

INFLUENCE OF
CAMBIAL AGEING, INITIAL SPACING, STEM TAPER AND GROWTH RATE
ON THE WOOD QUALITY OF THREE COASTAL CONIFERS

By

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ABSTRACT

As the forest industry in British Columbia becomes increasingly dependent on second-growth timber for its raw material supply, the question of wood quality becomes more relevant. Accelerated growth in forest plantations, coupled with an earlier harvest, will lead to changes in the quality of the timber harvested. The influence of cambial ageing, initial spacing, stem taper and growth rate was non-destructively evaluated on the wood quality characteristics of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don). The wood properties analysed included ring width, earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, whole-ring tracheid length and microfibril angle. Juvenile wood development was determined based on whole-ring relative density trends from pith to bark. A highly significant cambial age effect was noted for practically each wood property considered. An identical pattern of development, regardless of spacing or taper class, was identified for Douglas-fir via latewood proportion and whole-ring relative density, and for western hemlock via latewood width, earlywood relative density, latewood relative density, whole-ring tracheid length and microfibril angle. No identical results were identified for western redcedar. An increasingly non-significant relationship evolved over time for Douglas-fir between growth rate and whole-ring relative density. A slight, but increasingly negative relationship unfolded for western hemlock. An increasingly stronger negative relationship developed for western redcedar. The Kajaani FS-200 Optical Fibre Analyser was found inadequate for measuring tracheid length variability on the basis of 12 mm increment cores. A gradual decrease in juvenile wood ring count was commonly identified with increasing height. Generally speaking for both Douglas-fir and western hemlock, the larger the volume of crown foliage relative to length of branch-free stem, the lower the passage from juvenile wood to mature wood below the base of the live crown. In the case of western redcedar, the larger the volume of crown foliage relative to length of branch-free stem, the higher the passage. The use of a variable exponent taper equation was explored for predicting juvenile core development.

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1. GENERAL INTRODUCTION

Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is commonly found west of the Coast mountain range in British Columbia. Its distribution extends south along the Pacific coast for about 2200 km, from the upper limits of Vancouver Island to the western slopes of the Sierra Nevada in northern California (Burns and Honkala 1990). Mature standing timber volume within coastal British Columbia was estimated in 1995 at about 134 million cubic metres. Sawlog production that year totalled 4.25 million cubic metres, comprising 16.4 % of the region's total timber harvest (COFI 1996). Although a relatively minor commercial species, coastal Douglas-fir remains in high demand due to its high growth potential, as well as to its excellent strength qualities. It is widely used for the production of structural lumber, plywood, poles and pulp and paper products.

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is the most important commercial tree species in coastal British Columbia. Its range along the Pacific coast extends approximately 3200 km, from central California to the Kenai Peninsula in Alaska (Burns and Honkala 1990). Mature standing timber volume within coastal British Columbia was estimated in 1995 at about 1 184 million cubic metres. Harvest levels that year totalled 9.09 million cubic metres, accounting for 35.0 % of the region's total sawlog production (COFI 1996). Western hemlock is highly valued for its excellent strength, pulping and treating characteristics. Its wood is light and uniform in colour, is even-grained, lacks pitch and is excellent for machining.

The range of western redcedar (*Thuja plicata* Donn ex D. Don), along the Pacific coast, extends from northern California to southeastern Alaska (Burns and Honkala 1990). The species remains a commercially important element within British Columbia's coastal forest region even though volumes harvested in recent years have decreased substantially. Remaining standing timber reserves were estimated in 1995 at approximately 302 million cubic metres. Sawlog production that year totalled 5.87 million cubic metres, accounting for 22.6 % of the region's total timber harvest

(COFI 1996). Western redcedar is considered a valuable speciality wood due to its natural durability, low density, straight grain and high dimensional stability. Traditional uses include shingles and shakes, poles, pilings and house siding and interior panelling.

Wood quality is defined by Jozsa and Middleton (1994) as the attributes that make logs and lumber valuable for a particular end use. As the forest industry within coastal forest region of British Columbia becomes increasingly dependent on second-growth timber for its raw material supply, the question of wood quality will become more important. Recent trends in forest management have favoured relatively wide initial spacings, over a short rotation, to accelerate second-growth operability, and to achieve maximum stand value in the form of large diameter sawlogs. The main reason for advocating wider spacings is to increase the rate of diameter growth, which will increase proportionally with growing space until a maximum is reached by an open-grown tree (Smith *et al.* 1997). Such accelerated diameter growth, coupled with an earlier harvest, will lead to changes in the quality of the timber produced. Each tree will subsequently contain a greater proportion of juvenile wood at time of harvest. Whether this will have a major influence on the quality of future manufactured wood products remains uncertain.

Douglas-fir, western hemlock and western redcedar currently account for nearly three quarters of coastal British Columbia's annual timber harvest, the majority of which is old-growth. Past wood quality research in British Columbia has primarily focussed on the physical and mechanical aspects of this old-growth resource. More recent studies involving the above species have generally served to characterise the naturally regenerated, second-growth resource presently available for harvest (Jozsa and Kellogg 1986, Jozsa *et al.* 1989, Jozsa *et al.* 1998). Much of this information remains inadequate for evaluating the effects of current stand management practices on future second-growth wood quality. Sampling in past studies was most often conducted within irregularly-spaced, often mixed-species stands that had largely developed from unknown initial stocking densities. The effects of increased diameter growth on wood quality within uniformly-spaced, even-aged, single species stands are subsequently difficult to evaluate from this work. Such knowledge will ultimately be required from forest managers if future timber quality objectives within second-growth forest plantations are to be met. A better understanding of the effects of cambial ageing, initial spacing, stem taper and growth rate on second-growth wood formation is therefore required.

Data for this research were collected from a spacing trial established at the UBC Malcolm Knapp Research Forest near Haney, BC (Walters and Smith 1973). Douglas-fir, western hemlock and western redcedar were selected for study based on their commercial importance, and relatively wide distribution, within the coastal forest region of British Columbia. The site at Haney was chosen for its easy access, and also due to the fact that it represents one of the oldest spacing trials available for study in the province. These trials were originally established to assess the effects of initial spacing on tree and stand development. A non-destructive approach for wood property sampling was therefore employed to maintain the pattern of spatial distribution between trees, and to respect ongoing growth and yield studies.

The following research sought to provide information necessary for allowing rational decision making during the crop planning process of second-growth stands of Douglas-fir, western hemlock and western redcedar to meet product objectives. Two main objectives were addressed:

- (1) to analyse the effects of cambial ageing, initial spacing, stem taper and growth rate on the development of specific wood properties important to wood quality
- (2) to examine juvenile wood development within second-growth stands established over a range of initial spacing intervals

A literature review discussing the physiological aspects of wood formation, along with the effects of stand density management on tree development, is provided in Chapter 2. Additional information relating to wood quality is included under the headings Relative Density, Longitudinal Tracheid Length, Microfibril Angle and Juvenile and Mature Wood. A description of the data set, and the sampling techniques employed, is included under the Materials and Methods heading in Chapter 3. The two main objectives considered in this study are central to Chapters 4 and 5. Both chapters are organised in a similar manner, incorporating an introduction section, a data analysis section, a results and discussion section and a general summary. A final summary of the principal results obtained, and recommendations for future research, are presented in Chapter 6 under the heading General Conclusions. All literature cited is listed in Chapter 7. Supplementary Tables pertaining to Chapters 4 and 5 are included in Appendices I and II, respectively.

2. LITERATURE REVIEW

2.1 Mechanism of Wood Formation

A description of the physiology of wood formation can be divided into two developmental stages. The primary stage regulates height growth and overall tree form. Elongation of the main stem, branches and roots occurs as a result of active cell division in distally located apical meristems. The secondary stage involves the expansion in circumference of all root and stem axes accomplished through meristematic activity in the vascular cambium.

Primary growth is triggered in temperate zone conifers by an increase in temperature and photoperiod in early spring. The process is initiated once the rehydration and swelling of vegetative buds has occurred, prompting hormonal and enzymatic activity within the apical meristems. As cell division proceeds, older tissues formed behind the apical initials gradually undergo changes in size, shape and function (Reeve 1948). Further differentiation leads to the formation of three distinct primary tissues, namely the protoderm, the ground meristem and the procambium. The protoderm gives rise to the epidermis, a protective layer that is one-cell thick and which serves primarily to prevent the dessication of underlying tissues. The ground meristem develops into the cortex and pith and gives rise to the rays that originate from the pith. The inner and outer cells of the procambium differentiate radially into bundles of vascular tissue known as the primary xylem and primary phloem respectively. Groups of cells located in the centre of the procambium remain meristematic. These give rise to strands of cambium that eventually interconnect through the addition of meristematic cells originating from the surrounding parenchyma. Thus, a complete circumferential sheath of meristematic cells known as the vascular cambium is formed (Zimmermann and Brown 1971).

The same physiological processes that trigger the initiation of bud growth in early spring also reactivate the vascular cambium formed in previous years. Secondary growth begins immediately

beneath the newly activated buds and proceeds downward toward the stem base with the rehydration and swelling of dormant fusiform and ray initials (Wilcox 1962, Zimmermann and Brown 1971). The production of xylem and phloem cells is initiated shortly after, through the periclinal cell division of the cambial initials, and through the division of the xylem and phloem mother elements along the tangential-longitudinal plane (Bannan 1955, 1962). The anticlinal division of the cambial initials in the radial plane also takes place, allowing the vascular cambium to increase in circumference (Bailey 1923, Bannan 1957, 1962). Differentiation follows whereby the newly formed xylem and phloem cells increase in both length and diameter. The deposition of a secondary wall and the formation of pits begin toward the end of this stage. Once the secondary wall has been formed, no further enlargement of the cell occurs. Cells are considered mature once completely lignified and void of protoplasm (Wardrop 1964).

Annual xylem development within temperate softwoods is reflected through the formation of a concentric growth ring. Its thickness following deposition is highly variable at various positions about the stem. Such variability can be related to the rate of cell production observed during cambial activity, and to the length of time that the vascular cambium is active over the course of a season. However, the overlying cause of such variation is seemingly the relationship between crown size and length of stem that is devoid of branches (Farrar 1961, Larson 1963).

Cambial activity within a stem typically increases downward from the apex in a tapered fashion. The larger the volume of crown foliage, the greater the taper observed. Maximum ring width is normally attained in the vicinity of the base of the live crown where the cumulative contribution of all branches to cambial growth is greatest. Below the base of the live crown, ring width typically decreases in a continual fashion. A certain increase in thickness is sometimes observed as ground level is approached. Greater anchoring support and wind-firmness is thus provided (Duff and Nolan 1953, Farrar 1961, Larson 1963).

The width of all growth increments combined ultimately determines the form adopted by a tree stem. At one extreme is the form adopted by a young, open-grown tree that supports a long, vigorous crown over the length of its stem. A continual increase in ring width can be observed with decreasing height in such a tree, with the point of maximum ring development occurring toward

ground level. Additional ring swelling at ground level, to aid in maintaining tree stability, may also be observed, resulting in a highly tapered stem shape with buttressing (Farrar 1961, Larson 1963).

The other extreme of form is exemplified by a suppressed, stand-grown tree. The typical growth ring produced by such a tree is not only thinner throughout, but also begins to narrow immediately below the base of the live crown. Little or no basal thickening is generally observed at ground level. In severe cases, the annual sheath may fail to completely extend to the stem base, resulting in the formation of a missing or discontinuous growth ring. Over time, this concentration of growth in the general vicinity of the base of the live crown will result in the formation of a more-or-less cylindrically-shaped bole (Farrar 1961, Larson 1963).

Mature growth rings in all conifers are characterised by zones of earlywood tracheids, which function as conducting cells, and latewood tracheids, which mainly serve for mechanical support. Earlywood tracheids are most often slightly shorter, have larger radial diameters, thinner cell walls and generally possess a greater number of bordered pits that tend to be larger in diameter than those found in latewood (Panshin and de Zeeuw 1980, Zobel and Van Buijtenen 1989). Transitional latewood tracheids are also commonly associated with most conifers. These tracheids generally possess intermediate characteristics of both earlywood and latewood, and may be found in varying amounts between the two wood zones (Larson 1969).

Current thinking indicates that cambial growth is to a large extent controlled by hormonal interactions. The changes observed in tracheid development from earlywood and latewood are said to be a plastic response of the vascular cambium to varying concentrations of plant hormones at different periods within the growing season. Five groups of plant hormones are generally recognised. These include auxins, gibberellins, cytokinins, ethylene (growth promoters) and abscisic acid (growth inhibitor). In earlier studies, each of these hormone groups was often assigned to a very distinct function relative to plant growth. For example, auxins were considered solely responsible for stimulating cell enlargement, gibberellins for height growth, cytokinins for cell division and ethylene for fruit ripening. It is now recognised that each hormone group is present in varying quantities within the vascular cambium and each may be involved in controlling the production and differentiation of cambial derivatives. However, the extent and manner in which each hormone group

interacts with one another, and with other nonhormonal groups, in regulating cambial activity is still unknown (Little and Savidge 1987, Salisbury and Ross 1992, Little and Pharis 1995).

Auxins apparently play a predominant role in regulating cell division and promoting cell enlargement. Many studies support this assertion. An increase in the production of xylem and phloem in gymnosperms was observed following the application of exogenous auxin to disbudded, defoliated or phloem-severed stems (Larson 1962, Little and Wareing 1981, Little and Savidge 1987, Sundberg and Little 1991). Significant reductions in the basipetal flow of endogenous auxin and cambial growth were observed by the same authors when no exogenous auxin was added. The application of exogenous auxin to disbudded, defoliated or phloem-severed stems was also found to promote tracheid enlargement and cell wall thickening (Larson 1962, Sheriff 1983). A positive relationship was identified between the production of cambial derivatives and the concentration of exogenous auxin applied, up to an optimum level (Sheriff 1983, Little and Savidge 1987).

An increase in cell wall thickening has been correlated to the maturation of current-year needles, and with the resultant increase in carbohydrate supply within the stem (Larson 1964, Gordon and Larson 1968). Cell wall thickening entails the deposition of cellulose, hemicellulose and lignin within the tracheid secondary wall. Mainly reserve carbohydrates from storage tissues are used for this purpose during earlywood development. Buds and new shoots represent the major carbohydrate sink at this time, consuming most of the photosynthate production available from the older foliage (Kozłowski 1992, Hansen *et al.* 1997, Kozłowski and Pallardy 1997).

Approaching maturity, the newly developed foliage rapidly becomes a weaker sink for carbohydrates, and a net producer. A significant increase in the downward flow of assimilates toward the roots soon follows. Tracheid cell walls along the stem subsequently increase in thickness, indicative of latewood development (Larson 1964, Gordon and Larson 1968). This activity is maintained so long as carbohydrate sinks in competing meristems remain weaker, and so long as factors affecting carbohydrate conversion into secondary cell wall tissues (water availability, hormonal interactions, photoperiod, temperature) remain favourable (Kozłowski 1992, Hansen *et al.* 1997, Kozłowski and Pallardy 1997).

Auxin synthesis and photosynthate production were described by Larson (1969, 1973) as physiologically independent processes that could overlap in time and under certain conditions. This independence, it was hypothesised, was responsible for many of the changes in tracheid structure that could be observed within a growth ring from earlywood to latewood. Larson furthermore proposed that physiological gradients within a tree stem, in terms of both auxin and photosynthate availability, combined with the independence element, accounted for much of the variability in earlywood and latewood structure that could be observed at different heights along a tree stem. Larson nonetheless did recognise that the process of tracheid development was inherently more complex than the seemingly basic relationships proposed. Unequivocal evidence to support Larson's work remains unavailable, indicating how little is still understood with regard to the process of wood formation.

Larson (1969, 1973) stated that a sharp drop in auxin production, followed by a sharp increase in photosynthate availability, was generally associated with a sudden decrease in tracheid radial diameter and increase in cell wall thickness. He explained that an abrupt transition from earlywood to latewood would generally result from the above. Larson added that the development of transition wood took place under conditions where auxin production coincided with the export of photosynthate from the current year's foliage. The tracheids produced under such conditions would demonstrate either thickened cell walls with no subsequent change in radial diameter, or a narrower diameter with no apparent change in cell wall thickness. The subsequent transition from earlywood and latewood would, as a result, be very gradual, with the visible features of one wood type slowly blending into the other.

Larson (1969, 1973) suggested that high levels of auxin were present throughout the vascular cambium during early terminal shoot growth. As terminal shoot growth subsided, the levels of transported auxin within the vascular cambium would likewise begin to decrease, prompting the cambial regions furthest from the auxin source to initiate latewood production first. A thicker latewood increment would accordingly be produced at the stem base, tapering upward toward the apex to the point of disappearing. In contrast, earlywood width would remain similar in proportion to ring width, increasing downward from the apex and reaching a maximum in the vicinity of the base of the live crown. A continual decrease in earlywood width would follow as ground level was approached, with perhaps a slight increase in thickness displayed toward the stump due to buttressing.

Larson (1969, 1973) furthermore suggested that auxin levels within the vascular cambium of young trees that have a high proportion of their stems covered by branches would remain consistently high throughout the growing season. Mostly transitional latewood tracheids, demonstrating thickened cell walls and wide radial diameters, would subsequently develop within the outer portions of each annual ring. Following the cessation of terminal shoot growth, older trees possessing longer branch-free boles would see a marked drop in auxin concentration at points furthest from the crown. An abrupt transition from earlywood to latewood would subsequently develop for such trees. With increasing proximity to the active crown, and with increasing auxin levels, a more gradual earlywood to latewood transition would develop. Wood almost devoid of true latewood, but containing some transitional latewood tracheids, would be produced toward the apex where auxin levels within the cambium would have remained at a high throughout the growing season.

2.2 Competition Theory

Grime (1979) defines competition in terms of the capacity of neighbouring plants to capture and utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space. His plant strategy model predicts that those plants which are the best competitors for light will also be the ones most efficient at extracting moisture and nutrients from the ground. Such plants will be able to maintain the highest levels of growth. Strong tradeoffs exist between the ability to tolerate low resource supplies and the ability to grow rapidly and to exploit resources. Species that display a maximum capacity for resource capture will be the superior competitors. Once established, differences among competing plants will be maintained and magnified due to the positive feedback that exists between growth and resource capture.

Tilman (1988) defines competition as the utilisation, by two or more species, of shared resources that are in short supply. His resource-ratio model predicts that the superior competitor will be the species that can reduce the concentration of the limiting resource to the lowest level and still maintain its population. Tilman contends that the best competitor will be the species with the lowest resource requirements rather than the one that can grow the largest, the fastest, or is the first to colonise an area.

2.3 Shade Tolerance

The minimum light intensity at which the photosynthetic uptake of CO_2 within a tree becomes equal to its rate of release through respiration is commonly referred to as the compensation point. Trees that respire more rapidly typically require a greater amount of light to reach this level. As light intensity increases beyond the compensation point, a rapid increase in the rate of photosynthesis, and therefore in net CO_2 fixation, is observed. However, such increases are difficult to sustain and will at some point begin to diminish with further increases in light. A saturation point is eventually reached at which time further increases in light intensity will lead to no further gains in net CO_2 fixation. The particular light intensities at which compensation points and saturation points are reached in turn depend upon a combination of factors. These factors may include some of the following in addition to the various interactions possible; genotype, leaf type, leaf age, soil moisture, nutrient availability, air humidity, CO_2 concentration in the air, ambient temperature and insect and disease infestation (Larcher 1983, Kimmins 1987).

The capacity for a tree to grow in the shade of other trees varies widely with species. Those adapted to growing at reduced light intensities and high root competition are commonly referred to as shade tolerant. Such species generally have lower compensation points and saturation points than species adapted to higher light-intensity environments (Larcher 1983, Kimmins 1987). In the absence of a large-scale disturbance, relative shade tolerance becomes an important element in the ability of a tree to form part of a climax community in a given environment. A knowledge of shade tolerance and its implications for growth is therefore essential for explaining and predicting vegetation succession and in supporting stand-level silvicultural decisions during management planning.

For this and other purposes, tree species have often been arbitrarily classified in order of comparative shade tolerance based on their capacity to withstand low light conditions. Such a system has simplistically implied that shade tolerance for a species will remain more-or-less constant across the range of sites on which the species may be found, and for all stages of tree development. Contradicting classifications have therefore sometimes arisen. Krajina (1965) ranked *amabilis* fir (*Abies amabilis* Dougl. Ex Loud. Forbes) as the most shade tolerant tree species in the Pacific Northwest. Western hemlock and western redcedar were both ranked as equally high in shade

tolerance, but at a level inferior to that demonstrated by the amabilis fir. Minore (1979) considered western hemlock equal to amabilis fir as the most shade tolerant species in coastal British Columbia. Western redcedar was considered less tolerant than western hemlock. Western hemlock and western redcedar were both classified by Burns and Honkala (1990) as very shade tolerant, though western redcedar was considered perhaps slightly-less-so. Coastal Douglas-fir has been classified as intermediately shade tolerant by all of the above authors. A recent study of interspecific variation in shade tolerance, based on variations in light condition as well as in soil moisture and in nutrient availability, has suggested that shade tolerance is greatest in western redcedar, followed by western hemlock and Douglas-fir (Carter and Klinka 1992).

2.4 Idealised, Even-Aged, Single-Species Stand Development

An understanding of stand dynamics is essential in forest management. Forest stand dynamics describe the various changes that may be observed in forest stand structure as a function of time. Stand structure relates to the physical and temporal distribution of trees in a stand. The evolution of structure within an idealised, even-aged, single-species stand, as influenced by competition, can best be described through four general phases of development. In order of succession, these include the stand initiation stage, the stem exclusion stage, the transition stage and the steady-state stage (Oliver and Larson 1996).

The first stage of stand development is commonly referred to as stand initiation. During stand initiation, plant species developing from seeds, sprouts or advanced regeneration gradually recolonise open spaces created by a major disturbance such as fire, blowdown, insect infestation, disease infestation or logging activity. The duration of this stage varies widely, depending upon a combination of factors such as the intensity of disturbance, area of disturbance, growth rate of invading species, regeneration mechanisms of invading species, the coincidence of disturbance, seed crops and weather and also, on the density and multiplication rates of seed predators or competing shrubs (Oliver 1981). Little competition is observed among tree seedlings at this time because site resources are not yet fully exploited. The rate of tree development, if unimpeded by herbaceous competition, is mostly governed by physiological and genetic factors. Abiotic elements such as

climate, topography, aspect and the physical and chemical characteristics of the soil also play an important role (Oliver and Larson 1996).

The onset of competition within a single species, even-aged stand largely corresponds to the timing of crown closure. Complete crown closure is realised when the lower shaded branches of a tree die and the base of the live crown begins to recede. On similar quality sites, crown closure will occur later at the widest spacings, with the extreme of an open-grown tree experiencing little crown recession. Following crown closure, widely-spaced trees will be taller, will have wider crowns and will possess larger average diameter branches and stems than closely-spaced trees growing on similar sites (Curtis and Reukema 1970, Oliver and Larson 1996).

Stem exclusion is characterised by the onset of competition within a stand, and through the initiation of self-thinning. The intensification of competition during this stage gradually leads to the differentiation of the stand into four commonly identified crown class subgroups, namely the dominant, the codominant, the intermediate and the overtopped. Each crown class is defined by total tree height position relative to the general crown canopy structure, and by the proportion of tree crown surface exposed to direct sunlight (Kozlowski *et al.* 1991, Oliver and Larson 1996).

As the name suggests, dominant trees are those that extend above the general canopy layer and receive full sunlight along the top and upper sides of their large, well developed crowns. Codominant trees form the general canopy layer and intercept full sunlight from above, but comparatively little from the sides of their medium-sized crowns. Intermediate trees extend somewhat into the lower portions of the main canopy and receive small amounts of direct sunlight from above, but none from the sides. Crowns are typically narrow and short, resulting in limited leaf surface area and a low live-crown-ratio. Such trees maintain the potential to recover upon release, and to gradually emerge into either of the codominant or dominant crown class positions. Overtopped trees are those positioned entirely below the main canopy layer and which receive practically no direct sunlight. Such positioning results in the formation of small, sparse, flat-topped and often lopsided tree crowns. Overtopped trees have little chance of recovering upon release (Kozlowski *et al.* 1991, Oliver and Larson 1996, Smith *et al.* 1997).

The transition stage is initiated by a general decrease in upper canopy vigour as trees begin to age and decrease in vigour. Overstory tree heights and crown sizes become less uniform, with less overlapping occurring between adjacent branches. Individual tree mortality at this point is largely brought about by environmental factors such as windthrow, insects and disease. Openings created by the deaths of dominant and codominant trees are subsequently larger, and persist over a longer period of time. Gaps in the main canopy are slowly created, allowing sunlight to penetrate diagonally to the forest floor, and allowing for the subsequent establishment of a new stratum of herbs, shrubs and advanced regeneration (Oliver 1981, Peet and Christensen 1987, Oliver and Larson 1996).

A forest stand in the steady-state phase can be viewed as a patchwork of trees of various sizes and ages continuously undergoing the processes of stand initiation, stem exclusion and transition. Individual old-growth trees continue to die at irregular intervals, freeing up growing space in a spatially discontinuous pattern. Advanced regeneration is gradually released within such openings, forming a vertically stratified stand that contains trees of a wide range of ages, diameters and heights. Most often, the steady-state phase is never reached due to a major disturbance, such as fire, that completely destroys the forest stand and reverts it back to the stage of stand initiation. Barring such a disturbance, the ingrowth provided by the new trees eventually gives the stand an uneven-aged character, with a diameter distribution approaching a reverse-J shape. Volume lost through the periodic death of individual old trees is replaced by ingrowth provided by younger trees (Oliver 1981, Peet and Christensen 1987, Oliver and Larson 1996).

2.5 Wood Quality

A few of the basic principles governing tree development were advanced in the preceding discussion. The effects of crown development on wood formation, and on the subsequent patterns observed for earlywood, transition wood and latewood development, were also considered. The following discussion will address the concept of wood quality. Five wood properties important to the wood processing industry in terms of end-product quality and value, namely relative density, longitudinal tracheid length, microfibril angle, juvenile wood and mature wood, will be reviewed.

2.5.1 Relative Density

Relative density is considered by many as the best single measure of wood quality. Clear wood strength and stiffness, digester pulp yield and caloric content are all closely related to it. Its importance also stems from the fact that it can be easily altered for many species through silvicultural and genetic manipulation (Panshin and de Zeeuw 1980, Zobel and Van Buijtenen 1989). Relative density is defined as the ratio of the weight of a given volume of wood to the weight of an equal volume of water at 4 °C. It is commonly determined in small wood samples through gravimetric analysis (Smith 1954) and by x-ray densitometry (Parker *et al.* 1980, Jozsa and Myronuk 1986, Jozsa *et al.* 1987).

The basic relative density (oven-dry weight / green volume) of an annual growth ring is influenced by several wood characteristics such as cell wall thickness, cell diameter and most importantly, by the relative amounts of earlywood and latewood present. The greater the proportion of latewood, the higher the whole-ring relative density recorded. Relative density within a Douglas-fir annual growth ring was described by Jozsa and Middleton (1994) as ranging from a minimum of about 0.25 in the earlywood to a maximum of about 0.84 in the latewood. Relative density for western hemlock was described by Wilson (1964) as ranging from about 0.20 to 0.60 from earlywood to latewood, and for western redcedar from about 0.12 to 0.60, respectively. Jessome (1977) reported average whole-ring relative density values of 0.45, 0.42 and 0.33 for old-growth Douglas-fir, western hemlock and western redcedar, respectively.

Relative density variation within a tree is most often described in a horizontal sequence from pith to bark. Generally speaking, the variability displayed is strongly correlated with ring number from pith, but weakly correlated with growth rate (Megraw 1986, Jozsa *et al.* 1989, Jozsa and Middleton 1994). Average whole-ring relative density profiles established by Jozsa and Middleton (1994) for second-growth Douglas-fir (60 trees sampled), western hemlock (26 trees), western redcedar (10 trees), and for six other tree species from British Columbia, are illustrated in Figure 2.1.

Whole-ring relative density for Douglas-fir (Figure 2.1) averaged about 0.47 next to the pith, and decreased to a value of about 0.40 by ring 10. A steady increase followed until a more-or-less

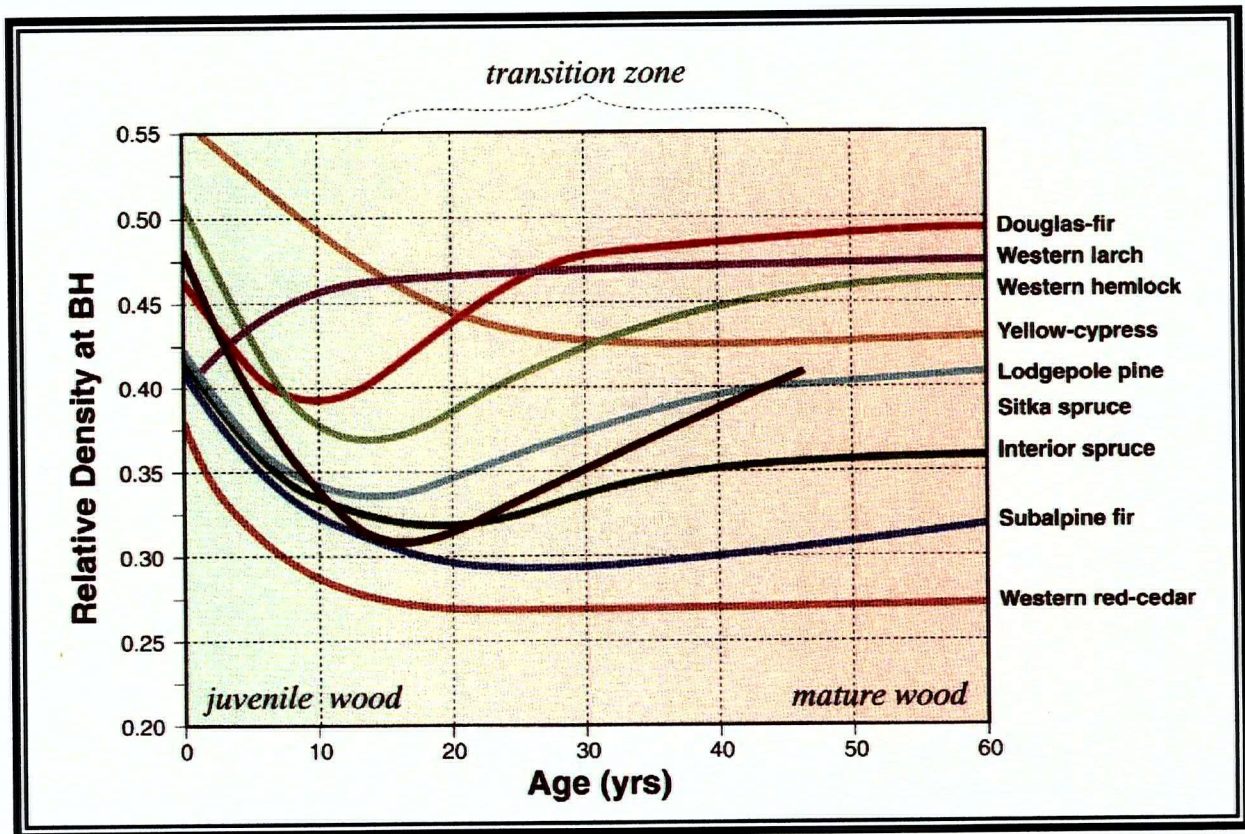


Figure 2.1 Average whole-ring relative density trends as displayed at breast height, and from pith to bark, for various second-growth native tree species from British Columbia (Jozsa and Middleton 1994).

steady value was attained by about ring 30. A similar pattern of relative density variation was observed for the species by Chalk (1953), Jozsa and Kellogg (1986), Megraw (1986) and Jozsa *et al.* (1989). Whole-ring relative density for western hemlock was at a maximum (about 0.51) next to the pith. A sharp decline to a minimum (about 0.38) at ring 14 was followed by a moderate increase to a more-or-less steady value by ring 40. Wellwood and Smith (1962), Krahmer (1966), Megraw (1985) and Jozsa *et al.* (1998) all reported similar whole-ring relative density profiles for the species. Western redcedar also displayed a maximum whole-ring relative density value (about 0.37) next to the pith. This value decreased to about 0.27 by ring 16, with very little subsequent variation displayed over time. Wellwood and Jurazs (1968) and Jozsa and Kellogg (1986) both reported a similar pattern of relative density variation for the species.

Some researchers have noted a decrease in whole-ring relative density following an increase in initial spacing. Such decreases were reported by Klem (1942) for Norway spruce (*Picea abies* (L.) Karst), by Cown (1981) for Caribbean pine (*Pinus caribaea* var. *hondurensis* Morelet) and by Yang (1994) for black spruce (*Picea mariana* (Mill.) B.S.P.). Klem (1952) reported no effect for Norway spruce at spacings narrower than 2 m, but observed a decrease in relative density at spacings greater than 3 m. Other researchers, such as Geyer and Gilmore (1965) for loblolly pine (*Pinus taeda* L.) and Baker (1967) for red pine (*Pinus resinosa* Ait.), have observed an increase in relative density. Others, such as Grigal and Sucoff (1966) for jack pine (*Pinus banksiana* Lamb.), Smith (1977) for slash pine (*Pinus elliottii* Engelm.) and Barse and Laidly (1980) for red pine, have observed no effect.

Smith (1980) studied the effects of initial spacing on radial growth and percentage latewood for 21-year-old Douglas-fir and 20-year-old western hemlock and western redcedar. The plots sampled were established at initial spacings of 0.91, 1.83, 2.74, 3.66 and 4.57 m (Haney spacing trials). Increased ring width, and a corresponding decrease in latewood proportion, were observed for all species as spacing increased. From the same plots studied by Smith (1980), Jozsa *et al.* (1998) analysed the effects of initial spacing (0.91, 2.74 and 3.66 m) on stemwood relative density for western hemlock. Both earlywood and latewood relative density, it was found, remained practically identical at breast height for all three spacings. A slight drop in latewood proportion, from a high of 33.3 % at 0.91 m, to a low of 26.0 % at 3.66 m, was also observed. Ultimately, it was concluded that wider spacings were capable of producing stemwood densities comparable to old-growth standards.

