chronologies (for the period A.D. 1886-1996) in the Bella Coola area of central coast British Columbia.

Principal component	**Eigenvalue**	**Variance (%)**	**Cumulative variance (%)**
1	4.38	48.7	48.7
2	2.16	24.0	72.7
3	0.78	8.7	81.4
4	0.64	7.1	88.5
5	0.32	3.6	92.1
6	0.25	2.8	94.9
7	0.19	2.2	97.1
8	0.18	1.9	99.0
9	0.10	1.0	100.0

NOTE: Eigenvalue is the sum of squares of the correlations between the component and the chronologies. Variance (%) refers to the percentage of total variance explained by the corresponding principal component.

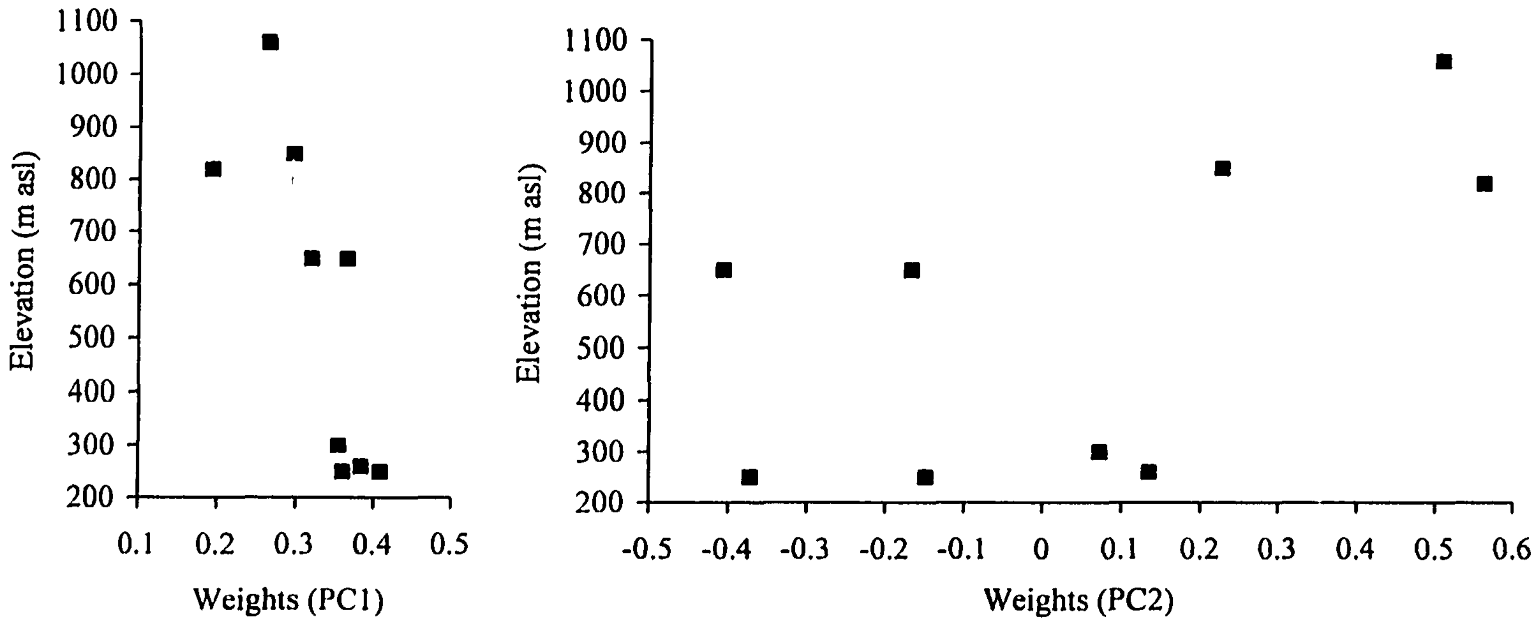


Figure 5.5 Weights associated with the nine sites for the first (a) and second (b) principal components of site tree-ring chronologies in the Bella Colla area of central coast British Columbia.

which increase slightly as elevation decreases. This pattern indicates that the growth variations at all sites are positively correlated with the first principal component, and the correlations are stronger at lower elevational sites than that at higher elevations. Therefore, the first PC reflects a common growth response throughout the nine sites, and a larger contribution of variance by the lower elevational sites. Regional climate variation is the most likely factor for such spatial response pattern because all the sites may experience the same relative changes as each new weather system crosses the area (Brubaker, 1980).

For the second PC, the weights of the three sites at highest elevation have large and positive values, and the weights of other six sites are near zero (for four sites) or have large negative values (for two sites). This indicates that the radial growth represented by the second PC has positive correlation with that at the three sites of highest elevation, little correlation with that at the four sites of near-zero weights, and negative correlation with that at the two sites of large negative weights. Therefore, the second PC reflects a contrasting growth response pattern at sites of different elevation. Environmental changes associated with elevational gradient, such as decrease in temperature and length of growing season with the increase in elevation, may lead to such spatial variation in radial growth (Lassoie, 1982; White, 1987). Factors other than elevation, such as slope aspect and local disturbance, may also influence the spatial pattern of radial growth in the second PC because sites of similar elevation have a wide range of weights and sites at different elevation have similar weights (Figure 5.5).

The growth variations represented by the first two PCs can be displayed by plotting the PC scores against the calendar years (Figure 5.6). The PC score for a given year is calculated by multiplying the tree-ring indices (expressed as departures from average) with the corresponding weights for each site and summing the products across the nine sites. The most striking features in the first PC are the large positive scores (greater than 4) in years of 1947, 1950, 1977, 1980-81, and 1984, and large negative score (smaller than -4) in year of 1991 (Figure 5.6a). The large positive scores indicate that above average growth is a dominant feature in these years throughout the study area. Likewise, the large negative score indicates a dominant feature of below average growth throughout the study area. This synchroneity of spatial growth pattern can also be reflected by directly comparing the observed growth patterns over the nine sites. Such comparison of site chronologies (Figure 5.4) shows that common intervals of enhanced growth occurred in the 1940s-early 1950s (significant in low elevation sites), and mid 1970s-1980s; and common reduced growth occurred in early 1990s. These common growth patterns are most likely a result of regional climatic variations; the relationships between the climatic variables and radial growth will be discussed in the next subsection.

The second PC shows persistent negative values from late 1900s to late 1950s and persistent positive values from 1960s to 1990s, (Figure 5.6b). Negative values mean that the sites with negative weights have above average growth and the sites with positive weights have below average growth. Likewise, positive values indicate above average growth for sites with positive weights and below average growth for sites with negative

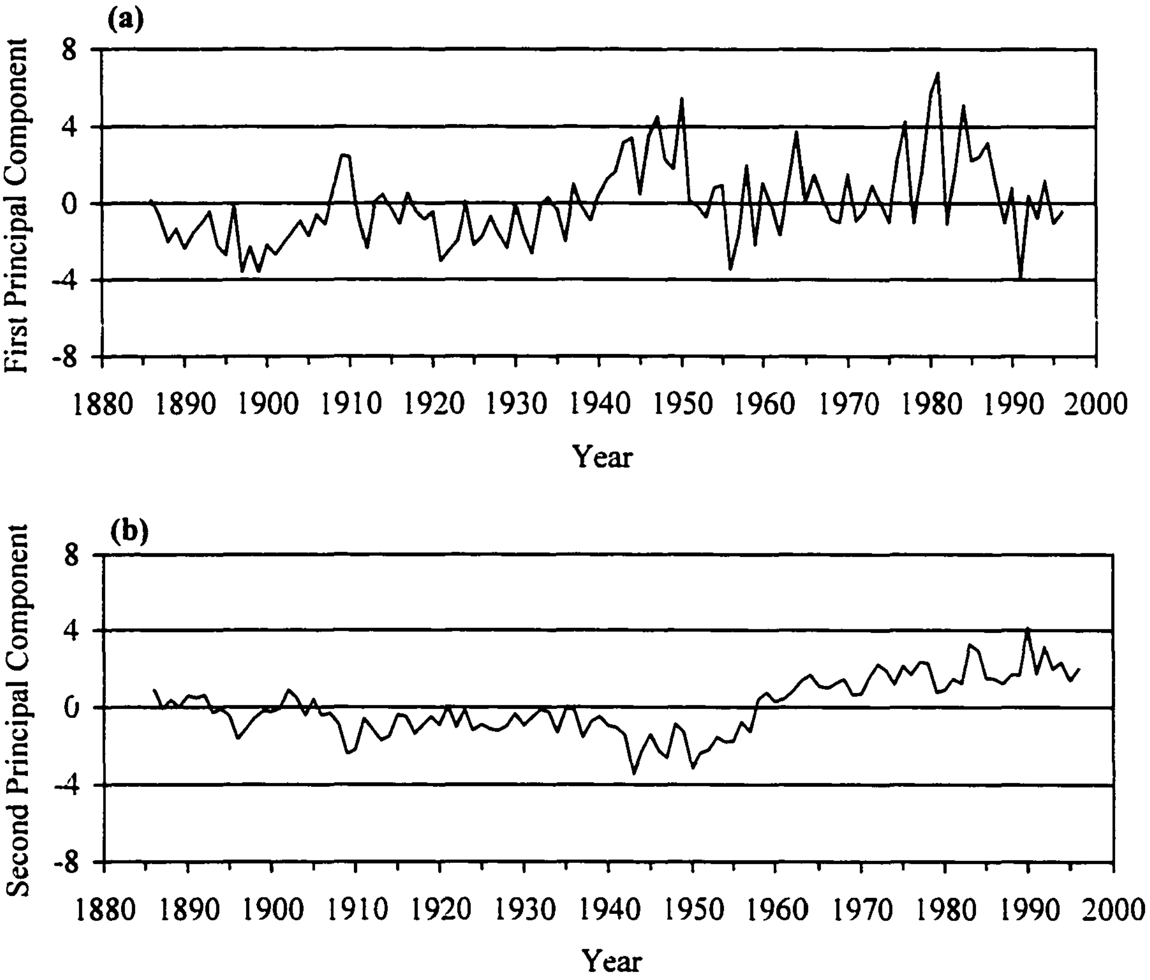


Figure 5.6 The first and second principal components of the Douglas-fir ring-width chronologies at nine sites in the Bella Coola area of central coast British Columbia.

weights. The contrasting growth patterns over different sites may suggest a different growth response to local site conditions. Could the temperature be responsible for such contrasting growth responses? A speculation is that an increase in growing season temperature might facilitate tree growth by increasing the leaf area and photosynthesis (due to closer to optimal temperature) at sites of higher elevation, but retard radial growth by increasing water loss (due to more evapotransporation) at sites of lower elevation (Brix, 1967; White, 1987). It is difficult, however, to relate the contrasting growth responses to specific factors because of the lack of climatic and disturbance records for sites of different elevation.

I attempted to explore the effects of temperature on tree-ring growth by examining the brightness and widths of earlywood and latewood at sites of different elevation because the density and widths of latewood have been reported to be sensitive to growing season temperature (Briffa et al., 1992, 1994; Luckman et al., 1997; Dobry and Klinka, 1998). Unfortunately, the attempt was not successful because of large measurement errors in recording the brightness and intra-ring widths data using the Windendro™ image system. These measurement errors were due to the problem of surface defects and extraneous color variation in tree-rings, e.g., heartwood discoloration, fungal staining and compartmentalization of wounds (Shigo, 1985; Kreber and Byrne, 1994; Sheppard et al., 1996; Frank, 1998). The measured ring-brightness data for such rings no longer represent the actual ring-density variable because of the disruption of the ring brightness-density relationships (Sheppard, 1999). Gradual changes from earlywood to latewood and extraneous discoloration also obscure the detection of the boundary between earlywood and latewood within a ring, hence introducing errors in reading earlywood- and latewood-widths (Sheppard, 1999). With the future development of the techniques in processing the extraneous wood color variation, the ring-brightness and intra-ring widths data for Douglas-fir may have potential for studying climate-growth response.

Climate-growth response

Since the first PC of the tree-ring chronologies at the nine sites reflects the common growth response to regional climatic variations, the scores of the first PC can be used to evaluate the regional climate-growth relationships. Because there are no sufficiently long climate records available for sites of different elevations, the best choice for growth response analysis is to use the climate record from the weather station at Stuie-Tweedsmuir (Figures 5.2, 5.3) as an approximation of the regional climate variation.

The computer program PRECON (Fritts, 1994) (see section 3.3.1) was used to examine the relationships between climatic variables and tree-ring growth represented by the first PC. The climatic variables consist of monthly mean temperature and total monthly precipitation for a 14-month period starting with August of the previous growth year ending with September of the current growth year. The results show that the tree-ring growth is positively correlated with the precipitation in May and July of the current year, and with the temperature in March, and negatively correlated with temperature in previous year's August (Figure 5.7). The response function represents fifty-nine percent of the variance in the first PC. It should be noted that the response function analysis using climate data at one site of low elevation and the first principal component of nine

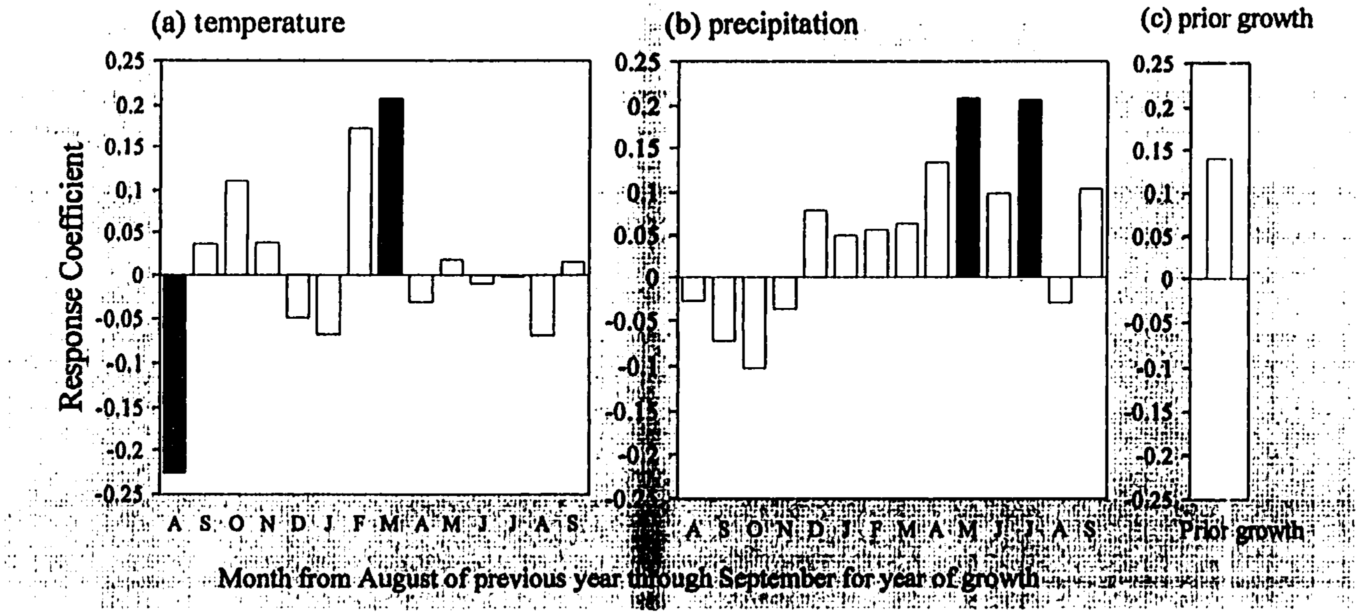


Figure 5.7 Response function coefficients relating monthly mean temperature and total precipitation to the first principal component of Douglas-fir ring-width chronologies at nine sites in the Bella Coola area of central coast British Columbia. The coefficients that are significant at $p \leq 0.05$ (based on bootstrapping tests) are shaded in dark. The response function represents 59 percent of the variance in the first PC.

chronologies only provide general information about the common climate-growth relationships for the region.

Artificial neural networks (ANN) are not appropriate for further modeling the nonlinear growth response in this situation because the first PC does not represent the exact growth response to the corresponding climate record, but rather a summarized common growth response in all the sites. In other words, the available climate-growth database contains too much noise making it difficult for the ANN to learn the real climate-growth relationships. In fact, the climate-growth response of Douglas-fir varies with different elevations as shown by the weights in the first two PCs, and the common growth response represented by the first PC only accounts for 48.7% of the total variance in the nine chronologies. In my experimentation with ANN modeling using such climate-growth database, the ANNs can memorize the climate-growth patterns in training set, but cannot generalize well for the testing set. This indicates that the ANNs have great power to learn the input-output patterns presented in the training set, but cannot generalize well if the training set contains too much noisy information (i.e., unobserved factors affecting the tree-ring growth).

5.3 Comparison of Growth Responses Under Different Climate Regimes

Comparison of the climate-growth relationships of Douglas-fir under regionally different climate, i.e., Central Coast vs. southern Vancouver Island, provides insights into growth response patterns under a wider range of climatic conditions. The comparison shows that the radial growth of Douglas-fir in both regions is positively related to the growing season precipitation (Figures 4.4, 4.9, and 5.7). This shared response suggests that the precipitation in the growing season limits sustained rapid growth and is a major radial growth controlling factor operating over a macro-regional scale. The length of the growing season in the Bella Coola area may be shorter than that on the southern Vancouver Island. As a consequence, only May and July precipitation are significantly related with the growth of Douglas-fir in the Bella Coola area, whereas April-July precipitation affects the tree's growth on the southern Vancouver Island.