Many attempts have been made to establish a relationship between ring width and relative density. Megraw (1986), Jozsa *et al.* (1989) and Abdel-Gadir *et al.* (1993) each reported a very weak to non-existent relationship for Douglas-fir. A weak, negative relationship for western hemlock (rings 20-24 analysed combined) was identified by DeBell *et al.* (1994) as a function of earlywood relative density ($r^2 = 0.16$) and whole-ring relative density ($r^2 = 0.39$). A non-significant relationship was identified for latewood relative density. Jozsa *et al.* (1998) also reported a weak, but consistently negative whole-ring relative density relationship for western hemlock, with relationships generally stronger for growth rings sampled within the juvenile wood zone, and weaker for those sampled within the mature wood. Little information concerning the relationship between ring width and relative density development is currently available for western redcedar.

A negative relationship between ring width and whole-ring relative density has occasionally been identified for Norway spruce (Klem 1942, Persson 1975, Olesen 1976, Johansson 1993, Lindstrom 1995). Stem taper has, as a result, sometimes been considered a predictor of relative density for the species, especially for stems grown within young, even-aged, single-species stands. Generally speaking, the greater the stem taper observed, the lower the mean relative density value recorded (Klem 1942, Johansson 1993, Lindstrom 1995). Little information is currently available for Douglas-fir, western hemlock and western redcedar with regard to this relationship.

2.5.2 Longitudinal Tracheid Length

The length of an average tracheid is often said to be roughly 100 times greater than its tangential width. The actual value ultimately depends upon the length of the fusiform initial from which it is derived. The greater the length of the fusiform initial, the longer the tracheid produced. The length of a fusiform initial, measured next to the pith, is itself strongly inherited. Genetics, cambial age, growth rate, and all the possible interactions involved, all contribute to the subsequent increases in length that are commonly displayed over time by most species (Larson 1994).

Accelerated diameter growth by a young tree typically requires a corresponding increase in the rate of anticlinal cell division to provide the necessary circumferential expansion of the vascular cambium. The frequency of anticlinal cell division at this point is such that an overabundance of fusiform initials are initially produced. The subsequent survival of each fusiform initial, it is thought, is largely dependent on contact with rays through which synthesised food material is translocated. The longer the fusiform initial, the greater the chance of contact. With aging comes the decline of the shorter, less efficient fusiform initials. These cells, even when bordered by rays, frequently lose their capacity for further division and either develop into ray initials, mature directly into xylem or phloem elements, or simply die out (Bannan 1967a, Philipson and Butterfield 1967). An overall increase in mean fusiform initial cell length is therefore said to occur from the above.

With tree maturity comes a diminishing rate of diameter growth, and a general decline in anticlinal cell division. Greater time is subsequently available between successive divisions for cell

tip elongation by the fusiform initials. Longer daughter initials are accordingly produced, and a greater survival ratio is also observed. Only small increases in mean fusiform initial cell length take place from then on. A genetically controlled maximum value is eventually reached at which time fusiform initial cell length fluctuations become largely attributable to seasonal changes in rate of cell division (Bannan 1967a, Philipson and Butterfield 1967).

Anticlinal cell division during the initial years of tree development is normally held constant throughout the growing season. The growth rings produced are generally wide and contain a high proportion of earlywood. A slight, but constant, increase in average fusiform initial length may be observed. As trees grow older, anticlinal cell division tends to concentrate in the final portion of the growing season. This results in a pattern of increasing fusiform initial cell length within the earlywood and early latewood zones, followed by a gradual or abrupt decline at the approach of cambial dormancy. Such late-season anticlinal divisions, in turn, generate the fusiform initials that will initiate periclinal division the following season. Despite the tendency for fusiform initial lengths to decrease at season's end, there is nonetheless a residual increase in cell length that is carried over from year to year (Bannan 1967a, 1967b).

The seasonal fluctuations in fusiform initial cell length noted above may lead to increases in mean tracheid length of 10 to 15 % from earlywood to latewood (Panshin and de Zeeuw 1980). Furthermore, earlywood and latewood tracheids, once fully developed, are both significantly longer than the fusiform initials from which they originated. Increases of 10 to 15 % may be observed. Such post-cambial cell elongation is typical of conifer tracheids and is largely a result of intrusive growth on the part of the cell tips (Wenham and Cusick 1975).

Tracheid length, when viewed from pith to bark, demonstrates a similar pattern of development for most conifer species. A rapid increase in tracheid length is normally displayed from the pith over the first 10 to 20 years of development, followed by more-or-less constant values over time. Hamm (1989) measured tracheid length for second-growth coastal Douglas-fir. Average values of 1.7, 2.7, 3.1 and 3.3 mm were obtained for rings 0-5, 11-15, 21-30 and 41-50, respectively. Wellwood and Smith (1962) measured tracheid length for western hemlock. Mean values of 1.8, 2.7, 3.2 and 3.6 mm were obtained for rings 1-10, 21-30, 31-40 and 71-80, respectively. Wellwood and

Jurazs (1968) measured tracheid length for western redcedar, and obtained a mean value of 2.5 mm at ring 10, 3.0 mm at ring 23, 3.5 mm at ring 50 and 4.0 mm at ring 120.

The general finding for softwoods is that initial spacing has little impact on tracheid length development. Klem (1942) for Norway spruce, Youngberg *et al.* (1963) for slash pine, Posey (1965) for loblolly pine and Persson (1975) for Norway spruce all concluded that no relationship existed. Little information has been compiled regarding the above for Douglas-fir, western hemlock and western redcedar.

The observation that an increasing rate of diameter growth brings about a corresponding increase in frequency of anticlinal cell division suggests that tracheid length variability is, to a certain extent, a function of growth rate. Faster diameter growth, it is assumed, will lead to the production of shorter tracheids. Conflicting results have nonetheless been reported in past studies for various conifer species. The effects of growth rate have frequently been confounded with those of cambial age. The correlation of tracheid length with rate of diameter growth has sometimes resulted in a positive, in a negative or in no relationship at all.

Smith *et al.* (1961) concluded that growth rate held no important effect on tracheid length development for either Douglas-fir or western hemlock. Age was identified as having the greatest impact on variability for both species. A total of 77 % of tracheid length variation for Douglas-fir was found attributable to ring number from pith. A value of 60 % was obtained for western hemlock. Wellwood and Smith (1962) associated 65 % of tracheid length variation for Douglas-fir to cambial age. Wellwood and Jurazs (1968) associated a value of 58 % for western redcedar.

2.5.3 Microfibril Angle

The cell wall of a tracheid is, to a large extent, a composite structure of thread-like filaments called microfibrils. Each microfibril constitutes a crystalline cellulose core encased in a shell of amorphous hemicellulose. On the basis of microfibril orientation, the resultant cell wall construction can be subdivided into four principal layers (Figure 2.2).

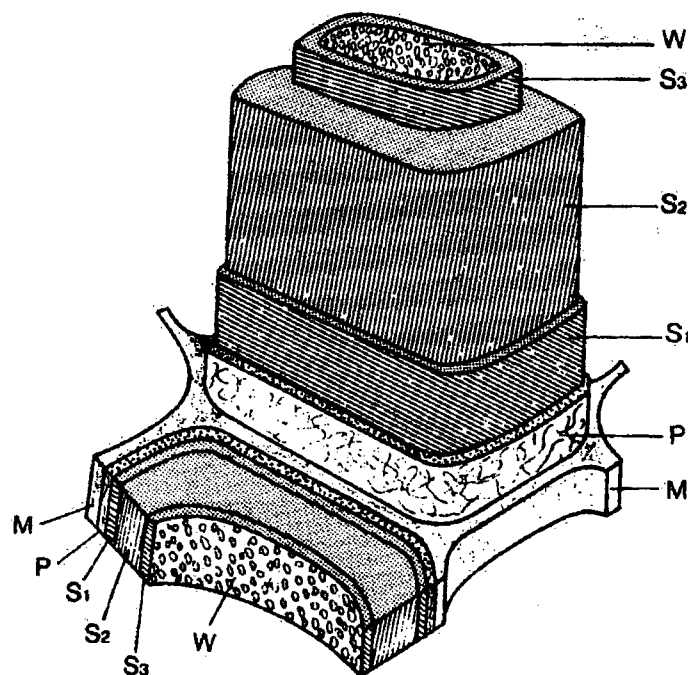


Figure 2.2 Schematic representation and microfibril angle orientation of tracheid cell-wall layers (adapted from Côté 1967).

The primary wall (P) is formed at the time of cambial division. It remains very thin, approximating $0.1\ \mu\text{m}$ throughout. Microfibrils found within this wall are loosely interwoven, and more-or-less randomly orientated. Such a loose network facilitates expansion and elongation during the subsequent period of cell enlargement. The secondary wall is characterised by a higher degree of parallelism of its microfibrils, and by the deposition of cell wall material in the form of successive sheets (lamellae). The secondary wall collectively includes three layers that generally integrate into one another. The S_1 layer lies immediately within the confines of the inner primary wall and never exceeds a thickness of about 0.1 to $0.2\ \mu\text{m}$ (4 to 6 lamellae). Microfibrils within this layer generally alternate in orientation between opposing surfaces. A left-handed upward spiral (S helix) relative to the longitudinal axis of the cell may be viewed from the outside of the layer. A right-handed (Z helix) arrangement may be observed from the inside. The helical angles observed may range from as high as 50 to 90° . The central S_2 layer is highly variable in thickness (1 to $5\ \mu\text{m}$, 30 to 150 lamellae) and may constitute upward of 80% or more of total cell wall volume. The term microfibril angle itself,

as commonly employed with regard to wood quality, refers to the mean helical angle observed within this particular layer. Microfibrils are typically closely packed and steeply aligned to the cell axis in a single Z helix. The S₃ layer lies adjacent to the cell lumen and constitutes a very thin layer ranging from 0.1 to 0.2 µm in thickness (4 to 6 lamellae). An alternating Z helix on the outside surface of the layer and an S arrangement on the inner surface may be viewed. Likewise to the S₁ layer, the helical angles observed may range from 50 to 90° (Fujita and Harada 1991, Booker and Sell 1998).

Also included in Figure 2.2 is the middle lamella (M). This component is primarily composed of pectin and is the rubbery substance responsible for cementing the outer primary walls of the individual cells together. Its development parallels the formation of the secondary wall and is associated with the stage of lignification. The warty layer (W) is deposited on the inner surface of the S₃ layer by the dying protoplasm during the final portion of the lignification stage. Its purpose remains unknown (Panshin and de Zeeuw 1980, Tsoumis 1991).

The mechanism governing microfibril angle development is still under debate. Current thinking suggests that microtubules play an important role in directing cellulose deposition. Strong correlations have been identified between the orientation of microtubule arrays and the orientation of newly deposited microfibrils within the secondary wall (Seagull 1989,1992, Fujita and Harada 1991, Salisbury and Ross 1992 Hisashi *et al.* 1994). Microtubules are generally present within the cytoplasm of a cell following division. These structures consist of long, hollow cylinders measuring about 25 nm on the outside and 12 nm on the inside. At the onset of cell enlargement, most microtubules are organised in a compressed helical band about the cell equator and are mostly positioned at right angles to the longitudinal axis. The control of this arrangement remains unknown. As cell enlargement proceeds, the helix arrangement expands and microtubules begin to move away from one another. The orientation of the microtubules within the helix accordingly changes, forming angles of up to 45° with the long axis of the cell. Cellulose formation is believed to be controlled by enzymes located on the plasmalemma, namely rosettes on the inner surface and globules on the outer surface. It is currently hypothesised that the movement of these rosette-globule complexes during cellulose synthesis is guided by the microtubules. It is through this association that microtubule orientation is believed to provide a pathway for cellulose deposition, with the direction of the deposition being essentially parallel to that of the microtubules (Salisbury and Ross 1992).

The overall design of the cell wall is believed to provide extra resistance within a tree stem against wind inflicted damage. A microfibril angle greater than zero effectively serves as a vibration damping mechanism at the cellular level to prevent intra-wall fracturing during swaying. Assuming adjacent tracheids within a tree stem possess similar microfibril angles, the double cell wall portions observed will display reverse microfibril orientations. Upon bending in the wind, one side of the stem will be compressed whereas the opposite side will be placed under tension. Since the organisation of microfibrils within the S_2 layer is at a slight angle relative to the longitudinal axis, individual cells when placed under compression will rotate slightly. Movement within the double cell wall portions will therefore be in opposing directions. The middle lamella will accordingly be placed in shear, but will not rupture due to its highly elastic nature. With the tree swaying back to its original position and beyond, the same tracheids will be placed under tension and will correspondingly rotate, but in the reverse direction. The middle lamella will once again be placed in shear and will accordingly dissipate the vibrational energy conveyed (Booker and Sell 1998).

The microfibril angle observed for most conifers is typically greatest near the pith, decreases rapidly as tracheids in increasingly distant growth rings are examined, and eventually stabilises (Megraw 1985, Cave and Walker 1994). Dadswell (1958) stated that microfibril orientation could decrease from a value of 55 to 20° from pith to maturity. Erickson and Arima (1974) reported a decrease in average microfibril angle for Douglas-fir, from a value of about 32° next to the pith, to about 7° by ring 30. Wellwood (1962) reported a somewhat smaller decrease between rings 1 and 27 for western hemlock, from about 22° to 11° for the earlywood zone, and from about 19° to 8° for the latewood zone. Little information regarding microfibril angle development has been compiled for western redcedar.

Erickson and Arima (1974) noted a weak relationship between growth rate and microfibril angle for Douglas-fir, with the variability observed largely a function of cambial age. Markstrom *et al.* (1983) noted that an increase in radial growth for Ponderosa pine (*Pinus ponderosa* Laws.) was not accompanied by a corresponding significant increase in microfibril angle. Herman *et al.* (1999) observed a positive relationship between growth rate and microfibril angle for Norway spruce. Slow-grown stems displayed the classic pattern of decreasing microfibril angle from pith to bark, whereas the faster-grown stems, following a thinning intervention, demonstrated a significant increase in value.

A mean microfibril angle of 29° was reported for the faster-grown trees, compared to 21° for the slower-grown stems. Very little information is available for western hemlock and western redcedar regarding the effects of ring width on microfibril angle development. Furthermore, very few studies have analysed the effects of initial spacing on microfibril angle development for the three species considered in this study.

Many studies have pointed to the existence of a strong, negative correlation between microfibril angle and tracheid length (Dadswell 1958, Erickson and Arima 1974, Briggs and Smith 1986). It was furthermore suggested by Meylan and Probine (1969) that microfibril angle development could vary as a function of cell diameter and cell wall thickness. Megraw (1985) suggested overall lumen geometry, stating that the long and narrow cell cavities typical of latewood tracheids favoured the deposition of a low microfibril angle, whereas the shorter and wider cavities typical of earlywood tracheids favoured a larger microfibril angle.

2.5.4 Juvenile and Mature Wood

Juvenile wood can be defined as that portion of the xylem first laid down near the centre of a tree. Regardless of tree age, it is always produced within the live crown. Its relative proportion below the base of the live crown is largely a function of species, cambial age, and distance of sampling point along the stem relative to the base of the live crown. Juvenile wood is characterised by greater variability in terms of wood properties. Mature wood typically demonstrates greater uniformity. Generally speaking, a lower average relative density, shorter tracheids, thinner cell walls, a lower proportion of latewood, a larger average microfibril angle, a lower cellulose content and a higher lignin content will be displayed within the juvenile wood core (Panshin and de Zeeuw 1980, Zobel and Van Buijtenen 1989, Zobel and Sprague 1998).

A range of 20 to 30 growth rings at breast height has been suggested as the extent of juvenile development within many conifers (Jozsa and Middleton 1994, Kennedy 1995). The actual number of growth rings identified ultimately depends upon the wood property used for defining a transition zone. Different wood properties will attain a more-or-less stabilised value (indicative of mature wood

development) at different ages. Also, there is no sharp demarcation between juvenile wood and mature wood, as one wood type systematically blends into the other as a tree ages. Transition age results have accordingly varied between studies, species, and even provenances (Zobel and Sprague 1998).

A boundary between juvenile and mature wood has most frequently been defined using whole-ring relative density trends from pith to bark, with a transition point between the two wood types selected where values began to stabilise (Bendtsen and Senft 1986, Di Lucca 1989, Abdel-Gadir and Krahmer 1993, Kucera 1994, Tasissa and Burkhart 1997). The age at which ring width (Bendtsen and Senft 1986, Kucera 1994, Yang *et al.* 1986, 1994), tracheid length (Bendtsen and Senft 1986, Kucera 1994, Yang 1994), tracheid diameter (Kucera 1994), microfibril angle (Bendtsen and Senft 1986), latewood relative density (Sauter *et al.* 1999), latewood proportion (Kucera 1994) and longitudinal shrinkage (Pearson and Gilmore 1971, Ying *et al.* 1994) stabilise have also been considered.

Kucera (1994) identified a close relationship between the culmination of annual height increment in Norway spruce, and the age at which whole-ring relative density attained a minimum value at stump level. An association was suggested between shade tolerance and relative density development, with a minimum whole-ring relative density value produced at an earlier age by the more shade intolerant species. Kucera also suggested that whole-ring relative density for shade intolerant species would stabilise sooner, resulting in a shortened period of juvenile wood formation. An abrupt transition, owing to the rapid decrease in incremental height growth, would subsequently be observed from juvenile wood to mature wood.

Jozsa *et al.* (1989) observed the following trends based on intra-ring relative density profiles established at breast height for 50-year-old Douglas-fir from Vancouver Island. Relative density within the juvenile wood core (first 20 years of growth) ranged from about 0.29 in the earlywood to 0.88 in the latewood. Annual growth rings averaged 5.8 mm in width, contained 30 % latewood, and averaged 0.46 in terms of whole-ring relative density. In contrast, the relative density of the mature wood zone ranged from about 0.28 in the earlywood to 0.95 in the latewood. Ring width averaged 3.2 mm, latewood proportion averaged 43 % and whole-ring relative density averaged 0.53.

Jozsa *et al.* (1998) observed the following trends based on intra-ring relative density profiles established at breast height for 90-year-old western hemlock from coastal British Columbia. Latewood proportion increased from 15 %, to 28 %, to 48 % over growth rings 6-15, 16-35 and 71-90, respectively. Ring width, over the same intervals, averaged 3.9, 2.6 and 1.1 mm, respectively. Whole-ring relative density averaged 0.39 at ring 10, 0.42 at ring 25 and 0.49 at ring 75.

Smith (1980) measured latewood proportion from 20-year-old western redcedar trees sampled at the Haney spacing trials. Mean breast height values were obtained based on a sample of 29 stems from five spacings ranging from 0.91 to 4.57 m. Average values equalling 18, 13, 9 and 13 % were obtained for growth rings 9, 12, 15 and 20, respectively. Very little information relating to mature wood development within second-growth timber is available for the species.

Average stemwood relative density, when described as a function of height for both Douglas-fir and western hemlock, is typically greatest at stump level (Okkonen *et al.* 1972, Jozsa and Kellogg 1986, Jozsa *et al.* 1998). Since concentrations of mature wood are generally at a maximum within this region, average stemwood relative density will be higher. A rapid decrease in relative density for both species follows as the base of the live crown is approached, and the proportion of juvenile wood within the stem increases. A final increase in stemwood relative density can be observed as the stem apex is neared. Only the innermost growth rings, representing extremely high relative density values for both species, make up the stem at this height.

Western redcedar demonstrates an opposite pattern of stemwood relative density variation, with the lowest values recorded at stump level, and the highest values observed within the live crown (Wellwood and Jurazs 1968, Okkonen *et al.* 1972, Jozsa and Kellogg 1986). A complete explanation for the above pattern of variation has never been provided. Wellwood and Jurazs (1968) nonetheless attributed it to the development of compression wood next to the pith, and to the fact that mature wood for the species remained comparatively low in relative density throughout its development. With a decreasing number of growth rings with increasing height, the inner juvenile core would gradually form a greater proportion of overall stem volume. With increasing height, the inner juvenile core would subsequently maintain a greater influence on stemwood relative density, hence the greater values observed.

3. MATERIALS AND METHODS

3.1 Data Collection

The material for this study was collected from a spacing trial established at the UBC Malcolm Knapp Research Forest (project 57-5, site-index 39.8 (50 years, breast height age) for Douglas-fir, 32.6 for western hemlock and 32.9 for western redcedar), located 60 km east of Vancouver near Haney, BC. Douglas-fir was initially planted during the fall of 1957 as 2+0 seedlings at square spacings of 0.91, 1.83, 2.74, 3.66 and 4.57 m (3, 6, 9, 12 and 15 ft). These represented initial stocking densities of 12076, 2986, 1332, 747 and 479 stems/ha. Western hemlock 2+0 seedlings and western redcedar 1+1 seedlings were planted on the same site, and in similar fashion, during the fall of 1958 and spring of 1959, respectively. All Douglas-fir and western hemlock seedlings were obtained from Green Timbers Nursery and were of unknown, but presumably, local provenance. The western redcedar seedlings were collected as wildlings from the UBC Research Forest. The spacing trials were laid out in 49-tree plots, and replicated twice. An additional 0.2 ha plot trial was laid out for Douglas-fir at each of the above spacings, and for western hemlock at 0.91 m only. Seedlings that died during the first season were replaced the following year with 3+0 stock. All plots were cleaned and weeded several times to eliminate brush competition (Walters and Smith 1973).

All trees located within the outer two rows of each 49-tree plot were disregarded during sampling to eliminate an edge effect. All trees located within the inner rows were initially inventoried to identify the stems suitable for wood quality sampling. Trees with forked stems were omitted along with those demonstrating excessive lean and crown dieback. All suitable stems within each spacing were then sorted from smallest diameter at breast height (dbh) to largest, with the range subsequently divided into three groups representing small, medium and large diameter trees. Six trees were randomly selected per spacing, two per group. Excessive mortality, coupled with poor quality in the residual stems, was generally observed within the 4.57 m spacing for western hemlock, prompting

the elimination of this spacing from the sampling frame. A total of 84 trees were thus selected, accounting for the five spacings available for Douglas-fir and western redcedar, and the four available for western hemlock.

Non-destructive sampling was carried out using a 5 mm and a 12 mm increment borer. Two core samples were bored immediately one (5 mm) above the other (12 mm) at breast height (1.3 m). Additional core samples (5 mm) were obtained at 2 m intervals from stump level (0.3 m) up to the base of the live crown. Whorls, as well as areas likely to contain compression wood, were avoided. Climbing gear and a handsaw to prune dead branches were used during this operation (Figure 3.1). Sampling for wood properties along a tree stem has traditionally been conducted through destructive means using stem analysis. Non-destructive sampling for wood quality as performed in this study, via a combination of tree climbing and increment boring, is uncommon in the literature.



Figure 3.1 Increment core collection at 2 m intervals from stump level up to the base of the live crown.

Sampling along the branch-free bole was conducted only when bark surfaces were dry and the risk of slipping was minimal. It was found during this procedure that trees growing at 0.91 m and 1.83 m for all species, and at 2.74 m for Douglas-fir, had crown positions too high (upward of 20 m), and too narrow in diameter (from 10 to 15 cm at the base of the live crown), to be safely climbed. Consequently, only the 3.66 and 4.57 m spacings for Douglas-fir, only the 2.74 and 3.66 m spacings for western hemlock and only the 2.74, 3.66 and 4.57 m spacings for western redcedar were sampled using this method.

































The base of the live crown for Douglas-fir and western hemlock was defined as the lowest whorl containing three or more live branches. For western redcedar, which does not possess clearly defined whorls, the third lowest living, healthy branch was used as the point of delineation. Increment core samples were collected at heights reaching 20 m in the case of Douglas-fir, 12 m in the case of western hemlock and 13 m in the case of western redcedar. All core samples were obtained from the southern aspect of each stem. The randomisation of this procedure would have proved difficult since mobility about the trees was very difficult during climbing. It was therefore decided, for the sake of consistency, that a common aspect would be used for all trees. Identification numbers were inscribed on each core using an indelible copy pencil, and all were stored and transported in plastic straws to avoid breakage. A total of 69 and 66 core samples were collected from the 3.66 and 4.57 m Douglas-fir spacings, respectively. Thirty-seven cores were collected from the 2.74 m spacing for western hemlock, and 43 additional cores were collected for the species at 3.66 m. A total of 51 cores were collected from the 2.74 m spacing for western redcedar, and 43 additional samples were collected for the species at each of the 3.66 and 4.57 m spacings.

Recently wind-thrown trees (foliage still green) from the 0.91 m Douglas-fir and western hemlock spacing trials (0.2 ha plots) were available in sufficient numbers to allow for destructive sampling through stem analysis. Six trees were randomly selected, by species, from those suitable for wood quality sampling. A chainsaw was used to cut 2.5 cm thick discs at breast height and at the required 2 m intervals from stump level up to the base of the live crown. Aspect was determined based on root collars which remained partially buried, and from which the direction of tree fall could be retraced. The southern aspect of each disc was marked with an indelible copy pencil immediately after sawing. A total of 69 disc samples were collected for Douglas-fir, and 50 for western hemlock.

The southern aspect of each disc was later cut to size using a bandsaw. Wood samples collected from each disc effectively replaced all 5 mm and 12 mm cores that would otherwise have been collected using the non-destructive sampling design.

The non-destructive sampling design employed in this study is summarised in Table 3.1. All wood sample collecting was conducted during the summer and fall of 1998. Fifty-four trees out of a possible 84 were intensively sampled along the branch-free sections of their respective boles. The remaining 30 trees, originating from the 1.83 and 2.74 m spacings for Douglas-fir, the 1.83 m spacing for western hemlock and the 0.91 and 1.83 m spacings for western redcedar were sampled exclusively at breast height, and using a 5 mm increment borer only. The above mentioned 30 trees were for the most part relatively small in diameter. Increment core collection using a 12 mm borer would have proved too damaging to the stems. This activity was subsequently restricted to the larger diameter stems found within the wider spacing intervals.

Table 3.1 Number of trees sampled, and sampling procedure, by species and spacing.

spacing (m)	Douglas-fir			western hemlock			western redcedar					
0.91	6				6				6			
1.83	6				6				6			
2.74	6				6				6			
3.66	6				6				6			
4.57	6								6			
total	30				24				30			

 : single 5 mm core collected per tree at breast height

 : 5 mm core, or disc sample, collected at 2 m intervals from stump level up to the base of the live crown

 : single 12 mm core collected per tree at breast height

Outside bark dbh was measured for each of the above trees using a diameter tape. Total tree height, height to base of live crown and crown width measurements were obtained using a metric tape and Suunto clinometer possessing a 90° scale. An average crown width was estimated for each sampled tree from eight live-branch length measurements taken every 45° around the perimeter of the crown, and in line with neighbouring trees. The value obtained for height to base of the live crown was subtracted from the total tree height to determine live-crown-length and subsequently, live-crown-ratio. The height over diameter ratio (hdr) was determined by dividing tree height (cm) by stem diameter at breast height (cm).

The following stem taper classification scheme was used to divide the population of sampled trees, by species (all spacings combined), into three groups. The slower-growing trees, classified within the suppressed taper class, were those with a $\text{hdr} \geq 100$. Such trees are typically spindly, are especially vulnerable to snow damage and windthrow, and ordinarily would not survive until a final harvest (Weetman and Farnden 1995, Smith *et al.* 1997). Intermediate taper class trees were categorised as those with a hdr ranging from 80 to 100. Such trees, along with those classified as suppressed, would be likely candidates for removal during a low-thinning exercise. The faster-growing trees, classified within the dominant taper class, were those with a $\text{hdr} \leq 80$. A value of 80 represents the maximum hdr that is normally targeted during crop planning (Weetman and Farnden 1995). Such trees are also representative of the wood quality that is potentially available at time of final harvest if a series of low-thinning exercises are applied during stand development. The fact that all trees were relatively young (41 years for Douglas-fir, 40 years for both western hemlock and western redcedar), even-aged, growing on the same site, and presumably of comparable genetic stock, permitted the above classification scheme.

3.2 X-ray Densitometry

All 5 mm cores, and all disc-derived wood samples, were taken to Forintek Canada Corporation's laboratory in Vancouver where direct reading x-ray densitometric techniques were applied to obtain annual growth and relative density data. Each wood sample was initially air-dried to approximately 8 % equilibrium moisture content, and then extracted in a Soxhlet apparatus in

ethanol-cyclohexane (1:2 by volume) for 24 hours. Samples were once again air-dried, followed by further extraction in distilled water for another 24 hours. A final period of air-drying was initiated after which individual samples were mounted on a twin-blade micro-saw and cut transversely from pith to bark in strips measuring 1.57 mm thick. All samples were marked and identified in five-year increments. A total of 216, 136 and 149 wood samples were prepared for Douglas-fir, western hemlock and western redcedar, respectively.

Scanning was conducted from pith to bark, and was initiated either at the beginning of the second growth ring from the pith, or in accordance with the first ring to lie at an angle less than 45° to the scan path. The scanning procedure itself involved passing an X-ray beam collimated to 0.25 x 1.00 mm, and operating at 15 to 20 KV, and at about 2 mA, through the wood strips and onto an X-ray detector. X-ray attenuation was directly proportional to the relative density of the wood being processed. A density calibration wedge was used to initially calibrate the system, and to recalibrate it following every five samples processed. Incremental and relative density values for each growth ring were measured in 0.01 mm increments and with 0.0254 mm resolution, respectively (Parker *et al.* 1980, Jozsa and Myronuk 1986, Jozsa *et al.* 1987).

Forintek Canada's Tree Ring Input Program (TRIP) was used for data acquisition. All relative density values obtained were expressed on a green volume and oven-dry weight basis. A 100-point relative density profile was obtained for each annual growth ring, regardless of its width. The wood properties analysed within each growth increment included ring width, earlywood width, latewood width, earlywood relative density, latewood relative density and whole-ring relative density. The earlywood to latewood boundary was set at a relative density of 0.54 for Douglas-fir, 0.52 for western hemlock and 0.44 for western redcedar. Boundaries separating the latewood zone of one ring and the earlywood zone of the following ring were established at 0.45, 0.42 and 0.34 for Douglas-fir, western hemlock and western redcedar, respectively. The above noted delineation values have all been commonly used in previous studies by researchers at Forintek Canada, and are based on hundreds of sample runs conducted for each species. Individual growth rings were assessed for latewood proportion (%) by dividing latewood width by whole-ring width.

3.3 Microfibril Angle

Microfibril angle sampling was conducted on all 12 mm core samples, with measurements obtained for every third growth increment from the pith. Cores were initially prepared for testing by five repeated cycles of soaking in water to saturation, followed by oven-drying at 100°C to induce checking in the cell walls. A total of 572 radial microtome sections 15 microns thick were cut and stored in 50 % ethyl alcohol. Prior to viewing, each microtome section was mounted on a microscope slide, to which a drop of water and cover slip were added. Angles were measured using a Carl Zeiss / Jena Jenamed transmitted-light microscope with video projection. A cursor was employed to trace the projected microfibrils, and measurements were recorded using the Jandel Video Analysis (JAVA) system. Angle measurements were conducted in line with checks, and with the longitudinal axis of the tracheid radial surface (Figure 3.2). Forty readings were captured at various random locations within the earlywood portions of each of the 196 Douglas-fir, 187 western hemlock and 189 western redcedar growth rings sampled. A total of 7840, 7480 and 7560 microfibril angle measurements were obtained for Douglas-fir, western hemlock and western redcedar, respectively.

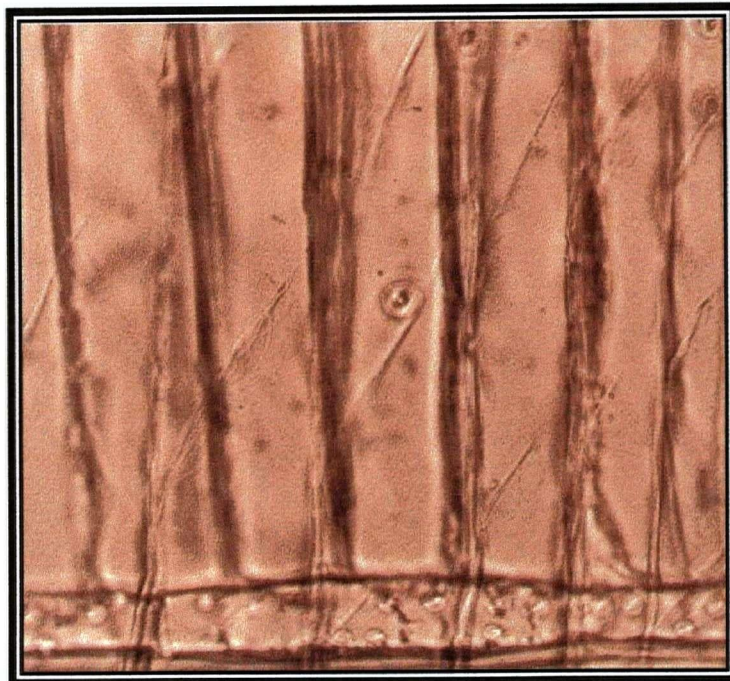


Figure 3.2 Radial section of western redcedar showing earlywood microfibril angle orientation (25x).