The differences in the climate-growth relationships for Douglas-fir between the Bella Coola area of the Central Coast and the Heal Lake site of southern Vancouver Island lie mainly in non-growing seasons. In the Bella Coola area, high temperature in previous year's August has a negative influence on tree's growth, an effect which might be explained by the increase in moisture deficit associated with high temperature, i.e., the higher the temperature, the more the water loss through evapotranspiration. The positive relationship between the temperature in March and the tree's growth in Bella Coola might be related to the break of winter dormancy and initiation of a variety of physiological activities (Lassoie, 1982). For the Heal Lake site of southern Vancouver Island, the temperature in previous year's September and November has a positive relationship with the tree's growth, and the precipitation in January shows negative correlation with the tree's growth. The role of these climatic variables might be related to the process of photosynthesis which is active in Douglas-fir trees in temperatures ranging from 2-25°C (optimal from 10-20°C) (Doehlert and Walker, 1981). Mild autumn and winter seasons with clear sky (less precipitation) can facilitate photosynthesis (Helms, 1965; Brubaker, 1980; Little et al., 1995; Livingston, personal communication, 1999). In contrast, photosynthesis may not be continually active during the autumn and winter in the Bella Coola area because of the colder temperatures which usually goes below 2°C in winter season (Figure 5.3).

In summary, the growing season precipitation is likely a major factor limiting the growth of Douglas-fir over a macro-regional scale in the coastal BC. The non-growing season climatic factors may contribute to the differences in the radial growth response between southeastern Vancouver Island and Central Coast BC.

Chapter 6 Late Holocene Growth Variations in Douglas-fir

Climate changes affect the radial growth of a tree through altering the disturbance and stress factors (see section 2.2 of chapter 2), and major climate changes have occurred several times in British Columbia in the Holocene (L. Heusser, 1983; C. Heusser et al., 1985; C. Heusser, 1995; Allen, 1995; Hebda, 1995; Heinrichs, 1999; Brown, 2000). The discovery of subfossil logs from the bottom of Heal Lake on southern Vancouver Island provides an opportunity to examine tree-ring growth patterns under historically different climate at the same location (Hebda, 1993a). Such tree-ring data are an important proxy record of palaeo-climate variation (Hebda, 1993b; Zhang, 1996). This chapter extends the previous dendrochronological study of the Heal Lake subfossil Douglas-fir (Zhang, 1996), and applies the knowledge of climate-growth response from chapters four and five to analyze the late Holocene radial growth patterns. Section 6.1 deals with the preparation and crossdating of the subfossil log samples. Section 6.2 presents the results of tree-ring chronologies. Section 6.3 describes the radial growth patterns in historically different climate regimes and focuses on a particularly marked change in radial growth at about 4000 years ago.

6.1 Preparation and Crossdating of Subfossil Log Samples

A large number of well-preserved logs were discovered from the bottom of Heal Lake of southern Vancouver Island in the fall of 1992 when the lake was drained by the Capital Regional District for additional space for municipal waste. Seven hundred and six disc samples were collected from these logs and were stored in the Pacific Forestry

Centre (PFC), Canadian Forest Service, Victoria, BC. Radiocarbon dates of selected samples indicate that the age of these logs varies from 150 +/-50 years before present (BP) to 9230 +/-60 years BP. In a previous study of these subfossil logs (Zhang, 1996), the tree species were identified from microscopic examination of wood anatomy, and the ring-widths were measured at PFC using a MEASU-CHRON system. The results showed that most of the logs were Douglas-fir and tree-rings of these logs contained a useful proxy record of environmental changes, particularly for variation of spring precipitation. One hundred and twenty six log discs and 29 living trees of Douglas-fir were crossdated to form a continuous ring-width chronology for the last two millennia (Zhang, 1996). In this section, the focus is on the crossdating of the rest of the subfossil logs so as to extend tree-ring chronologies further back in time.

6.1.1 *Preparation of Subfossil Samples*

The development of tree-ring chronologies and the study of ring growth patterns often require repeated examination and comparison of ring features on the original wood samples. The 706 subfossil log discs, however, were in a large volume and piled up densely in a shed at the PFC (Figure 6.1), making it difficult to find any particular samples for re-examination. To facilitate further study, a narrow strip of wood was cut (using a table saw) from each of these log discs to reduce the sample volumes (Figure 6.2). The location of the strip chosen for cutting was determined by several factors, e.g., long ring-series, sensitive rings, and free from rot. The strip samples are stored in a set of shallow drawers at the Royal British Columbia Museum (RBCM). The residuals of the log discs have been retained in the collections of RBCM.

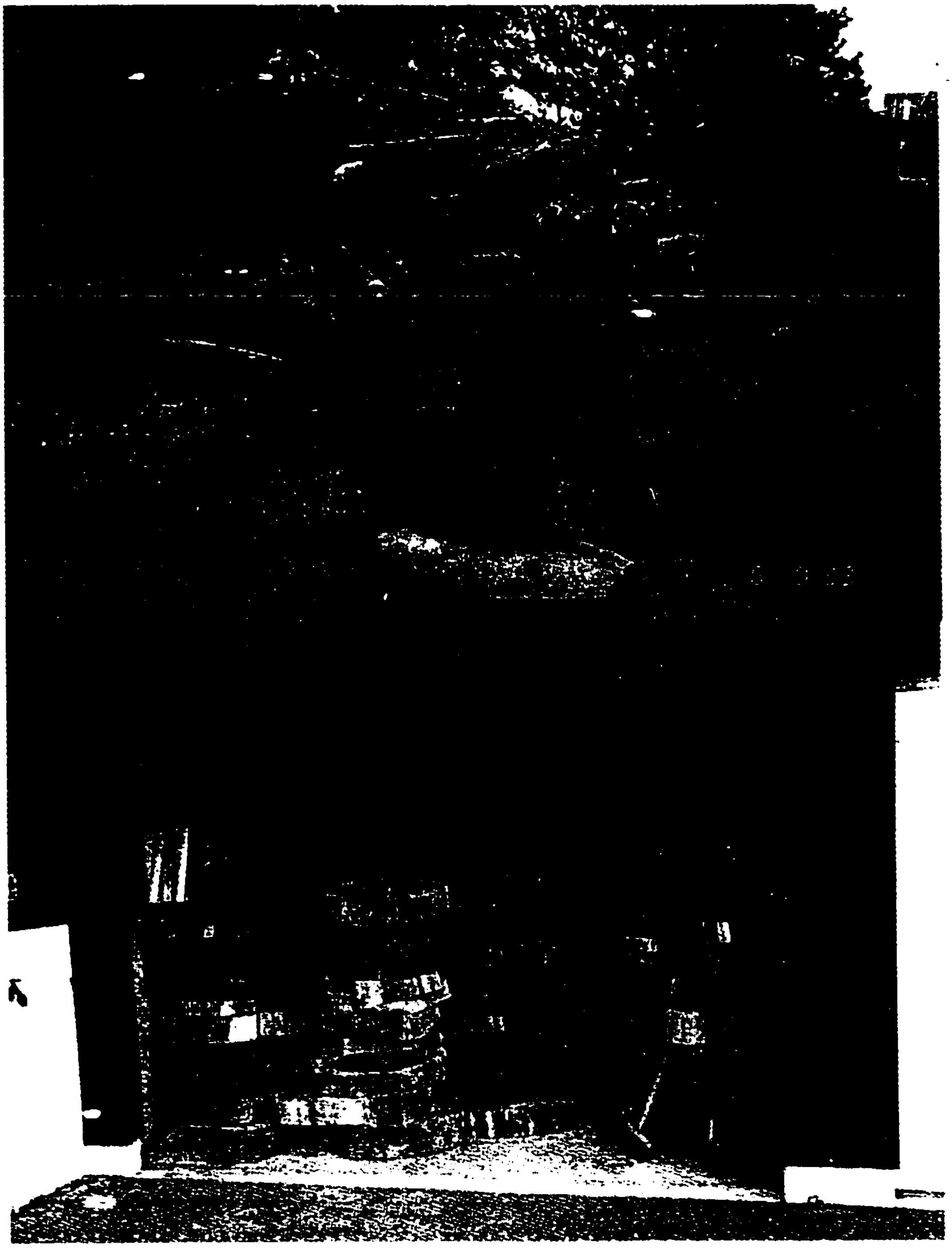


Figure 6.1 Subfossil logs and discs stored at the Pacific Forestry Centre, Canadian Forest Service, Victoria, British Columbia.

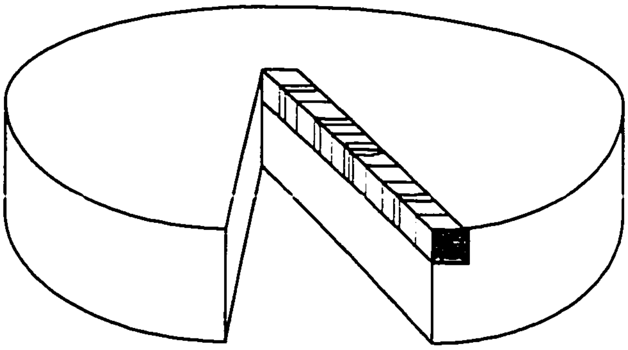


Figure 6.2 Illustration of a strip sample cut from a Heal Lake log disc.

The cross-sectional surface of each strip sample was polished with a series of sandpaper grits (100, 220, 320, 400, and 600) to bring out the ring features clearly (Swetnam et al., 1985). It is more convenient to examine ring characteristics from the strip samples than log discs, thus facilitating direct visual comparison and crossdating of ring sequences.

6.1.2 *Crossdating of Subfossil Samples*

The tree-rings of the subfossil Douglas-fir samples were compared using a variety of crossdating techniques including skeleton plot, graphical examination, computer-aided checking (program COFCHA), and visual examination (see section 3.2). Radiocarbon dates of selected samples (Table 6.1) were used to anchor the floating ring sequences to an interval of time. This work of crossdating consumed much time and effort because the undated logs could have grown at any time in the past nine millennia. To date, 79 subfossil samples have been crossdated into five floating groups (Tables 6.2-6.6), each having an interval of at least five sample replicates per year. Each annual growth ring of the samples in the five floating groups was assigned with a relative calendar year based on the radiocarbon dates of the component samples within the chronology (Table 6.1).

There remain 501 log disc samples either singly or in groups of less than five sample replications that have not been placed into chronologies. These samples are not analyzed in this study because it is difficult to distinguish growth patterns resulting from microsite conditions and stand environment if only a single or a few (e.g., less than five) samples are available. Nevertheless, for those samples that have been radiocarbon dated,

Table 6.1 Radiocarbon dates of selected samples from Heal Lake subfossil logs. Samples No. 1-10 are incorporated into the floating chronologies in this study.

No.	Sample ID	Number of rings	Rings for dating[1]	C-14 dates (year BP)[2]	Calibrated calendar years (year B.C.)[3]
1	HLL098	303	93-(97)-101	2250 +/- 48	397-[384-(365, 275, 264)-202]-183
2	HLL069	174	17-(20)-24	2540 +/- 50	803-[790-(767)-446]-412
3	HLL026	166	10-(15)-20	2610 +/- 70	897-[814-(793)-766]-432
4	HLL569	352	7-(10)-12	2860 +/- 50	1210-[1078-(1008)-917]-835
5	HLL527	316	7-(9)-11	2880 +/- 50	1236-[1187-(1047, 1040, 1013)-940]-899
6	HLL670	341	7-(9)-11	2900 +/- 50	1285-[1208-(1069, 1064, 1050, 1034, 1021)-974]-904
7	HLL699	335	9-(11)-13	2900 +/- 50	1285-[1208-(1069, 1064, 1050, 1034, 1021)-974]-904
8	HLL064	238	60-(65)-70	3390 +/- 50	1859-[1736-(1687, 1669, 1660, 1648, 1640)-1559]-1517
9	HLL020	225	10-(15)-20	3450 +/- 60	1918-[1863-(1736, 1701, 1695)-1638]-1532
10	HLL517	181	32-(35)-37	3520 +/- 50	2009-[1917-(1864, 1843, 1826, 1818, 1814, 1793, 1778)-1739]-1663
11	HLL063	271	7-(12)-16	3720 +/- 50	2279-[2197-(2130, 2081, 2068, 2059, 2044)-1978]-1933
12	HLL070	313	17-(22)-26	3740 +/- 50	2396-[2210-(2136, 2078, 2072)-1983]-1945
13	HLL167	242	30-(33)-36	4230 +/- 50	2918-[2893-(2883, 2766, 2764)-2643]-2602
14	HLL032	195	10-(15)-20	4270 +/- 70	3077-[2918-(2890)-2713]-2603
15	HLL056	154	11-(14)-17	5720 +/- 60	4759-[4685-(4540)-4462]-4407

16	HLL047	183	30-(35)-39	6520 +/- 60	5571-[5516-(5439)-5353]-5327
17	HLL986	102	60-(65)-70	6940 +/- 60	5945-[5840-(5754)-5703]-5666
18	HLL043	235	90-(95)-99	6990 +/- 70	5974-[5942-(5927, 5914, 5847, 5819, 5809)-5732]-5679
19	HLL036	181	17-(20)-22	7360 +/- 64	6361-[6217-(6177)-6058]-6015
20	HLL046	172	50-(55)-60	7930 +/- 64	7034-[7001-(6756, 6743, 6713)-6616]-6561
21	HLL428	143	11-(17)-23	8490 +/- 72	7585-[7546-(7504)-7447]-7422
22	HLL091	78	15-(18)-20	9230 +/- 60	8413-[8345-(8329, 8312, 8246, 8231, 8202)-8095]-8083

[1] The number of rings is counted from the pith side to bark side, and the middle-ring of the dated segment is indicated in the brackets;

[2] the dates underlined are reported from Beta Analytic Inc., Miami, Florida, USA, and the rest of the dates are reported from the Radiocarbon Dating Laboratory, Geological Survey of Canada, Ottawa.

[3] the dates are in the sequence of "2 sigma maximum-[1 sigma maximum-(intercept(s))-1 sigma minimum]-2 sigma minimum" (Stuiver and Reimer, 1993), and the underlined intercept years are used as anchor years for the floating chronologies.

Table 6.2 Subfossil Douglas-fir samples crossdated for floating chronology I.

No.	Sample ID	Span of years (year B.C.)[1]	No. of rings	No. of segments[2]	No. of flags[3]	Correlation of ring-widths with the mean of the remaining series
1	HLL098	371-69	303	11	1	0.50
2	HLL580	236-82	155	6	0	0.64
3	HLL547	230-87	144	6	0	0.62
4	HLL061	340-91	250	10	0	0.66
5	HLL134	359-93	267	11	1	0.59
6	HLL440	250-94	157	6	0	0.63
7	HLL022	240-107	134	5	0	0.55
8	HLL513	246-109	138	5	0	0.72
9	HLL934	246-109	138	5	0	0.72
10	HLL016	249-110	140	5	0	0.62
11	HLL021	241-110	132	5	0	0.60
12	HLL258	357-114	244	10	1	0.52
13	HLL322	250-129	122	4	0	0.56
14	HLL673	300-143	158	6	1	0.39
15	HLL125	321-151	171	7	0	0.52
16	HLL449	356-178	179	7	0	0.54
17	HLL465	347-187	161	6	0	0.66
18	HLL421	422-170	213	6	1	0.49
Total or Mean			3206	121	6	0.58

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[1] The age in years is estimated based on calibrated radiocarbon date of sample HLL098 (see Table 6.1).

[2] The segments are 50-year in length with 25-year overlap in successive segments.

[3] The flags are segments for which the correlation of the ring-widths with the mean of the remaining series is 0.32 or less ($p \leq 0.05$).

Table 6.3 Subfossil Douglas-fir samples crossdated for floating chronology II.

No.	Sample ID	Span of years (year B.C.)[1]	No. of rings	No. of segments[2]	No. of flags[3]	Correlation of ring-widths with the mean of the remaining series
1	HLL069	779-606	174	7	0	0.46
2	HLL026	777-612	166	7	2	0.48
3	HLL450	787-624	164	6	2	0.38
4	HLL397	810-649	162	6	1	0.59
5	HLL523	832-666	167	7	0	0.67
6	HLL142	866-677	190	7	0	0.58
7	HLL979	858-684	175	7	0	0.61
8	HLL668	807-686	122	5	0	0.51
Total or Mean			1320	52	5	0.54

[1] The age in years is estimated based on calibrated radiocarbon date of sample HLL069 (see Table 6.1).

[2] The segments are 50-year in length with 25-year overlap in successive segments.

[3] The flags are segments for which the correlation of the ring-widths with the mean of the remaining series is 0.32 or less ($p \leq 0.05$).

Table 6.4 Subfossil Douglas-fir samples crossdated for floating chronology III.

No.	Sample ID	Span of years (year B.C.)[1]	No. of rings	No. of segments [2]	No. of flags[3]	Correlation of ring-widths with the mean of the remaining series
1	HLL569	1017-666	352	13	0	0.69
2	HLL670	1033-693	341	13	0	0.67
3	HLL699	1041-707	335	13	0	0.69
4	HLL527	1029-714	316	12	0	0.71
5	HLL574	971-824	148	6	0	0.67
6	HLL582	991-849	143	6	0	0.60
7	HLL317	1000-852	149	6	1	0.50
8	HLL310	1030-865	166	6	0	0.49
9	HLL353	1013-884	130	6	0	0.55
10	HLL610	1010-886	125	5	0	0.65
11	HLL609	1010-892	119	4	0	0.70
Total or Mean			2324	90	1	0.65

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[1] The age in years is estimated based on calibrated radiocarbon date of sample HLL569 (see Table 6.1).

[2] The segments are 50-year in length with 25-year overlap in successive segments.

[3] The flags are segments for which the correlation of the ring-widths with the mean of the remaining series is 0.32 or less ($p \leq 0.05$).

Table 6.5 Subfossil Douglas-fir samples crossdated for floating chronology IV.

No.	Sample ID	Span of years (year B.C.)[1]	No. of rings	No. of segments[2]	No. of flags[3]	Correlation of ring-widths with the mean of the remaining series
1	HLL575	1491-1291	201	8	0	0.69
2	HLL362	1455-1298	158	6	0	0.50
3	HLL287	1526-1313	214	8	0	0.74
4	HLL305	1523-1316	208	8	0	0.78
5	HLL293	1535-1352	184	8	0	0.69
6	HLL264	1703-1417	287	11	0	0.61
7	HLL355	1565-1429	137	6	0	0.57
8	HLL335	1585-1444	142	6	0	0.64
9	HLL064	1724-1487	238	9	0	0.69
10	HLL396	1663-1496	168	7	1	0.46
11	HLL243	1658-1499	160	7	0	0.57
12	HLL062	1685-1501	185	8	0	0.61
13	HLL130	1721-1536	186	7	0	0.68
14	HLL256	1754-1547	208	8	0	0.69
15	HLL404	1671-1562	110	4	0	0.59
16	HLL465	1774-1565	210	8	0	0.51
17	HLL267	1723-1569	155	6	0	0.56
18	HLL109	1750-1578	173	7	4	0.38
19	HLL286	1845-1585	261	7	0	0.55
20	HLL288	1745-1585	161	6	0	0.73
Total or Mean			3746	145	5	0.62

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[1] The age in years is estimated based on calibrated radiocarbon date of sample HLL064 (see Table 6.1).

[2] The segments are 50-year in length with 25-year overlap in successive segments.

[3] The flags are segments for which the correlation of the ring-widths with the mean of the remaining series is 0.32 or less ($p \leq 0.05$).

Table 6.6 Subfossil Douglas-fir samples crossdated for floating chronology V.

No.	Sample ID	Span of years (year B.C.)[1]	No. of rings	No. of segments[2]	No. of flags[3]	Correlation of ring-widths with the mean of the remaining series
1	HLL099	1616-1461	156	5	2	0.58
2	HLL359	1673-1483	191	7	2	0.55
3	HLL294	1776-1511	266	10	0	0.52
4	HLL254	1760-1512	249	10	0	0.48
5	HLL020	1752-1528	225	9	0	0.65
6	HLL443	1744-1564	181	7	0	0.68
7	HLL571	1831-1569	263	11	0	0.69
8	HLL683	1698-1583	116	4	0	0.64
9	HLL376	1860-1605	256	10	0	0.66
10	HLL695	1716-1610	107	4	0	0.56
11	HLL712	1832-1631	202	8	0	0.77
12	HLL423	1859-1652	208	8	2	0.52
13	HLL517	1852-1672	181	8	0	0.85
14	HLL508	1850-1673	178	7	1	0.68
15	HLL479	1858-1673	186	8	0	0.80
16	HLL597	1819-1678	142	5	0	0.76
17	HLL106	1932-1681	252	8	1	0.71
18	HLL593	1842-1692	151	6	0	0.60
19	HLL702	1863-1742	122	5	0	0.64
20	HLL467	1892-1744	149	6	0	0.71
21	HLL393	1890-1752	139	5	0	0.76
22	HLL528	1884-1758	127	5	0	0.66
Total or Mean			4047	156	8	0.64

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[1] The age in years is estimated based on calibrated radiocarbon date of sample HLL517 (see Table 6.1).

[2] The segments are 50-year in length with 25-year overlap in successive segments.

[3] The flags are segments for which the correlation of the ring-widths with the mean of the remaining series is 0.32 or less ($p \leq 0.05$).

their ring-width sequences are plotted and presented in Appendix 1. These individual samples have sensitive tree-rings and their ring-width series may provide useful information for readers of different interests, e.g., ancient tree biology, ecology, and disturbance. For example, the oldest log, HLL091, shows wide ring-widths (from 2 mm to 7.5 mm) in the first 40 years and an average of above 1 mm in the rest of the years (Appendix 1), suggesting that the microsite stress factors (e.g., substrate, climate, and competition) to this individual tree were not severe. Combined with the results from pollen analysis at the same location (Allen, 1995), which indicate a warming temperature and decreased moisture and an open canopy, the wide rings might reflect, in part, a condition of low competition stress. Another example of obtaining environmental information from these individual logs is to examine notable changes in ring-widths such as the positive growth spike in the year about 5769 B.C. in log HLL986 (Appendix 1). Examination of the wood indicates that this spike occurs in compression wood and is dominated by latewood growth, suggesting that it is probably a result of tree tilting by landslide (Jacoby et al., 1992; Sheppard and White, 1995). Corroborative evidence from other sources is needed to identify whether the growth spike reflects a local slope instability or a large-scale seismic event.

The difficulties of crossdating the 501 remaining samples include the following.

1). The growth interval of a sample does not overlap with that of other samples. In some intervals of the past, there might have been only a few or even no logs preserved in Heal Lake because the availability of logs for deposition was limited. For example, the trees that at one time lived on the surrounding slopes of the lake might have been removed by forest fire, or have not been deposited into the lake because of the lack of transportation mechanisms such as flooding and storm. Therefore, for those samples that were isolated in different time-intervals, their tree-ring series cannot be crossdated.

2). The overlap period between the growth interval of two samples is too short (e.g., shorter than 30 years) to crossdate securely. The chances that two tree-ring patterns of different periods being similar are greater for a short sequence than for a long sequence (Pilcher, 1990). Therefore, coincidence of similar tree-ring patterns from trees for a short time interval does not necessarily mean that they crossdate. Moreover, comparison of tree-rings from the bark-side portion of a tree with those from the pith-side is difficult because a tree usually grows faster in the juvenile period than in the old-age period (Fritts, 1976).

3). A sample may have few pointer years (years with extreme ring features common in many trees) to assist crossdating with other trees living at the same time. Some trees may have lived in a suitable micro-site condition that dampens the signal of pointer years. Others may have been affected frequently by local factors (e.g., competition with neighboring trees, and gap habitat), making it difficult to recognize the signal of pointer years. Consequently, tree-rings from these samples are dominated by their local environmental controls and can hardly be crossdated with each other.

Radiocarbon dates of the uncrossdated samples show that some of these subfossil logs were living in the past 6th, 7th, 8th, and 9th millennia (Table 6.1). This holds promise for the extension of the tree-ring chronology further back in time. Additional radiocarbon analysis is needed to assist the crossdating of these samples. Additional subfossil samples from other sites in this region, if available, may help increase sample replications and bridge the gaps between isolated floating sequences.

6.2 Floating Tree-Ring Chronologies

The five groups of crossdated samples (79 samples in total), each with at least 5 sample replications, were used to develop ring-width chronologies according to the standard procedures described in section 3.2. The age of each floating chronology was approximated from the calibrated radiocarbon date of the component sample by taking the intercept age of calibration curve as the anchor year for the middle-ring of the dated segment (Table 6.1). The actual ages of the floating chronologies are located somewhere forward or backward in time within a possible range suggested by the radiocarbon analysis (Table 6.1). Higher probabilities are encountered around the intercept ages (Stuiver and Reimer, 1993).

The dendrochronological characteristics of the five floating chronologies are presented in Table 6.7. The values of the mean sensitivity and serial correlation coefficients showed that the tree-rings of the subfossil samples are sensitive to, and contain common signals of standwide environmental changes (Table 6.7) (Brubaker, 1982). Similar to the record from living trees (Table 5.1), the subfossil Douglas-fir has high autocorrelation in ring-width series, suggesting that the growth of Douglas-fir in the preceding year strongly affected the growth in the following year. This observation reveals that similar physiological preconditioning occurred under the past different climatic regimes (Allen, 1995, Hebda, 1995).

Table 6.7 Dendrochronological characteristics of the floating tree-ring chronologies derived from the subfossil Douglas-fir logs at Heal Lake, southern Vancouver Island (The chronology length includes the interval with a minimum of 5 sample replications).

Floating chronology	**Chronology length**	**Number of logs**	**Mean sensitivity**	**Serial correlation**	**First-order autocorrelation**
Chronology I	264 years (356-93 BC)	18	0.19	0.58	0.90
Chronology II	142 years (807-666 BC)	8	0.21	0.54	0.85
Chronology III	194 years (1017-824 BC)	11	0.17	0.65	0.95
Chronology IV	394 years (1745-1352 BC)	20	0.17	0.62	0.90
Chronology V	336 years (1863-1528 BC)	22	0.20	0.64	0.89

The five floating tree-ring chronologies are presented in Figures 6.3-6.7. Also plotted in these figures are the life span of each sample and the sample depth of the chronology. There appear to be overlaps between chronologies II and III, and between IV and V, suggesting that the record from subfossil logs might in part be continuous as long as the sequences are not erroneously dated by radiocarbon analysis. Further examination of the ring characteristics (e.g., the width and darkness of earlywood and latewood) of these samples showed possible connections between chronologies I and II, II and III, and IV and V. The ring-width sequences of many "bridge" samples also show statistically significant correlations at different levels (Tables 6.8-6.10). There is a likelihood for such connections to be real (based on ^{14}C ages and tree-ring patterns) and, therefore, the chronologies I, II and III, and IV and V are combined respectively into two extended chronologies (Figures 6.8 and 6.9). It should be noted that no reliable crossdating can be obtained for these connections and the correlation coefficients between some "bridge" samples are very low (Tables 6.8-6.10). This is because the overlap periods are relatively short and the occurrence of marker rings is insufficient and inconsistent.

The age of the combined floating chronology I-II-III was estimated based on the radiocarbon date of sample HLL098 (in chronology I) by assigning the middle-ring of the dated segment, i.e., ring No. 97, with the intercept age on calibration curve, i.e., 365 B.C. Accordingly, the age of the samples in chronology II was moved 170 years forward in time, and the age of the samples in chronology III was moved 60 years forward in time. This approximation of age is reasonable because it makes the radiocarbon ages of the seven component samples (No. 1-7 as shown in Table 6.1) all fall within the one-sigma

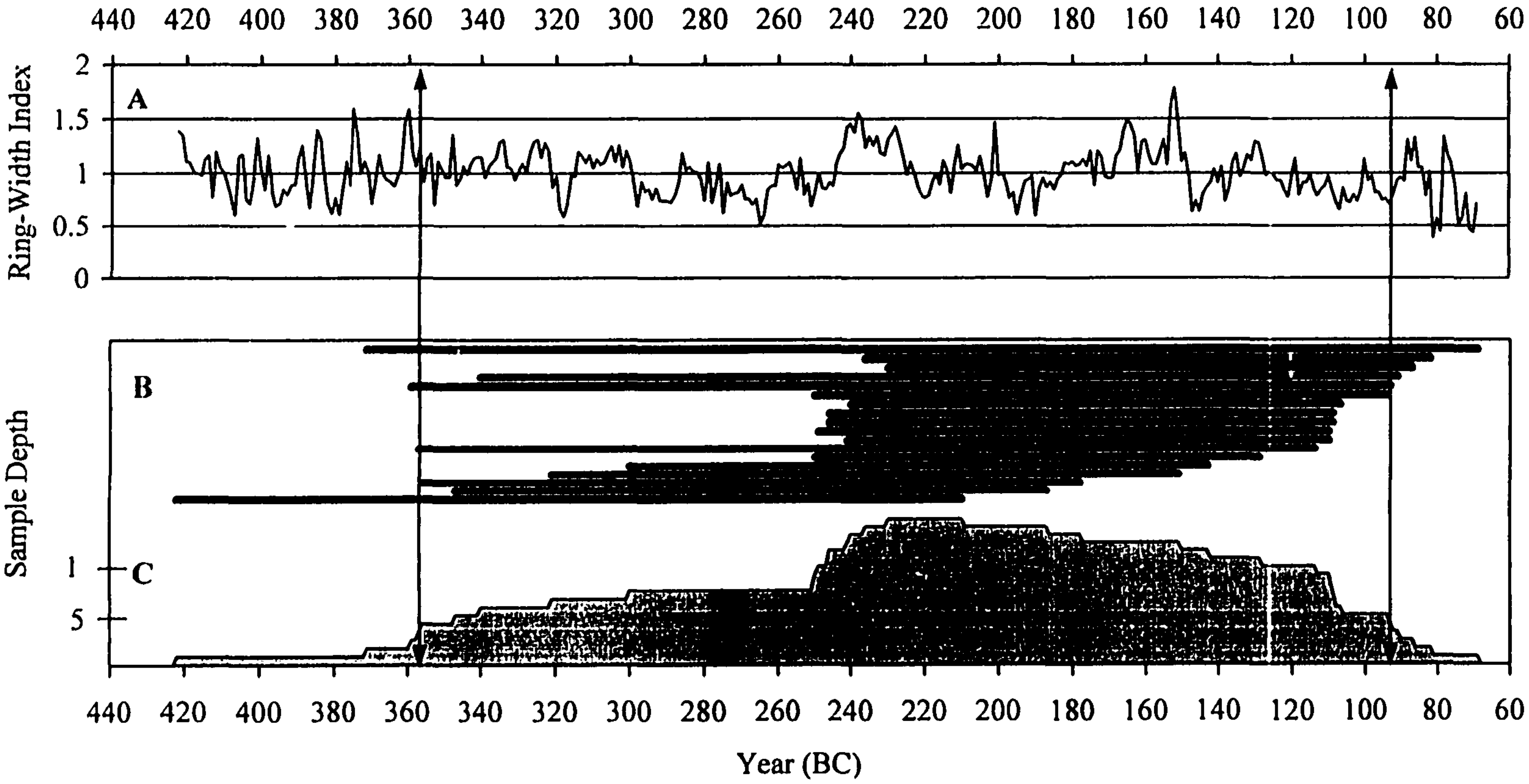

Figure 6.3 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for Douglas-fir floating chronology 1 on southern Vancouver Island, British Columbia. The samples are placed in sequence presented in Table 6.2. Arrows indicate beginning and end of intervals with 5 samples or more.

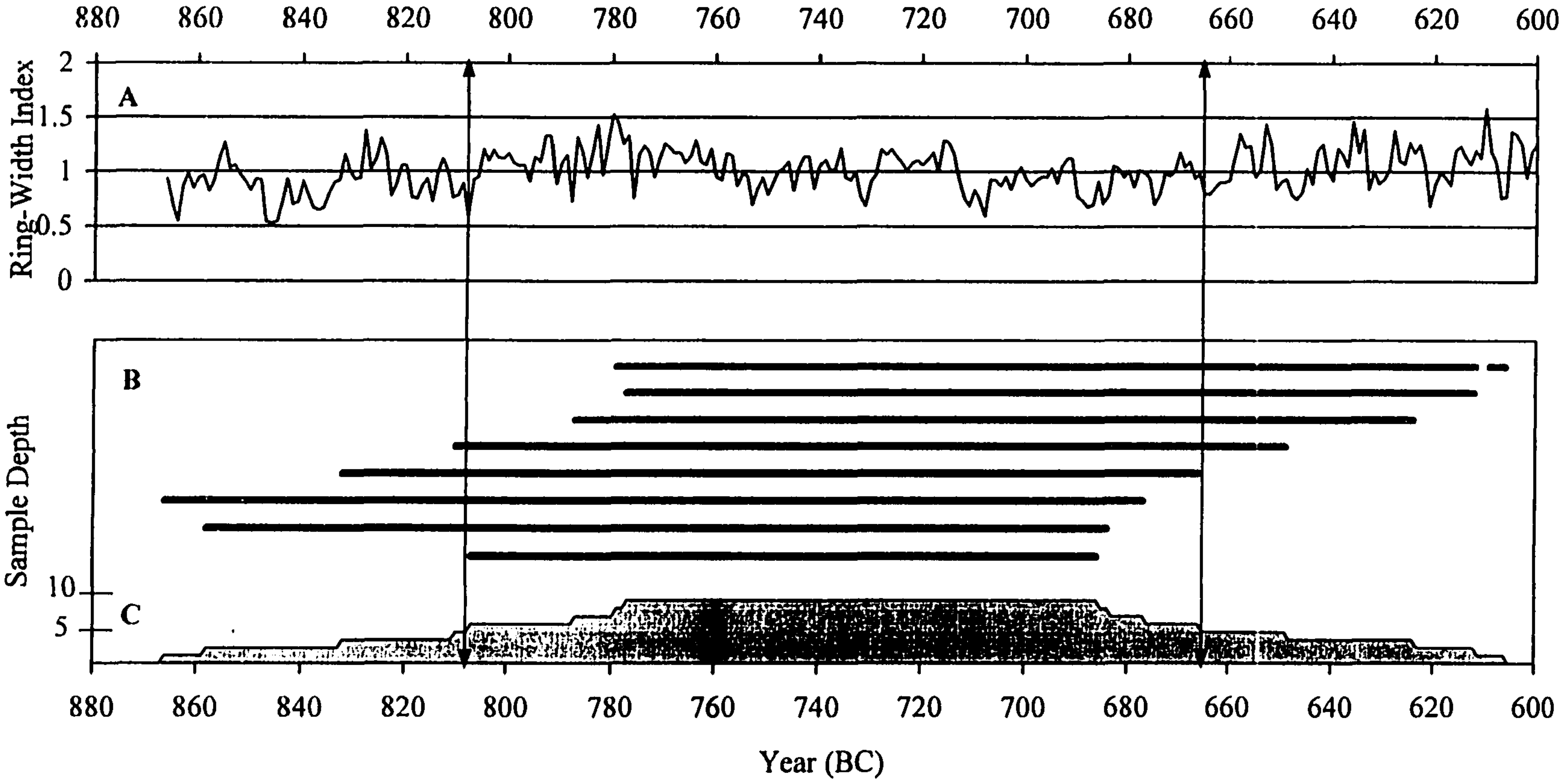

Figure 6.4 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for Douglas-fir floating chronology II on southern Vancouver Island, British Columbia. The samples are placed in sequence presented in Table 6.3. Arrows indicate beginning and end of intervals with 5 samples or more.