3.4 Longitudinal Tracheid Length

As was the case for microfibril angle sampling, longitudinal tracheid length sampling was also conducted on all 12 mm core samples, and measurements were also obtained for every third growth increment from the pith. Growth ring sections not utilised for the production of microfibril angle microtome slides were used during this exercise. Each section was first split longitudinally into earlywood and latewood portions, and approximately six match-sized splints were subsequently produced from each portion. Care was taken to produce the longest splints possible. Those originating from the edge of the wood cores, and therefore containing a higher proportion of broken tracheids, were discarded. In the narrowest growth rings where accurate splintering by razor blade was impossible, earlywood and latewood portions were left grouped together. Splints were placed into individual test tubes and macerated by mixing equal parts of glacial acetic acid and 30 % hydrogen peroxide (Franklin's solution), followed by boiling in a steam bath for three hours. Once uniformly translucent, the splints were thoroughly washed with water. Tracheid length measurements were obtained using two separate procedures.

The first approach consisted of preparing individual fibre slurries, by diluting a single macerated splint from each growth ring sampling point with approximately 20 ml of water inside a vial, and then briefly shaking. The slurries were then strained through a 200 mesh SS screen in a No. 3 Buchner funnel. The resultant strained slurries were transferred to slides and allowed to dry. Individual tracheids were viewed using the same video analysis system employed for obtaining microfibril angle measurements. The system was initially calibrated for tracheid length measurement using a stage micrometer.

A total of 502 slides (180 Douglas-fir, 150 western hemlock and 172 western redcedar) were prepared and sampled in this manner for the earlywood, with the same number repeated for the latewood. An additional 92 slides (18 Douglas-fir, 48 western hemlock and 26 western redcedar) accounted for the narrowest growth rings where earlywood and latewood were sampled combined. Forty unbroken tracheids were measured at random locations on each slide. A total of 15120, 13920 and 14800 tracheid length measurements were accordingly obtained for Douglas-fir, western hemlock and western redcedar, respectively. A mean tracheid length value, based on the 40 measurements

obtained at each growth ring sampling point, was calculated for both earlywood and latewood. The following formula was used to estimate mean whole-ring tracheid length:

$$(1) \quad WRT = \frac{(\%E \times ED \times ET) + (\%L \times LD \times LT)}{(\%E \times ED) + (\%L \times LD)}$$

where

<i>WRT</i>	mean whole-ring tracheid length
<i>%E</i>	earlywood proportion
<i>ED</i>	mean earlywood relative density
<i>ET</i>	mean earlywood tracheid length
<i>%L</i>	latewood proportion
<i>LD</i>	mean latewood relative density
<i>LT</i>	mean latewood tracheid length

A substantial decrease in tracheid radial diameter, and a corresponding increase in tangential cell wall thickness, are typical of intra-ring development from earlywood to latewood. Generally speaking, the larger the lumen diameter and the thinner the cell wall, the lower the relative density recorded (Panshin and de Zeeuw 1980). It was assumed at the onset of this study that a decrease in relative density would equate to a lower number of tracheids per unit of wood. It was furthermore assumed that a longer mean tracheid length would be associated with latewood development, and that latewood proportion would remain smaller than earlywood proportion for most growth rings sampled.

Since an equal number of tracheids were measured for both earlywood and latewood at each growth ring sampling point, an arithmetic mean (sum of the tracheid length measurements divided by the number of tracheids measured) would have resulted in an overestimation of the whole-ring tracheid length value. By considering earlywood relative density, latewood relative density,

earlywood proportion and latewood proportion, equation 1 took into account the variation in tracheid count, and in tracheid length within a growth increment, that can be expected as a function of both ring number from pith and growth rate. The use of Equation 1 was impossible in cases where earlywood and latewood length were sampled combined. An arithmetic mean whole-ring tracheid length value was obtained in such cases.

The second approach for measuring tracheid length involved use of the Kajaani FS-200 Optical Fibre Analyser. The total number of samples processed per species, and per wood type, was identical to that described for method 1 (502 earlywood, 502 latewood, 92 whole-ring). Individual fibre slurries of approximately 1000:1 by weight were initially prepared for all wood samples. Each water and tracheid solution was then fed by vacuum into a narrow capillary tube. The low tracheid concentration, along with the fine capillary tubing, ensured that a discrete procession of straightened fibres would be fed into the Kajaani. A laser beam within the device was used to project the image of passing tracheids onto an array of light diodes. The number of diodes covered corresponded to the length of the tracheids being measured (Kajaani Electronics Ltd. 1986). A minimum of 20 000 tracheids per fibre slurry were accordingly processed. A mean tracheid length value for each earlywood and latewood segment, and for the narrower growth rings sampled as a whole (earlywood and latewood combined), was estimated using the length-weighted formula provided by Kajaani Electronics Ltd. (1986). Mean whole-ring tracheid length was estimated using Equation 1.

4. STUDY OF WOOD FORMATION IN RELATION TO CAMBIAL AGE, INITIAL SPACING, STEM TAPER AND GROWTH RATE

4.1 Introduction

Wood quality is an arbitrary term used to evaluate the suitability of a certain wood characteristic for a particular end-use. The wood processing industry has long considered relative density and tracheid morphology as prime indicators of wood quality. Clear lumber strength and stiffness, as well as increased pulp yields, have generally been associated with higher relative density values. Longitudinal tracheid length has long been associated with the tearing, bursting, tensile and folding properties of a sheet of paper. A large microfibril angle has been identified with lower stiffness properties in lumber, as well as with increased longitudinal shrinkage and with subsequent higher levels of degrade during drying. Large microfibril angle values are now being recognised as having a negative impact on the tensile and tear strength of paper (Panshin and de Zeeuw 1980, Zobel and van Buijtenen 1989).

The increased variability in wood properties displayed by second-growth timber is often seen as a major drawback to its efficient use as a raw material. Numerous studies have associated this lack of uniformity to a shortened growing period prior to harvest, and to an increased rate of diameter growth. The purpose of this portion of the study was therefore to analyse the effects of cambial ageing, initial spacing, stem taper and growth rate on the development of specific wood properties important to wood quality in second-growth timber.

The first objective was to profile and compare ring width, earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, whole-ring tracheid length and microfibril angle development as a function of ring number from pith. Profiles for each species were established according to both initial spacing and taper class.

The following hypotheses were tested:

- H_{4.1}: there are no time effects (i.e., the developmental profile for a wood property, displayed as a function of ring number from pith, is horizontal)
- H_{4.2}: there are no overall differences between groups (i.e., the mean value recorded over time for a wood property is similar for all groups, the between-units factors have no effect)
- H_{4.3}: there are no interactions between groups involving time (i.e., the growth curves displayed for a wood property are parallel for all groups considered)

The second objective was to investigate the effects of accelerated diameter growth on earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, whole-ring tracheid length and microfibril angle development over time. The effects of cambial ageing on the above wood properties were investigated concurrently. The following hypothesis was tested:

- H_{4.4}: an increase in ring width has no effect on earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, longitudinal tracheid length and microfibril angle development

A third objective was to evaluate the effectiveness of the Kajaani FS-200 Optical Fibre Analyser for obtaining tracheid length measurements from 12 mm increment cores.

A fourth objective was to profile and compare the development of intra-ring relative density by species. The subsequent plots were to depict the changes observed in earlywood and latewood content as a function of both taper class and time. All intra-ring profiles were to be included in a general summary, serving in the process to consolidate the results obtained for all wood properties relating to x-ray densitometry in preceding analyses.

4.2 Data Analysis

4.2.1 Univariate Repeated Measures Analysis

Average ring width, earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density and whole-ring relative density profiles were plotted by initial spacing and taper class. Average profiles for whole-ring tracheid length and microfibril angle were plotted by initial spacing only due to the smaller number of spacings sampled for each wood property. Classification by taper class would have proved redundant. All chronologies were plotted as a function of ring number from pith to facilitate comparisons between the variables listed above.

A univariate repeated measures analysis of variance (based on a split-plot ANOVA model in which time was the split-plot factor) was used to assess the within-subjects effects of ring number from pith, between-subjects effects of initial spacing and taper class, and related interactions (spacing x ring, taper class x ring) on all wood properties considered. The following model was used:

$$(2) \quad y_{ijl} = u + \alpha_i + d_{i(l)} + \beta_j + (\alpha\beta)_{ij} + e_{(ij)l}$$

where

y_{ijl}	dependent variable
u	general mean
α_i	effect of the i^{th} treatment
$d_{i(l)}$	random experimental error within treatment (<i>error 1</i>)
β_j	effect of the j^{th} ring
$(\alpha\beta)_{ij}$	interaction between spacing and ring, or taper class and ring
$e_{(ij)l}$	random experimental error on repeated measures (<i>error 2</i>)
i	1, 2, ..., k (treatment level, i.e., specific spacing interval, or taper class)
j	1, 2, ..., t (ring number from pith)
l	1, 2, ..., r (experimental unit, i.e., tree at a specific growth ring)

A significant interaction involving either initial spacing and ring number from pith (spacing x ring) or taper class and ring number from pith (taper class x ring) implied nonparallel profiles of development over time between a minimum of two treatment levels. A corresponding significant treatment effect pointed to differences between a minimum of two treatment levels when their respective effects on the wood property in question were averaged over time. Alternatively, a non-significant treatment effect indicated no differences among treatment levels. The relative gains and losses displayed essentially cancelled out over time.

A non-significant interaction implied parallel trends of development for all treatment levels considered. A corresponding significant treatment effect pointed to differences between a minimum of two treatment levels when their respective effects on the wood property in question were averaged over time. Alternatively, a non-significant treatment effect implied an identical pattern of development over time for all treatment levels considered.

A repeated measures design is defined as a collection of measurements obtained at fixed intervals in time or space from an experimental unit undergoing some treatment regimen that does not change. The nature of such repeated data demands an alternative approach to analysis. Measurements obtained from successive growth rings often demonstrate a pattern of serial autocorrelation, thus violating the assumption of independence. Furthermore, the levels of a repeated measures factor, in this case ring number from pith, cannot be randomised. There is an order to the establishment of growth rings. For example, the tenth growth increment cannot be randomly assigned to the ninth position which naturally precedes it during tree development. Since the development of the tenth ring is to a certain extent predictable from the ninth, stronger correlations may exist between these two adjacent observations than between observations that are well separated in time. This lack of randomisation may also heighten the problem of heteroscedasticity between pairs of repeated measures. If the variances and correlations for all repeated measures are held constant, a condition known as compound symmetry is maintained, and the repeated measures analysis will provide reliable F-tests. If the conditions of compound symmetry do not hold, biased statistical tests with inflated Type I error may result (Moser *et al.* 1990, Meredith and Stehman 1991, Gumpertz and Brownie 1992, Nemec 1996).

The assumption of compound symmetry was assured using Greenhouse and Geiser's (1959) and Huynh and Feldt's (1976) epsilon correction factors (ϵ). These factors, when multiplied by the numerator (effect) and denominator (error) degrees of freedom, yielded the corrected degrees of freedom to be used in the ensuing F-tests. If the variances and correlations of the repeated measures remained constant over time, the two correction factors provided values approximating one. The lower the correction factor, the larger the deviation from compound symmetry, and the stronger the required correction due to heteroscedasticity and autocorrelation (Moser *et al.* 1990, Meredith and Stehman 1991, Gumpertz and Brownie 1992, Kuehl 1994, Nemec 1996).

The SAS procedure employed for the univariate approach was PROC GLM with the REPEATED statement (SAS Inc. 1989). The choice of the univariate approach for analysing the repeated measures data was based upon sample size. All trees selected for analysis were relatively young. Since the total number of trees sampled was, for the most part, less than the number of repeated measures collected, the multivariate approach could not be considered. All data were initially tested for heteroscedasticity, with square root or log-transformations subsequently applied to temper the effects of outliers, to obtain normality, and for variance stabilisation.

In order to conduct a univariate repeated measures analysis using PROC GLM, values for all dependent variables must be present for an observation (SAS Inc. 1989). Missing values, especially from growth rings nearest the bark, were common for each species where crushing had occurred during the collection of the 5 mm core samples. Incomplete growth rings from heavily suppressed trees were also a factor at the narrower spacings. Certain trees that presented large amounts of missing x-ray densitometry data subsequently had to be eliminated from the individual data sets. These included trees #61 (1.83 m) and #30 (3.66 m) for Douglas-fir, trees #1 (0.91 m) and #464 (1.83 m) for western hemlock and trees #24 (0.91 m) and #70 (1.83 m) for western redcedar. A total of 28 Douglas-fir trees (rings 4 to 33), 22 western hemlock (rings 4 to 30) and 28 western redcedar (rings 5 to 27) were subsequently available for analysis.

For consistency, the data set used for the plotting of each variable was the same as that considered during each corresponding repeated measures analysis. The average profiles established for each of the above mentioned spacings is subsequently based upon a sampling of five trees rather

than six. The mean profiles established as a function of taper class are in turn based upon the following tree count subtotals; suppressed (12 Douglas-fir, 14 western hemlock, 9 western redcedar), intermediate (10 Douglas-fir, 5 western hemlock, 4 western redcedar) and dominant (6 Douglas-fir, 3 western hemlock, 15 western redcedar). Data sets for whole-ring tracheid length and microfibril angle remained complete. Profiles for either of these two wood properties were accordingly based upon a sample of six trees.

The data analysed by repeated measures analysis were drawn from the non-shaded portions of each profile (illustrated in Figures to follow, in section 4.3.1 onward) where values from all trees were available for each time period sampled. Profile sections depicted within the shaded regions contain missing data. These were established from the subset of trees that did not present missing values. Values preceding ring 3 and succeeding ring 33 were truncated in all profiles due to frequently missing data (e.g., pith missed during increment core collection, crushing in outer growth rings during boring). Rings 3 to 33 also correspond to the sampling scheme adopted for both whole-ring tracheid length and microfibril angle development. The presence of discontinuous growth rings within the outer sections of five heavily suppressed western redcedar trees created problems during analysis, accounting for the lack of data within the 0.91 m spacing and within the suppressed taper class following ring 27.

4.2.2 Regression and Correlation Analysis

Linear regression and correlation analysis were used to evaluate the effects of ring width on earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, whole-ring tracheid length and microfibril angle development. Data from all spacings sampled were initially pooled to assess a wider range of growth rates by species. Analyses were conducted on a yearly basis to display observed trends, and to locate points in time at which significant responses were obtained. The SAS procedures PROC REG, and PROC CORR, were employed (SAS Inc. 1989).

The following model was used:

$$(3) \quad y_i = \beta_0 + \beta_1 x_i + e_i$$

where

y_i	dependent variable
β_0	y intercept coefficient
β_1	slope coefficient
x_i	independent variable
e_i	independent, normally distributed random error term

4.2.3 Intra-Ring Relative Density Development

One hundred relative density measurements, regardless of ring width, were obtained during x-ray densitometry analysis for each growth increment processed. Average breast height profiles, depicting intra-ring relative density development over time, were subsequently established using these data. Relative density values obtained from five consecutive growth increments (ring class), as well as from the trees categorised within each taper class, were averaged at each of these 100 relative density positions. All profiles were plotted by taper class, and as a function of both ring width and latewood proportion. Profiling according to initial spacing was avoided since the exercise would have been largely redundant. Profiling according to taper class was preferred since it offered a clearer depiction of the effects of competition and crown morphology on ring width and relative density development over time.

4.3 Results and Discussion

The ranges in stem and crown dimensions observed in this study are summarised according to initial spacing and taper class in Tables 4.1 and 4.2, respectively (Appendix I). Mean values for each spacing were obtained from a total of six trees. Mean values listed for each taper class are based upon the following subtotals; suppressed (13 Douglas-fir, 16 western hemlock and 11 western redcedar), intermediate (10 Douglas-fir, 5 western hemlock and 4 western redcedar) and dominant (7 Douglas-fir, 3 western hemlock and 15 western redcedar). Excessive mortality within the narrower Douglas-fir and western hemlock spacings (mostly as a result of windthrow and snow breakage) brought about increased variability in the physical attributes of the trees left standing. Certain specimens were openly growing, whereas others were severely repressed. Mortality within the wider spacings was not as apparent. The effects of competition and subsequent crown class differentiation were nonetheless discernible within these spacings through the disparity in stem and crown dimensions observed.

4.3.1 Ring Width

Mean ring width development is presented by initial spacing in Figure 4.1, and by taper class in Figure 4.2. Ring width development for all species was initially subject to an increase, followed by a continual decrease, to a point at which more-or-less constant values were maintained. This increase was generally of greater duration at the wider spacings and for the dominant taper class (lowest *hdr*) where larger ring width values were also attained. Minimum constant values were reached at an earlier age as spacing interval decreased, and these values tended to be lower than those observed at the wider spacings. Minimum constant ring width values were also achieved at an earlier date by trees classified as suppressed (highest *hdr*). Minimum values for these trees also tended to be lower than those attained by the more dominant taper classes. Western hemlock demonstrated the greatest overall homogeneity over the range of growth increments considered. Initial increases, and subsequent drops in ring width, were less than those observed at corresponding spacing intervals and taper classes for both Douglas-fir and western redcedar. Greater variation in ring width would have been expected had the 4.57 m spacing been available for sampling.

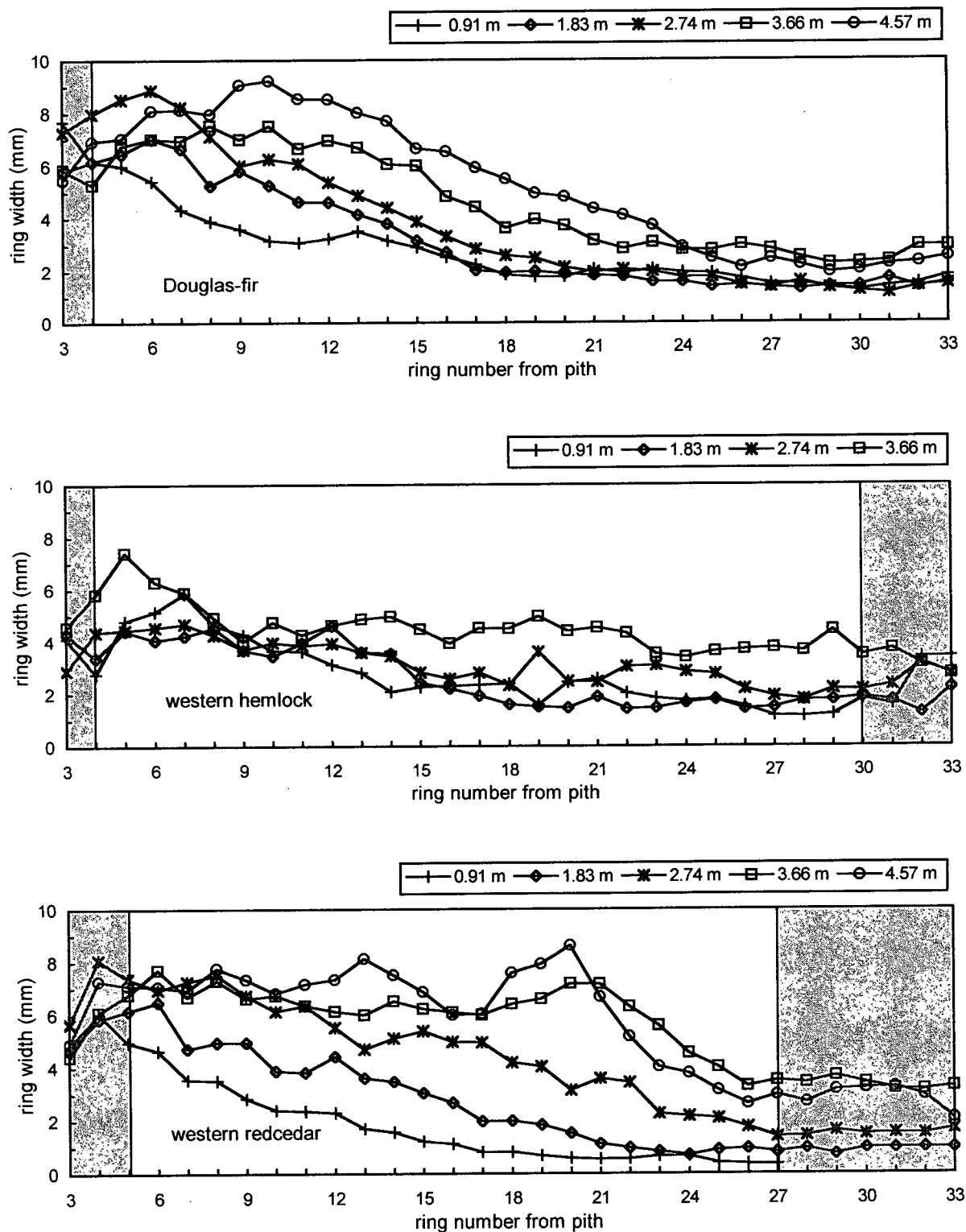


Figure 4.1 Mean ring width (mm) profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

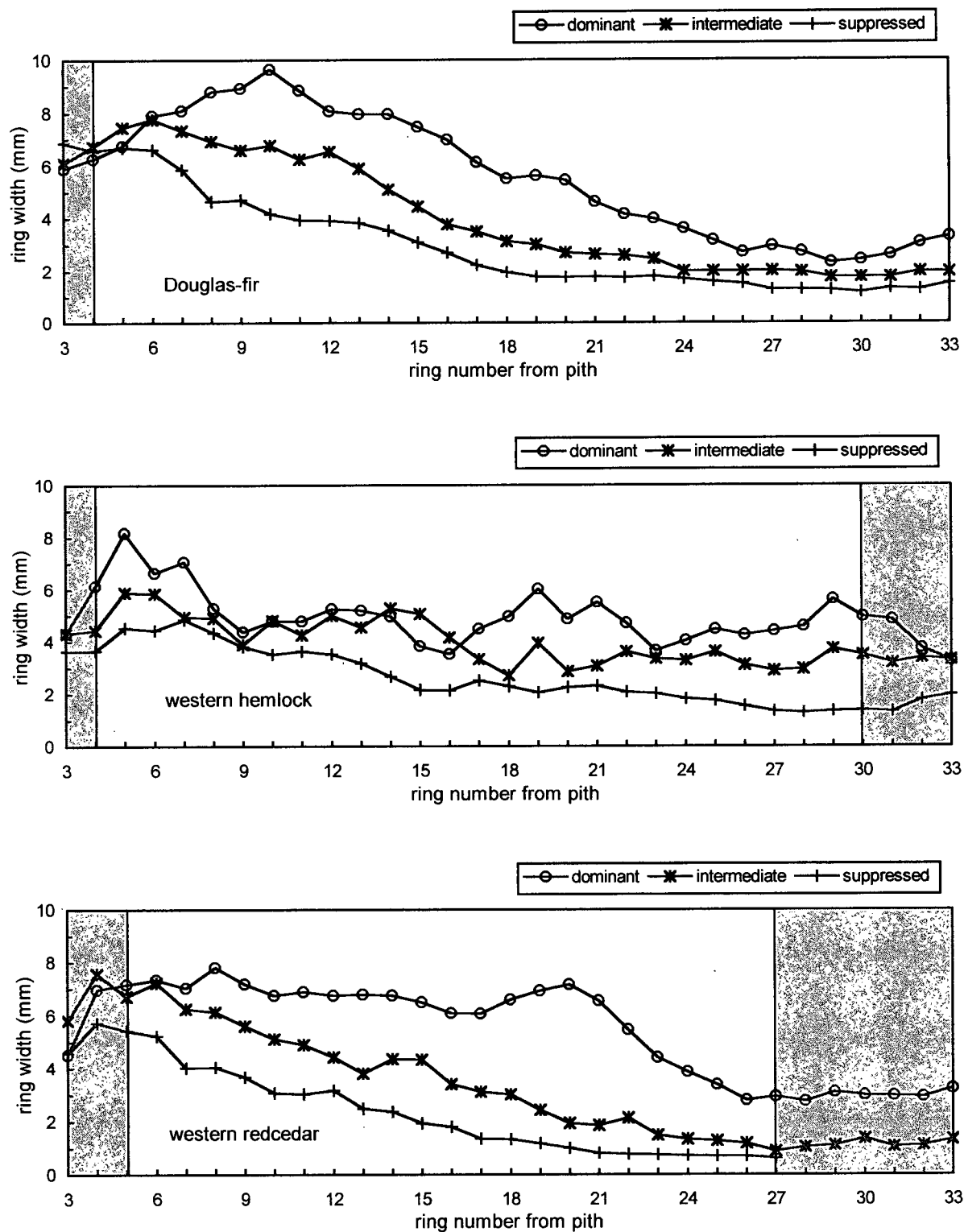


Figure 4.2 Mean ring width (mm) profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

The relationship between ring width development and available growing space is well documented within the literature. It is generally recognised that diameter growth commands a very low priority in the hierarchy of photosynthate allocation within a tree, well behind maintenance respiration, fine root, flower and seed production and terminal and lateral shoot growth (Kozlowski *et al.* 1991, Kozlowski 1992). Larson (1973) states that the overlying cause of ring width variation within a tree is the relation of crown size to the length of stem devoid of branches. An increase in ring width at breast height is therefore strongly associated with growing space, up to the limit associated with an open-grown tree (Larson 1969, Kozlowski 1971, Larson 1973).

The sudden increase in competition following crown closure did little to affect the rate of crown recession observed for western hemlock. The extreme shade tolerance displayed by the species resulted in deep crowns and extensive live-crown-ratios even at very high stand densities (Tables 4.1 and 4.2). Ring width development, especially within the intermediate and dominant taper classes, continued to progress at a more-or-less steady pace. It is interesting to note that maximum incremental growth within the dominant taper class for western redcedar carried on at a regular pace up to about ring 20. That observed within the dominant taper class for Douglas-fir (intermediate shade tolerance) reached a high at ring 10, and decreased in a continuous fashion thereafter. Ring width development within conifers typically reaches a maximum in the lower sections of the live crown where the cumulative growth contribution of all branches is greatest (Farrar 1961, Larson 1963). Crown recession within the dominant taper class for western redcedar took longer to initiate due to the greater shade tolerance displayed by the species. The base of the live crown therefore remained in close proximity to breast height over an extended period of time. Maximum ring width development was accordingly maintained over a greater proportion of the growth increments sampled at this height.

Basic statistics for ring width are summarised by initial spacing in Table 4.3a (Appendix I), and by taper class in Table 4.4a (Appendix I). A minimum average ring width value was obtained for all species at the narrower spacings and within the suppressed taper class. Maximum values were observed at the wider spacings and within the dominant taper class. Coefficient of variation values for Douglas-fir and western redcedar were greatest at the narrower spacings and within the suppressed taper class where intensive competition was stifling diameter growth. The same held true,

but to a much lesser extent, for the more shade tolerant western hemlock. Many of the more narrowly-spaced trees for Douglas-fir and western redcedar had experienced poor ring width development following crown closure, and were now showing signs of impending mortality through the meagre amounts of crown foliage displayed. Incremental growth within these trees was now practically nonexistent. Ring width distributions were, as a result, heavily skewed toward the smaller values.

Results of the repeated measures analyses conducted on ring width, and as a function of initial spacing and taper class, are presented in Tables 4.3b and 4.4b, respectively (Appendix I). The within-subjects effects of ring number from pith were highly significant ($\alpha = 0.01$) for all species. Time effects will therefore be considered in forthcoming regression and correlation analyses that will include ring width measurements collected at successive intervals of time. The interactions involving initial spacing and ring number from pith (spacing x ring), and taper class and ring number from pith (taper class x ring), were highly significant for both Douglas-fir and western redcedar. The corresponding treatment effects for both species were also highly significant. Non-significant spacing x ring and taper class x ring interactions were obtained for western hemlock. Treatment effects were highly significant in each case.

As expected, an increase in ring width was strongly associated with an increase in the amount of available growing space, and correspondingly, with an increase in the amount of crown foliage. The mean levels recorded over time were invariably different for each species. Results obtained as a function of initial spacing and taper class, for both Douglas-fir and western redcedar, were similar with respect to the following. The widely-spaced and dominant taper class trees displayed a prolonged increase in ring width development from the pith. Rapid diameter growth was maintained over a longer period by such trees. The average ring width recorded over time was, as a result, significantly thicker. The narrowly-spaced and suppressed taper class trees initially displayed a rapid decrease in ring width, followed by relatively very poor incremental growth. The average ring width recorded over time for such trees was significantly thinner. Similar results would most likely have been obtained for western hemlock had the 4.57 m spacing for the species been available for sampling.

4.3.2 Earlywood Width

Mean earlywood width development is illustrated by initial spacing in Figure 4.3, and by taper class in Figure 4.4. All earlywood curves essentially mimicked the shapes of their ring width counterparts featured in Figures 4.1 and 4.2. Yearly dips and rises were, for the most part, reproduced by both variables. The initial increase in earlywood width was sustained over a longer period by the wider spacings, and by the dominant taper class. Higher maximum values were subsequently attained by these groups. Minimum constant values were once again reached at an earlier age as spacing decreased, and by those trees identified within the suppressed taper class. The minimum values attained also tended to be lower than those observed at both the wider spacings and by the dominant taper class.

Current thinking indicates that earlywood development is to a large extent controlled by hormonal interactions involving varying concentrations of auxins, gibberellins, cytokinins, ethylene and abscisic acid at different periods of the growing season. However, it is generally recognised that auxins exert a predominant role. The rate of periclinal cell division, as well as final tracheid diameter, are both said to be strongly tied to the presence of this growth promoter. The extent and manner in which the other hormone groups interact with auxin during earlywood development remains unclear (Little and Savidge 1987, Salisbury and Ross 1992, Little and Pharis 1995).

The dominant taper class, as the name suggests, supported the largest volumes of foliage and therefore maintained the greatest potential for auxin synthesis. Trees from this taper class, as well as from the wider spacings, never experienced severe competition. Large volumes of crown foliage were continually supported, with high live-crown-ratios displayed. Earlywood production at breast height was therefore maintained at a greater level (compared to the other taper classes) throughout stand development. Minimum constant values in Figures 4.3 and 4.4 were reached at an earlier date by the narrower spacings, and by the trees associated with the suppressed taper class. Such trees experienced greater levels of competition, and accordingly possessed the smallest crown attributes. Auxin levels within these trees presumably remained lower throughout stand development. The earlywood width values observed were accordingly narrower than those achieved at the wider spacings, and by the trees associated within the dominant taper class.