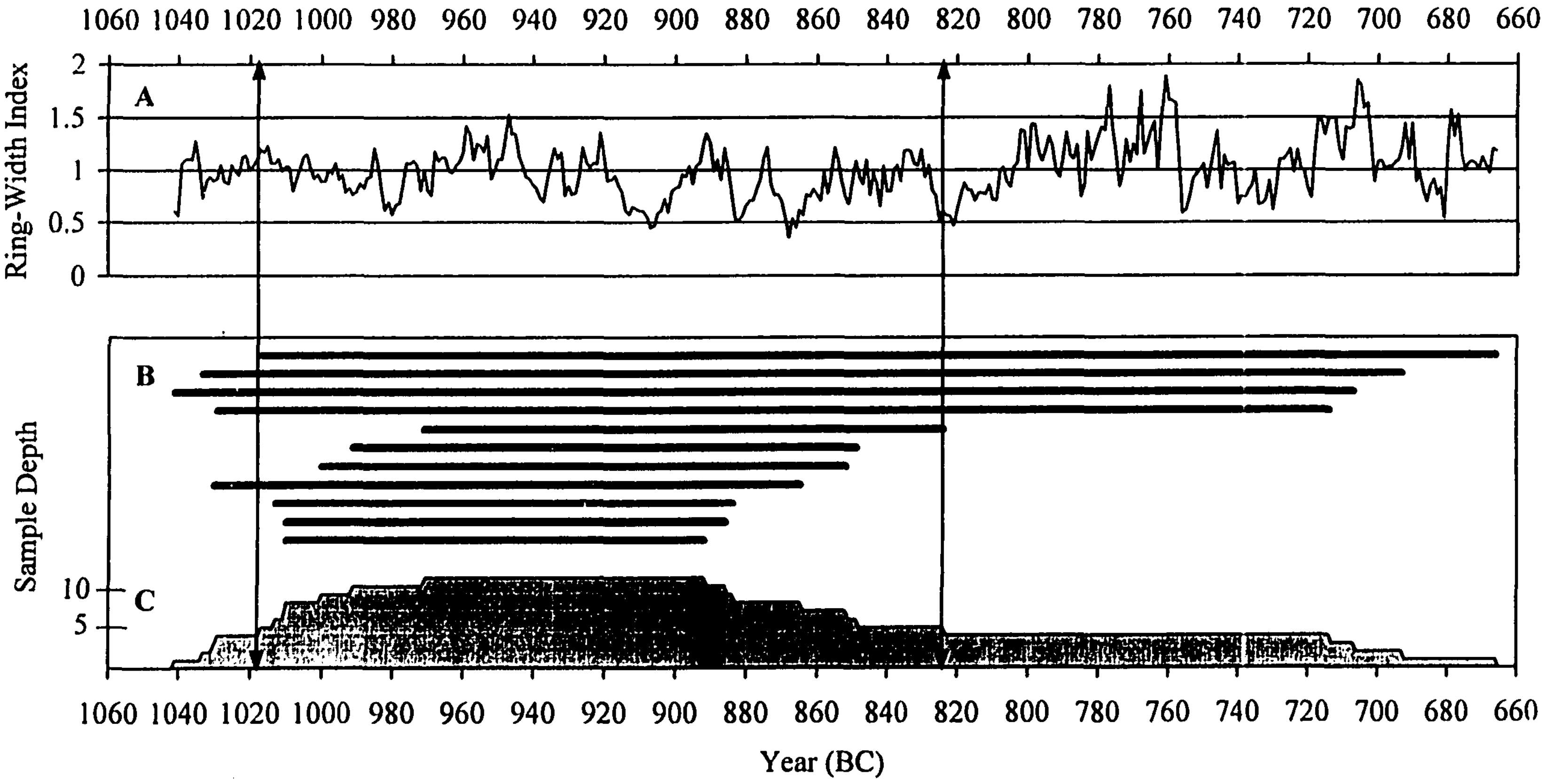

Figure 6.5 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for Douglas-fir floating chronology III on southern Vancouver Island, British Columbia. The samples are placed in sequence presented in Table 6.4. Arrows indicate beginning and end of intervals with 5 samples or more.

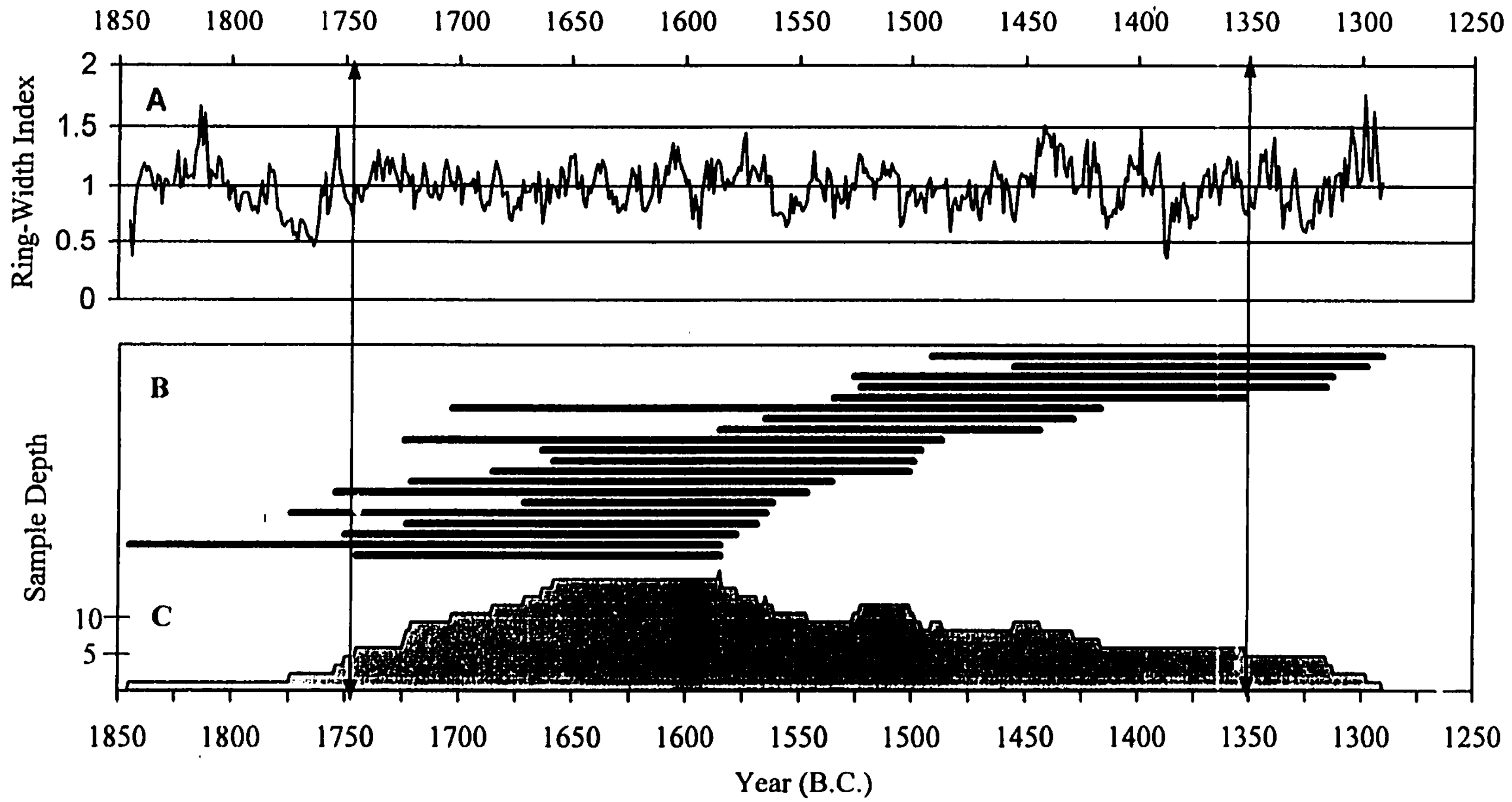

Figure 6.6 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for Douglas-fir floating chronology IV on southern Vancouver Island, British Columbia. The samples are placed in sequence presented in Table 6.5. Arrows indicate beginning and end of intervals with 5 samples or more.

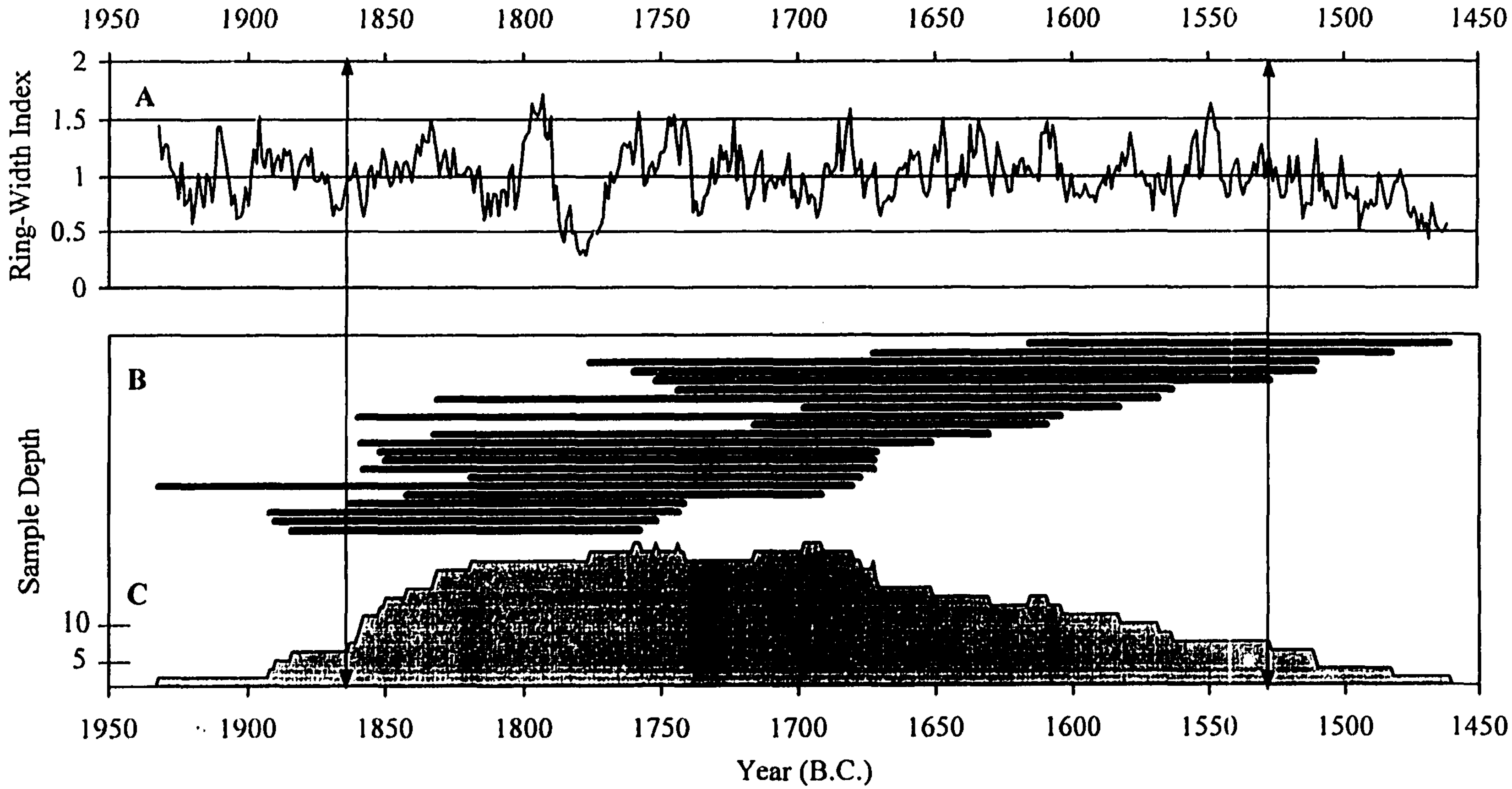

Figure 6.7 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for Douglas-fir floating chronology V on southern Vancouver Island, British Columbia. The samples are placed in sequence presented in Table 6.6. Arrows indicate beginning and end of intervals with 5 samples or more.

Table 6.8 Samples with possible overlap intervals (greater than 30 years) between floating chronologies I and II. The correlation coefficients significant at $p \leq 0.05$ for sample sizes of 32, 62, and 92 are 0.35, 0.25, and 0.21, respectively.

Chronology	Sample ID	Number of years in overlap with the other chronology	Correlation of ring-widths with the other chronology
Chronology I	HLL098	34	0.19
	HLL421	85	0.55
Chronology II	HLL069	85	0.48
	HLL026	79	0.45
	HLL450	67	-0.02
	HLL397	42	0.01

Table 6.9 Samples with possible overlap intervals (greater than 30 years) between floating chronologies II and III. The correlation coefficients significant at $p \leq 0.05$ for sample sizes of 32, 62, and 92 are 0.35, 0.25, and 0.21, respectively.

Chronology	Sample ID	Number of years in overlap with the other chronology	Correlation of ring-widths with the other chronology
Chronology II	HLL397	38	0.03
	HLL523	60	-0.15
	HLL142	94	0.30
	HLL979	86	0.09
	HLL668	35	0.24
Chronology III	HLL569	94	0.28
	HLL670	67	0.23
	HLL699	53	0.24
	HLL527	46	0.16

Table 6.10 Samples with possible overlap intervals (greater than 30 years) between floating chronologies IV and V. The correlation coefficients significant at $p \leq 0.05$ for sample size of 32, 62, and 92 are 0.35, 0.25, and 0.21, respectively.

Chronology	Sample ID	Number of years in overlap with the other chronology	Correlation of ring-widths with the other chronology
Chronology IV	HLL264	38	0.32
	HLL064	59	0.54
	HLL130	56	0.30
	HLL256	89	0.47
	HLL465	109	0.49
	HLL267	58	0.44
	HLL109	85	0.34
	HLL286	180	0.51
	HLL288	80	0.53
Chronology V	HLL099	156	0.52
	HLL359	158	0.54
	HLL294	130	0.36
	HLL254	129	0.32
	HLL020	113	0.40
	HLL443	77	0.60
	HLL571	72	0.03
	HLL683	58	0.37
	HLL376	36	0.44
	HLL695	31	0.30

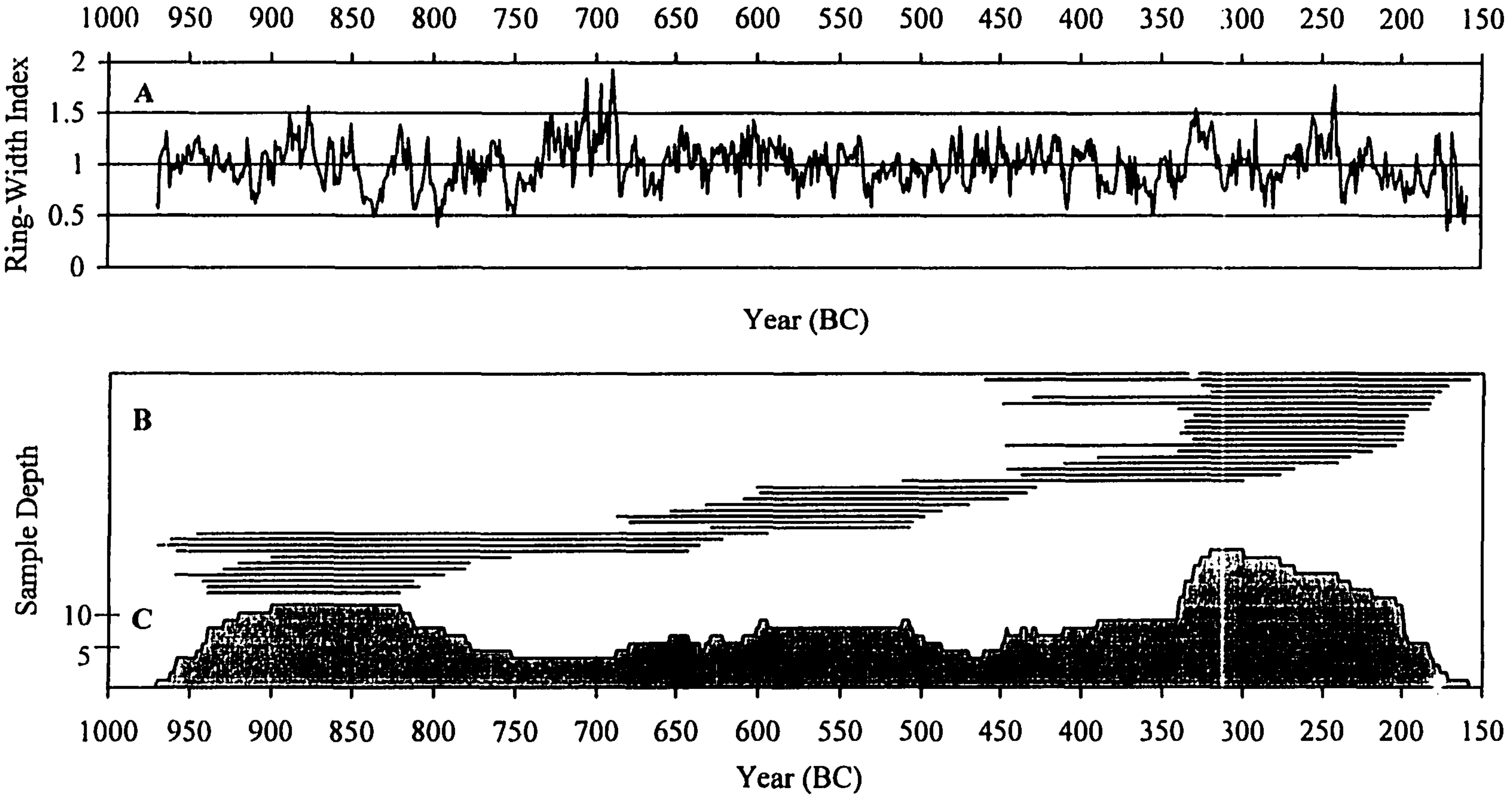

Figure 6.8 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for I-II-III-connected Douglas-fir floating chronology on southern Vancouver Island, British Columbia. The approximate age is derived from the calibrated radiocarbon date of sample HLL098.

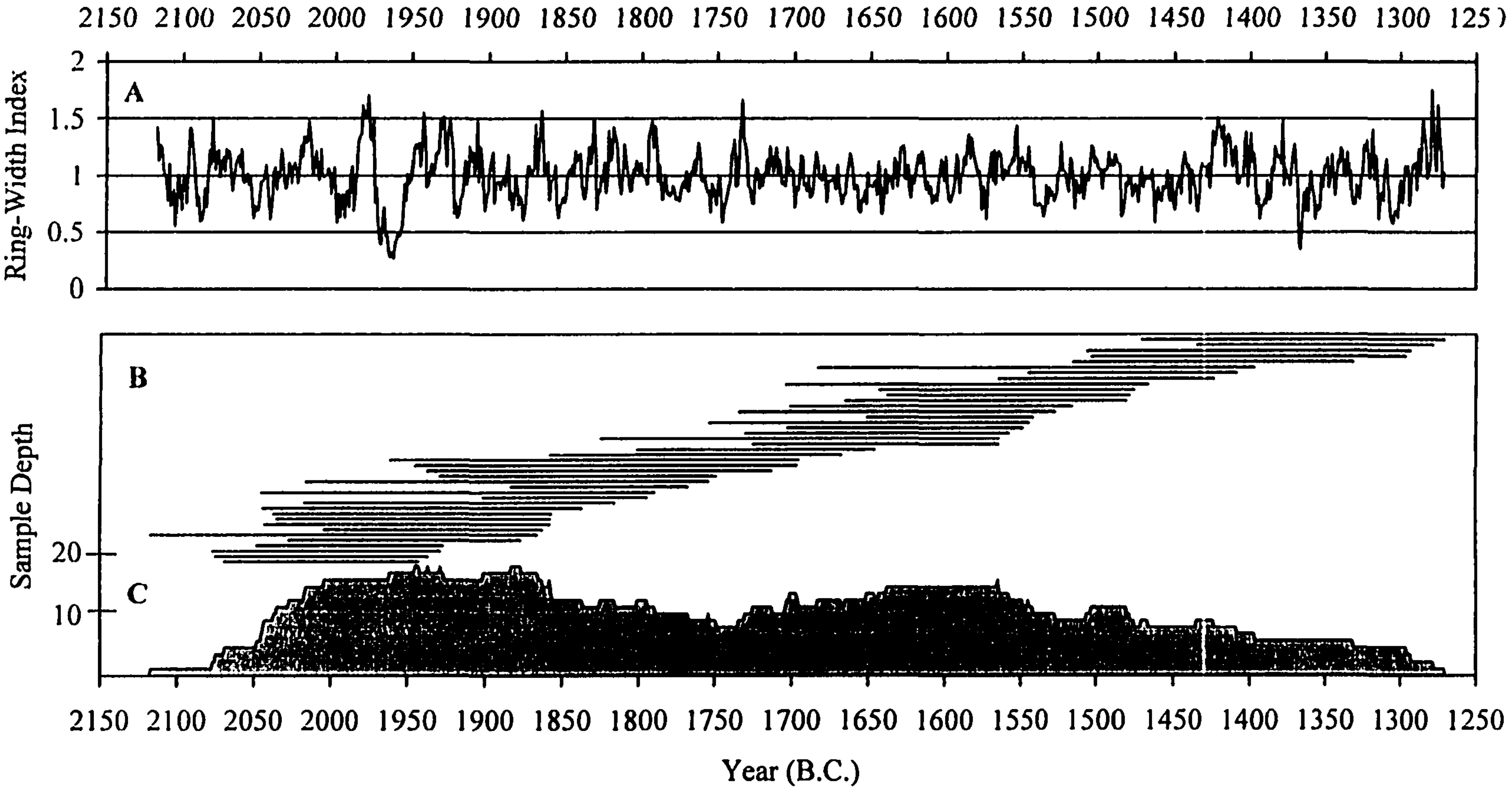

Figure 6.9 Ring-width indices (A), bar chart of sample life span (B), and shaded curve of sample replication (C) for IV-V-connected Douglas-fir floating chronology on southern Vancouver Island, British Columbia. The approximate age is derived from the calibrated radiocarbon date of sample HLL064.

range of the calibrated radiocarbon ages. This combined chronology, which spans the period ca. 970 B.C. - 159 B.C., cannot be crossdated with the previously developed two-millennium long chronology, which spans the period 130 B.C. - A.D. 1992 (Figure 6.10) (Zhang, 1996), indicating a gap between the two chronologies.

The age of the combined floating chronology IV-V was estimated based on the radiocarbon date of sample HLL064 (in chronology IV) by assigning the middle-ring of the dated segment, i.e., ring No. 65, with the intercept age on calibration curve, i.e., 1640 B.C. Accordingly, the age of the samples in chronology IV was moved 20 years forward in time, and the age of the samples in chronology V was moved 180 years backward in time, which was within the two-sigma range of the calibrated radiocarbon ages for samples HLL020 and HLL517 in chronology V (Table 6.1).

I tried to anchor the floating chronologies to a narrower range by comparing the ring patterns with the long tree-ring chronologies of bristlecone pine (*Pinus aristata* Englem.) in the White Mountains of east-central California, USA (Ferguson, 1969). Unfortunately, no confident match positions could be found. This is probably due to the differences in growth response characteristics of different species and in climatic regimes of different regions. Although insufficient soil moisture limits the growth of both species, high precipitation and low temperature in previous autumn have positive effects on growth in bristlecone pine (LaMarche, 1974) but negative effects on growth of Douglas-fir. Furthermore, bristlecone pine is subject to an inland climate, whereas Douglas-fir is subject to a coastal climate. These differences, together with the influence of local

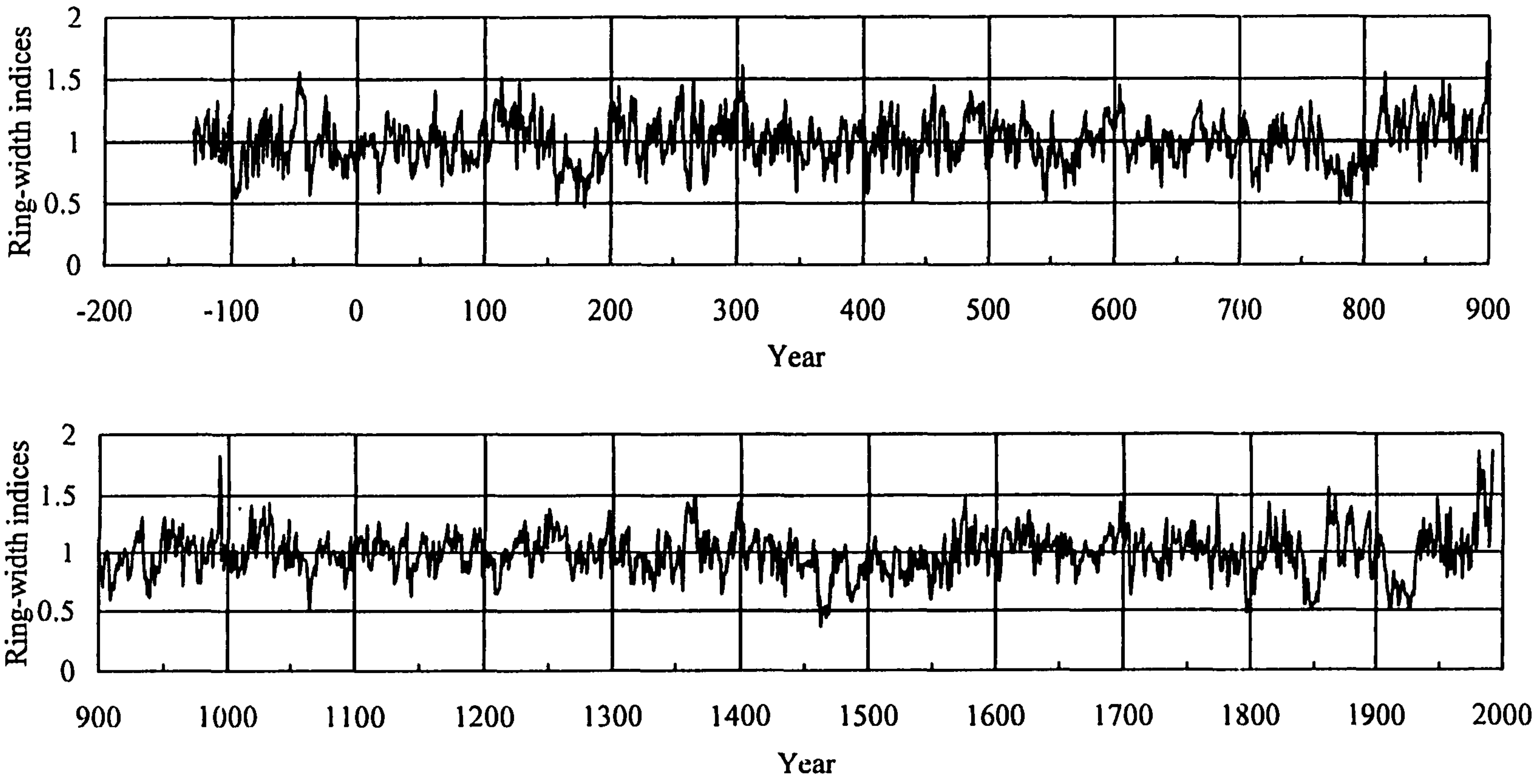

Figure 6.10 A 2122-year ring-width chronology of Douglas-fir at Heal Lake site, southern Vancouver Island, British Columbia, Canada (from Zhang, 1996).

disturbances, make it difficult to place the floating Douglas-fir chronologies in confident positions on the bristlecone pine chronology.

The following analysis of the tree-ring variations is based on the two combined chronologies (Figures 6.8, 6.9). It is realized that the temporal position of these chronologies is floating, and the connection of the individual chronologies may not be correct. These shortcomings restricted the usefulness of the chronologies for analyzing growth features in exact dates and in the interval of connections. Nevertheless, they do not influence very much the analysis of growth patterns exhibited in the individual chronologies because the temporal position of these chronologies is relatively well-fixed by the radiocarbon dates and there are limited interactions between/among these chronologies due to the short intervals and fewer sample numbers in the overlaps. The combined chronologies, if dated correctly, allows for examination of longer time series of environmental variations. These tree-ring data will be submitted to the International Tree-Ring Data Bank (Grissino-Mayer and Fritts, 1997) so that other researchers can use them for large-scale network studies of climate variations (Fritts, 1991; Meko et al., 1993).

6.3 Radial Growth Variations in Historically Different Climate

Pollen analysis at the Heal Lake site of southern Vancouver Island (Allen, 1995) indicates that the climate was warm and moist between 8000 and 2600 years BP, moderate-cool and moist-wet between 2600 and 150 years BP, and exhibited a trend of increasing moisture and decreasing temperature from 5900 to 2600 years BP. Studies of tree-ring growth at the same location under these different climatic regimes provide high resolution (year-by-year) records of the range of variability in environments. Such knowledge is useful for understanding the environmental changes and the ecological processes within a forest (Morgan et al., 1994).

6.3.1 *Overall Growth Variations*

The floating tree-ring chronologies at Heal Lake represent radial growth patterns of Douglas-fir for periods between about 2048 B.C. - 1332 B.C. (717 years long with a minimum of five samples for most of the years) (Figure 6.9) and between about 946 B.C. - 183 B.C. (764 years long with a minimum of five samples for most of the years) (Figure 6.8). In these periods, there are intervals in which the radial growth fluctuated slightly around the long-term mean for more than a century, and intervals in which the growth varied rather strongly above and below the average within a century. Examples of the former growth pattern include intervals between about 1730 B.C. - 1430 B.C. (300 years long) and about 670 B.C. - 340 B.C. (330 years long) during which the ring-width indices are close to 1 and within the range [0.5, 1.5]. Examples of the latter growth pattern include intervals between about 2010 B.C. - 1920 B.C. (90 years long), 1420 B.C. - 1320 B.C. (100 years long), and 870 B.C. - 680 B.C. (190 years long) during which the variation of ring-width indices reaches or exceeds the range [0.5, 1.5].

The tree-ring chronologies also show evidence of sustained positive growth for as long as five decades, e.g., the interval between 730 B.C. - 690 B.C. Longer-term growth trends may not be represented in the chronologies because they may have been removed during the process of standardization (Cook et al., 1995) which is designed to detrend the intrinsic biological growth trend (see section 3.2.3).

6.3.2 *Growth Anomalies*

Significant growth anomalies in which the ring-width indices were persistently above 1.5 or below 0.5 for at least five years occurred two times in the floating tree-ring chronologies (Figure 6.9). Figure 6.11 shows the enlarged graph of tree-ring indices for the interval of these two growth anomalies. The first one was a positive growth which started in about 1986 B.C. (ring-width index being close to 1) and culminated in about 1982 B.C.-1978 B.C. (ring-width indices being greater than 1.50). Following this growth surge the ring-width indices decreased rapidly to below 0.5 within only seven years. The trajectory of the decrease showed a "bump-like" pattern: major decrease for a few years followed by one or two years of slight recovery before the occurrence of another major decrease (Figure 6.11). The growth suppression lasted eight years from about 1967 B.C to 1960 B.C. (ring-width indices being smaller than 0.50) before it recovered to normal (ring-width index being close to 1) in about 1953 B.C. The overall above normal growth was a 12-year period from 1986 B.C. to 1975 B.C. with the highest ring-width index (=1.70) occurred in about 1978 B.C. The overall below normal growth was a period of 22-year period from 1974 B.C. to 1953 B.C. with the lowest ring-width index (=0.27) occurred in about 1962 B.C. These two growth anomalies were well replicated by 14 individual samples of subfossil Douglas-fir (Figure 6.12). The synchronous growth response in many trees suggested that the changes in growth were caused by environmental factors operating at the stand level (or even larger-scale) rather than at the micro-site scale specific to individual trees.