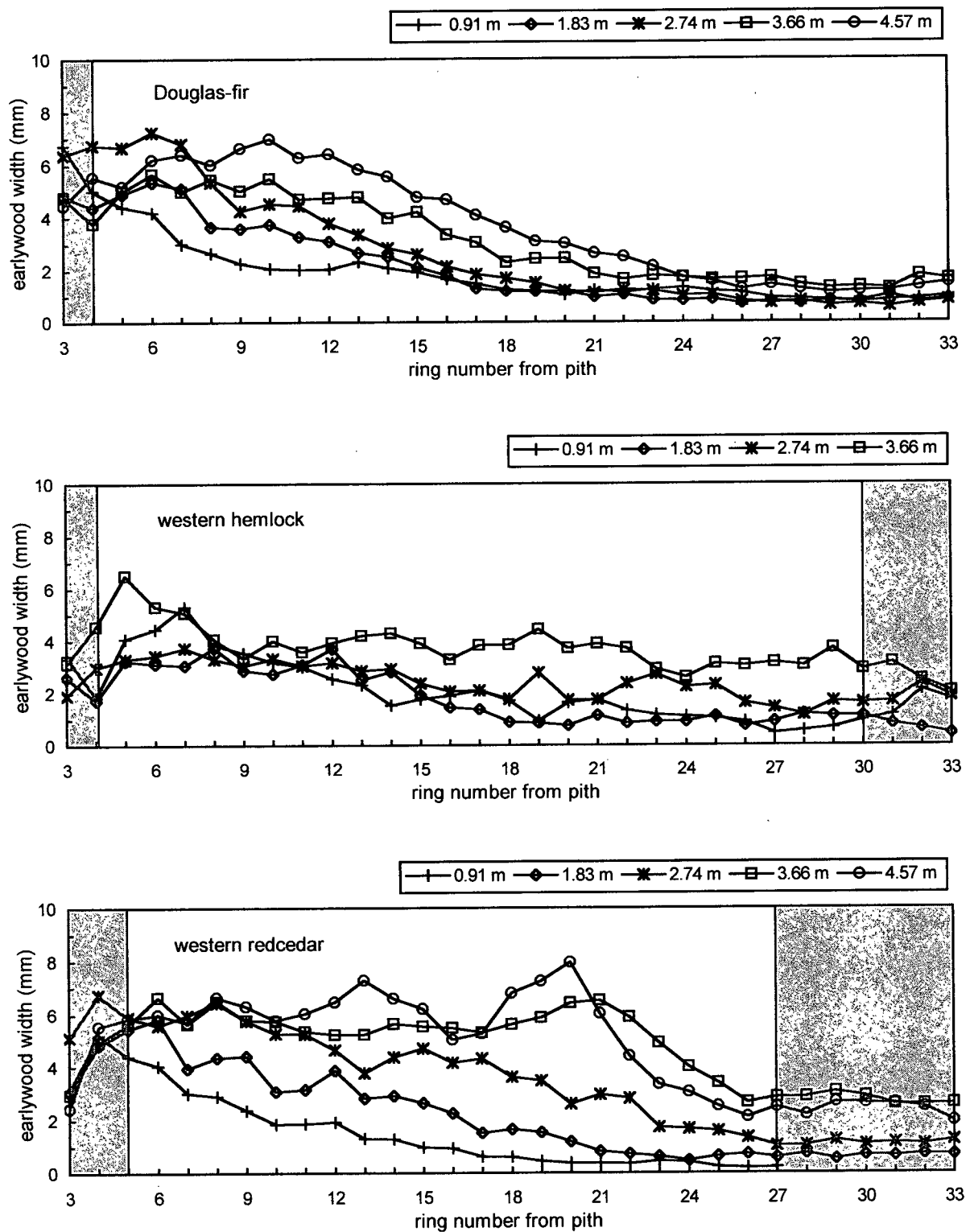


Figure 4.3 Mean earlywood width (mm) profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

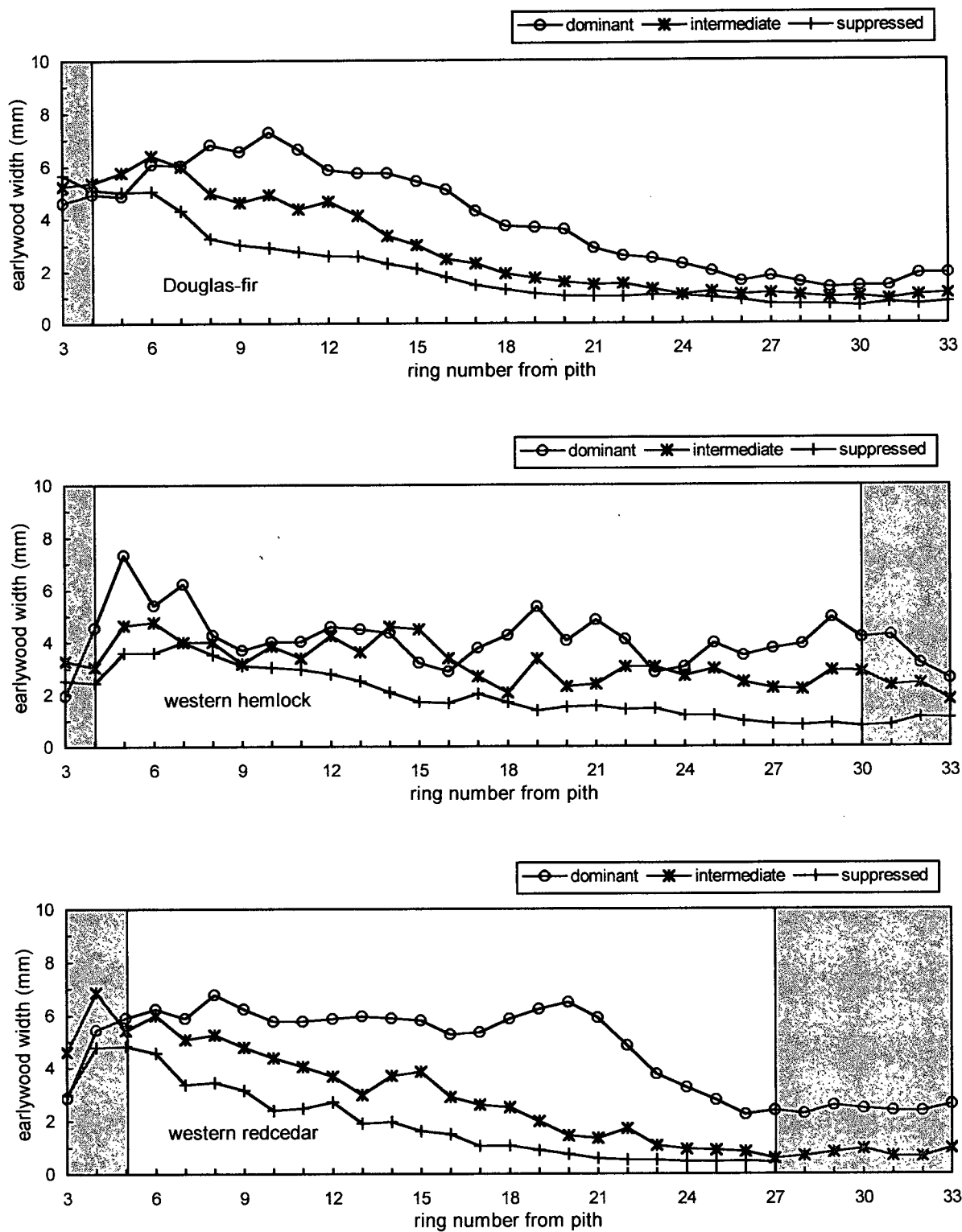


Figure 4.4 Mean earlywood width (mm) profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

Maximum earlywood thickness along a tree stem (in similar fashion to ring width) is generally observed in the vicinity of the base of the live crown. The larger the volume of crown foliage, the thicker the earlywood increment generally produced (Farrar 1961, Larson 1963). The production of a maximum earlywood width value within the western redcedar dominant taper class was maintained up to approximately ring 20 (Figure 4.4). Since crown recession within this taper class proceeded slowly (Table 4.2), the base of the live crown remained in close proximity to breast height for an extended period of time. Earlywood development within this general area was subsequently favoured.

The production of a maximum earlywood width value within the Douglas-fir dominant taper class dropped rapidly following the high reached at ring 10. The species, being intermediate in shade tolerance, demonstrated a more pronounced rate of crown recession. The point of maximum earlywood width was therefore moving up along the stem in line with the receding crown base, and earlywood width at breast height was accordingly decreasing.

Mean earlywood width development for western hemlock, in part due to the high shade tolerance displayed by the species, was once again the most homogeneous over the range of growth rings sampled. Very little change over time was observed within the dominant and intermediate taper classes. Greater variability, especially within the dominant taper class, would have been expected had the 4.57 m spacing interval been available for sampling.

Basic statistics for earlywood width are presented by initial spacing in Table 4.5a (Appendix I), and by taper class in Table 4.6a (Appendix I). Results are similar to those displayed for ring width in Tables 4.3a and 4.4a. A minimum average earlywood width was obtained for all species at the narrower spacings and within the suppressed taper class. Maximum values were observed at the wider spacings and within the dominant taper class. Only a shortened period of accelerated earlywood development was displayed prior to crown closure by the more narrowly-spaced trees. The intensification of tree-to-tree competition for the same trees was now reducing earlywood development to practically nothing. Coefficient of variation values were therefore greatest at the narrower spacings, and within the suppressed taper class, where earlywood width distributions remained heavily skewed toward the smaller values.

Results of the repeated measures analyses conducted on earlywood width, and as a function of initial spacing and taper class, are presented in Tables 4.5b and 4.6b, respectively (Appendix I). The effects of time were highly significant for all species. The spacing x ring and taper class x ring interactions were highly significant for both Douglas-fir and western redcedar. The corresponding treatment effects were also highly significant. The spacing x ring and taper class x ring interactions for western hemlock were both non-significant. Highly significant treatment effects were obtained in each case.

Identical repeated measures analysis results were obtained for both earlywood width and ring width. The widely-spaced and dominant taper class trees for both Douglas-fir and western redcedar displayed a prolonged increase in earlywood width development from the pith. The narrowly-spaced and suppressed taper class trees initially displayed a rapid decrease in earlywood width, followed by very poor incremental growth. An increase in available growing space, analysed as a function of either initial spacing or taper class, maintained a highly significant and positive effect on the mean level recorded over time. Comparable results would most likely have been obtained for western hemlock had the 4.57 m spacing been available for sampling.

The effects of growth rate on earlywood width development are presented in Tables 4.7, 4.8 and 4.9 (Appendix I) for Douglas-fir, western hemlock and western redcedar, respectively. The relationship between earlywood width and ring width remained exceptionally strong over time for all species. Highly significant results were obtained in all cases. Regression equations at all growth increments provided excellent fits. Coefficient of determination values were, for the most part, superior to 0.90. Practically all earlywood width variability was therefore associated with ring width. Correlation values remained highly positive throughout. Slope coefficients for Douglas-fir decreased in a more-or-less constant fashion from ring 3 to 33. Such a decline points to a decreasing proportion of earlywood within each growth ring as a function of time. Slope coefficients observed for western hemlock and western redcedar remained practically identical, indicating very little change over time in the ratio of earlywood width to ring width.

4.3.3 Latewood Width

Mean latewood width development is presented by initial spacing in Figure 4.5, and by taper class in Figure 4.6. An increase in latewood width was initially observed for Douglas-fir. This increase was generally of greater duration at the wider spacings and within the dominant taper class where larger values were subsequently attained. A gentle but continuous decrease in latewood width followed until more-or-less steady values were displayed by about ring 25. A decrease in latewood width was initially observed for both western hemlock and western redcedar. Values for western hemlock generally stabilised following ring 9, whereas those for western redcedar declined in a slow but continuous fashion. Slightly greater latewood width values were generally maintained for both Douglas-fir and western redcedar at the wider spacings and within the dominant taper class. Differences were minimal for western hemlock, with profiles largely superimposed on one another.

Larson (1969) stated that high concentrations of auxins generally remained within the vascular cambium of a young, open-grown tree following the cessation of height growth. Large diameter tracheids would accordingly be produced throughout the growing season, and accelerated incremental growth would be maintained. Maintenance respiration within a young, open-grown tree is also said to be at a minimum compared to that displayed by an older tree of similar crown size, but possessing a larger and longer branch-free stem (Oliver and Larson 1996). Proportionally speaking, greater amounts of photosynthate are available within the younger tree for both cambial growth and cell-wall thickening. According to Larson (1969), these conditions will likely lead to the development of a great number of large-diameter, thick-walled transition wood tracheids at breast height within the younger tree during the latter portion of the growing season.

It can therefore be assumed that widely-spaced trees, possessing greater quantities of crown foliage, will produce a greater number of transition wood tracheids at time of crown closure. Oliver and Larson (1996) stated that when trees within an idealised even-aged, evenly-spaced stand grew in height at an equal rate, they would maintain the crown sizes they had at crown closure. It can therefore also be assumed, so long as height growth is maintained at a similar level for all stems considered, that even-aged, widely-spaced trees will continuously produce greater quantities of transition wood at breast height following the onset of crown recession.

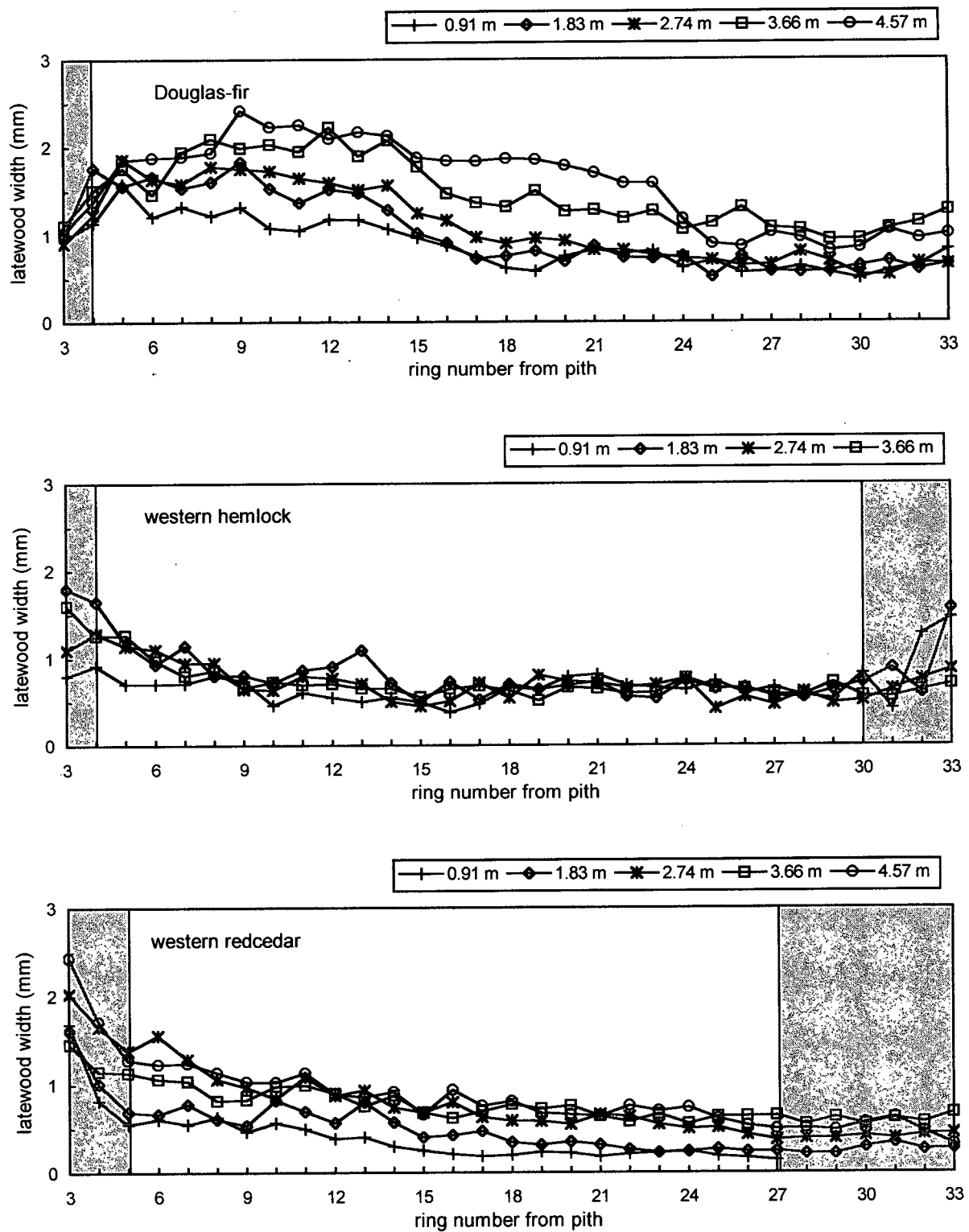


Figure 4.5 Mean latewood width (mm) profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

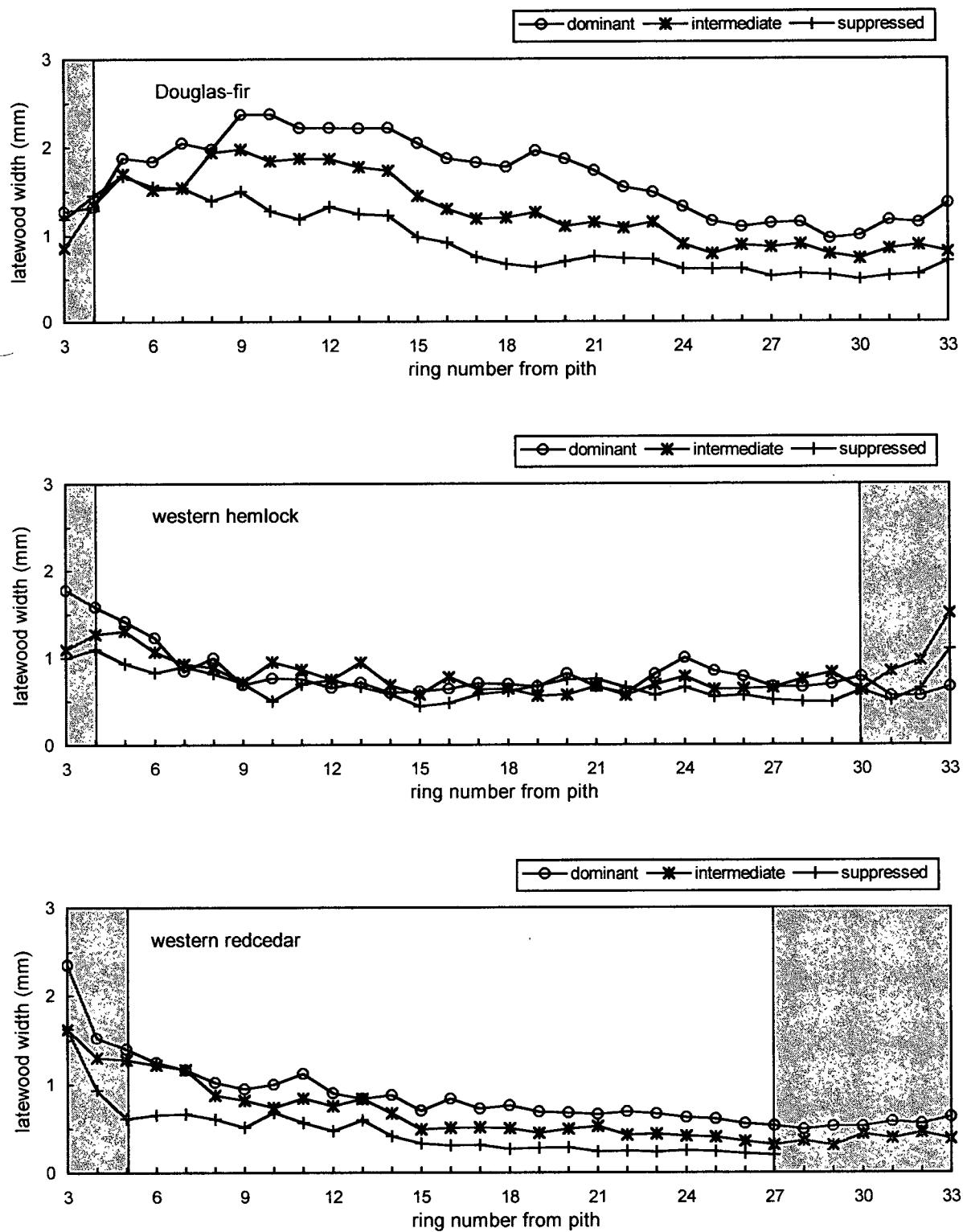


Figure 4.6 Mean latewood width (mm) profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

Larson (1969, 1973) suggested the existence of physiological gradients within the vascular cambium in terms of both auxin and photosynthate availability. These gradients, he remarked, remained in constant change and were largely affected by period of growing season, by overall tree age and by the relative length of the branch-free stem. Based on Larson's work, it can therefore be assumed that auxin levels at breast height will begin to decrease earlier within a growing season in accordance with the progression of crown recession. The greater the distance from breast height to the base of the live crown, the earlier the decline. The overall availability of photosynthates for cell wall thickening will also decrease due to the greater maintenance respiration needs of the developing tree. Consequently, less transition wood will likely develop at breast height, and a corresponding abrupt transition from earlywood to latewood will emerge.

Past crown and stem measurements relating to the trees sampled in this study were obtained from the BC Ministry of Forest's Research Branch in Victoria, and from Reukema and Smith (1987). The ring number from pith at which a maximum latewood width was achieved by each Douglas-fir profile in Figure 4.5 corresponds well to the tree ages at which crowns began to lift. Crown recession within the three narrowest Douglas-fir spacings attained breast height at tree ages ranging from about 6 to 8. The tree ages in this case correspond roughly to about 4 or 5 growths increments from the pith. Crown recession within the two wider spacings reached breast height between rings 10 and 12. Crown recession within the 0.91 m spacing for both western hemlock and western redcedar began at about ring 16. That within the wider spacings for both species started at about ring 20.

Crown recession proceeded very rapidly for Douglas-fir following crown closure. Crown recession for western hemlock was very slow, whereas that observed for western redcedar proceeded at an intermediate pace. These patterns of crown recession are reflected for each species in the corresponding latewood width profiles illustrated in Figure 4.5. In general, the faster the rate of crown recession, the greater the decline in latewood width displayed over time.

The initial sharp decline in latewood width for both western hemlock and western redcedar can perhaps be attributed to the presence of compression wood. Such wood is often found in large concentrations within the inner cores of both species. Its development is associated with the stiffening of small diameter, often drooping leaders that are subjected to wind stresses (Krahmer

1985, Kennedy 1995). The lack of variability between the various western hemlock profiles can perhaps be attributed to the gradual earlywood to latewood transition that typically develops for the species regardless of cambial age or rate of growth. Since an abrupt transition rarely develops, less variability in latewood width will be observed over time. This is in contrast to both Douglas-fir and western redcedar which may see a range of earlywood to latewood transitions, from gradual within the inner core, to abrupt toward the bark (Panshin and de Zeeuw 1980, Hoadley 1990).

Basic statistics for latewood width are summarised by initial spacing in Table 4.10a (Appendix I), and by taper class in Table 4.11a (Appendix I). Smaller mean values were displayed within the 0.91 m spacing, and within the suppressed taper class, for both Douglas-fir and western redcedar. The 4.57 m spacing and the dominant taper class both produced the largest mean values. However, the increases observed did not translate into major changes, amounting to less than 1 mm in most cases. Mean latewood width was practically the same for all western hemlock spacings and taper classes. Coefficient of variation values for both Douglas-fir and western redcedar were greatest at the narrower spacings and within the suppressed taper class where the distributions for latewood width remained positively skewed. Coefficient of variation values for western hemlock were generally the same throughout, save for the 0.91 m spacing which was considerably lower.

Results of the repeated measures analyses conducted on latewood width, and as a function of initial spacing, are presented in Table 4.10b (Appendix I). Time effects were highly significant for all species. The spacing x ring interaction was non-significant for both Douglas-fir and western hemlock. Corresponding treatment effects were highly significant for Douglas-fir, and non-significant for western hemlock. A non-significant, but notable, spacing x ring interaction ($p = 0.0912$) was obtained for western redcedar using Greenhouse and Geisser's eps. A weak but significant interaction ($p = 0.0304$) was obtained using Huynh and Feldt's eps. Such conflicting results indicate borderline parallelism between a minimum of two profiles. Of the two adjustment methods, Greenhouse and Geiser's eps is considered more conservative (Kuehl 1994). By using it only, a parallel pattern of latewood development can be implied for all spacings considered. The corresponding treatment effects were highly significant.

Results of the repeated measures analyses conducted on latewood width, and as a function

of taper class, are presented in Table 4.11b (Appendix I). The taper class x ring interaction for Douglas-fir produced a non-significant result ($p = 0.0553$) using Greenhouse and Geisser's eps, and a significant result ($p = 0.0294$) using Huynh and Feldt's eps. Treatment effects were highly significant. A non-significant taper class x ring interaction was obtained for western hemlock. Treatment effects were also non-significant. The taper class x ring interaction for western redcedar, as opposed to results obtained for initial spacing in Table 4.10b, produced a definite non-significant result. Treatment effects remained highly significant.

An increase in available growing space had little effect on the pattern of latewood width development observed for western hemlock. Identical trajectories were identified as a function of both initial spacing and taper class. An increase in growing space also did not affect the pattern of latewood development observed for either Douglas-fir or western redcedar. All spacing and taper class profiles were identified as parallel. Highly significant and positive treatment effects were nonetheless observed in each case. A significantly thicker mean latewood increment was accordingly produced by the more widely-spaced, dominant taper class trees. Alternately, the more narrowly-spaced, suppressed taper class trees produced a significantly thinner mean latewood increment.

The effects of growth rate on latewood width are presented in Tables 4.12, 4.13 and 4.14 (Appendix I) for Douglas-fir, western hemlock and western redcedar, respectively. Results for Douglas-fir grew stronger with time such that coefficient of determination values following ring 14 were practically all superior to 0.80. The very low correlation coefficients observed next to the pith, and the very high values ($r \geq 0.87$) following ring 14, attest to an increasingly strong interdependence between latewood width and ring width in the later years of tree development. Slope coefficients increased in a continual fashion, pointing to an increasing latewood proportion as a function of time. The results obtained for western hemlock indicate a very weak relationship between latewood width and ring width. Regression equations were mostly non-significant, or significant at the $p = 0.05$ level. The results obtained for western redcedar indicate an increasingly strong relationship between latewood width and ring width. Practically no latewood width variability was associated with ring width next to the pith. Highly significant results were obtained from ring 14 onward. Correlation coefficients generally increased in value over time, remaining positive throughout. Slope coefficients remained more-or-less stable, suggesting little actual change in latewood width relative to ring width.

4.3.4 Latewood Proportion

The development of mean latewood proportion is presented by initial spacing in Figure 4.7, and by taper class in Figure 4.8. The profiles illustrated for Douglas-fir were practically identical in both time and space. All exhibited a very gradual increase in latewood proportion from pith to bark. Latewood proportion for both western hemlock and western redcedar initially declined in value to about ring 6. Such a decrease was perhaps due to the presence of compression wood within the inner cores of both species. Latewood proportion within the wider spacings, and within the dominant taper classes, increased very little thereafter. Important gains were observed within the narrower spacings and within the suppressed taper classes.

A comparison of profiles for earlywood width (Figure 4.3), and latewood width (Figures 4.4), reveals that the development of latewood proportion was to a large extent a function of earlywood width development. Comparatively speaking, latewood width varied little by species. Only slight decreases were observed over time for Douglas-fir, and even slighter decreases were observed for western redcedar. Western hemlock remained practically unchanged. In the case of Douglas-fir, a similar ratio of earlywood to latewood was maintained for each growth ring sampled. The gradual increase in latewood proportion displayed over time was largely due to ongoing greater decreases in earlywood width relative to latewood width. In the case of western hemlock and western redcedar, the rapid initial decline in latewood proportion corresponded, in large part, to a rapid initial increase in earlywood width from the pith. Latewood proportion for the wider spacings, and within the dominant taper class, increased little following ring 6, reflecting the fact that earlywood width also varied little. Latewood proportion for the narrower spacings, and within the suppressed taper class, displayed the greatest overall increases in value over time. Only marginal earlywood production was displayed by these groups during the final years of growth.

Basic statistics for latewood proportion are summarised by initial spacing in Table 4.15a (Appendix I), and by taper class in Table 4.16a (Appendix I). Mean latewood proportion was greatest at the narrower spacings and within the suppressed taper class. Coefficient of variation values for Douglas-fir and western redcedar were also highest within these two groups. Extreme competition was limiting earlywood production during the final years of development. Many of the

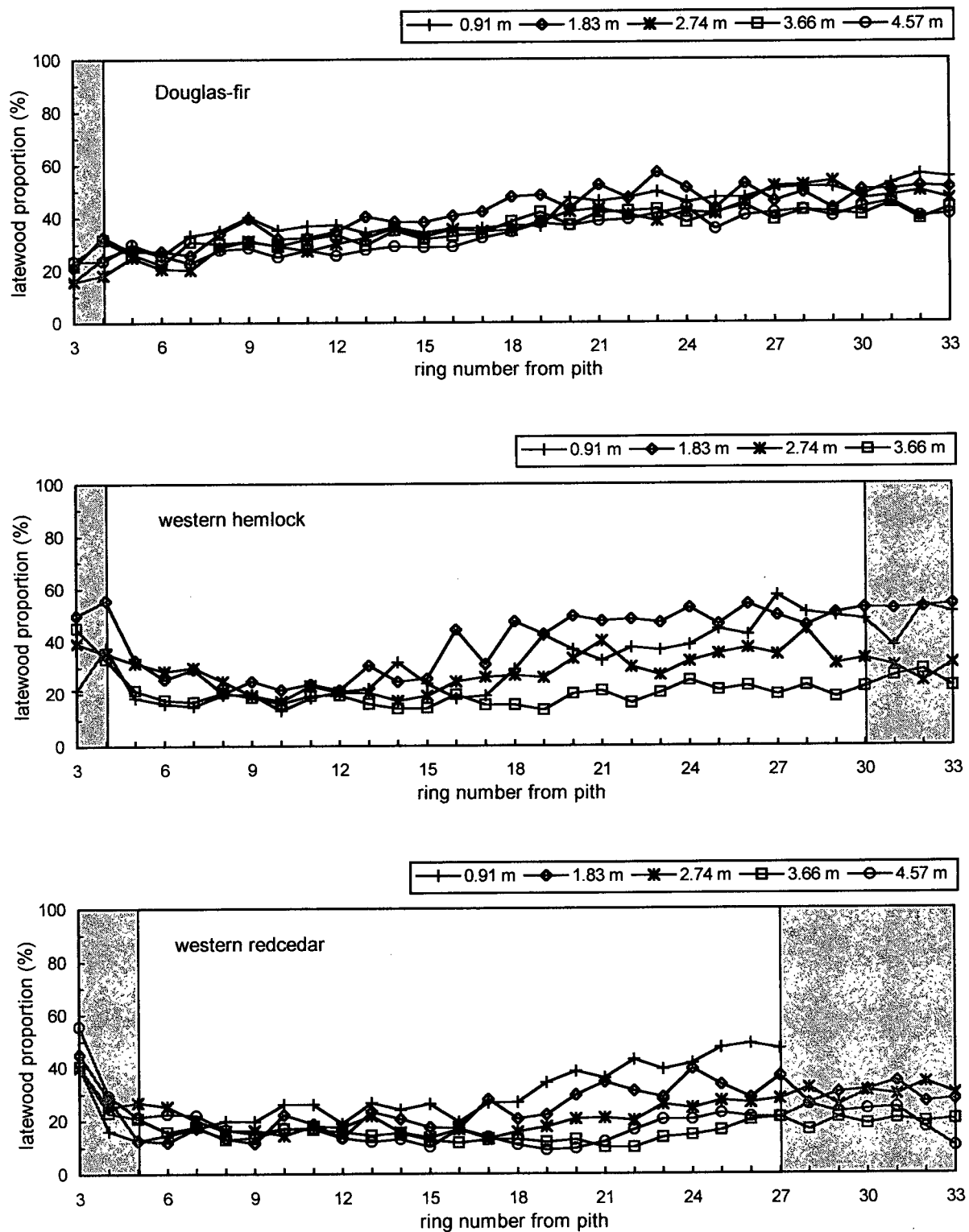


Figure 4.7 Mean latewood proportion (%) profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

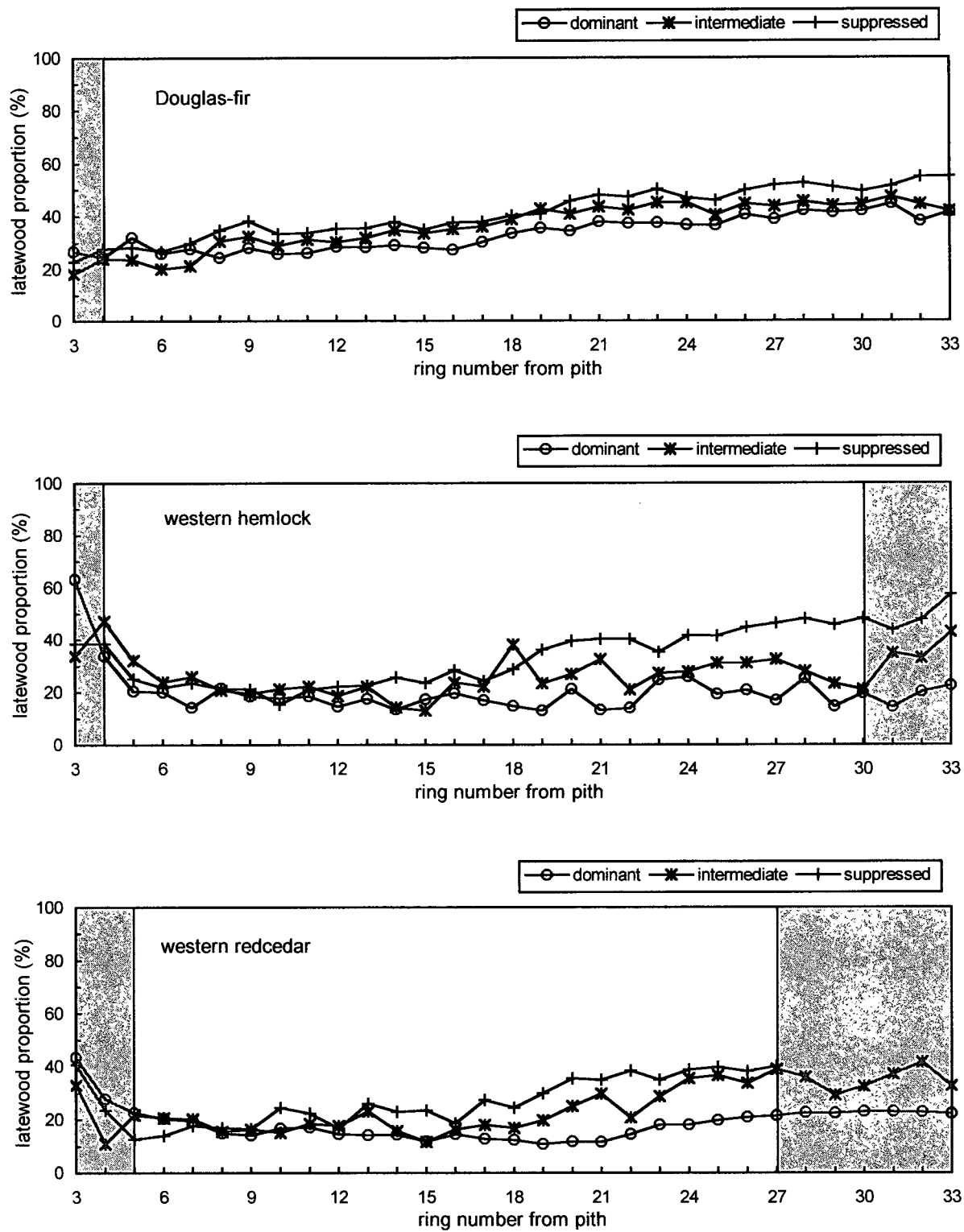


Figure 4.8 Mean latewood proportion (%) profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

growth increments sampled from the slowest growing trees demonstrated a proportion of latewood approaching 100 %, hence the greater variability. Latewood proportion for western hemlock did not follow any specific pattern of variability as a function of initial spacing or taper class. Crown recession for the species was slow. The effects of competition on wood formation for the species were therefore tempered.

Results of the repeated measures analyses conducted on latewood proportion, and as a function of initial spacing and taper class, are presented in Tables 4.15b and 4.16b, respectively (Appendix I). The effects of time on the development of latewood proportion were highly significant for all species. The spacing x ring and taper class x ring interactions for Douglas-fir were both non-significant. Treatment effects for spacing were non-significant. Treatment effects for taper class were also non-significant, but borderline ($p = 0.0694$). Non-significant spacing x ring and taper class x ring interactions were obtained for western hemlock. Treatment effects for spacing were highly significant, whereas treatment effects for taper class produced significant results only ($p = 0.0446$). Highly significant interactions and treatment effects were obtained as a function of both initial spacing and taper class for western redcedar.