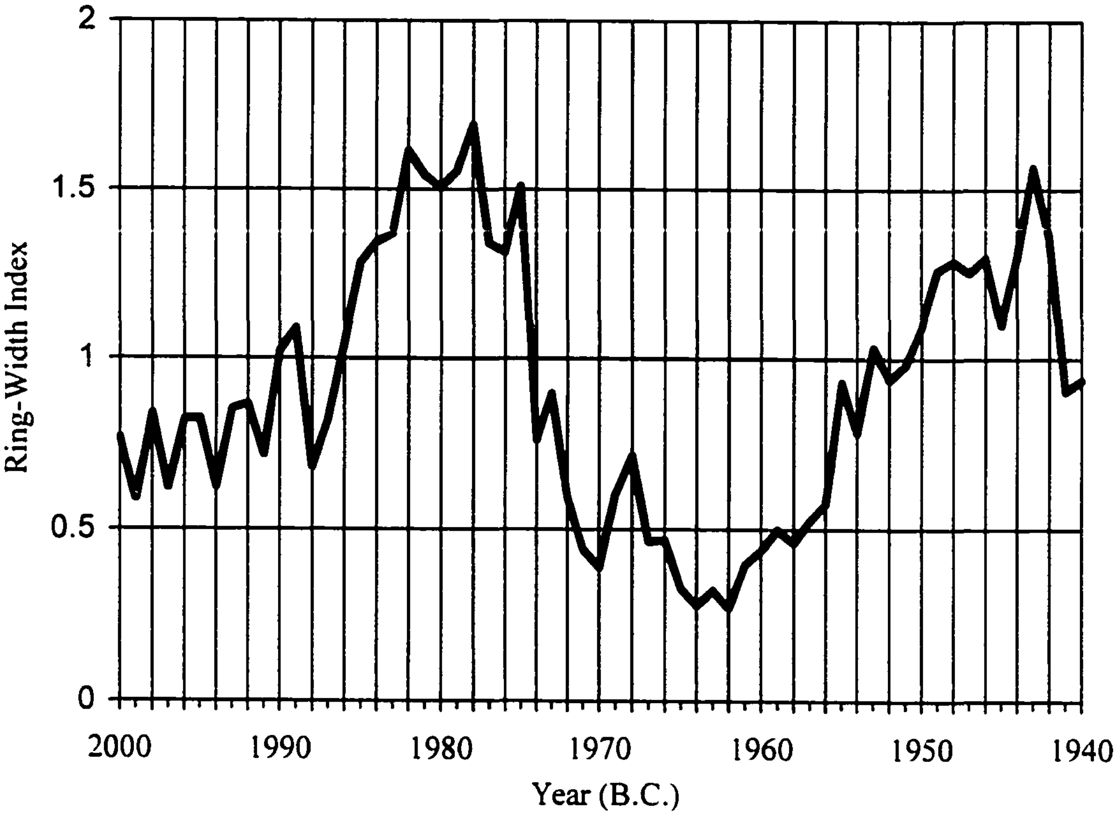

Figure 6.11 Enlarged chronology graph showing the year-by-year changes in ring-width indices for the interval of significant growth anomalies near 2000 B.C.

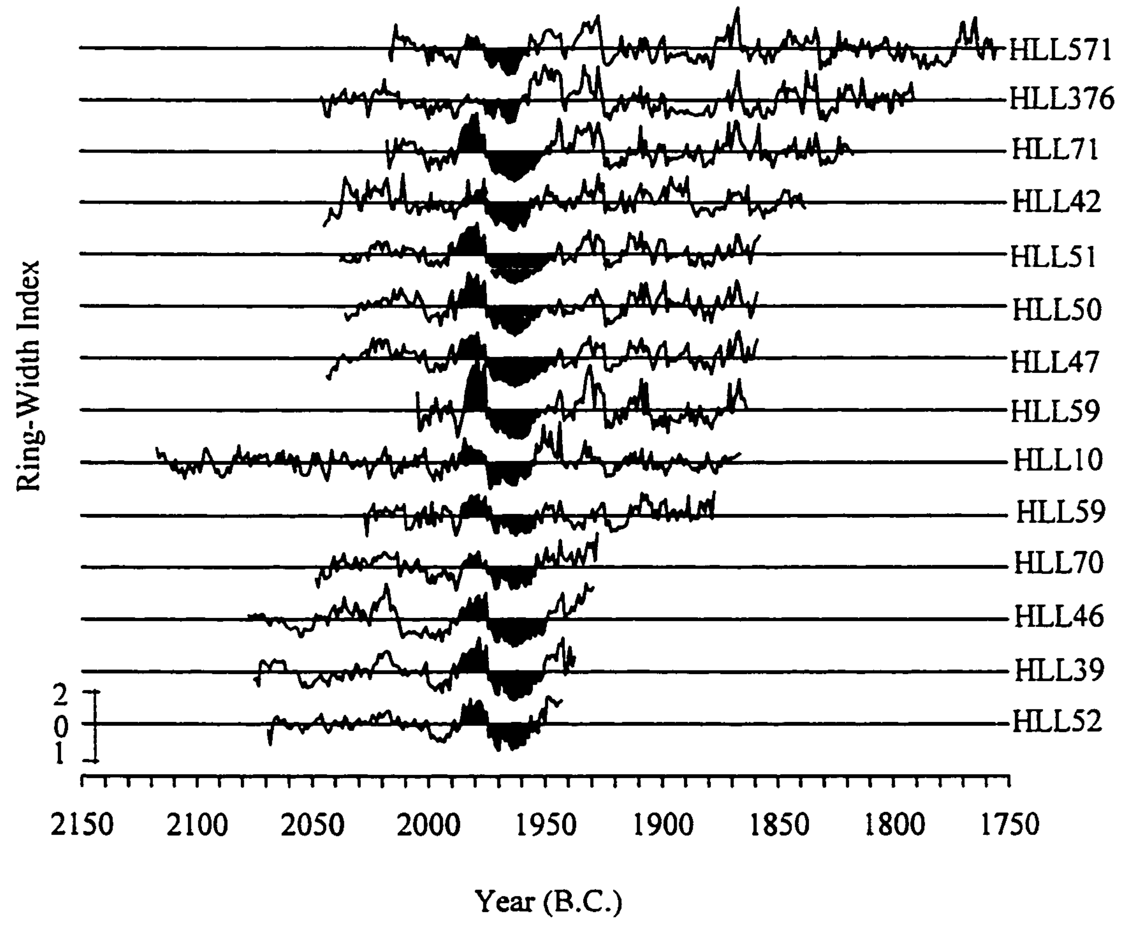

Figure 6.12 Ring-width indices of 14 individual subfossil Douglas-fir logs (labeled on the right of each series) showing growth anomalies in about 1982 B.C.-1978 B.C. (positive growth) and 1967 B.C-1960 B.C. (negative growth).

To understand the factor(s) responsible for such rapid and large changes in growth is important to know whether these growth anomalies represent a local or more widespread event. Wildfire is not likely the causal factor for the two growth anomalies because fire scars and long-lasting post-fire growth release patterns are not present in any of the 14 samples. Windstorm is not likely a causal factor either because of the absence of reaction wood and long-lasting growth release pattern resulting from the thinning effect (see section 2.2.2). Although insect attack could cause severe reduction in radial growth, the observed pattern of growth anomalies does not resemble that expected following insect outbreaks (section 2.2.2). The observed growth reduction shows a "bump-like" pattern rather than a smooth decrease, and the growth release following the suppression is not significant and persistent. Furthermore, the magnitude of the growth suppression never appears a second time in any other floating chronologies. Therefore, insect outbreak is not likely a major factor for the observed growth suppression.

I speculate that climatic changes are the most likely causal factor for these two significant growth anomalies. First, climatic changes are a large-scale phenomenon that affects virtually all the trees in a forest stand. Second, climatic changes can result in a rapid and significant change in the radial growth of Douglas-fir by altering its resource availability and growth conditions (section 2.2.1). For instance, a severe spring frost could cause damage to temperature-related physiological processes such as bud initiation and production of hormonal substances (e.g., auxin) that are important in controlling cambial cell activities (Kozlowski and Pallardy, 1997). Furthermore, climatic changes such as severe droughts in growing seasons can act as a stand disturbance that disrupt the structure of the canopy-understory-root zone system (see the two-level linear aggregate model presented in section 3.1), and result in "bump-like" pattern of growth decrease. The small recovery in growth could be explained, in part, by the reduced competition stress to individual trees due to the change in stand structure under an overall drought situation. It is especially notable that the occurrence of the two growth anomalies falls within a climatic transition from the regionally warm moist mesothermic to the moderate and moist modern climate, a trend of decreasing temperature and increasing precipitation (Allen, 1995; Hebda, 1995).

Pollen studies on Vancouver Island showed that there was a *Quercus garryana* maximum in the mid-Holocene (approximately 6,000 B.C. to 2000 B.C.) indicating a warm temperature probably warmer than the modern value (Hebda, 1995). After 2,000 B.C. the climate cooled and became moister approaching modern values as indicated by the decreased pollen values in *Quercus garryana* and the establishment of modern vegetation such as community primarily of Douglas-fir on the Saanich Peninsula (Zirul, 1967; L. Heusser, 1983; Allen, 1995) and western hemlock in the upland areas (C. Heusser, 1960).

The dates of the two tree-ring growth anomalies fall within the climatic transition around 2,000 B.C. It should be noted that these dates were obtained from the combined chronology IV-V which used the radiocarbon date of the sample HLL064 for the anchor year (Figure 6.9). These dates are within the two-sigma range of the calibrated radiocarbon date of sample HLL517 (in chronology V) (Table 6.1), which records directly the signals of the two growth anomalies. It is possible that the dates of the two growth anomalies could be moved 10 years backward or 124 years forward in time and still be within the two-sigma ranges of the calibrated radiocarbon dates of sample HLL517 and HLL064, but it is unlikely that they could be moved further forward because there is no evidence of crossdating between samples in chronologies IV and V in positions other than that shown in the IV-V connected chronology. If the two growth anomalies indeed occurred around the 2,000 B.C. interval, then it might suggest that the climate variation during a transition from one climatic condition to another could be of high amplitude over a short interval. Such climate changes could act as a stand disturbance that disrupts the stand structure and alters the stress conditions to the growth of individual trees. The implications of the growth patterns and anomalies revealed in the chronologies will be discussed in the section of synthesis in next chapter.

Chapter 7 Discussion, Implications and Conclusions

The goal of this study was to examine the spatio-temporal patterns of radial growth of Douglas-fir in relation to climatic variables in coastal British Columbia. To do so, climate-growth relationships were modeled using the technique of Artificial Neural Network (ANN) as well as the traditional approach of multiple linear regression. A broader spectrum of the Douglas-fir growth response was obtained by examining the growth patterns over spatially different climate regions and under historically different climate regimes. This chapter summarizes the major findings of the study and discusses their applications and implications. Section 7.1 discusses the conceptual and technical findings, i.e., the two-level linear aggregate model for tree-ring analysis and the Artificial Neural Networks (ANNs) for modeling nonlinear climate-growth relationships. Section 7.2 presents a synthesis of the radial growth of Douglas-fir in relation to climate. Section 7.3 provides suggestions for future research and conclusion remarks.

7.1 The Conceptual and Technical Advances

7.1.1 *The Two-Level Linear Aggregate Model for Tree-Ring Analysis*

Finding 1: *A two-level linear aggregate model is considered to be an improved conceptual framework for interpretation of tree-ring data in environmental studies. The focus of the first level is the individual trees, and the growth controlling factors consist of stresses and single tree disturbances. The focus of the second level is the forest stand, where the collective growth behavior of forest trees is affected by climate and standwide* *disturbances. There are interactions among environmental factors within a level and between the two levels.*

Although the basic idea of viewing tree-rings as a linear aggregate of several signals is the same in both the original (Cook, 1987) and the new (two-level) models, the two-level linear aggregate model provides a clearer conceptual framework than the original model for understanding and interpretation of variation of tree-ring attributes using the contemporary concepts of stress and disturbance in forest ecology (Pickett et al., 2000). First, the new model clearly distinguishes and defines the two levels of target systems. This not only establishes a basis for unambiguous interpretation of the impact of either local or standwide disturbances, but also presents a clear structure for using individual trees to extract standwide signals.

Second, the new model recognizes the interactions and transformations between different environmental factors. For example, severe climatic events can cause changes in stress state to individual trees and can be further transformed into a stand-wide disturbance if the stress-induced mortality disrupts stand structure.

Third, the new model does not single out the age-related growth trend (A_t) from other component factors, but rather considers it as part of the overall growth pattern that represents, as much as possible, the potential growth of a tree in the absence of changes in the factors being studied. The detrending curve fitted to the measured ring-width series is an integration of the effects of one or more stresses and disturbances depending on the purpose of the study. For example, if the standwide climate and disturbance are of primary interest as in this study, the detrending curve reflects, to a large extent, the combined signals of substrate stress, competition stress (the part not related to stand disturbances), and disturbances unique to the tree. This broad concept of overall growth pattern is more consistent with the standardization process in the development of stand tree-ring chronology.

7.1.2 *Using ANN Techniques to Model Climate-Tree-Ring Growth Responses*

Finding 2: *Artificial Neural Network provides an innovative technique to modeling nonlinear climate-tree-ring growth responses.*

Modeling the nonlinear and complex relationships between climate and tree-ring growth is of significance in dendroclimatic studies, but difficult to implement using traditional linear regression approaches. To overcome this difficulty, I explored the feasibility of applying ANN technique in modeling climate-growth response using the climate and tree-ring database for Douglas-fir on southern Vancouver Island, British Columbia (BC). The results show that the ANN models are able to extract nonlinear growth response patterns from the observed climate/tree-ring data sets, and to generate more accurate predictions than multiple linear regression approaches. The ANN-extracted climate-growth relationships can be displayed by a series of scenario analyses; for example, when all other input variables are held fixed at their means, the limiting effect of April-July precipitation on tree-growth decreases with increased precipitation.

The application of ANN technique in dendroclimatic studies is an advance in the modeling of nonlinear and complex climate-growth responses. First, the ANN has nonlinear activation functions embedded within the hidden neurons, and each input signal is spread over several hidden neurons where it is processed together with other received signals (see section 3.3.1 and Figure 3.3). These features give neural networks the flexibility to model nonlinear and complex systems (Haykin, 1994). Second, the ANN relies less on statistical assumptions on the actual distribution of the data, and can use many simple and problem-independent activation functions (usually sigmoid function) to model complicated nonlinear relationships between input and output variables (Bengio et al., 2000; Zhang and Gupta, 2000). This study demonstrates that the ANN models, if designed and trained properly, could perform better than traditional linear regression approaches currently used.

Despite the benefits of the ANN technique, the problem of overlearning presents a major obstacle to the construction of well-performing ANN models in dendroclimatology. An ANN usually contains many free parameters (i.e., the synaptic weights) and is much less parsimonious than traditional methods. Overlearning makes it difficult for a neural network to distinguish the essential climate-growth response from the specific noisy features, and is an inevitable consequence of any climate/growth database that contains low sample numbers (insufficient) and includes features arising from non-climatic factors (noisy).

In my experimentation of the ANN modeling, I found that the overlearning problem could be avoided by reducing the size of the neural network according to prior knowledge of the way the biological system works, and by using the early-stopping technique. Reducing the size of a neural network, e.g., reducing the number of neurons and inter-neuron connections, can reduce the learning flexibility of the neural network because of the smaller number of free parameters (i.e., the synaptic weights associated with each connection between neurons) within the network (Haykin, 1994; Zhang and Gupta, 2000). Designing the experiment of ANN modeling according to prior knowledge of the biological system, e.g., the number of major limiting factors and the temporal sequence of the limiting factors, can help the network learn more effectively. The procedure of early-stopping, as used in the pioneering work of ANN climate reconstruction by Woodhouse (1999), is also demonstrated to be an effective way to overcome the problem of overlearning in this study. However, it should be used with caution because when the testing set is allowed a "monitoring" role in the training process, the selection of the neural networks might be biased by the testing set, i.e., creating a new and indirect overlearning to the patterns in the testing set.

This study demonstrates that there are variations in the performance of ANN models developed over different training/testing sets. The best-performing model (i.e., best memorization for training set and generalization for testing set) might not necessarily be the best representation of the climate-growth response, because it might be obtained just by chance due to the noise distribution over the specific training/testing sets (LeBaron and Weigend, 1998). Therefore, it is better to develop models using diverse sample splitting methods, and take the "expert panel", rather than the "single guru" strategy for practical applications. By using an "expert panel", the apparent accuracy of a prediction is not as good, but the models collectively represent the real range of possible values and decrease the possibility of making extreme false predictions. There is no standard way for splitting the samples and for choosing the size of training/testing sets, although dividing the data into half size is most frequently used.

The ANN modeling of climate-growth response is currently at an early stage of development. Many procedures for developing ANN models still rely on trial-and-error experimentation with different designs of network training. For example, in the studies by Guiot et al. (1995) and Keller et al. (1997) for modeling the effect of pollution on tree growth in the Alps region, 24 monthly mean temperature and total monthly precipitation were selected as input variables, and a fully connected architecture with five hidden neurons was designed for processing input signals. In my study, well-performing ANN models were obtained by selecting a small number of input variables, and by designing partially connected neural networks with a small number of neurons in the hidden layer. The prior knowledge of the climate-growth relationships is incorporated into the model by designing specific ANN architectures. The contemporary advance of ANN theory has allowed the planting of traditional regression equations into the ANN architecture (Zhang and Gupta, 2000). The recently updated software, *NeuroModeler* version 1.2 (Zhang, 2000), has incorporated such hybrid techniques and opened the door for practical construction of knowledge-based ANN models. Extracting the essential knowledge from small and noisy training set is a common task in many fields, e.g., sensitivity analysis of crops to ozone pollution, forecasting El Niño-Southern Oscillation events, nonlinear modeling in complex engineering system, etc. (Goh, 1995; Wang and Zhang, 1997; Roadknight et al., 1997; Tangang et al., 1998). It is expected that a valid and optimal procedure for developing growth-response ANN models will be found with the advance of ANN research and more applications of ANN technique in dendroclimatic studies.

Besides the problem of overlearning, the ANN model has another shortcoming, i.e., lack of explanatory capability. An established growth-response ANN model appears to operate like a "black-box" that takes in an input of climatic signals and gives out an output of tree-ring indices without presenting any comprehensible lines of reasoning relating the input to the output values. Although the processing of the input signals inside the "black-box" follows the numerically stored knowledge of the climate-growth relationships, and the output can be expressed as a series of mathematical equations, e.g., equations (1), (2) and (3) in section 3.3.1, it is practically impossible to evaluate the input-output relationships directly from these equations and the synaptic weights. The reason is that the forms of the activation functions used in a neural network are normally problem independent, and the overall effect of the synaptic weights relating to a specific input variable is unrecognizable because of the interwoven neural connections and hidden layer neural interactions (mathematical manipulations) in the network. It is worth repeating that the mathematical equations used in a neural network are not the expectation function (as in a regression model) describing the input-output relationships, but rather they are approximation equations to that expected functional relationship. Moreover, each input signal is distributed in parallel and processed throughout the network. Therefore, climate-growth relationships can hardly be interpreted directly from the mathematical equations and the synaptic weights of a neural network. Instead, the interpretation can be implemented, as in this study, by simulating the output growth responses to a series of input climatic scenarios.