An increase in available growing space had little effect on the development of latewood proportion for Douglas-fir. Identical trajectories were identified as a function of both initial spacing and taper class. Parallel profiles of development were also identified for western hemlock. Highly significant and negative treatment effects on the overall mean levels obtained were nonetheless identified as a function of both initial spacing and taper class. A significantly lower mean latewood proportion value was therefore associated with the more widely-spaced, dominant taper class trees. A significantly higher mean value was associated with the narrowly-spaced, suppressed taper class trees. All interactions for western redcedar, and all treatment effects, yielded highly significant results. The development of latewood proportion within the narrowly-spaced, suppressed taper class trees demonstrated a steep initial decline from the pith, followed by a continual increase in value over time. The mean value recorded over time for such trees was significantly higher. The development of latewood proportion within the widely-spaced, dominant taper class trees demonstrated less of an initial drop in value from the pith, and relatively stable values thereafter. The mean value recorded over time for such trees was significantly lower.

The effects of growth rate on latewood proportion are presented in Tables 4.17, 4.18 and 4.19 (Appendix I) for Douglas-fir, western hemlock and western redcedar, respectively. Slope coefficients for all species became somewhat increasingly negative towards the bark, indicating a slight but strengthening relationship. In other words, the wider the growth ring observed as a function of time, the smaller the proportion of latewood identified. The relationships for Douglas-fir were mostly significant, but weak. Coefficient of determination values remained low throughout. Correlation coefficients were moderately negative. Results for western hemlock were equally weak during the initial years of development. The relationships did strengthen somewhat following ring 20. Best results were obtained for western redcedar. Relationships were largely non-significant during the initial years of development. Highly significant results were obtained between rings 17 and 31. Coefficient of determination values obtained during this period were generally greater than 0.50. Important amounts of latewood proportion variability during the later years of development were consequently associated with ring width.

4.3.5 Earlywood Relative Density

Mean earlywood relative density development is presented by initial spacing in Figure 4.9, and by taper class in Figure 4.10. A decrease in value was initially observed for all species. Lower minimum values for Douglas-fir were subsequently attained at the narrower spacings and by the suppressed taper class. A constant, gentle increase in earlywood relative density followed for all profiles. Slightly greater values were displayed by the suppressed taper class during the final years of development. In the case of western hemlock, hardly any subsequent increase in earlywood relative density was observed following the initial low reached at about ring 10. Relatively constant values were displayed thereafter by all profiles. Western redcedar demonstrated the greatest overall variability. Mean values were essentially the same for all spacings and taper classes during early development. A steep decline in earlywood relative density was initially observed to about ring 6. A slow but continual decrease in value followed at the wider spacings and within the dominant taper class. Relatively stable values were observed within the 1.83 m spacing and within the intermediate taper class. The 0.91 m spacing and suppressed taper class both demonstrated a slight increase in value that grew steeper with time.

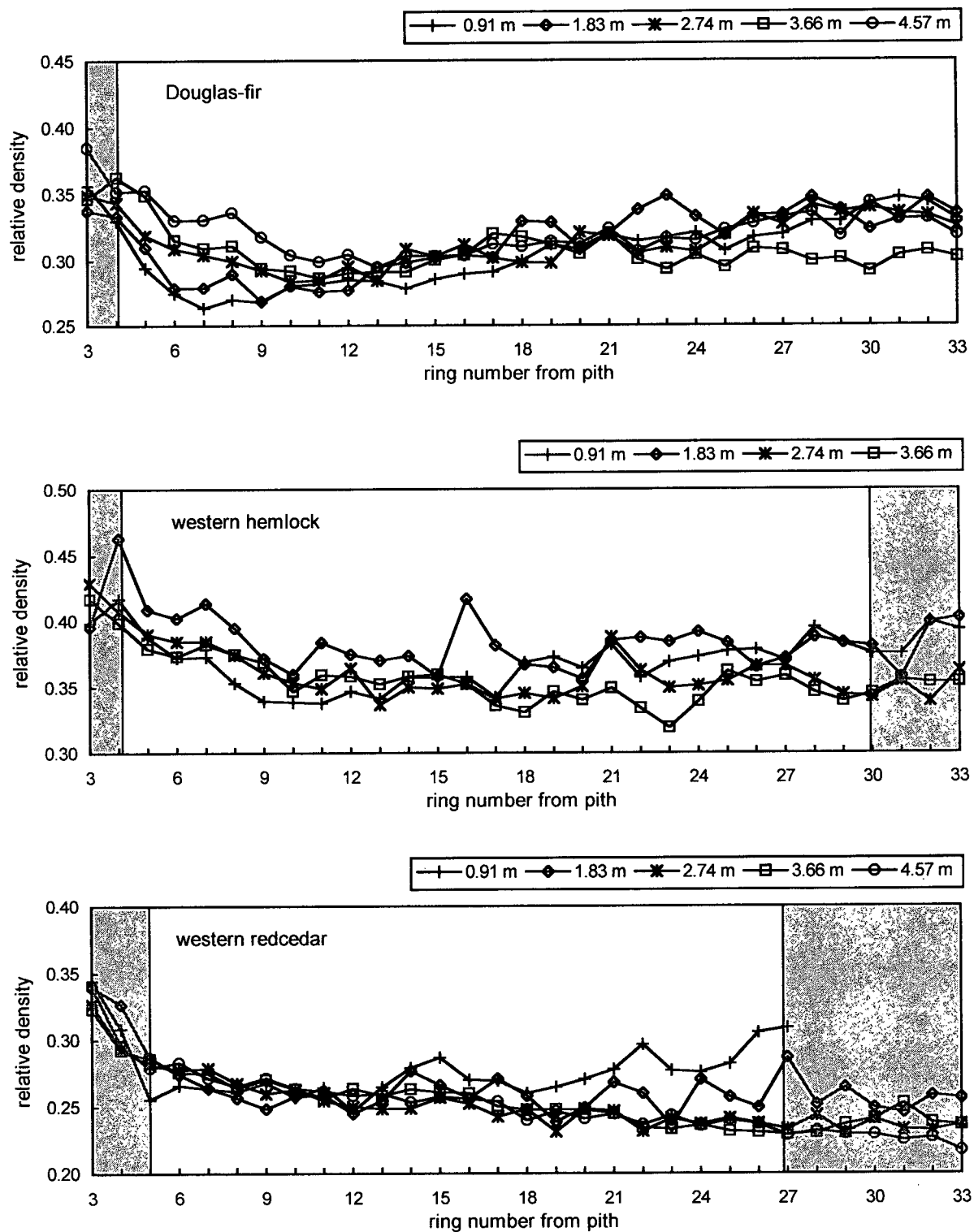


Figure 4.9 Mean earlywood relative density profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

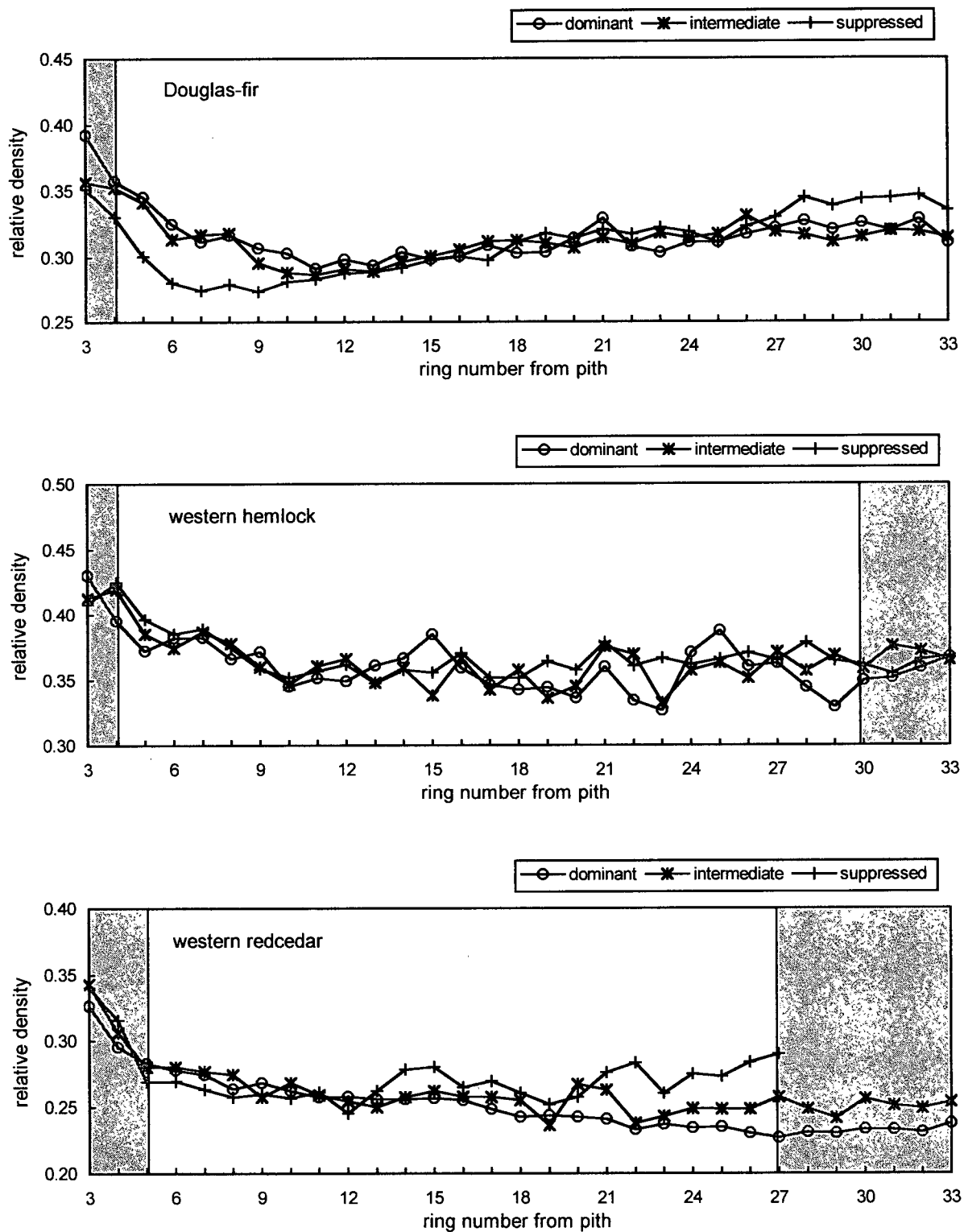


Figure 4.10 Mean earlywood relative density profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

Maximum earlywood relative density for each species was observed immediately next to the pith. These high values can perhaps be linked to the presence of compression wood and also, to the particular morphology demonstrated by these first-formed tracheids. Earlywood tracheids are typically shortest next to the pith, resulting in an increased number of cross-walls per unit of wood. More importantly, these first-formed earlywood tracheids are much smaller in radial diameter than in succeeding growth rings. Smaller radial diameters correspond to a greater proportion of cell wall per unit of volume and consequently, to a higher relative density (Megraw 1986, Kennedy 1995). The relative density of the wood substance which constitutes the cell wall of any tracheid approximates 1.5 g/cm³ in the oven-dry state. Little variation about this value exists both within and between species. Generally speaking, the larger the lumen diameter and the thinner the cell walls, the lower the relative density recorded (Panshin and de Zeeuw 1980).

Erickson and Harrison (1974) measured earlywood tracheid diameter variability at breast height within 30-year-old Douglas-fir. Hyperbolic increases in value were observed over time in both the radial and tangential directions. Radial diameter values increased sharply from a mean value of 25 μm near the pith, to almost 40 μm by ring 16. Tangential diameter values showed a more moderate increase, from a mean value of 22 μm near the pith, to almost 32 μm at ring 12. Diameter measurements following these rings displayed only moderate increases in value along both planes. Little information exists with regard to earlywood tracheid diameter development, both radially and tangentially, for western hemlock and western redcedar. The mean values that are offered in the literature serve mostly to differentiate between earlywood and latewood, but fail to describe the effects of time and growth rate on the variability of development within each wood type.

Conifer tracheids generally display a gradual increase in cell wall thickness from the pith outward. Increases ranging from 15 to 70 % may be observed for latewood tracheids during the first 30 years of growth. Smaller, more variable increases in cell-wall thickness may be observed for earlywood tracheids over the same time period (Larson 1966). Generally speaking, earlywood cell-walls are thinner radially than tangentially. For latewood tracheids, the radial cell-wall is normally thicker (Panshin and de Zeeuw 1980).

Little information is available with regard to earlywood cell wall thickness development for

Douglas-fir, western hemlock and western redcedar. The effects of cambial ageing and growth rate on such development remains largely unknown. Many of the studies that do report mean earlywood and latewood values offer little indication as to where sampling was conducted in terms of distance from the pith, and location within a growth ring. The data that are available most often corresponds to the radial plane only. Obtaining radial and tangential cell-wall thickness measurements, along with corresponding data on earlywood tracheid diameter development, would account for much of the earlywood relative density variation observed in this study. Furthermore, this information would allow for the establishment of relationships between the various patterns of earlywood development identified in each tree, with the various changes displayed in crown morphology and competitive status over time.

With the profiling of earlywood tracheid diameter and cell-wall thickness development from pith to bark, the following assumptions regarding earlywood relative density development could in turn be verified. An initial hyperbolic increase in tracheid diameter, coupled with an almost linear rate for increase in cell wall thickening, would partially account for the initial decrease in earlywood relative density displayed by each species. For Douglas-fir, the eventual stabilisation in tracheid diameter development (Erickson and Harrison 1974) would have to be accompanied by an increase in the rate of cell-wall thickening to produce the subsequent increase in earlywood relative density. In the case of western hemlock, the eventual stabilisation of tracheid diameter and cell wall thickening would have to occur at about the same time to produce a somewhat constant earlywood relative density. In the case of western redcedar, very little increase in the magnitude of cell wall thickening would have to occur from the pith. The production of increasingly larger tracheid diameters would subsequently bring about a decrease in earlywood relative density. An eventual stabilisation of tracheid diameter would in turn produce relatively stable values.

Of interest in Figure 4.9 is that a lower minimum relative density was observed for Douglas-fir at the narrower spacings, and a higher minimum value at the wider spacings. Such differences can perhaps be explained on the basis of fusiform initial cell development. An increase in rate of diameter growth within a young tree typically requires a rapid expansion of the vascular cambium. This expansion is accomplished primarily through an increase in the number of fusiform initials. The faster the rate of anticlinal cell division, the shorter the average length, and the narrower the tangential

diameter of the daughter initials produced (Bannan 1967a, Philipson and Butterfield 1967). It can therefore be assumed that larger tangential tracheid diameters and longer tracheid lengths developed at the narrower spacings first, where cambial growth was slower. A direct consequence of these slightly longer and wider earlywood tracheids was a lower earlywood relative density. This assumption, regarding changes in tracheid morphology as a function of growth rate, would have to be verified for each species using microscopy.

The suppressed taper class for Douglas-fir and western redcedar demonstrated slight increases in earlywood relative density during the final years of development. Earlywood width development at this time was demonstrating an important reduction in activity (Figure 4.4). Live-crown-ratios (especially for western redcedar) were extremely low, and crown widths were especially narrow (Table 4.2). The trees sampled generally displayed extended translocation pathways, and presumably a smaller capacity for auxin synthesis. A decrease in earlywood tracheid radial diameter, along with little corresponding change in cell wall thickness, was likely underway. A large number of transition wood tracheids were subsequently being produced within the earlywood zones, leading to an increase in overall earlywood relative density. Once again, these changes in tracheid radial diameter, and in cell-wall thickness, would have to be verified for both species using microscopy.

Basic statistics for earlywood relative density are presented by initial spacing in Table 4.20a (Appendix I), and by taper class in Table 4.21a (Appendix I). The mean values observed by species varied little as a function of initial spacing or taper class. Coefficient of variation values were slightly greater at the narrowest spacings for both Douglas-fir and western redcedar, and remained relatively stable for western hemlock. Slightly greater coefficient of variation values were displayed by the suppressed taper class for all species.

Results of the repeated measures analyses conducted on earlywood relative density, and as a function of initial spacing and taper class, are presented in Tables 4.20b and 4.21b, respectively (Appendix I). Time effects were highly significant for all species. The spacing x ring interaction for Douglas-fir was significant ($p = 0.0332$) using Greenhouse and Geisser's eps, and highly significant ($p = 0.0094$) using Huynh and Feldt's eps. The taper class x ring interaction invariably produced highly significant results. Non-significant treatment effects were obtained in each case. Non-

significant interactions and treatment effects were obtained for western hemlock as a function of both initial spacing and taper class. Highly significant spacing x ring and taper class x ring interactions were obtained for western redcedar. Non-significant treatment effects were obtained in each case.

An increase in available growing space had little effect on the development of earlywood relative density. The mean levels recorded over time for Douglas-fir, western hemlock and western redcedar did not differ as a function of either initial spacing or taper class. Parallel profiles were furthermore identified for western hemlock. Such results imply an identical pattern of earlywood relative density development for all spacings and taper classes considered. Non-parallel profiles were identified for both Douglas-fir and western redcedar. The narrowly-spaced, suppressed taper class trees were undergoing intensified levels of competition. A steep drop in earlywood relative density from the pith was being followed by a more-or-less continual increase in value over time. The widely-spaced, dominant taper class trees were displaying a more gentle initial drop in value, followed by greater stability during subsequent earlywood relative density development.

The relationships observed between earlywood relative density and ring width are displayed for Douglas-fir, western hemlock and western redcedar in Tables 4.22, 4.23 and 4.24 (Appendix I), respectively. Very weak relationships were generally obtained for all species. A certain increase in earlywood relative density for Douglas-fir was generally associated with faster growth between rings 6 and 9. A certain decrease was observed from ring 25 onward. However, the relationships obtained during these periods remained weak, accounting for only 15 to 45 % of total variability. The relationships obtained for western hemlock were consistently weak and, except for ring 21, non-significant. Results for western redcedar were equally weak. Non-significant relationships were generally identified. The few significant results intermittently obtained between rings 14 and 28 generally provided poor fits, accounting for only 15 to 43 % of total variability.

4.3.6 Latewood Relative Density

Mean latewood relative density development is illustrated by initial spacing in Figure 4.11, and by taper class in Figure 4.12. Douglas-fir displayed the greatest overall increase in latewood

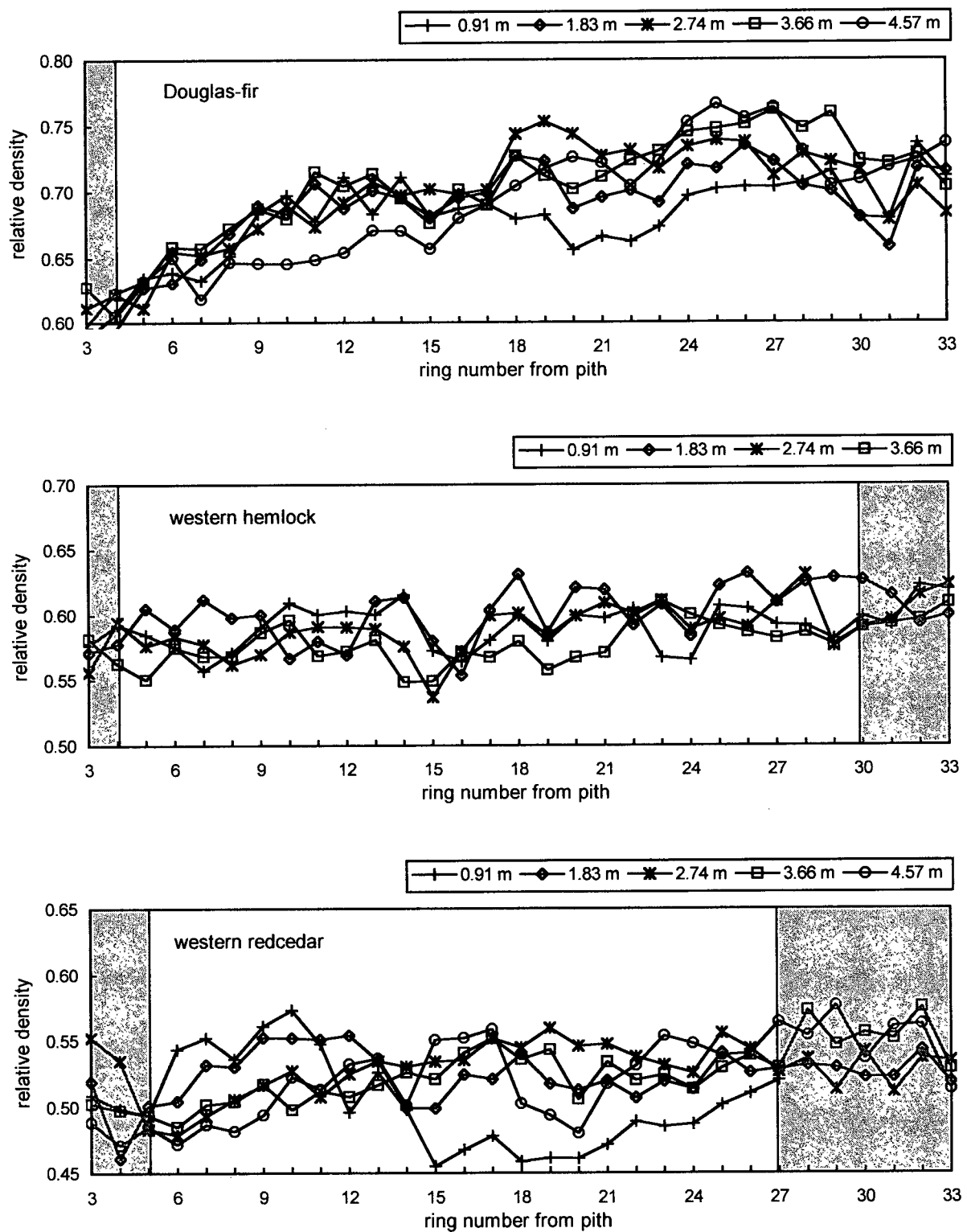


Figure 4.11 Mean latewood relative density profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

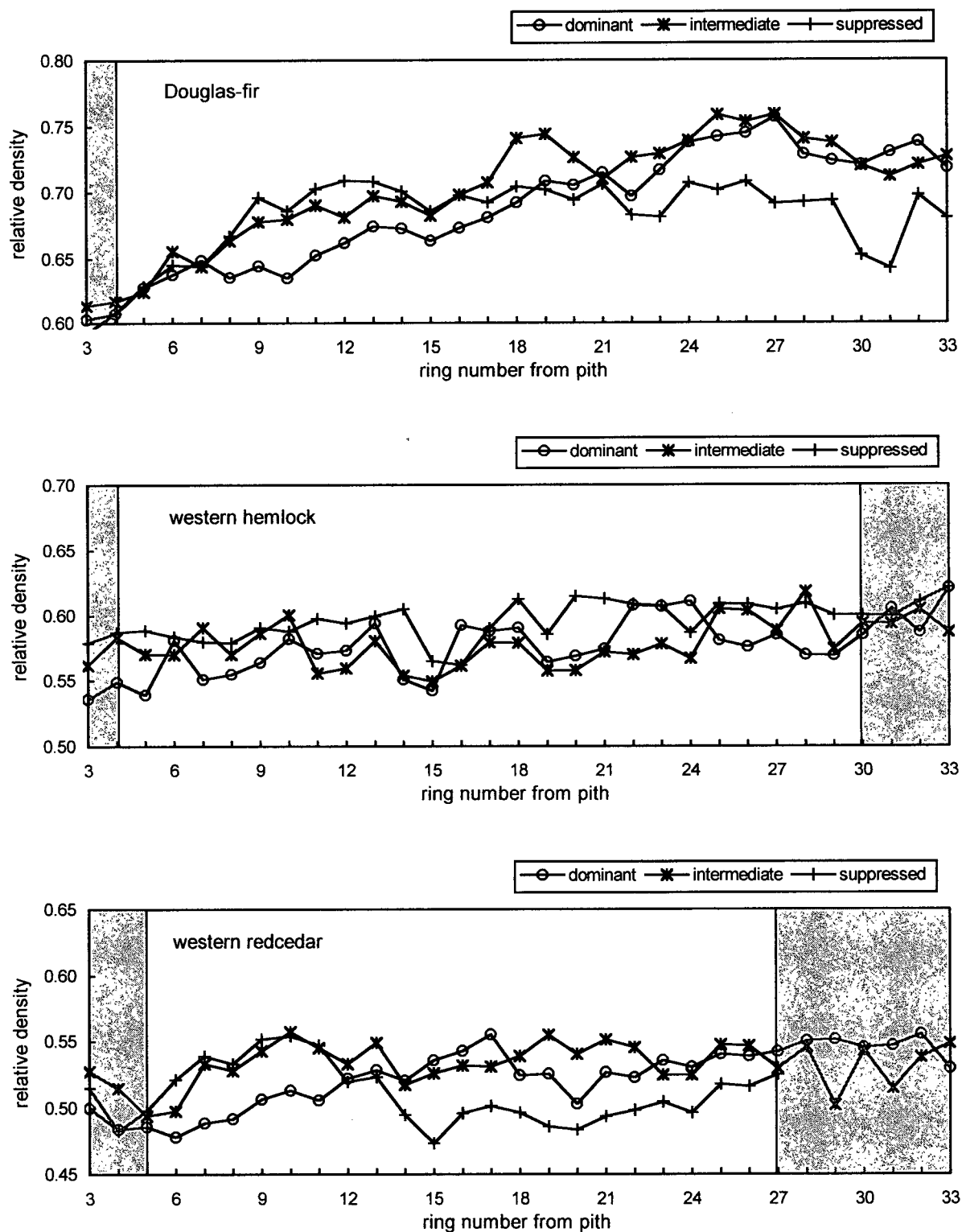


Figure 4.12 Mean latewood relative density profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

relative density over time. All profiles demonstrated a rapid initial gain from the pith, followed by a gentle increase to a more or less constant value. The 4.57 m spacing and the dominant taper class both experienced the slowest, yet steadiest initial increase. Relatively stable values within the narrower spacings, and within the suppressed taper class, were attained at an earlier date and at a lower average value. Western hemlock demonstrated the least variation. Profiles for both spacing and taper class remained largely superimposed on one another and demonstrated very little change over time. In the case of western redcedar, only a minor increase in latewood relative density was observed from pith to bark at the wider spacings and within the dominant taper class. The 0.91 and 1.83 m spacings, and the suppressed taper class, did experience slightly greater initial increases to about ring 10, followed by sharp decreases to about ring 15, and more-or-less stable values thereafter.

It was noted in section 4.2.5 that little information was available regarding earlywood tracheid diameter development for Douglas-fir, western hemlock and western redcedar. Little concurrent information is also available in terms of latewood diameter development, both radially and tangentially. Such information, along with corresponding data on latewood cell wall thickness, would account for most latewood relative density variation observed in this study. This information would also allow for the verification of the assumptions made in the forthcoming discussion regarding the effects of age and growth rate on transition wood and latewood tracheid development. Combined, the earlywood and latewood tracheid morphological data would explain much of the variation in whole-ring relative density that exists from pith to bark. This information would, in turn, allow for the establishment of stronger links between the various identified patterns of wood formation, and the various changes in crown morphology and competitive status displayed over time.

A great quantity of radially wide tracheids are generally produced throughout the growing season by a young tree at time of crown closure. Toward the end of the growing season, some of these tracheids may display thickened cell walls, hence transition wood (see section 4.2.3). If tracheid radial diameter at this time also displays a certain decrease in breadth, the transition wood produced will begin to contribute to overall latewood development. The earlywood to latewood boundary was set in this study at a relative density of 0.54 for Douglas-fir, 0.52 for western hemlock and 0.44 for western redcedar. In order to profile relative density development, transition wood for all species was subsequently classified under this criteria as either earlywood or latewood. A large quantity of

transition wood, displaying a relative density slightly greater than a value listed above, would therefore have lead to a slight decrease in mean overall relative density within a corresponding latewood increment. In turn, a large quantity of transition wood, displaying a value slightly lower than one listed above, would have brought about a slight increase in mean overall relative density within a corresponding earlywood increment.

The production of transition wood within a tree may carry on indefinitely. A minimum amount is generally produced within all growth increments. Roughly speaking, the slower the rate of crown recession, the longer the period during which large quantities of transition wood will be produced in successive growth rings at breast height. With time, and with continuing crown recession, an increasingly sharper drop in auxin gradients at breast height will be observed following the cessation of height growth (Larson 1969). An increasingly sharp decline in tracheid radial diameter development will typically follow within the latewood zone. Cell wall thickening at this time will proceed largely unaffected, so long as the respiration needs within the tree are met. Fewer transition tracheids will accordingly be produced, and a greater number of latewood tracheids will develop. The mean relative density recorded within the latewood zone will therefore increase, and an increasingly abrupt transition from earlywood to latewood will take shape.

The development of latewood relative density within the wider spacings and dominant taper class, for both Douglas-fir and western redcedar, was gradual when viewed from pith to bark. The presence of large quantities of transition wood within the first few growth rings may have accounted for the initially low values. The progressive changes observed over time, from a gradual to an abrupt earlywood to latewood transition, would account for the slow, yet steady rise in value. An abrupt transition, coupled with the formation of mostly latewood tracheids within each latewood zone, would account for the high values at which latewood relative density eventually plateaus. The profiles displayed for western redcedar illustrated a much more gradual increase in value over time. This was perhaps partially due to the greater shade tolerance displayed by the species. Crown recession for western redcedar was much slower than for Douglas-fir (Reukema and Smith 1987). Translocation pathways from the base of the live crown to breast height were much shorter (Tables 4.1 and 4.2). The changes observed in wood formation over time, and subsequently in the progression from a gradual to an abrupt intra-ring relative density transition, were likely tempered.

A steeper initial rise in latewood relative density was displayed by the narrower spacings and by the suppressed taper class for both Douglas-fir and western redcedar. This rapid increase can perhaps be attributed to an earlier date for crown closure, and accordingly, to smaller tree crowns and to longer translocation pathways. It is therefore presumable that a sudden drop in auxin gradients at breast height occurred first within these slower growing trees. A corresponding decrease in transition wood production also presumably occurred first, with an increasingly greater proportion of latewood tracheids produced within each subsequent latewood zone. The progression from a gradual to an abrupt intra-ring relative density transition within these trees was, in effect, taking place at a faster pace.

The lower steady-state values observed within the narrower spacings and by the suppressed taper class for both Douglas-fir and western redcedar during the final years of development can perhaps be attributed to an intensification in competition. A return to the production of large quantities of transition wood within the latewood zones was conceivably taking place. A continual decrease in the ratio of crown attributes to total tree size was influencing the pattern of wood formation displayed at breast height. Crown sizes for both species remained small, and the distance from breast height to crown base was increasing (Tables 4.1 and 4.2). Auxin gradients within the vascular cambium at breast height were therefore presumably in a continual decline. Photosynthate availability was also presumably in sharp decline due to ever increasing demands for maintenance respiration. The potential for further increases in both auxin and photosynthate synthesis within these trees was limited. With minimal auxin and photosynthate availability, tracheids produced within the latewood zones remained radially narrow, and cell walls remained thin. The latewood relative density observed subsequently fell short of that recorded by the faster growing trees.

Latewood relative density varied little for western hemlock as a function of either time, initial spacing or taper class. This lack of variability can perhaps be attributed to the gradual transition from earlywood to latewood that typically develops for the species regardless of cambial age or growth rate (Panshin and de Zeeuw 1980). Since transition tracheids are continually produced, less variability in latewood relative density will be observed over time. Crown recession for the species was, in addition, very slow for all spacings and taper classes considered. Large volumes of crown foliage, and a relatively short distance from breast height to crown base, were typical of most trees

sampled (Tables 4.1 and 4.2). Such factors may have compounded the effects of the species' natural inclination to develop a gradual transition from earlywood to latewood and therefore, to produce comparatively stable latewood relative density values over time.

Basic statistics for latewood relative density are presented as a function of initial spacing in Table 4.25a (Appendix I) and as a function of taper class in Table 4.26a (Appendix I). The mean and coefficient of variation values observed for each species varied little according to both initial spacing and taper class. The greatest homogeneity encountered was within and among the various initial spacings and taper classes sampled for western hemlock.

Results of the repeated measures analyses conducted on latewood relative density, and as a function of initial spacing and taper class, are presented in Tables 4.25b and 4.26b respectively (Appendix I). Highly significant time effects were obtained for all species during the initial spacing analysis. Highly significant time effects were obtained during the taper class analysis for Douglas-fir only. Significant effects were obtained in the case of western redcedar. Non-significant (Greenhouse and Geisser) and significant time effects (Huynh and Feldt) were obtained for western hemlock. For consistency, time effects will nonetheless be considered for all species in forthcoming regression and correlation analyses. A non-significant spacing x ring interaction, and a significant ($\alpha = 0.05$) taper class x ring interaction, was obtained for Douglas-fir. Non-significant spacing x ring and taper class x ring interactions were obtained for western hemlock. The spacing x ring and taper class x ring interactions for western redcedar were both highly significant. Treatment effects for all species were consistently non-significant.

An increase in available growing space had little effect on the development of latewood relative density. The mean levels recorded over time for Douglas-fir, western hemlock and western redcedar did not differ as a function of either initial spacing or taper class. Parallel profiles were identified for western hemlock. Ring number from pith, by taper class, was identified as having little impact on latewood relative density development. Such results imply an identical, somewhat horizontal, pattern of development for all spacings and especially, for all taper classes considered. Non-parallel profiles were identified for western redcedar. The narrowly-spaced, suppressed taper class trees were undergoing intensified levels of competition. A rapid initial increase in latewood

relative density was being followed by a sharp decrease, and then by comparatively stable values. The widely spaced, dominant taper class trees were displaying a gradual initial rise in latewood relative density, followed by relatively stable values.