The challenge of directly interpreting the input-output relationships from the line of reasoning inside the ANN "black box" has attracted considerable research effort in many fields (Healy and Caudell, 1997; Tickle et al. 1998). Garson (1991) proposed a method to assess the relative importance of the input variables by partitioning the hidden-to-output connection weights into components associated with each input variable. Benítez et al. (1997) analyzed the equality between neural networks and fuzzy rule-based systems and used fuzzy rules to interpret the behavior of neural networks. Other methods of supplementing neural networks with explanation capability include giving the hidden neurons a phase space interpretation, and applying spectral analysis to measure the nonlinearity of a network (Hsieh and Tang, 1998; Tangang et al., 1998). With the continuing research on interpretation of ANN, the knowledge embedded in the "black box" will come to light and allow users to see the functional relationships between the input and output variables.

The climate and tree growth relationships revealed by the ANN models can provide guidance to build transfer function models, which use tree-ring data as predictor variables and climate data as predictand variables, a reverse problem of the growth-response process. The transfer functions can also be developed using ANN technique to capture the nonlinear and complex relationships between tree-rings and climate variables (Woodhouse, 1999). However, ANN models for transfer function cannot be produced if a tree-ring value (used as an input) corresponds to several different climatic conditions (used as output). Using tree-ring chronologies of different species that have different response to the regional climate can reduce the flexibility of input-output relationships, and thus help develop neural networks in such situations.

7.2 Radial Growth of Douglas-fir in Relation to Climate: a Synthesis

7.2.1 *Climate-Growth Relationships*

Finding 3: *The radial growth of Douglas-fir on southern Vancouver Island responds nonlinearly to prior growth and six climatic variables (i.e., total precipitation in previous August, current January and April-July, and monthly mean temperature in previous September, November, and current August), and there are interactions among the effects of these variables.*

Finding 4: *In the mountainous region of central coast, the radial growth of Douglas-fir is autocorrelated with previous year's growth, positively correlated with precipitation in May and July, and with temperature in March, and negatively correlated with temperature in previous year's August. There is also contrasting pattern in growth response between sites at high elevation and low elevation.*

This study has added significantly to the understanding of the climate-growth responses of Douglas-fir in coastal British Columbia. The ANN modeling of growth response of Douglas-fir trees at Heal Lake site reveals nonlinear relationships between climatic variables and tree-ring growth. For instance, when other input variables are set at their means, the ANN model shows that the effects of April-July precipitation on tree-ring growth slightly decrease with the increase in precipitation (Figure 4.9). In the Bella Coola area of central coast BC, the difference in elevation-related site conditions and the lack of climatic data for each site precludes the establishment of site specific ANN growth-response models.

Principal component (PC) analysis of the nine site chronologies in the Bella Coola area indicates that the first two PCs represent as much as 72.7% of the total variance in the site chronologies. The first PC reflects a common growth response throughout the nine sites, and the second PC reflects a contrasting growth response pattern among sites of different elevations. Comparisons of radial growth of Douglas-fir at different sites show that all chronologies are highly autocorrelated, and growing season precipitation seems to be a common factor affecting tree-ring growth. Despite the similarities in growth variation at sites of different elevations, notable differences in radial growth are apparent. This observation reflects that there are differences in local growth conditions (e.g., stand structure and disturbances) and/or in growth response patterns at different sites. Identification of the specific factors responsible for such differences is difficult if solely based on the chronologies, although the growth patterns might provide some clues (see section 2.2). Information about the site history (e.g., climate and disturbances) is needed to explain the growth variations.

The climate-growth relationships revealed in this study are in general agreement with findings of other studies of Douglas-fir in the Pacific Northwest. The most common patterns are positive correlations of growth with precipitation in the growing season and with growth of the previous year (Lassoie and Salo, 1981; Henderson and Brubaker, 1986; Peterson and Heath, 1990; Robertson et al., 1990; Little et al., 1995). In the rainshadow areas of coastal BC, low precipitation and moderately high temperatures in summer combine to produce prolonged soil moisture stress, which is apparently severe enough to be the dominant climatic influence on radial growth (Robertson et al., 1990; Little et al., 1995). The storage of photosynthates and the retention of needles play a role in preconditioning the growth in the following year (Fritts, 1976; Lassoie, 1982). In low elevation sites, high precipitation and mild temperature in winter can recharge soil moisture and allow the accumulation of photosynthates (Waring and Franklin, 1979), although cloudy conditions in winter may inhibit growth potential by reducing photosynthesis because of low light levels (Little et al., 1995). In high elevation sites, cold temperatures in late fall and winter may inhibit photosynthesis and, thus, the conditions in non-growing season may have less effect on growth than those in the growing season (Lassoie, 1982).

Climate change is occurring now (Karl et al., 1997), and the continued increase of greenhouse gases in the atmosphere (Keeling et al., 1995) will result in warmer temperatures and various changes in precipitation according to simulations of general circulation models (Kellogg and Zhao, 1988; Mitchell et al., 1990; Houghton et al., 1996; Zwiers and Kharin, 1998). The increase in temperature may enhance radial growth of Douglas-fir by increasing the rate of net photosynthesis and the length of growing season, especially for high elevation sites (LaMarche, 1974; Lassoie, 1982; Larcher, 1995). On the other hand, it may also have negative influence on radial growth by reducing the production of leaves (Olszyk et al., 1998) and increasing the rates of respiration (therefore reducing photosynthate production and storage) and evapo-transpiration (therefore reducing the moisture availability) (Lassoie, 1982). Although the total annual precipitation will likely increase (Karl et al., 1997; Zwiers and Kharin, 1998), changes in seasonal distribution of precipitation would probably affect Douglas-fir growth more than would changes in total annual precipitation. If the increased precipitation occurs in fall and winter time, the associated cloudy conditions will probably reduce the accumulation of photosynthate, hence producing negative effects on tree-ring growth.

The ANN model for climate-growth response of Douglas-fir at the Heal Lake site of southern Vancouver Island also suggests a difference in the growth environment between the first half of the last century and the latter half. This is indicated in figure 4.8, which shows that the ANN modeled tree-ring growth diverges from the actual growth for the testing years in the latter half of the last century. This phenomenon suggests that the climate-growth relationships learned by the ANN were complicated by additional factors that emerged in the later half of the century. Such additional factors might be related to the increase in atmospheric CO_2 concentration, the climatic extremes in recent decades, or the occurrence of disturbances (LaMarche et al., 1984; Briffa et al., 1998, Guak et al., 1998; Mann et al., 1998). This also implies that caution should be taken when using present climate-growth relationships to interpret tree-rings under historically different climatic regimes. Understanding the effects of those additional factors on tree-ring growth in the recent period is important for understanding the causes and limits on past tree growth (Briffa and Osborn, 1999).

The knowledge of climate-growth relationships is useful for practical forest management. It helps make skillful predictions of the impacts of future climatic change on forest productivity and for planning of annual allowable cut to cope with the climate change. With the right planning we could be in a position to achieve optimal management to allow for timber yields for economic needs while maintaining the long-term health of sustainable forests.

7.2.2 *Climate from Tree-Rings*

Finding 5: *Growing season precipitation is likely a major growth controlling factor operating over a macro-regional scale. Assuming this relationship in the past, the floating ring-width chronologies of subfossil Douglas-fir at Heal Lake site of southern Vancouver Island reflect, in part, the variation in regional precipitation in the past 3rd and 4th millennia. The occurrence of different patterns in ring-width chronologies, e.g., intervals of slight fluctuation and strong variation, suggests different precipitation regimes in the past.*

Ring-width chronologies from living Douglas-fir trees at three sites on southern Vancouver Island and nine sites in central coast region reveal regional similarities in the radial growth responses (see sections 5.1.2, 5.2.2. and 5.3). This suggests that Douglas-fir trees throughout coastal British Columbia are responding to some form of macro-regional climate forcing. Since moisture stress, in addition to prior year's growth, is a common dominant factor affecting tree-ring growth, the climate forcing is probably playing its role by modulating the availability of moisture through changes in the amount of precipitation and the rate of evapo-transpiration.

The climate of Pacific Northwest is, to a large extent, regulated by the proximity of the Pacific Ocean, which is noted as a seat of low-frequency climate variability (Latif and Barnett, 1994; Mantua et al., 1997). The regional precipitation patterns are associated with the Aleutian low phase of the Pacific/North America (PNA) teleconnection pattern in the atmospheric circulation aloft (Wallace and Gutzler, 1981; Minobe, 1997; Cayan et al., 1998). The synchronous enhanced (or reduced) radial growth exhibited in the Douglas-fir tree-ring chronologies in coastal British Columbia may reflect the wet (or dry) modes of the PNA pattern. The temperature variability driven by Pacific Decadal Oscillation (PDO), an index of sea surface temperature in the north Pacific (Zhang et al., 1997), and El Niño / Southern Oscillation (ENSO) related teleconnections (Ropelewski and Halpert, 1986; Hoerling et al., 1997; Cayan et al., 1999) may contribute to the tree-ring variability as well (Kadonaga et al., 1999; Gedalof and Smith, 2000).

The link of tree growth to climate implies that tree-rings may serve as a proxy recorder of the paleoclimate of this region. The tree-ring chronologies of subfossil Douglas-fir at Heal Lake site of southern Vancouver Island exhibit different patterns in the past four millennia (Figures 6.8-6.10). The floating chronologies developed in this study show intervals of slight fluctuation, e.g., between about 1730 B.C. - 1430 B.C., and 670 B.C. - 340 B.C., and intervals of strong variation, e.g., between about 2010 B.C. - 1920 B.C., 1420 B.C. - 1320 B.C., and 870 B.C. - 680 B.C. The previously developed two-millennium long chronology also shows such pattern of slight fluctuation and strong variation over different time intervals (Zhang, 1996). This pattern suggests that the forcing mechanisms of the growth controlling factors (in which the growing season precipitation is a major factor operating over macro-regional scale) were not always the same in the past and the changes could occur rapidly (e.g., within a decade). Quantitative reconstruction of a specific climatic variable from tree-rings is, however, difficult because tree-ring variations are influenced by a complex of factors including seasonal precipitation and temperature, and a variety of standwide disturbances. Combined with other high resolution proxy records from nearby sites such as the varved sediments obtained from the Ocean Drilling Program in Saanich Inlet (Bornhold et al., 1998), the long time-series of tree-ring data at Heal Lake site will offer comparative clues to understanding the regional climate variations in the late Holocene. The tree-ring data also add a relatively long record for a region not well represented by long tree-ring records, and will contribute to large-scale network studies of climate variations (Fritts, 1991; Meko et al., 1993; Grissino-Mayer and Fritts, 1997).

In addition, long tree-ring records provide forest managers with a baseline of natural variability, which permits predictions to be made of the economic costs associated with climatic change (Larson and Kelly, 1998; Parsons et al., 1999). The range of variability derived from long tree-ring records also helps managers predict outcomes from forest practices (Landres et al., 1999; Swetnam et al., 1999) and, therefore, choose appropriate management designs to reconcile with individual species needs (Cissel et al., 1994).

7.2.3 *Growth Anomaly Around About 2000 B.C.*

Finding 6: *An interval of significant growth anomaly around ca. 2000 B.C. is discovered in the floating tree-ring chronology of subfossil Douglas-fir at Heal Lake site of southern Vancouver Island.*

A notable finding of this study was the discovery of significant growth anomalies in subfossil Douglas-fir at Heal Lake of southern Vancouver Island in the interval ca. 1980s B.C. - 1950s B.C. An abrupt enhanced growth started in ca. late 1980s B.C. and culminated in ca. 1982 B.C. - 1978 B.C. during which the ring-width indices were persistently above 1.5; this was followed by an abrupt reduced growth which culminated in ca. 1967 B.C. - 1960 B.C. during which the ring-width indices were persistently below 0.5 (Figure 6.9). The decrease in ring-width indices from above 1.5 to below 0.5 took place within a decade and the trajectory showed a "bump-like" pattern, i.e., a year of slight recovery after a few years of major depression.

The pattern of growth anomalies in the interval ca. 1980s B.C. - 1950s B.C., which were well replicated over 14 individual samples (Figure 6.12), suggests that this interval probably included a severe climatic event or an unstable climate with rapid and large changes. Reconstruction of Holocene vegetation types in British Columbia based on pollen evidence indicate a relatively warm and moist mid-Holocene and a cooler and wetter late Holocene with the transition occurred in ca. 2000 B.C. (Allen, 1995; Hebda, 1995; Heinrichs, 1999; Brown, 2000). Long tree-ring records from bristlecone pine growing in the White Mountains of California (Ferguson, 1969) and oak (*Quercus robur*) from west Europe (International Tree-Ring Data Bank, 2000), however, do not show comparable growth anomalies around 2000 B.C. (Figure 7.1). Caution should be taken when comparing tree-ring chronologies of different species and from regions of different climatic and ecological regimes because tree-ring growth is subject to a complex of factors including tree's genetics and environmental conditions at microsite, local and regional scale (Frits, 1976; Hughes and Diaz, 1994; Baillie, 1995). Nevertheless, it is to be hoped that the plot of ring-width chronologies from these different regions (Figure 7.1) will serve to show the growth patterns for readers of different interest. Comparison of the tree-ring characteristics directly from the wood at these different regions may provide more reliable information about the spatial patterns of environmental changes. If the growth anomalies identified in this study did indeed fall into a time of climate transition, then the tree-ring patterns may imply that the climate in the transition period was quite unstable and the climatic extremes could reach exceptionally high magnitude within a decade. Such climatic extremes, e.g., spring frost and growing season droughts, can cause forest stand disturbance by disrupting the forest structure through increasing stress to individual plants (see the two-level model of tree-ring analysis in section 3.1). According to Cayan et al. (1998) and Corti et al. (1999) such climatic extremes could be related to an increased frequency of oscillations between states in natural atmospheric circulation regime and/or to strong regional climatic instability.

The abundance of subfossil logs in the mid-late Holocene may also provide further evidence of the climatic transition at ca. 2000 B.C. The accumulation and preservation of ancient Douglas-fir trees in Heal Lake may be primarily due to a regional lake-level rise, which inundated fallen logs on the lake's shore. Increased precipitation

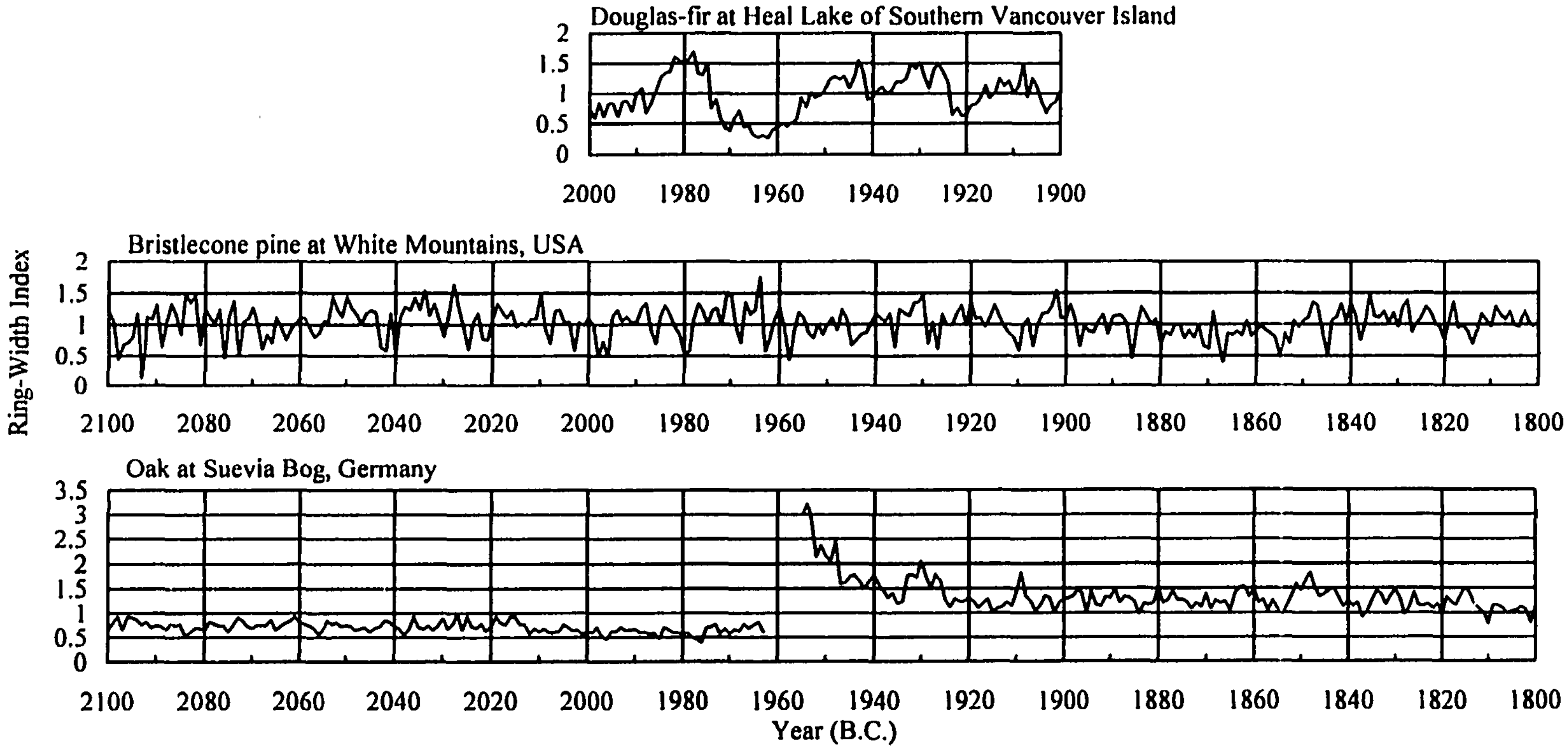

Figure 7.1 Comparison of the growth anomalies at about 1980s-1950s B.C. among ring-width chronologies of subfossil Douglas-fir (floating) at Heal Lake of southern Vancouver Island, bristlecone pine at White Mountains, USA (Ferguson, 1969), and oak at Suevia Bog, Germany (International Tree-Ring Data Bank, 2000). The oak chronology is not continuous and its dates are determined by crossdating with ring-width series of oak trees at other sites in Europe (Baillie, 1995).

and decreased temperature (therefore reduced evaporation) might be a factor that contributed to the water-level rise. Although the subfossil logs discovered in Heal Lake represent much of the Holocene, there seems to be a large number of logs in the period of mid-late Holocene.