Parallel profiles were identified for Douglas-fir as a function of initial spacing, and non-parallel profiles (borderline, $p = 0.0240$) were identified as a function of taper class. Such results demonstrate the increasing effect of tree-to-tree competition, and the decreasing effect of initial spacing, on tree development over time, and on subsequent wood formation. The intensified levels of competition resulted in a sharper initial gain in latewood relative density by the suppressed taper class trees. Steady-state values were eventually attained by these same trees, but at a lower maximum level relative to that displayed by the intermediate and dominant taper classes.

The effect of ring width on latewood relative density development is presented for Douglas-fir, western hemlock and western redcedar in Tables 4.27, 4.28 and 4.29 (Appendix I), respectively. Correlation coefficients for Douglas-fir were generally low, but negative, between rings 3 and 18, and generally low, but positive, from ring 19 onward. Slightly lower relative density values were therefore associated with the wider growth rings near the pith, and slightly higher relative density values were generally associated with the wider growth rings near the bark. The best regression fits were obtained from ring 24 onward. From 17 to 48 % of total latewood relative density variation was associated with ring width during this period. The relationships obtained for western hemlock were largely non-significant. Small amounts of latewood relative density variability were associated with ring width development during early development, with coefficient of determination values never surpassing a maximum of 0.44. A string of significant results was observed for western redcedar between rings 5 and 11, and between rings 15 and 17. From 17 to 41 % of total latewood relative density variation during these periods was associated with ring width. Correlation coefficients were for the most part moderately negative up to about ring 14, implying slightly lower latewood relative density values with the wider growth rings next to the pith.

4.3.7 Whole-Ring Relative Density

Mean whole-ring relative density development is presented by initial spacing in Figure 4.13, and by taper class in Figure 4.14. Similar profiles were obtained for Douglas-fir by Wellwood and Smith (1962), Erickson and Harrison (1974), Jozsa and Kellogg (1986), Megraw (1986), Jozsa *et al.* (1989) and Jozsa and Middleton (1994). Similar profiles were obtained for western hemlock by Wellwood and Smith (1962), Jozsa and Kellogg (1986), Jozsa and Middleton (1994) and Jozsa *et al.* (1998). Similar profiles were obtained for western redcedar by Jozsa and Kellogg (1986) and Jozsa and Middleton (1994).

A similar pattern of whole-ring relative density development for Douglas-fir was generally displayed by all spacings and taper classes. A slight decline in value from the pith, to a minimum between rings 6 and 7, was initially displayed by all profiles. A steady increase in value followed, with a general levelling-off initiated at about ring 20. Whole-ring relative density development for western hemlock demonstrated greater variability. A steep decline was initially demonstrated by all profiles to about ring 10. Values within the 3.66 m spacing and within the dominant taper class oscillated thereafter, but generally demonstrated no subsequent gains. Increases in whole-ring relative density within the 0.91, 1.83 and 2.74 m spacings were initiated beginning at about ring 15. Values within the intermediate and suppressed taper classes also increased progressively from this point onward, with the latter demonstrating the largest gains over time. Western redcedar, though initially comparable to both Douglas-fir and western hemlock, displayed the steepest initial decline in whole-ring relative density to about ring 5. Few subsequent changes were observed within the 2.74, 3.66 and 4.57 m spacings, and within the dominant taper class. A gradual increase in value followed within the 0.91 and 1.83 m spacings. Similar increases were noted by the intermediate taper class. The largest gains over time were displayed by the 0.91 m spacing and by the suppressed taper class.

Basic statistics for whole-ring relative density are presented as a function of initial spacing in Table 4.30a (Appendix I), and as a function of taper class in Table 4.31a (Appendix I). The mean values observed for Douglas-fir were invariably greater than those obtained for western hemlock, and much greater than those obtained for western redcedar at corresponding spacings and taper classes. Mean relative density for Douglas-fir varied little as a function of initial spacing and taper class.

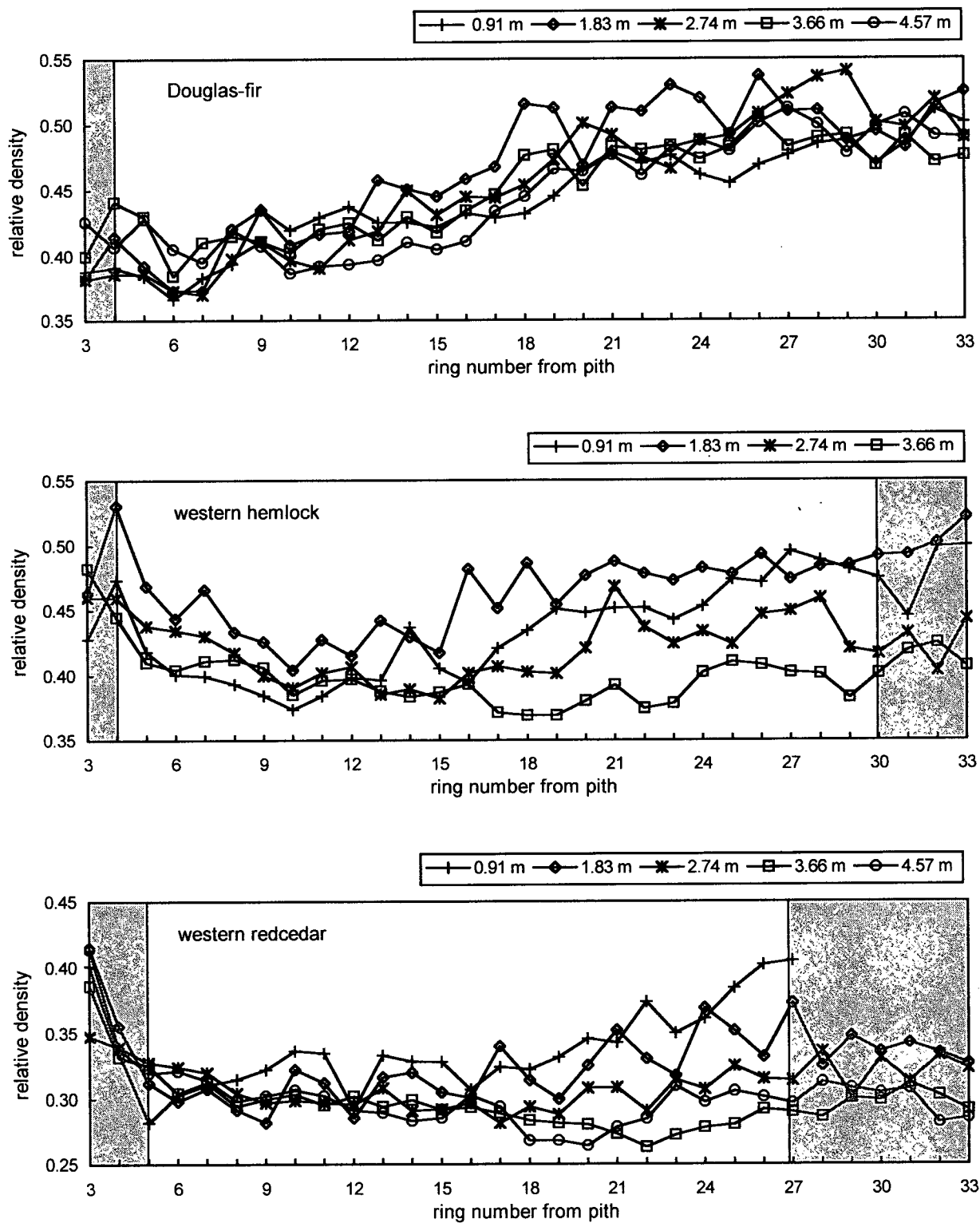


Figure 4.13 Mean whole-ring relative density profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

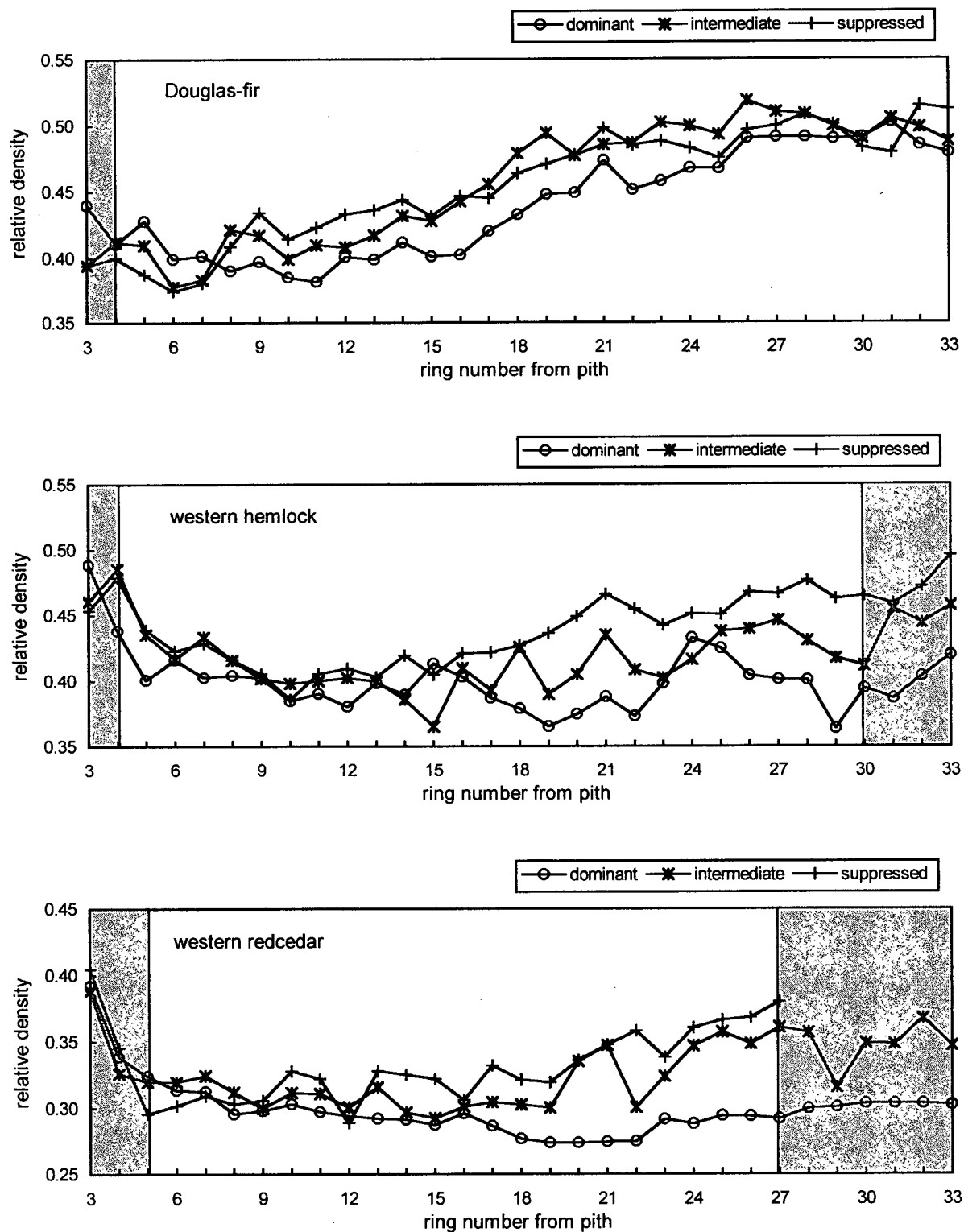


Figure 4.14 Mean whole-ring relative density profiled by taper class and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

Slightly higher mean values were observed for both western hemlock and western redcedar at the narrower spacings and within the suppressed taper class. Coefficient of variation values varied little for both Douglas-fir and western hemlock. Somewhat higher values were observed for western redcedar as spacing narrowed and within the suppressed taper class.

Results of the repeated measures analyses conducted on whole-ring relative density, and as a function of initial spacing and taper class, are presented in Tables 4.30b and 4.31b, respectively (Appendix I). Time effects were highly significant for all species. Non-significant spacing x ring and taper class x ring interactions were obtained for both Douglas-fir and western hemlock. Treatment effects for Douglas-fir were equally non-significant. Those obtained for western hemlock were highly significant as a function of initial spacing, and non-significant as a function of taper class.

An identical pattern of whole-ring relative density development was accordingly identified for all Douglas-fir spacings and taper classes considered. An identical pattern of development was also identified for western hemlock, but as a function of taper class only. Nonparallel profiles, and highly significant treatment effects, were identified for the species by initial spacing. Such conflicting results largely stem from the extreme measurements obtained, at most growth ring sampling points, from trees #411 and #458 within the 1.83 m spacing interval. In addition, the average profile illustrated for the 1.83 m spacing in Figure 4.13 was based upon a sample of five trees. Tree #464 was not included due to large amounts of missing data. Consequently, the mean values plotted over time were consistently higher than at all other spacings. The average whole-ring relative density profile displayed for the suppressed taper class in Figure 4.14 was based upon a sample of 13 trees. The effect of the much greater values demonstrated by trees #411 and #458, on mean whole-ring relative density development, were subsequently tempered once integrated into this data set.

The spacing x ring and taper class x ring interactions for western redcedar were both highly significant. Significant and highly significant treatment effects were obtained by initial spacing and taper class respectively. Nonparallel whole-ring relative density profiles were accordingly identified as a function of both initial spacing and taper class. The widely-spaced, dominant taper class trees demonstrated little subsequent rise in whole-ring relative density following the initial decrease in value from the pith. Significantly lower mean values were recorded over time for these trees. The profiles

established for the narrowly-spaced, suppressed taper class trees demonstrated a steeper initial drop in value from the pith, followed by a gradual increase over time. Significantly higher mean values were recorded over time for these trees.

The effects of ring width on whole-ring relative density are presented in Tables 4.32, 4.33 and 4.34 (Appendix I) for Douglas-fir, western hemlock and western redcedar, respectively. Although results for Douglas-fir were generally significant, most equations fit poorly. Strong relationships were obtained from rings 8 to 16, but with coefficient of determination values never surpassing a high of 0.40. In the case of western hemlock, ring width had a slightly increasing negative impact on whole-ring relative density development over time. If one discounts rings 31 to 33 (smaller sample size), a pattern of increasing significance was observed with age. Results from rings 3 to 17 were for the most part non-significant, or significant at the $\alpha = 0.05$ level only. Strong relationships were obtained from rings 18 through 29, with 14 to 55 % of total variation attributable to ring width during this period. Western redcedar displayed the strongest overall relationships, with regression equations for the most part significant from ring 13 onward, and with 38 to 62 % of total variation attributable to ring width during this period. Slopes and correlation values became increasingly negative with distance from the pith. A decrease in whole-ring relative density over time was therefore increasingly associated with an increase in ring width development.

4.3.8 Whole-Ring Tracheid Length

Sampling variability for earlywood and latewood tracheid length is summarised in Tables 4.35, 4.36 and 4.37 (Appendix I) for Douglas-fir, western hemlock and western redcedar, respectively. All values were obtained by means of image analysis. Tracheid length variability was estimated based on a potential sample pool of 240 measurements (6 trees per spacing, 40 tracheid measurements per growth ring sampling point). Similar tracheid length statistics, obtained by means of the Kajaani FS-200 Optical Fibre Analyser, are presented in Tables 4.38, 4.39 and 4.40 (Appendix I) for Douglas-fir, western hemlock and western redcedar, respectively. A single length-weighted mean value was calculated for each earlywood and latewood segment processed. Tracheid length variability for the Kajaani was therefore available based on a maximum of six values only.

The mean latewood tracheid length values observed in Tables 4.35, 4.36 and 4.37 were, for the most part, greater than those listed for earlywood. Increases in length of up to 15 % were observed in certain cases. Data collected for both wood types were subsequently compared at each growth ring sampling point, and at identical spacings, using a standard t-test for differences between two means. Positively significant differences were identified for 42 % of the growth rings sampled for Douglas-fir, 55 % for western hemlock and 76 % for western redcedar. These results justify the use of Equation 1 for estimating whole-ring tracheid length.

The earlywood and latewood data sets described in Tables 4.35 to 4.40 remained incomplete in instances where growth rings sampled were too narrow for accurate splintering by razor blade. A mean tracheid length value for the entire growth ring in question (earlywood and latewood sampled collectively) was obtained in such cases. These measurements were added to those previously estimated using Equation 1. Complete whole-ring tracheid length data sets (rings 3 through 33) were subsequently acquired for each spacing interval considered.

Mean whole-ring tracheid length development is illustrated by initial spacing in Figure 4.15. Dual sets of plots were established for each spacing interval to accommodate the two measurement methods used. The tracheid length relationships observed as a function of time are well documented in the literature. A relatively rapid increase in value was initially displayed by each species, followed by a gradual decrease in rate of development. Relatively stable whole-ring tracheid length values began to appear during the final years of growth.

Successive dips and rises were identified in many profiles using both measurement systems. A precise depiction of tracheid length development was accordingly provided by species. Greater accuracy was nonetheless obtained through image analysis. Only long, intact tracheids were considered during sampling. The Kajaani based profiles invariably demonstrated lower mean values throughout. Whole-ring tracheid length was gravely underestimated using this procedure. The longer the mean tracheid length value obtained through image analysis, the greater the discrepancy. Data collected using both systems were subsequently compared at each growth ring sampling point, and at identical spacings, using a standard t-test for differences between two means. Highly significant differences ($P \leq 0.001$) were obtained in all cases (data not shown).

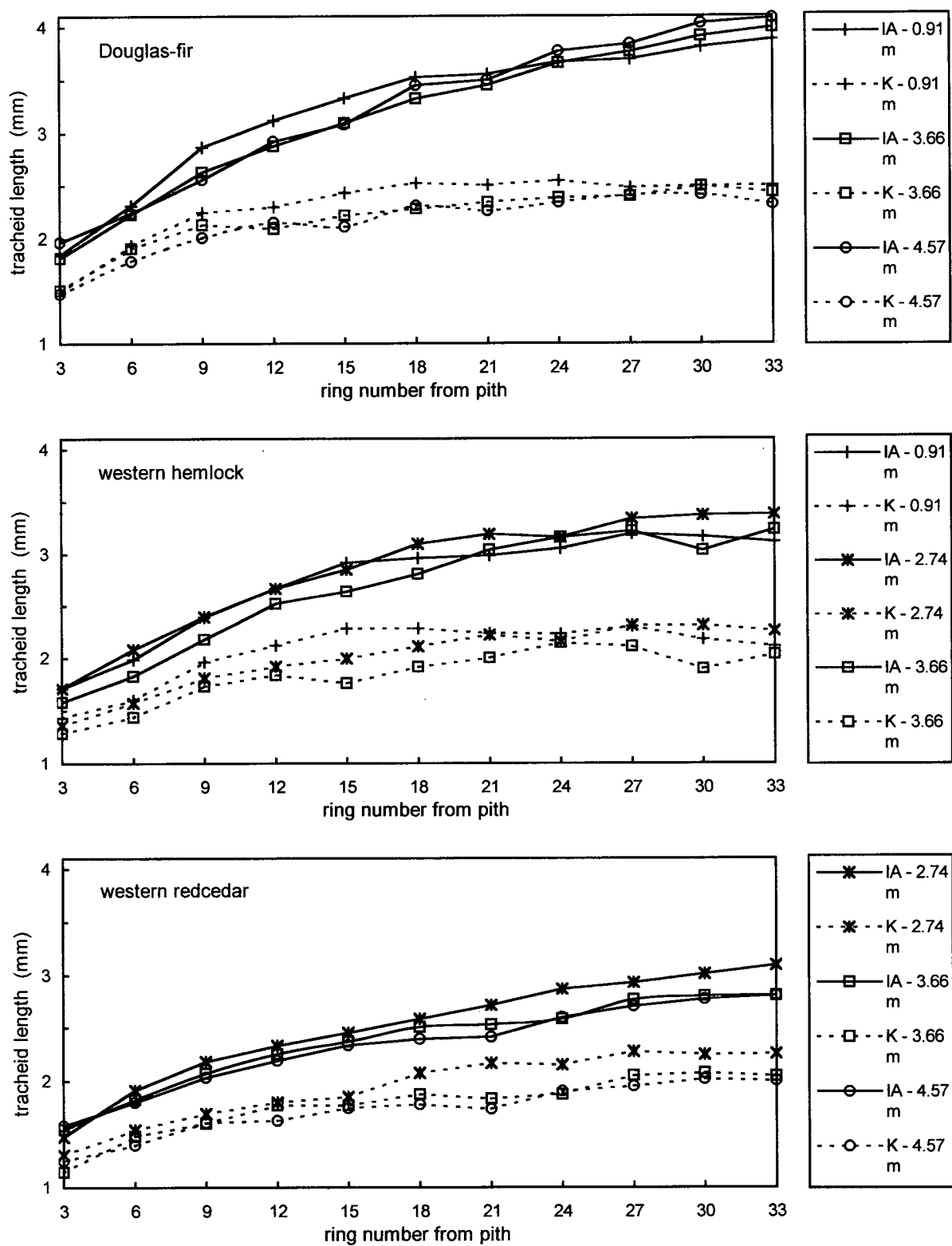


Figure 4.15 Mean whole-ring tracheid length (mm) measured using 1) image analysis (IA) and 2) the Kajaani FS-200 Optical Fibre Analyser (K). Profiles established by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

The length-weighted formula applied to the Kajaani data was therefore ineffective for masking the influence of the large number of broken tracheids processed. The length-weighted formula applied has repeatedly been used in previous research for Kajaani-based tracheid length analysis (Pirainen 1985, Hamm 1989, Hatton and Hunt 1989, Luukkonen *et al.* 1990, Bergqvist *et al.* 1996, Evans *et al.* 1997, Herman *et al.* 1998, Muneri and Balodi 1998). The weighting of tracheid length data by a second power, as performed in this study, is recommended as standard procedure by the manufacturer (Kajaani Electronics Ltd. 1986). However, the use of a third, or even a fourth power, would certainly have produced results more in line with those obtained through image analysis.

Tracheid length variability was non-destructively assessed using 12 mm increment cores. The limited dimensions of these cores may have introduced two possible sources of error that could have lead to an underestimation of tracheid length by the Kajaani system. Firstly, it is obvious that a large number of tracheids were cut during increment boring. Even though 12 mm core samples were collected, and only the central portions of these were macerated, the processing of a large number of damaged elements within the Kajaani was unavoidable. Secondly, the greater the mean length of the tracheids being sampled, the greater the probability that they would incur damage upon increment core collection. Tracheid measurements obtained during the foregoing studies were conducted on the basis of either wood chips, or from cross-sectional discs (minimum 2 cm thickness) obtained by means of stem analysis (destructive sampling on both counts). Such wood samples presented a much lower proportion of broken tracheids per unit of wood volume macerated.

Few studies have evaluated the effectiveness of the Kajaani system for measuring tracheid length from increment cores. A notable exception was the research conducted by Bergqvist *et al.* (1996), which investigated the effects of radial increment core diameter on tracheid length measurement in Norway spruce. Rings 31 through 87 from a single, slow-growing log were sampled collectively, earlywood and latewood combined, with no longitudinal shearing of the core edges performed. Eight core samples were collected per core diameter considered, namely 4, 8 and 12 mm. Wood chips were used as a control. Approximately 13 % of all tracheids originating from the wood chips were characterised as damaged following maceration. About 31 % of those obtained from the 12 mm cores were likewise identified as such. Tracheid damage for the 4 and 8 mm diameter core samples approximated 70 and 44 %, respectively. The length-weighted mean values obtained from

the wood chips, and from each of the core diameters sampled, were significantly different. The smaller the core diameter, the greater the influence of broken tracheids on the estimation of a mean tracheid length. The length-weighted mean values obtained from the wood chips, and from the 12, 8 and 4 mm increment cores, equalled 3.06, 2.75, 2.62 and 2.20 mm, respectively.

It is difficult to pinpoint the various sources of error that could have led to the tracheid length differences illustrated in Figure 4.15. The maceration procedure employed in this study (Franklin's solution) has long been used for breaking down wood samples into individual tracheids. The Kajaani system itself was initially calibrated using the recommendations and calibration fibres provided by the manufacturer (Kajaani Electronics Ltd. 1986). A weakness of the system is perhaps the 0.4 mm diameter capillary tubing (also designed to handle hardwood vessel elements) which sometimes allows overlapping tracheids to be simultaneously processed. A maximum tracheid length value of 7.2 mm (the largest length class recordable by the instrument) may accordingly be observed. Tracheid lengths exceeding 6.0 mm were commonly encountered. Such lengths go well beyond the ranges normally identified for the three species considered. Additionally, it is easy to imagine a single long tracheid being measured at half its true length as a result of folding in the middle. This scenario is conceivable in a situation where a tracheid is fed into the capillary tubing midriff first. The fact that the majority of tracheids sampled in this study were juvenile attests to a generally thin cell wall structure. The thinner the tracheid cell wall, the greater the likelihood of such folding. No method of verification was proposed by the manufacturer to identify and/or eliminate such measurements.

Along with broken tracheid sections and midriff folding, a shorter mean tracheid length could also have originated from the inclusion of ray tracheid measurements within the individual data sets. Ray tracheids normally make up from about 5 to 9 % of total wood volume for the three species considered in this study (Panshin and de Zeeuw 1980). These cells normally range from about 0.1 to 0.2 mm in length (Tsoumis 1991). The Kajaani system records tracheid length measurements within 0.2 mm classes, ranging from 0.0 to 7.2 mm. Since the Kajaani system is unable to distinguish between individual cell types, ray tracheids are systematically treated as longitudinal tracheids. In certain cases, upward of 20 % of the tracheids processed for one growth ring were grouped within the first two classes alone (0.0 to 0.2 mm, 0.2 to 0.4 mm). Tracheid length distributions subsequently became heavily skewed toward the smaller classes, leading to an inevitable decrease in mean length.

The specific objective of this portion of the study was not to compare the effectiveness of the Kajaani system relative to image analysis. Each measurement method was designed with a distinct application in mind. Image analysis has long been used for obtaining accurate tracheid length measurements. It is the cheapest method available in terms of equipment expenditure. Only a microscope and eyepiece micrometer are required. The process of measurement however, is quite labourious and time-consuming. Simply obtaining 40 tracheid length measurements from a single growth ring sample in this study (slide preparation time included) often required more than one hour to complete. The Kajaani system was designed with industrial purposes in mind. The system is fully automated and does not require specific skills to operate. Large numbers of tracheid length measurements can be rapidly obtained. The measurement time for one growth ring sample in this study (minimum of 20 000 tracheids processed) generally fluctuated between three and five minutes.

The purpose of this exercise was to see if the Kajaani system could be used to obtain accurate tracheid length measurements from 12 mm increment cores. The prospect of being able to rapidly and accurately process such samples would further encourage non-destructive wood quality research. Based on the previous study conducted by Bergqvist *et al.* (1996), it was conceivable that accurate measurements could be obtained from 12 mm increment cores if sampling were conducted on a more discerning basis. Only the central portions of the increment cores collected would be retained for analysis. Care would be taken to produce the longest splints possible for subsequent maceration. The longitudinal edges of the cores would be sheared to eliminate as many damaged tracheids as possible.

As demonstrated in Figure 4.15, significantly shorter tracheid lengths were nonetheless obtained for each species, and at all growth ring sampling points, using the Kajaani system. The system was shown to be inadequate for measuring tracheid length variability on the basis of 12 mm increment cores. Only the tracheid length data collected as a function of image analysis were therefore considered during the subsequent initial spacing and growth rate analyses.

The general finding from past studies is that initial spacing has little impact on tracheid length development for conifers. Douglas-fir, western hemlock and western redcedar have all received little attention in the literature with respect to the above. Certain trends were nonetheless observed in this study (Figure 4.15). A slightly greater increase in whole-ring tracheid length was originally

demonstrated by the 0.91 m spacing for Douglas-fir. The 3.66 and 4.57 m spacings both demonstrated slower initial development, but greater mean values toward the bark. In the case of western hemlock, somewhat shorter tracheids were produced at the 3.66 m spacing up to about ring 21. A somewhat parallel pattern development was demonstrated for all western redcedar spacings considered. Generally speaking, the wider the spacing, the shorter the tracheid length produced.

Basic statistics for whole-ring tracheid length are presented in Table 4.41a (Appendix I). Longer tracheids were, without exception, produced by Douglas-fir, and shorter tracheids by western redcedar. The mean value recorded over time varied little according to initial growing space. Slightly lower values were observed for both western hemlock and western redcedar at the wider spacings. Coefficient of variation values remained fairly constant by species.

Results of the repeated measures analyses conducted on whole-ring tracheid length, and as a function of initial spacing, are presented in Table 4.41b (Appendix I). Time effects were highly significant for all species. A highly significant spacing x ring interaction and non-significant treatment effects were obtained for Douglas-fir. The narrower the spacing, the faster the initial increase in tracheid length from the pith, with longer tracheids produced by the wider spacings during the final years of development. In the case of western hemlock, the spacing x ring interaction and treatment effects were both non-significant. An identical pattern of development was subsequently identified for all spacings considered. Significant effects would perhaps have been obtained had the 4.57 m spacing been available for sampling. A non-significant spacing x ring interaction and significant treatment effects were obtained for western redcedar. All profiles were subsequently identified as parallel. The narrower the spacing, the lower the mean level recorded. A significant interaction effect would perhaps have been obtained had the 0.91 and 1.83 m spacings also been sampled.

The effects of ring width on whole-ring tracheid length development are presented in Table 4.42 (Appendix I). Very little variation in whole-ring tracheid length variability was generally associated with ring width. The relationships observed by species were generally non-significant. Most correlation coefficients remained low, and for the most part negative, indicating perhaps a slight reduction in tracheid length with increased growth rate. This was presumably the case for both Douglas-fir and western hemlock during early development.

4.3.9 Microfibril Angle

Sampling variability for microfibril angle is summarised in Table 4.43 (Appendix I). Each mean and standard deviation value was calculated based on a data set of 240 measurements (six trees per spacing, 40 microfibril angle measurements per growth ring sampled). All values were obtained from the earlywood portion of each growth ring selected. There were no missing values.

Mean microfibril angle development is illustrated according to initial spacing in Figure 4.16. The trends observed from pith to bark are similar to those generally reported for conifers in general (McMillin 1973, Erickson and Arima 1974, Megraw 1985, Cave and Walker 1994). Microfibril angle was greatest near the pith for all species. Values at the narrowest spacings, for both Douglas-fir and western redcedar, decreased more rapidly and began to stabilise earlier. A relatively stable microfibril angle was attained at about ring 12 in the case of the 0.91 m spacing for Douglas-fir, and at about ring 18 in the case of the 2.74 m spacing for western redcedar. The foregoing spacings both maintained lower values during the later years of development. All microfibril angle profiles displayed for western hemlock remained similar in shape and size over time. Mean values decreased rapidly during the initial years of growth, and continued to do so afterward, but at a much reduced rate.

Conducting microfibril angle measurements remains a time consuming procedure when performed using optical means. The process of obtaining 40 microfibril angle values from a single growth ring sample in this study (microtome slide preparation time included) often took over one hour to complete. Indirect methods were therefore sought in past studies for the purpose of estimation. Tracheid length was suggested as an obvious predictor, perhaps because of the ease through which such measurements could be obtained. Tracheid length development typically includes a rapid increase in value from the pith (Figure 4.15). A gradual decrease in rate of development generally follows, after which relatively stable values can be viewed. The above stated trend is more-or-less opposite to that illustrated for microfibril angle development in Figure 4.16.

Past studies have since pointed to the existence of a negative correlation between the two variables. The shorter the tracheid length for a particular species, the larger the microfibril angle recorded (Echols 1955, Dadswell 1958, Erickson and Arima 1974, Megraw 1985, Briggs and Smith

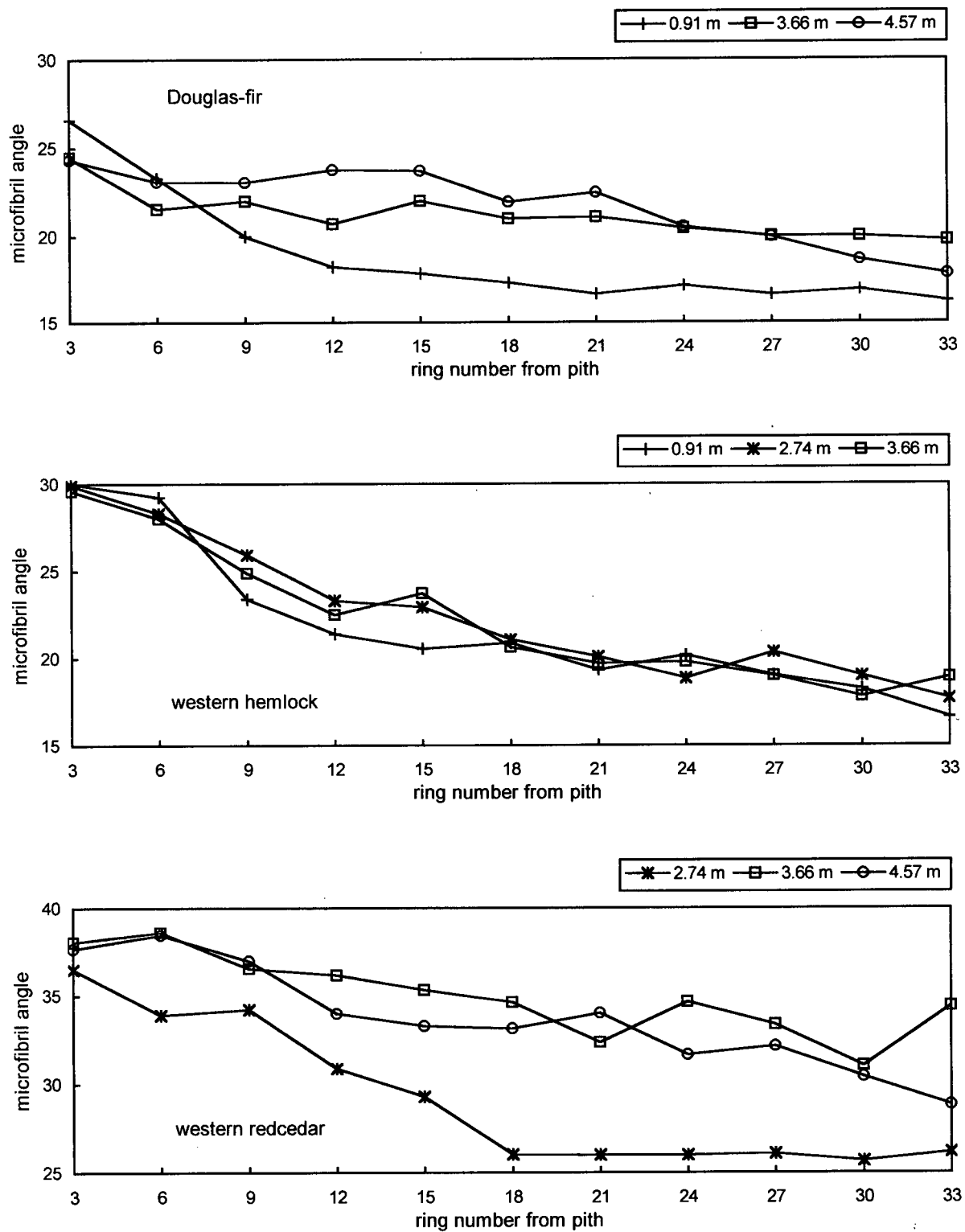


Figure 4.16 Mean microfibril angle profiled by initial spacing and as a function of ring number from pith for Douglas-fir, western hemlock and western redcedar.