Examination of the five floating chronologies and a previously studied two-millennium long chronology (Figure 6.10) (Zhang, 1996) of Douglas-fir at the same site reveals that the growth anomaly with an abrupt and persistently high magnitude similar to that of about 1980 B.C. - 1950 B.C. has occurred only one other time, i.e., in the A.D. 1980s. This observation suggests that we might have already entered into an interval of unstable climate. Given that the current global climate is changing, it is natural to ask what might be the pattern of such changes in the future? While general circulation models (GCMs) can provide us with relevant information based on the physics of a variety of processes in the atmosphere, ocean, and land, tree-rings in an analogous climate situation at ca. 2000 B.C. may serve as a biological time capsule to highlight the pattern of its changes. For example, the tree-ring pattern in the climate transition period at ca. 2000 B.C. suggests two climatic extremes with one favourable to tree growth and the other infavourable. This leaves us the question: Whether the future climate will have an interval of extreme dry growing seasons? GCMs have shown that the average interval between precipitation events will increase in the middle latitudes under CO_2 doubling (Cubasch et al., 1995; Zwiers and Kharin, 1998). It is possible that the longer interval between precipitation events, together with the increased evapotranspiration under a warmer climate, will produce a prolonged drought condition in the growing season. Forest ecosystems do not respond to climatic forcing as coherent units, rather, the individual species do (Hebda and Whitlock, 1997). The tree-ring patterns at ca. 2000 B.C. perhaps provide us with a lesson of climatic instability (and unpredictability?) during a time of climate transition. There is a potential of extracting further information from the tree-rings in this interval by analyzing other parameters such as density, widths, and carbon isotopes of the total ring as well as the earlywood and latewood (Brix, 1972; Francey and Farquhar, 1982; Jozsa and Robertson, 1987; Briffa et al., 1992; Livingston and Spittlehouse, 1993, 1996)

7.3 Suggestions for Future Research and Concluding Remarks

Suggestions for further research include the following.

1) Refinement of growth response models: The radial growth of Douglas-fir is a result of cambial cell division and the subsequent cell enlargement and maturation. This growth process is regulated by a variety of biophysical activities and biochemical reactions which are affected by a complex of environmental factors. Modeling the climate-growth response by considering a small number of climatic factors is only an approximation of such complex process. Continued refinement of the growth response ANN models using new techniques (e.g., the knowledge-based neural networks (Zhang and Gupta, 2000)) and additional data relating environmental factors and tree-rings (e.g., disturbances) is necessary to improve the accuracy of the models and, in particular, to help test if the climate-growth relationships are changing under the recent global warming conditions. For example, with longer series of climate-tree-ring data set and record of

detailed site history, the ANN model for climate-growth response can be refined and tested more rigorously.

2) Adding sample depth to floating tree-ring sequences: The standwide environmental signal of a tree-ring chronology becomes stronger with the increase in sample numbers. The sample depth for historical tree-ring chronologies is usually limited by the availability of ancient wood. The large amount of undated Heal Lake subfossil logs holds potential to add sample depth to floating tree-ring sequences. Many of the subfossil logs need to be radiocarbon dated to help narrow the range of the floating sequences. Collection of ancient logs from other lakes, if possible, will also help adding sample numbers. With more radiocarbon dates and laborious crossdating work, it is possible that the sample depth of many floating tree-ring sequences can be added and the information about standwide environmental changes can be obtained.

3) Further analysis of the growth anomalies at ca. 4000 year BP: The growth anomalies in this interval are considered as a result of climatic extremes in an unstable climatic transition period. The magnitude, rapidity, and persistence of the growth anomalies in this interval are the most significant in the past four millennia for the Heal Lake subfossil logs. This study only analyzed the ring-widths of these samples. However, the tree-rings in this interval may contain more information of the environment than those disclosed from the ring-widths. Further studies of other tree-ring parameters, such as the widths of earlywood and latewood (caution should be taken to the sample surface defects that affect the precision of measurement using the Windendro™ image system), the density of earlywood and latewood, and the carbon isotopes in tree-rings, will help us

understand whether the temperature or precipitation or a combination thereof were the predominant factor for the growth anomalies. This will further shed light for the understanding of the patterns of climatic changes in a climatic transition period.

In conclusion, the two-level linear aggregate model for tree-ring analysis facilitates better understanding and unambiguous interpretation of the effects of stress and disturbance on tree-ring growth. Artificial Neural Network (ANN) provides an innovative technique for modeling nonlinear and complex climate-growth relationships in dendroclimatic studies. The growing season precipitation and prior growth state are the two most important factors affecting the radial growth of Douglas-fir on macro-regional scale of coastal BC. The difference in growth response between southern Vancouver Island and Bella Coola of central coast lies mainly in non-growing season factors. The tree-ring chronologies of subfossil Douglas-fir show significant growth anomalies around ca. 4000 years BP and both intervals of relatively low fluctuation and strong variation in the past four millennia. Applying the conceptual and technical findings gained from this study to dendroclimatic analysis will improve our ability to interpret past tree-ring variations and to predict the effects of future climate on forest growth. The knowledge of climate-tree-ring growth relationships and growth patterns provides us with information of growth response and a reference of natural variability that will ultimately be of value to Douglas-fir forest management and climate studies in coastal British Columbia.

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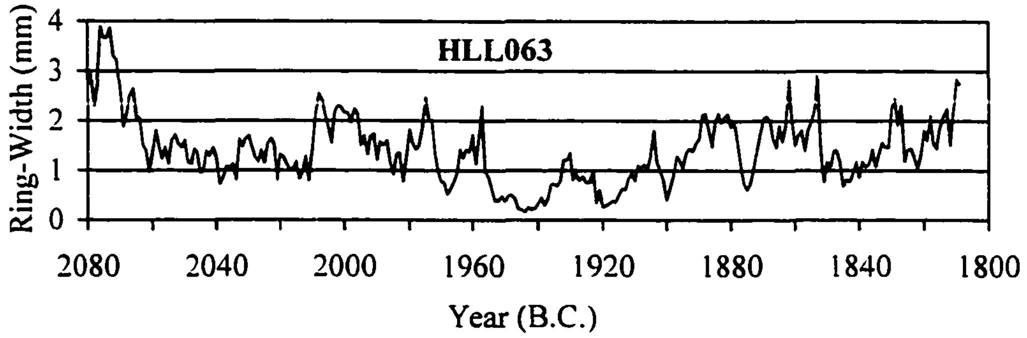
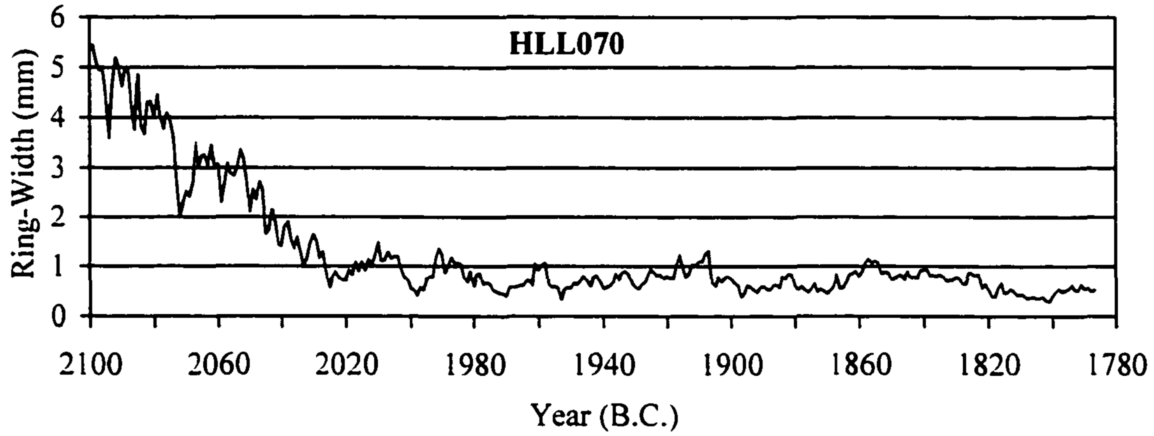
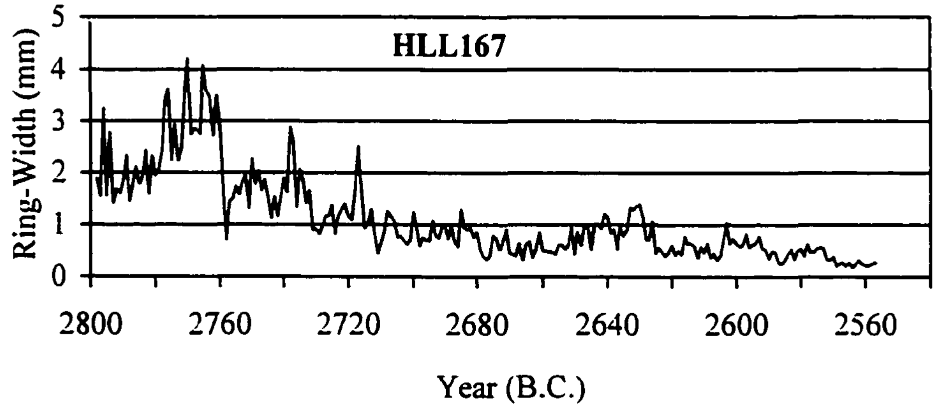
Appendix 1: Single floating ring-width sequences of ^{14}C-dated subfossil Douglas-fir logs discovered at the Heal Lake site of southern Vancouver Island, British Columbia.







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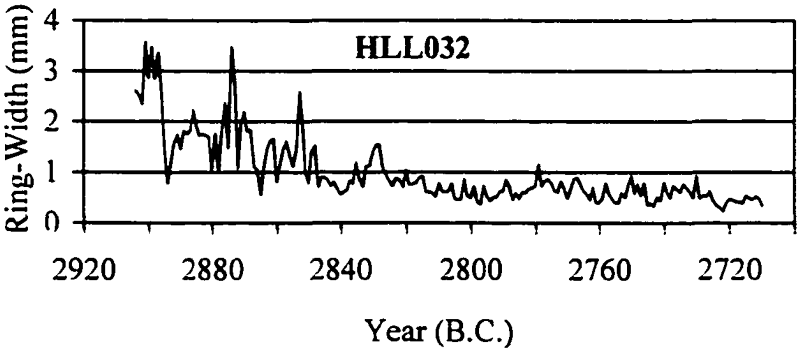
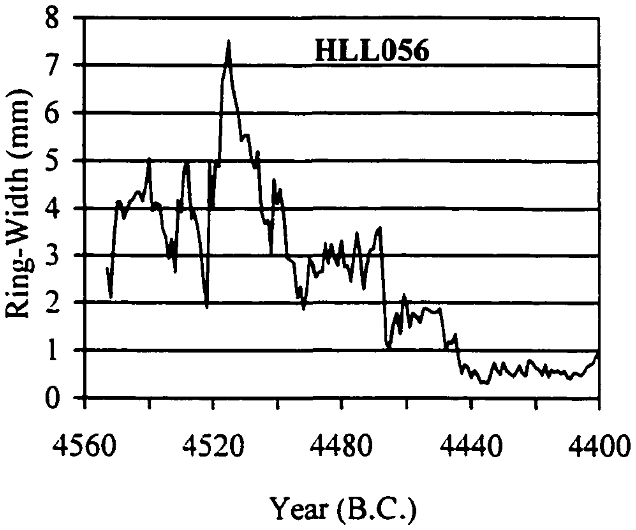
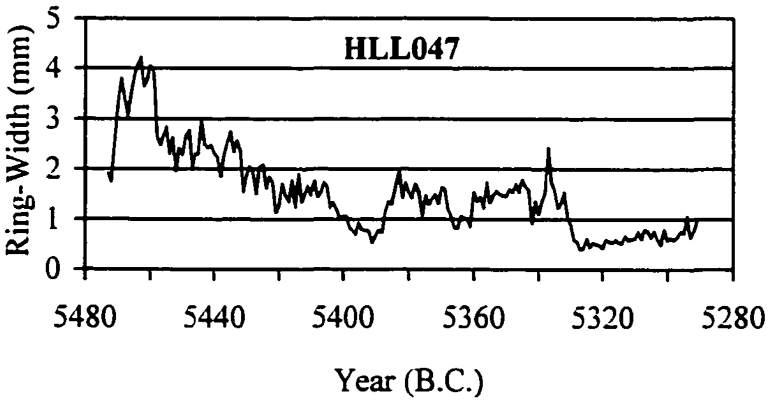
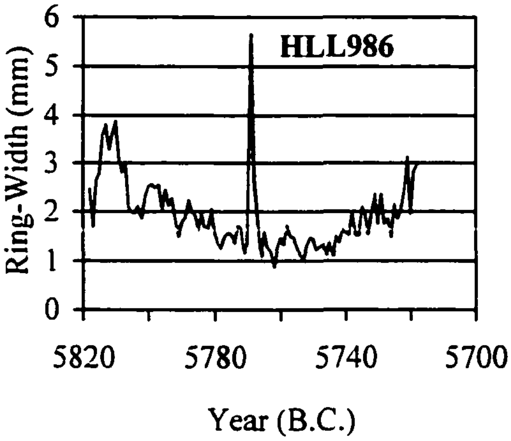
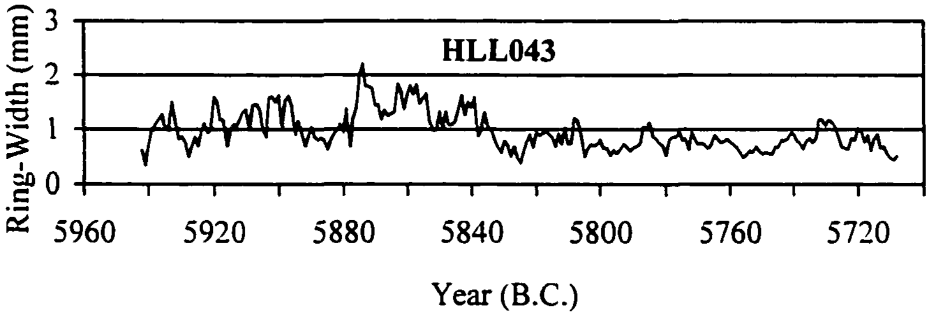


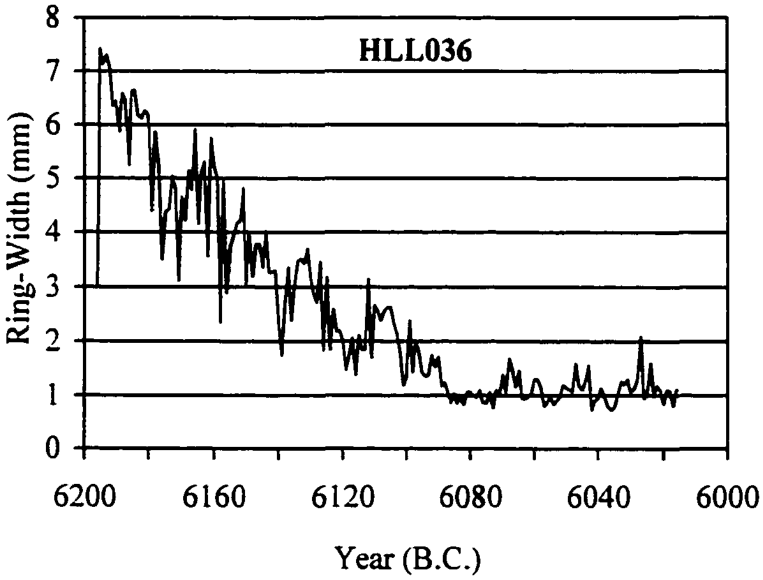




Appendix 1 (continued)







Appendix 1 (continued)