1986). Even though the strength of the correlations varied widely from study to study, a cause and effect relationship between the two variables has nonetheless evolved over time. Such a relationship is frequently assumed and reported.

However, it remains unlikely that tracheid elongation is the main precursor to microfibril angle development. Though a correlation might exist between the two variables, the relationship is most likely haphazard. The reasoning behind this statement is that important increases in tracheid length are characteristic of the stage of post-cambial cell enlargement. Concurrent increases in tracheid radial diameter are also inherent to this stage of development. The deposition of microfibrils in accordance with the profiles illustrated in Figure 4.17 occurs largely during the subsequent stage of secondary wall formation. The lignification of the compound middle lamella is largely complete at this time, and further expansion of the cell is therefore limited (Fujita and Harada 1991). The term microfibril angle itself commonly refers to the mean helical angle observed within the S_2 layer of the secondary wall. This definition was common to all the wood quality and related studies reviewed during this research.

Cell-wall thickness would perhaps be a more logical choice for predicting microfibril angle, inasmuch as both variables are intimately linked to the stage of secondary wall development. A sinusoidal trend of decreasing microfibril angle is generally known to exist within a growth ring from earlywood to latewood (Cave and Walker 1994, Herman *et al.* 1999). A similar, but reverse trend, is known to exist for cell wall thickness. Higher microfibril angle values are generally associated with thin-walled, earlywood tracheids. Lower microfibril angle values are generally associated with thicker-walled, latewood tracheids (Panshin and de Zeeuw 1980).

Little information is available with regard to intra-ring microfibril angle development for Douglas-fir, western hemlock and western redcedar. Large amounts of variability undoubtedly exist for each species as a function of cambial age, and perhaps even growth rate. The limited microfibril angle data that is available most often comes in the form of single mean values generated from a collection of growth rings. Intra-ring profiles demonstrating microfibril angle variability over time are largely unheard of. Such information would be most useful for the establishment of relationships between the various patterns of microfibril angle development identified in a tree, with the various

changes in crown morphology and competitive status displayed over time. These data would also allow for the subsequent evaluation of cell wall thickness as an effective predictor of microfibril angle variability. Relationships could in turn be established as a function of overall tracheid morphology by including corresponding tracheid diameter and tracheid length data, alongside cell wall thickness data, into the prediction model.

The possibility of using cell-wall thickness as a surrogate measure for microfibril angle would be beneficial in future tree breeding programs, and to wood quality research in general. Modern x-ray diffraction techniques capable of efficiently sampling large numbers of tracheids for microfibril angle do exist, but these systems remain expensive and limited in availability. Scanning technology is readily available for the rapid and inexpensive measurement of cell wall thickness in both the radial and tangential directions. It is likewise possible to prepare microtome sections for microfibril angle viewing along both the radial and tangential planes. In order to obtain corresponding cell wall thickness and microfibril angle data, measurements would have to be conducted at fixed percentage intervals relative to overall ring width.

Basic statistics for microfibril angle are summarised in Table 4.44a (Appendix I). The mean values obtained for western redcedar were consistently greater than those observed for both Douglas-fir or western hemlock at common spacing intervals. Average values for western hemlock remained largely unchanged over the three spacings sampled. Greater microfibril angle variability was noted at the narrower spacings for both Douglas-fir and western redcedar. Coefficient of variation values for western hemlock varied little throughout.

Results of the repeated measures analyses conducted on microfibril angle, and as a function of initial spacing, are presented in Table 4.44b (Appendix I). Time effects were highly significant for all species. The spacing x ring interaction and treatment effects for Douglas-fir were both highly significant. Such results imply a nonparallel pattern of development, as well as differences between a minimum of two spacings when their respective effects on microfibril angle are averaged over time. The fact that the interaction in question occurred between rings 6 and 9 downplays the results obtained. Relatively similar average microfibril angle values should have been observed at ring 3 for all spacings considered. All trees were still more-or-less openly growing at this time. All had been

established on the same site and were, presumably, of similar provenance. The highly significant interaction obtained should therefore be accepted with caution.

A non-significant spacing x ring interaction and non-significant treatment effects were obtained for western hemlock. An identical pattern of microfibril angle development was accordingly identified for all spacings considered. A non-significant spacing x ring interaction was obtained for western redcedar, along with significant treatment effects. The narrower the spacing interval for the species, the steeper the initial decline in microfibril angle, and the earlier the time at which relatively stable values were eventually attained.

Microfibril angle and whole-ring relative density are both known to have a significant influence on the strength properties of wood. Generally speaking, the higher the microfibril angle value and the lower the whole-ring relative density recorded, the lower the rigidity and the lower the tensile and tear strength of the lumber produced (Cave and Walker 1994, Walker and Butterfield 1995). The preceding microfibril angle results for Douglas-fir and western hemlock contrasted with those obtained as a function of whole-ring relative density in section 4.2.7. An identical pattern of whole-ring relative density development was identified for all Douglas-fir spacings considered. Comparable whole-ring relative density profiles were illustrated for western redcedar at the 2.74, 3.66 and 4.57 m spacings in Figure 4.13. Even though similar whole-ring relative density profiles were observed for each species, greater stiffness properties can nonetheless be expected from the narrower spacings where significantly lower mean levels were recorded over time for microfibril angle.

The effects of ring width on microfibril angle development are presented in Table 4.45 (Appendix I). A significantly positive relationship was observed for Douglas-fir between rings 9 and 21. The wider the growth ring produced at such time, the greater the corresponding microfibril angle deposited. Non-significant relationships were obtained for western hemlock at all ages. Equations for the species fit poorly, with coefficient of determination values generally remaining close to zero. The relationships observed for western redcedar, even when significant, remained weak. In similar fashion to Douglas-fir, most correlation coefficients remained low and positive, indicating perhaps a slight increase in microfibril angle with increasing ring width.

4.4 General Summary

The purpose of this portion of the study was to analyse the effects of cambial age, initial spacing, stem taper and growth rate on the development of specific wood properties important to wood quality in second-growth timber. The following discussion summarises the principal results obtained.

The first objective was to profile and compare ring width, earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, whole-ring tracheid length and microfibril angle development as a function of ring number from pith. A univariate repeated measures analysis was used to assess the effects of initial spacing and taper class on the development of the above-mentioned variables. The first hypothesis tested suggested that cambial age had no effect on the development of each wood property considered:

$H_{4.1}$: there are no time effects (i.e., the developmental profile for a wood property, displayed as a function of ring number from pith, is horizontal)

The influence of cambial age on wood formation in conifers can be attributed to two principal causes. Firstly, an initial sharp increase in fusiform initial cell length, followed by relatively stable values, is typically observed within the vascular cambium as a function of time (Bannan 1967a). Secondly, as crown recession proceeds along a tree stem, physiological gradients within the tree stem are gradually modified, and the subsequent process of wood formation at any specific height interval below the live crown is accordingly altered (Larson 1969). Pith to bark variability at breast height was therefore expected in this study for all wood properties considered.

The hypothesis of no time effects was not rejected in one instance only. A largely horizontal, non-significant ($p = 0.0767$), pattern of development was identified for western hemlock when latewood relative density was profiled as a function of taper class. Similar mean latewood relative density values per taper class were therefore identified at each growth ring sampling point. Highly significant time effects were identified in all other cases, and the hypothesis of no time effects was rejected each time.

The second hypothesis tested suggested that initial spacing and taper class had no effect on the mean level recorded over time for each wood property considered:

H_{4.2}: there are no overall differences between groups (i.e., the mean value recorded over time for a wood property is similar for all groups, the between-units factors have no effect)

A summary of the between-subjects effects obtained by wood property, and by species, is presented in Table 4.46. The hypothesis of similar mean levels was not rejected whenever a non-significant result was obtained. Such results suggested that the mean value recorded over time for a specific wood property remained similar for all initial spacings, or for all taper classes considered. When compared, the various profiles would basically demonstrate very little separation over time, with relative gains and losses largely cancelling each other out. Significant results implied differences between a minimum of two initial spacings, or between a minimum of two taper classes, when treatment effects were averaged over time. The hypothesis of similar means for all groups considered was rejected in such cases.

Table 4.46 Summary of between-subjects effects, by species, for both initial spacing and taper class.

wood property	Douglas-fir		western hemlock		western redcedar	
	initial spacing	taper class	initial spacing	taper class	initial spacing	taper class
ring width	**	**	**	**	**	**
earlywood width	**	**	**	**	**	**
latewood width	**	**	ns	ns	**	**
latewood proportion	ns	ns	**	*	**	**
earlywood relative density	ns	ns	ns	ns	ns	ns
latewood relative density	ns	ns	ns	ns	ns	ns
whole-ring relative density	ns	ns	**	ns	*	**
whole-ring tracheid length	ns		ns		*	
microfibril angle	**		ns		*	

** : significant at P < 0.01

* : significant at P < 0.05

ns : non-significant

The third hypothesis tested suggested that initial spacing and taper class had no effect on rate of development for each wood property considered:

H_{4.3}: there are no interactions between groups involving time (i.e., the growth curves displayed for a wood property are parallel for all groups considered).

A summary of the interaction effects obtained by wood property, and by species, is presented in Table 4.47. The hypothesis of no interactions involving time was not rejected whenever a non-significant result was obtained. A parallel pattern of development was accordingly implied for all initial spacings, or for all taper classes considered. Significant results implied a nonparallel pattern of development between a minimum of two initial spacings, or between a minimum of two taper classes. Interactions involving time were therefore involved, suggesting a change in the rate of development for the wood property being tested. The hypothesis was rejected in such cases.

Table 4.47 Summary of interaction effects, by species, for both initial spacing and taper class.

wood property	Douglas-fir		western hemlock		western redcedar	
	spacing x ring	taper x ring	spacing x ring	taper x ring	spacing x ring	taper x ring
ring width	**	**	ns	ns	**	**
earlywood width	**	**	ns	ns	**	**
latewood width	ns	ns	ns	ns	ns	ns
latewood proportion	ns	ns	ns	ns	**	**
earlywood relative density	*	**	ns	ns	**	**
latewood relative density	ns	*	ns	ns	**	**
whole-ring relative density	ns	ns	ns	ns	**	**
whole-ring tracheid length	**		ns		ns	
microfibril angle	**		ns		ns	

** : significant at P < 0.01

* : significant at P < 0.05

ns : non-significant

The second objective was to investigate the effects of accelerated diameter growth on earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, whole-ring tracheid length and microfibril angle development over time. Growth rate in this study was defined as ring width. The following hypothesis was tested:

$H_{4.4}$: an increase in ring width has no effect on earlywood width, latewood width, latewood proportion, earlywood relative density, latewood relative density, whole-ring relative density, longitudinal tracheid length and microfibril angle development.

A highly significant cambial age effect for $H_{4.1}$ was identified for practically each wood property considered. The only notable exception was latewood relative density for western hemlock when profiled by taper class. Cambial age was henceforth considered as a covariate in all regression and correlation analyses. Hypothesis testing for growth rate was accordingly conducted at discrete growth intervals. A significant test suggested either a positive or a negative effect of ring width on the development of the wood property being analysed, and the subsequent rejection of $H_{4.4}$. A non-significant test implied no association with ring width. For consistency, this procedure was extended to all wood properties, including western hemlock latewood relative density profiled by taper class.

Having disregarded cambial age as a covariate would have resulted in significant relationships with inflated coefficient of determination values for most wood properties. Such an exercise was originally pursued during a preliminary analysis. When each growth ring was considered as a separate entity, only some relationships had coefficient of determination values greater than, or equal to, the one initially obtained by way of a single, overall relationship. Such results go a long way in explaining why relative density, tracheid length and microfibril angle variability in past studies have often been associated with changes in growth rate. Cambial age was frequently overlooked as an important contributor to variation.

Results of the growth rate analyses conducted on all wood properties are featured in Figures 4.17, 4.18 and 4.19 for Douglas-fir, western hemlock, western redcedar, respectively. Results are summarised by way of correlation coefficients, with black dots identifying non-significant relationships ($P < 0.05$), and the subsequent non-rejection of $H_{4.4}$.

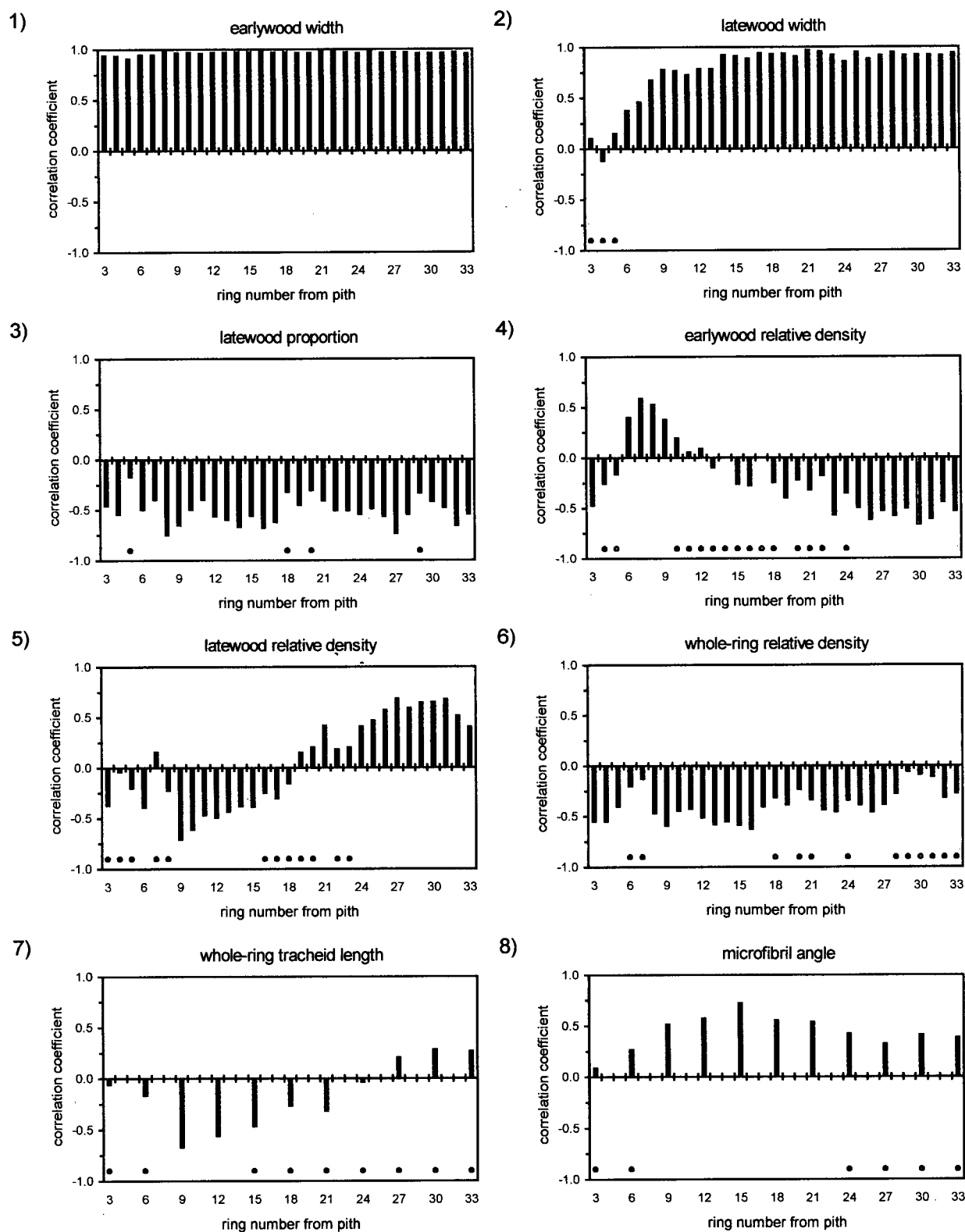


Figure 4.17 Summary of correlation coefficients obtained for Douglas-fir, illustrating the effects of ring width on the development of various wood properties at specific growth intervals from the pith (• indicates correlation coefficient not significant at $P < 0.05$).

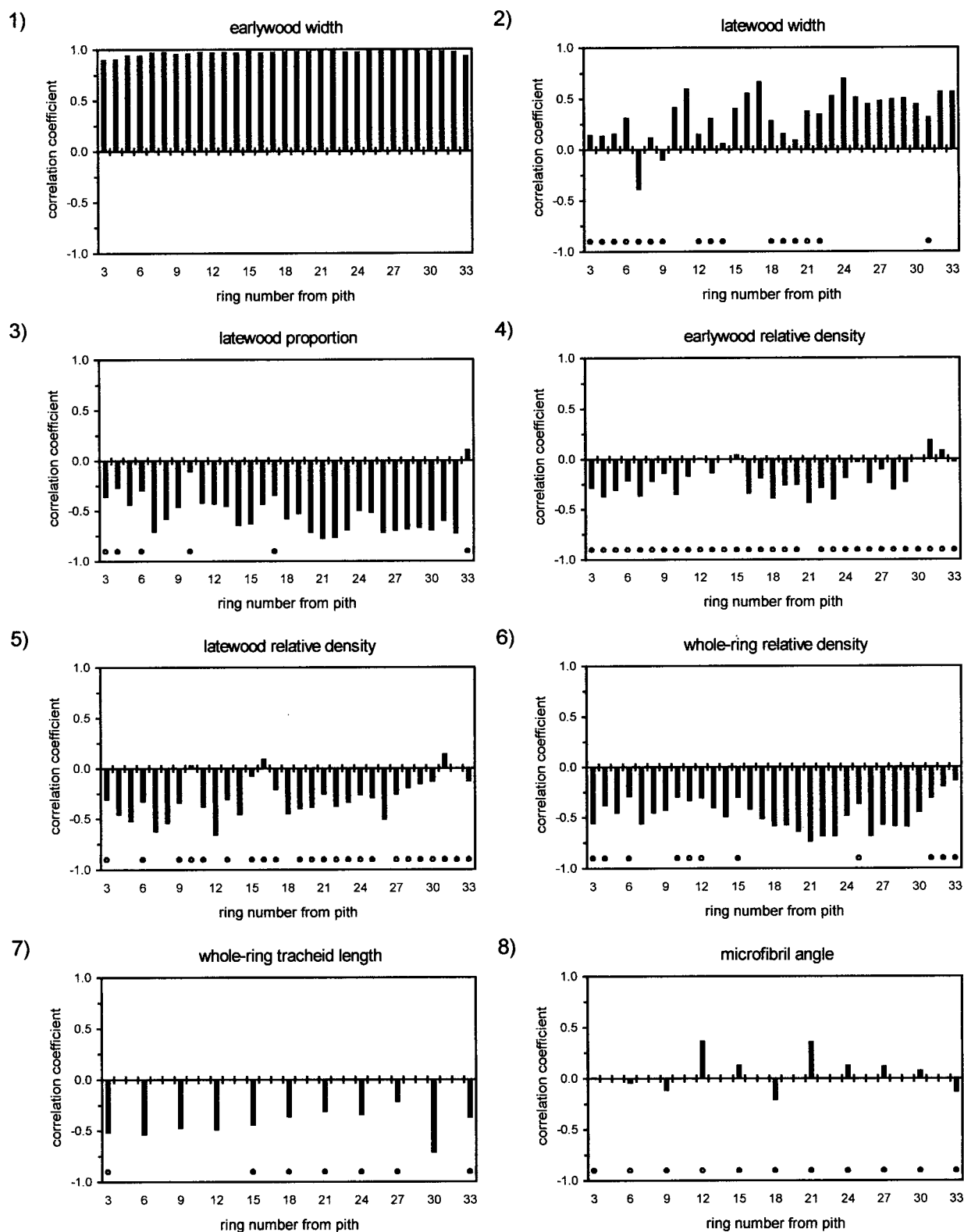


Figure 4.18 Summary of correlation coefficients obtained for western hemlock, illustrating the effects of ring width on the development of various wood properties at specific growth intervals from the pith (• indicates correlation coefficient not significant at $P < 0.05$).

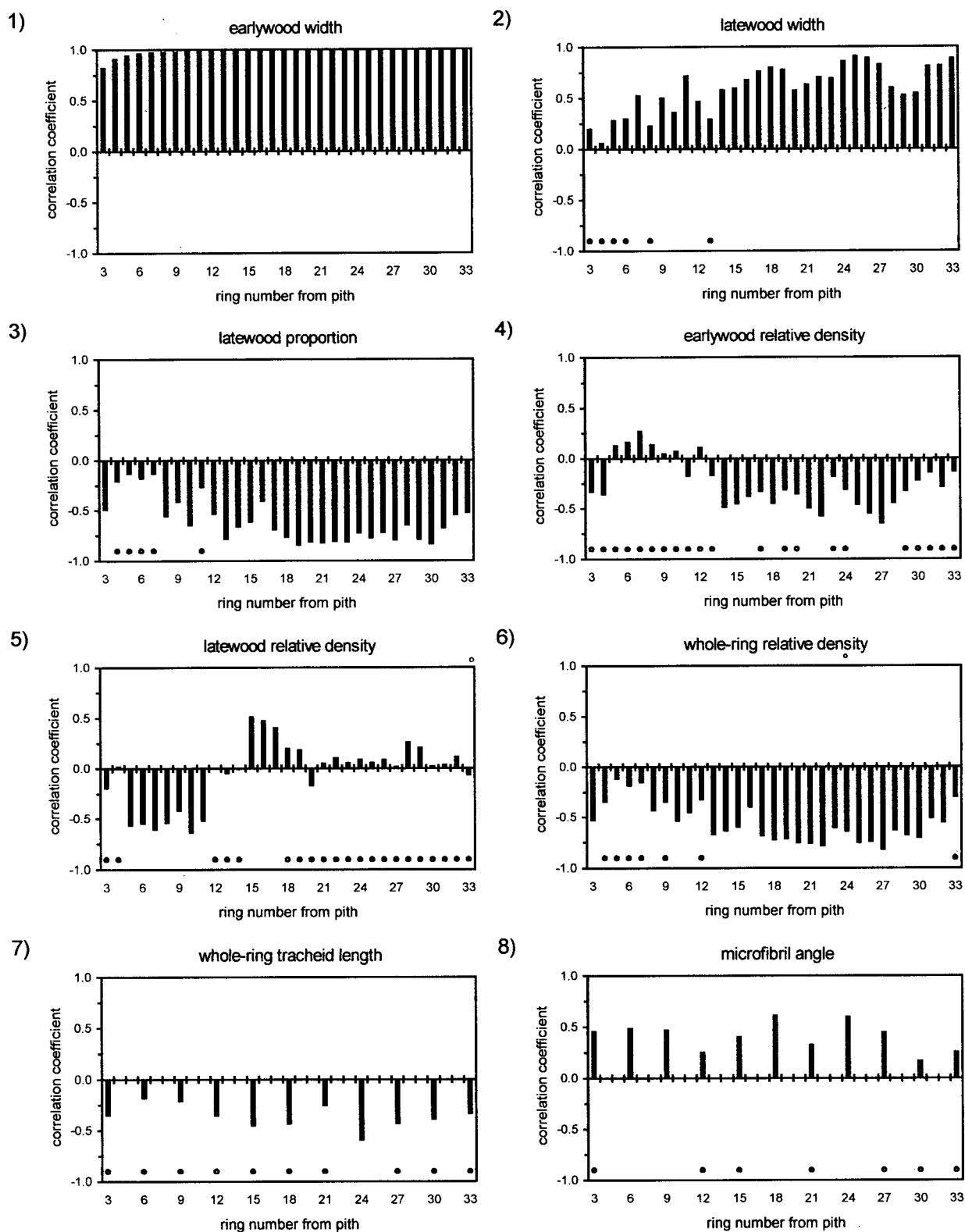


Figure 4.19 Summary of correlation coefficients obtained for western redcedar, illustrating the effects of ring width on the development of various wood properties at specific growth intervals from the pith (• indicates correlation coefficient not significant at $P < 0.05$).

- 1) Practically all earlywood width variability was associated with ring width. A highly significant, positive effect on earlywood width development was identified at all ages. Slope coefficients for Douglas-fir decreased in a more-or-less constant fashion over time, suggesting a continual decrease in the ratio of earlywood width to ring width within successive growth increments. Slope coefficients for both western hemlock and western redcedar remained more-or-less stable, suggesting very little change in the ratio of earlywood width to latewood width over time.
- 2) A positive relationship between latewood width and ring width was identified whenever significance was achieved. Large amounts of variability for Douglas-fir ($r \geq 0.87$) were associated with ring width from about ring 14 onward. A weak relationship was generally identified for western hemlock, with largely non-significant results obtained up to ring 22. A somewhat stronger relationship ($r \geq 0.53$) was observed for western redcedar following ring 13. Slope coefficients for Douglas-fir increased in a more-or-less constant fashion over time, pointing to a continual increase in latewood proportion within successive growth rings. Slope coefficients for western hemlock and western redcedar remained more-or-less stable, suggesting very little change over time in the ratio of latewood width to ring width.
- 3) A negative relationship was identified between latewood proportion and ring width whenever significance was achieved. The relationships observed over time for Douglas-fir were largely significant, but for the most part weak ($r \leq -0.76$). Results obtained for both western hemlock and western redcedar were mostly non-significant during the initial years of development. Results for western hemlock did strengthen somewhat following ring 20. Results for western redcedar became increasingly strong from ring 17 onward.
- 4) Very little earlywood relative density variability for each species was generally associated with ring width development. The significant relationships that were observed for Douglas-fir remained positive between rings 6 and 9, and negative from ring 25 onward. The results obtained for western hemlock were consistently non-significant, except for ring 21. Results for western redcedar were equally weak. The few significant results intermittently obtained

between rings 14 and 28 were consistently negative.

- 5) Very little latewood relative density variability for each species was generally associated with ring width development. The significant relationships that were observed for Douglas-fir remained negative between rings 9 and 15, and positive from ring 24 onward. Western hemlock demonstrated a largely non-significant relationship throughout. The few significant results that were observed for the species remained negative. Significantly negative results for western redcedar were obtained between rings 5 and 11. Significantly positive results were obtained between rings 15 and 17. Practically no latewood relative density variability for the species was associated with ring width thereafter.
- 6) A weak to moderately strong, negative relationship was generally identified between whole-ring relative density and ring width. The relationships obtained for Douglas-fir became increasingly non-significant as a function of time. Conversely, a somewhat increasing pattern of significance was displayed for western hemlock. An increasingly stronger relationship was obtained for western redcedar, with the strongest relationships of all displayed from ring 13 onward ($r \leq -0.82$).
- 7) A weak, negative relationship was generally observed between whole-ring tracheid length and ring width whenever significance was achieved. However, most relationships were identified as non-significant. The few significant results commonly obtained for both Douglas-fir and western hemlock did suggest a slight reduction in whole-ring tracheid length following an increase in diameter growth during early development.
- 8) A weak, positive relationship was generally identified between microfibril angle and ring width whenever significance was achieved. Significant relationships were obtained for Douglas-fir between rings 9 and 21. Non-significant relationships were obtained for western hemlock at all ages. Significant relationships were intermittently obtained for western redcedar between rings 6 and 24. The few significant results obtained for Douglas-fir and western redcedar did suggest a slight increase in microfibril angle following an increase in ring width development.

A third objective was to evaluate the effectiveness of the Kajaani FS-200 Optical Fibre Analyser for obtaining tracheid length measurements from 12 mm increment cores.

A precise depiction of mean whole-ring tracheid length development was provided for each species using both image analysis and the Kajaani FS-200 Optical Fibre Analyser. Successive dips and rises in whole-ring tracheid length development were frequently identified using both systems. Greater accuracy was nonetheless obtained by way of image analysis. Only undamaged tracheids were considered for sampling via this method. The Kajaani based profiles invariably demonstrated lower mean values throughout. The longer the mean tracheid length value obtained through image analysis, the greater the discrepancy.

Mean whole-ring tracheid length estimated through image analysis was subsequently compared to the corresponding mean values obtained using the Kajaani system. Highly significant differences ($P \leq 0.001$) were repeatedly identified at each growth ring sampling point. The Kajaani FS-200 Optical Fibre Analyser was shown to be inadequate for measuring tracheid length variability on the basis of 12 mm increment cores. The high proportion of broken tracheids present within these core samples invariably produced a significantly lower mean value. The length-weighted formula applied to the Kajaani data (Kajaani Electronics Ltd. 1986) was judged ineffective for masking the influence of the large number of broken tracheids processed. Image analysis, though extremely tedious, was considered a more reliable option in the context of this study.

The fourth objective was to profile and compare the development of intra-ring relative density by species. The illustrated profiles would serve to consolidate many of the observations and results obtained in the preceding analyses. All profiles were established by both taper class and ring class (average relative density values obtained from five consecutive growth increments). Ring class 29-33 was omitted for both western hemlock and western redcedar due to large quantities of missing data.

Average intra-ring relative density profiles, plotted as a function of ring width, are illustrated in Figures 4.20, 4.21 and 4.22 for Douglas-fir, western hemlock and western redcedar, respectively. Ring width development evolved along a similar path for all taper classes considered. An increase in value was generally observed from the pith, followed by a gradual decrease to a more-or-less

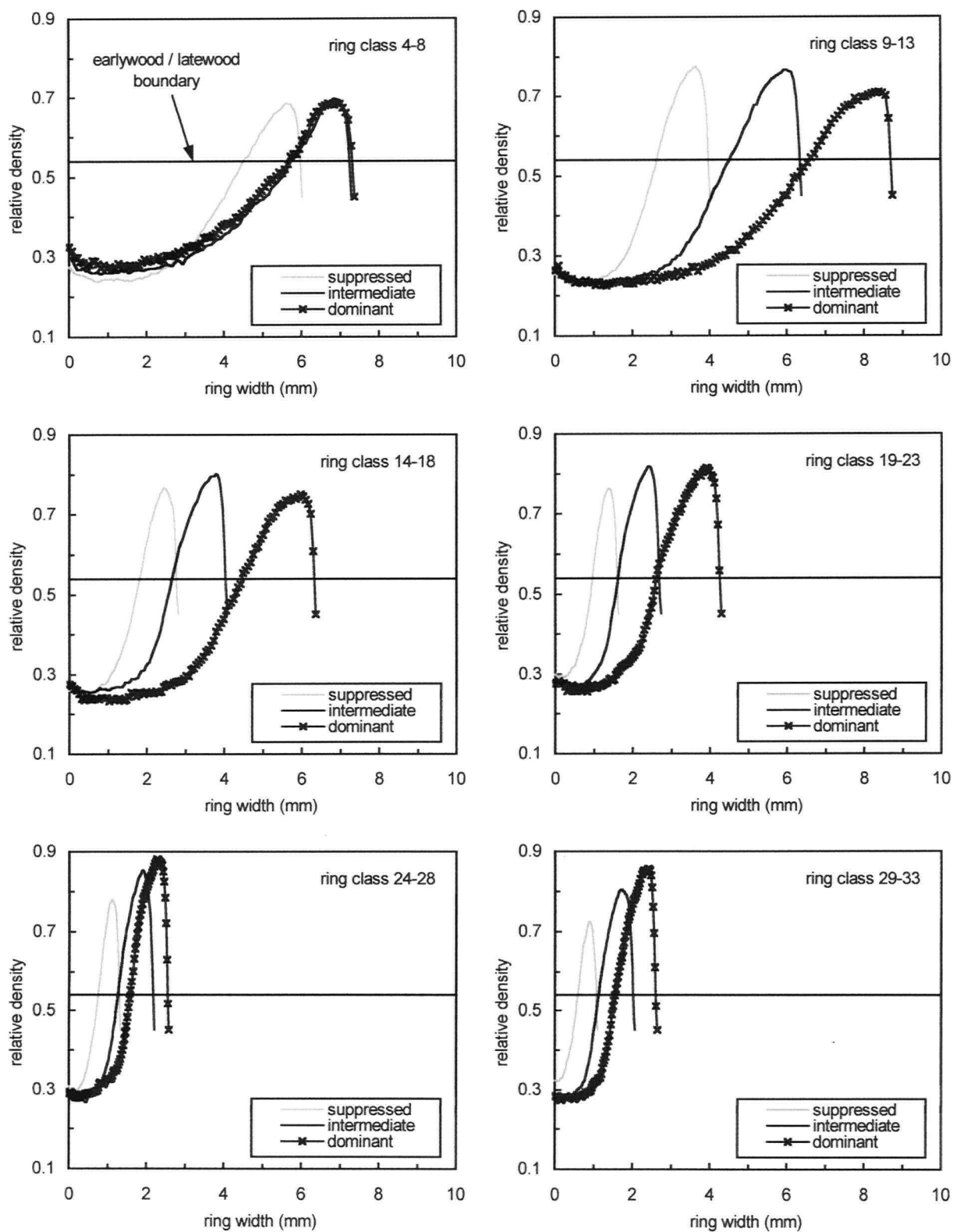


Figure 4.20 Intra-ring relative density development profiled by taper class and ring class, and as a function of ring width (mm) for Douglas-fir.

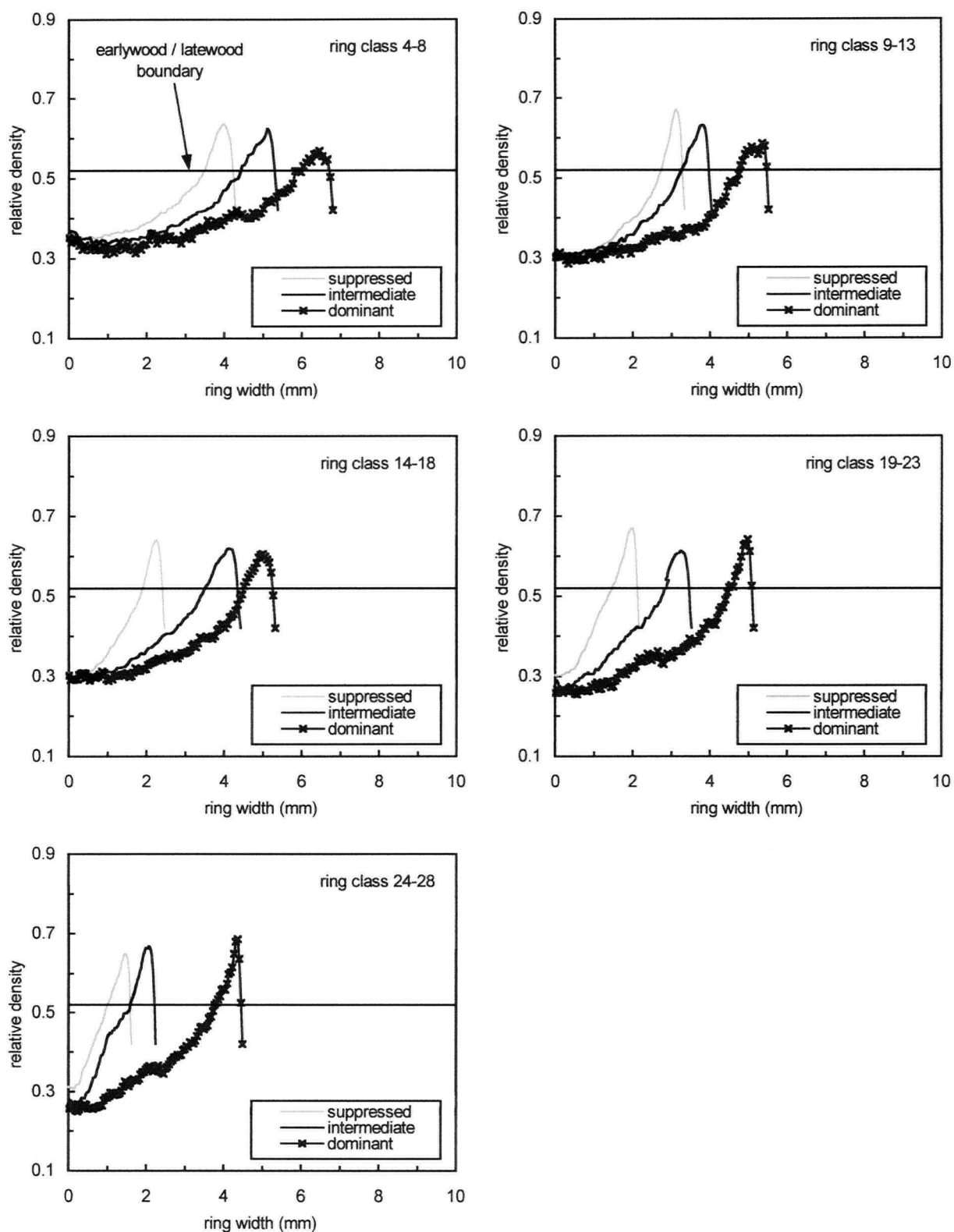


Figure 4.21 Intra-ring relative density development profiled by taper class and ring class, and as a function of ring width (mm) for western hemlock.

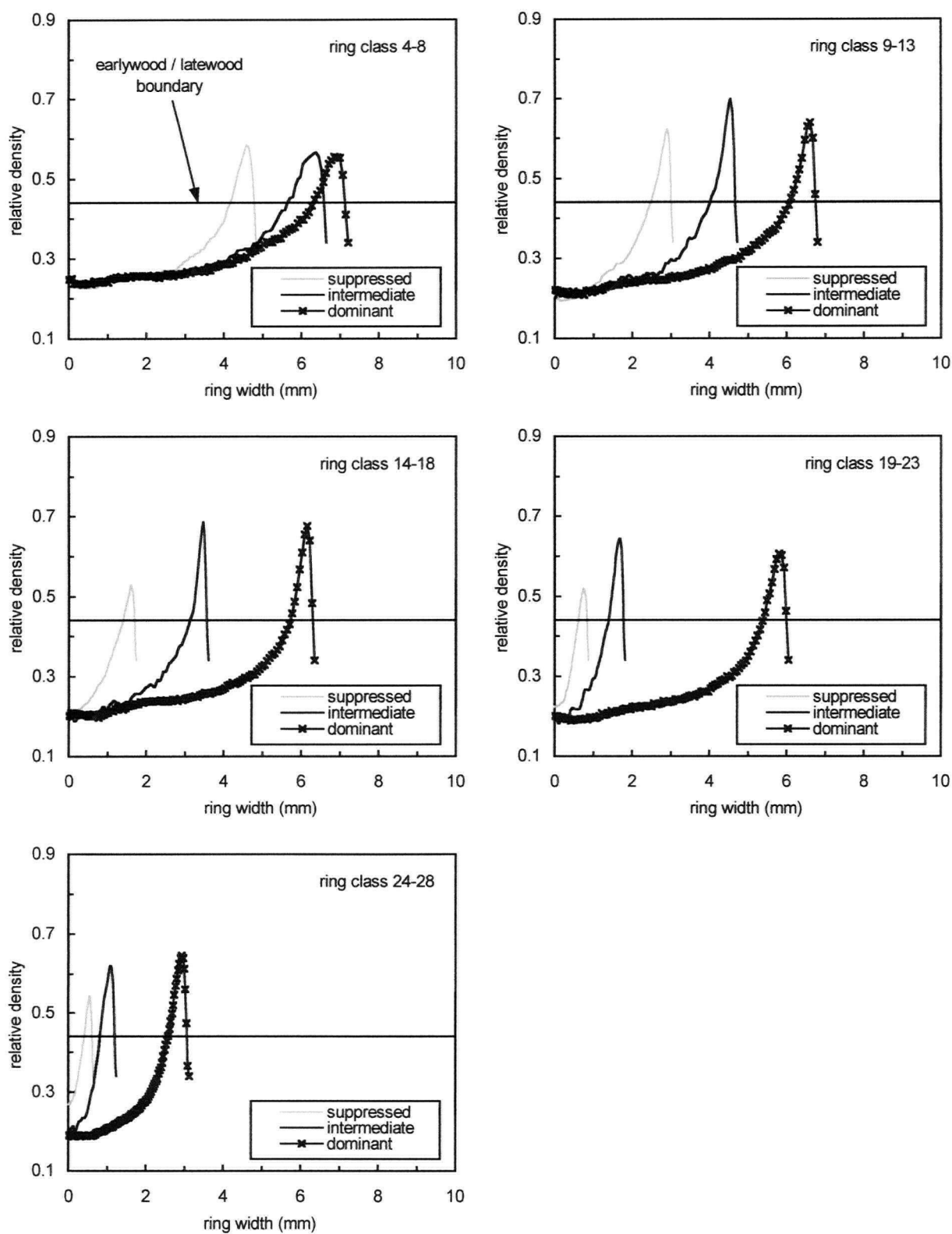


Figure 4.22 Intra-ring relative density development profiled by taper class and ring class, and as a function of ring width (mm) for western redcedar.

steady state. The greater capacity for photosynthesis associated with the dominant taper class led to greater diameter growth prior to crown closure, and to a subsequent wider maximum ring width. The earlier onset of crown closure within the suppressed taper class led to a sharp decrease in mean ring width from the onset of ring class 4-8. Subsequent decreases within the dominant taper class took longer to initiate, and were not as abrupt. The greater the shade tolerance displayed, the later the onset of crown recession, and the slower the rate of its progression. Western hemlock subsequently displayed the least ring width variation over time.

The relationship between earlywood width and ring width was especially strong for all species. Important increases in earlywood width were observed from the pith for all taper classes considered. Subsequent decreases in earlywood width were displayed at an earlier date by the suppressed taper class. Trees within this group were the first to undergo crown closure, and to initiate crown recession. Greater maximum earlywood width values were attained by the dominant taper classes prior to crown closure. Such trees, through their larger volumes of crown foliage, continually maintained the greatest potential for incremental growth. Earlywood increments within the dominant taper class were accordingly wider over the span of growth rings sampled. The intensification of competition within the suppressed taper classes was reflected in large part through the rapid narrowing of the earlywood. A similar pattern of narrowing was also observed within the dominant taper classes, but at a much reduced rate.

The development of latewood width was much less variable. Only marginal changes in latewood width were displayed over time for western hemlock. Modest changes were observed for western redcedar. The greatest overall variability was demonstrated by Douglas-fir. Latewood width for both western hemlock and western redcedar was invariably thicker at ring class 4-8 than at any other age. A period of accelerated latewood thickening was observed for Douglas-fir from the onset of ring class 4-8. This increase was sustained over a longer period by the dominant taper class, and a greater maximum value was subsequently attained by this group. A gradual decrease in latewood width to a more-or-less constant value followed for all taper classes.

The production of increased amounts of transition wood during the initial years of tree development was largely responsible for the creation of a gradual transition zone from earlywood to

latewood. With time, a general decline in transition wood production brought about an increasingly abrupt transition from earlywood to latewood. The ongoing change from a gradual to an abrupt intra-ring transition can perhaps be associated with the progression of crown recession. The greater the crown recession over time, the greater the extent that physiological gradients are modified along the stem. Douglas-fir demonstrated the lowest overall shade tolerance and accordingly, the greatest amount of crown lifting. The species correspondingly demonstrated the greatest variability in terms of wood formation, from a gradual intra-ring transition near the pith, to an abrupt transition near the bark. A more gradual rate of crown recession was observed for western redcedar, and a much slower rate was observed for western hemlock. More-or-less consistent growth ring characteristics were accordingly produced over time by both species. As the profiles at ring class 24-28 indicate, increasingly abrupt transitions could be expected for both species with further crown lifting.

Average intra-ring relative density development is profiled as a function of standardised ring width (%) in Figures 4.23, 4.24 and 4.25 for Douglas-fir, western hemlock and western redcedar, respectively. An increasing proportion of latewood over time was generally observed for all species. Taper class profiles were essentially the same prior to crown closure (approximately ring class 4-8). Subsequent increases in latewood proportion were first observed within the suppressed taper class. Latewood proportion within the dominant taper class generally remained static over the longest period. Douglas-fir continually displayed the greatest values overall. The proportion of latewood for both western hemlock and western redcedar was substantially lower at all ages.

The earlywood to latewood boundary was set in this study at a relative density of 0.54 for Douglas-fir, 0.52 for western hemlock and 0.44 for western redcedar. In order to profile relative density development, transition wood was classified under this criteria as either earlywood or latewood. A large quantity of transition wood, displaying a relative density slightly greater than a value listed above, would therefore have led to a slight increase in latewood width, and to a corresponding slight decrease in mean latewood relative density. In turn, a large quantity of transition wood, displaying a relative density slightly lower than a value listed above, would have brought about a slight increase in both earlywood width and mean earlywood relative density. A notable portion of the variability observed in terms of earlywood width, latewood width, earlywood relative density and latewood relative density was therefore linked to the presence of transition wood.

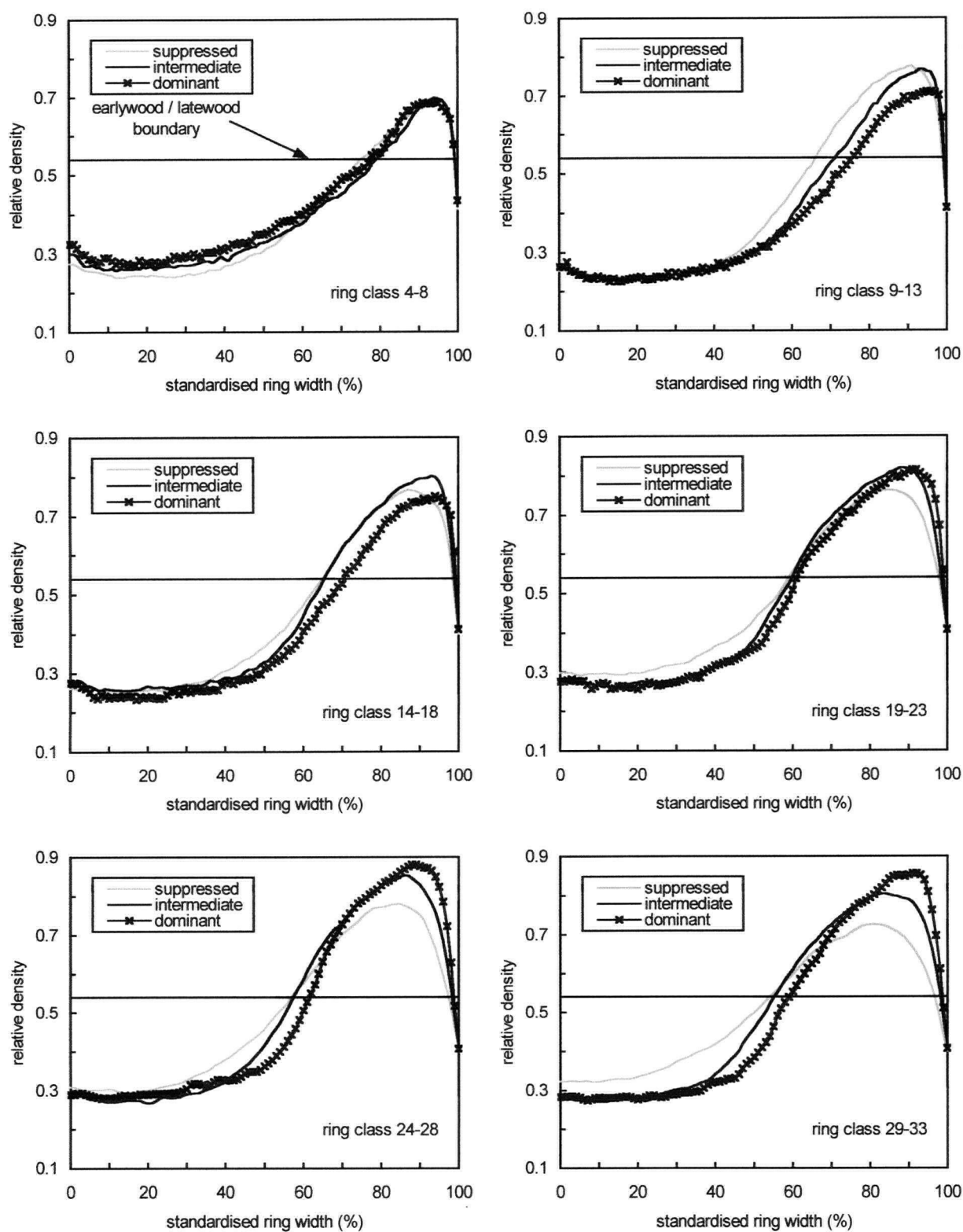


Figure 4.23 Intra-ring relative density development profiled by taper class and ring class, and as a function of standardised ring width (%) for Douglas-fir.

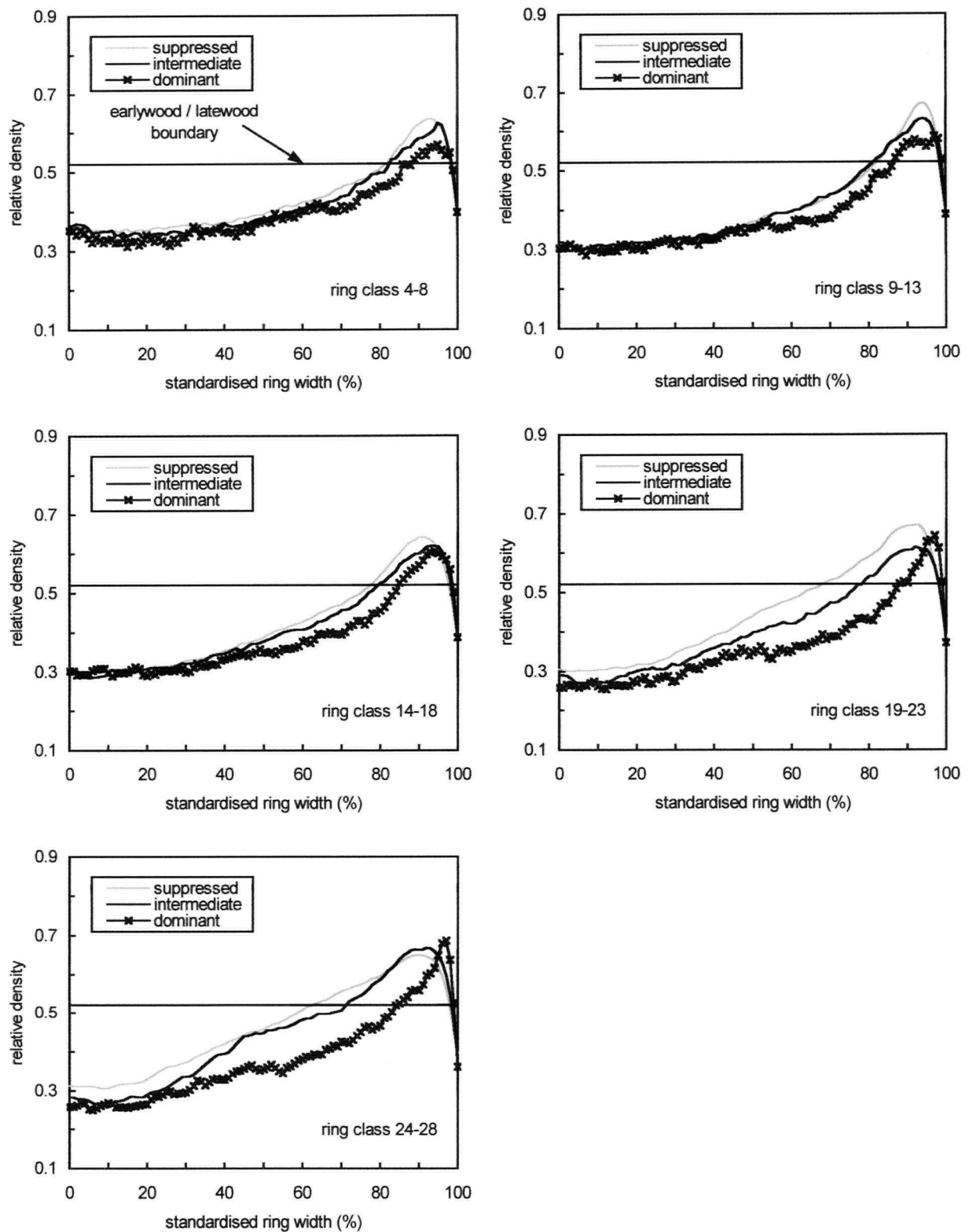


Figure 4.24 Intra-ring relative density development profiled by taper class and ring class, and as a function of standardised ring width (%) for western hemlock.

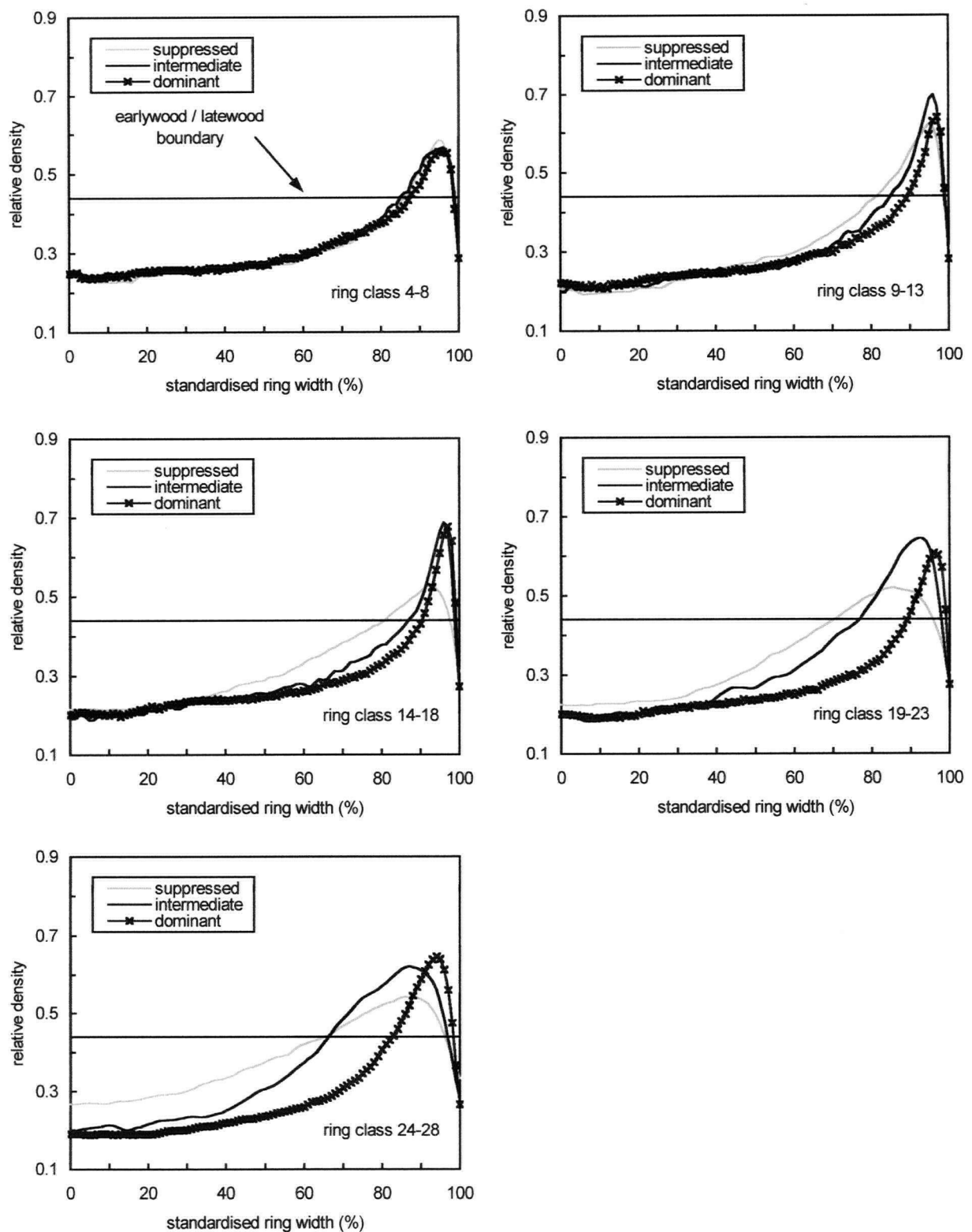


Figure 4.25 Intra-ring relative density development profiled by taper class and ring class, and as a function of standardised ring width (%) for western redcedar.

The minimum earlywood relative density values attained from the onset of ring class 4-8 varied little by taper class. Slight increases in value were nonetheless common to the suppressed taper class during the final years of development. Greater variability was observed for latewood relative density. Maximum values within each taper class profile were practically the same prior to crown closure (roughly ring class 4-8). Subsequent increases in value, followed by decreases, were observed at an earlier date within the suppressed taper class. The dominant taper class consistently required a longer period of time to reach a maximum latewood relative density value. The maximum values achieved were generally maintained over the range of growth rings sampled. Subsequent decreases in maximum latewood relative density, along with corresponding increases in minimum earlywood relative density, are foreseeable within this group as a function of further cambial ageing and crown recession.

Greater homogeneity in terms of intra-ring relative density was generally displayed during the initial years of development. Greater amounts of transition wood were produced at this time. A maximum value for latewood relative density had not yet been achieved. As crown recession proceeded, an increasingly greater range between minimum earlywood relative density and maximum latewood relative density developed for all taper classes. The intensification of tree-to-tree competition within the suppressed taper class eventually brought about a slight increase in minimum earlywood relative density, and a corresponding decrease in maximum latewood relative density. Greater intra-ring relative density uniformity was once again achieved at this time through the renewed production of transition wood.

Changes in whole-ring relative density were largely brought about by corresponding changes in either earlywood relative density, latewood relative density, latewood proportion, or through various combinations of the above. An increase or decrease in latewood proportion was in turn linked to changes in either earlywood width, latewood width, or both. Changes in earlywood width, and to some extent latewood width, were both a function of ring width development. The possible sources of whole-ring relative density variation for each species considered in this study are detailed in the following paragraphs. Results obtained through the foregoing growth rate and repeated measures analyses will be referenced. For brevity, only the taper class results will be considered.

In the case of Douglas-fir, changes in earlywood width and latewood width (except near the pith) were strongly associated with ring width. A somewhat similar ratio of earlywood to latewood was therefore maintained at each growth ring sampling point, regardless of ring width. Only small amounts of variability for latewood proportion were therefore associated with growth rate. An identical pattern of latewood proportion development was subsequently identified for all taper classes. Slope coefficients from relationships between earlywood width and ring width decreased in a more-or-less constant fashion. Slope coefficients for latewood width increased. Ongoing decreases in earlywood width were therefore greater relative to latewood width. A gradual increase in latewood proportion over time was subsequently observed for all taper classes.

Slightly higher earlywood relative density values and slightly lower latewood relative density values were associated with the wider growth rings during early development. In turn, slightly lower earlywood relative density values and slightly higher latewood relative density values were associated with the wider growth rings toward the bark. The mean levels obtained for both earlywood relative density and latewood relative density did not vary over time. However, the profiles identified for each variable were recognised as nonparallel. The lower earlywood relative density values initially identified within the suppressed taper class were in effect countered by comparatively higher latewood relative density values. The same pattern held true during the final years of development. Higher earlywood relative density values within a specific growth increment were generally associated with lower latewood relative density values.

Douglas-fir whole-ring relative density therefore remained comparable in value for each taper class at each growth ring sampling point. The general increase in whole-ring relative density over time was largely due to ongoing increases in latewood proportion. The greater the proportion of latewood, the higher the whole-ring relative density value recorded. An identical pattern of whole-ring relative density development was subsequently identified for all taper classes. Ring width therefore had little impact on whole-ring relative density development over time.

In the case of western hemlock, very little variability for earlywood relative density and latewood relative density was associated with ring width development. Identical taper class profiles were identified in each case. Earlywood width variability was in turn strongly associated with ring

width development, whereas very little association was displayed for latewood width. Parallel profiles were identified in each case. Highly significant and non-significant treatment means were obtained respectively. Slight decreases in earlywood width, with little corresponding change in latewood width, were therefore being displayed over time as a function of decreasing ring width.

Parallel profiles of development were accordingly identified for latewood proportion, with significantly different ($p = 0.0446$) mean levels recorded over time. Latewood proportion within the dominant taper class varied little over time. Earlywood width development was largely maintained at a more-or-less constant level, and in line with ring width development. The suppressed taper class displayed an increasingly larger proportion of latewood as time passed. Earlywood development within this taper class was largely reduced during the final years of growth. Latewood proportion at this time therefore became increasingly associated with ring width development.

An identical pattern of whole-ring relative density development was subsequently identified for western hemlock. Ring width accordingly had little impact on whole-ring relative density variability, save for a minor increase in the strength of the relationship during the mature wood portion of tree development. Slightly greater whole-ring relative density values were displayed by the suppressed taper class at this time. These values largely corresponded to the production of narrower earlywood increments and subsequently, to a slightly greater proportion of latewood.

In the case of western redcedar, slightly lower latewood relative density values were associated with the wider growth rings during the early years of development. In turn, slightly lower earlywood relative density values were associated with the wider growth rings toward the bark. The mean levels obtained for both earlywood relative density and latewood relative density did not vary over time. Nonparallel profiles were nonetheless identified for each variable, as a result of the minor fluctuations observed within the suppressed taper class.

Changes in earlywood width were strongly associated with ring width development. Latewood width variability became increasingly associated with ring width development over time. A nonparallel pattern of development was identified for earlywood width. A parallel pattern of development was identified for latewood width. Significantly different mean levels over time were

recorded in each case. The suppressed taper class displayed a steady decline in earlywood width over time that mirrored corresponding decreases in ring width. The dominant taper class demonstrated an important reduction in earlywood width during the final years of development only. Minor, but constant, decreases in latewood width were displayed throughout by all taper classes. Comparatively narrower latewood width values were continually produced by the suppressed taper class.

Profile development for latewood proportion was accordingly nonparallel, with significantly different mean levels recorded over time. Latewood proportion within the suppressed taper class displayed a steeper initial decline from the pith, to a lower minimum value. Earlywood width within this taper class was the first to reach a maximum, but at a lower value relative to the other taper classes. The steady decline in earlywood width that followed led to a slow, but steady increase in latewood proportion over time. The dominant taper class demonstrated a steadier initial decline in latewood proportion from the pith, with relatively stable values thereafter. A maximum earlywood width was produced by this taper class over an extended period of time. A similar ratio in the decline of earlywood width to latewood width was therefore being maintained at each growth ring sampling point.

Ultimately, the minor earlywood relative density decreases observed within the suppressed taper class were countered by minor increases in latewood relative density at corresponding points of time. A nonparallel pattern of whole-ring relative density development was accordingly identified for western redcedar, with significantly different mean levels recorded over time. A steeper drop in whole-ring relative density was initially displayed by the suppressed taper class. This sudden drop largely paralleled the sharp decrease observed for latewood proportion. A higher whole-ring relative density value was attained by this taper class during the final years of growth. Such values largely corresponded to the narrower earlywood increments produced, and subsequently, to a slightly greater proportion of latewood. An increasingly negative relationship was accordingly identified over time for the species between whole-ring relative density variability and ring width development.

5. STUDY OF JUVENILE AND MATURE WOOD DEVELOPMENT

5.1 Introduction

Juvenile wood is often considered inferior in wood quality due to the greater variability displayed in terms of wood properties. In contrast, mature wood generally demonstrates less variability, rendering it more valuable to the wood processing industry. There exists no sharp demarcation between the two wood types, with one generally blending into the other as a tree ages. Defining a juvenile wood transition zone has accordingly received much attention in past studies. Complicating the work has been the failure by researchers to agree upon a common transition variable. Different wood properties will generally attain a more-or-less steady state at a unique point in time relative to tree development. Longitudinal tracheid length, microfibril angle, lignin-cellulose ratio, ring width, latewood proportion, latewood relative density and whole-ring relative density have all been considered for analysis. Transition age results have accordingly varied between studies.

Non-destructive sampling for juvenile wood was accomplished in this study using a 5 mm increment borer. The use of a 12 mm increment borer was avoided for such work to prevent excessive tree damage, unacceptable in the context of the Haney spacing trials. Tracheid length and microfibril angle data were, as a result, unavailable for defining a juvenile wood transition zone. Only a select number of wood properties, measurable by way of x-ray densitometry, were subsequently available for analysis. Ring width was perhaps the most straightforward choice available. Wider growth rings are typically produced within the juvenile wood core, and narrower growth rings are generally maintained throughout mature wood development. A transition from juvenile wood to mature wood can therefore be pinpointed using visual means only (Bendtsen and Senft 1986, Kucera 1994, Yang *et al.* 1986, 1994). Such an approach was avoided in this study since ring width was shown in Figures 4.17, 4.18 and 4.19 to be a poor surrogate for relative density, tracheid length and microfibril angle variability, hence wood quality.

Whole-ring relative density was preferred, as it is often considered the best single measure of wood quality. Whole-ring relative density was described in section 4.4 as a composite wood property that developed as a function of earlywood width, latewood width, latewood proportion, earlywood relative density and latewood relative density. In an industrial setting, each of these individual wood properties would be difficult to associate with end-product value. Whole-ring relative density would be much easier to relate, providing a simple measure of clear wood strength and stiffness. Whole-ring relative density is furthermore a concept familiar to most people practising silviculture, making it a rational choice for incorporating the aspect of juvenile wood development into forest management.

The purpose of this portion of the study was to examine juvenile wood development within second-growth stands established over a range of initial spacing intervals. The first objective was to determine a juvenile wood to mature wood transition point based on whole-ring relative density trends from pith to bark. Profiles depicting juvenile wood distribution by height interval for each tree sampled were to be established according to both ring number and radial distance from the pith.

The second objective was to study the relationship between crown recession and mature wood development along the stem. Based on previous research, the passage from juvenile wood to mature wood is believed to occur at, or just below, the base of the live crown (Larson 1969, 1973). Wood formation at breast height, as illustrated in Figures 4.21 to 4.26, is strongly associated with changes in crown structure over time. The greater the ratio of crown foliage to length of branch-free stem, the lower the proportion of latewood, the greater the amount of transition wood, and the lower the whole-ring relative density produced within successive growth rings. In section 4.3.7 (Figure 4.14), a slower increase in whole-ring relative density at breast height, especially for western hemlock and western redcedar, was generally associated with increased diameter growth. Relatively stable values characteristic of mature wood development had yet to be achieved by many of the faster growing trees sampled. Crown recession was nonetheless well underway, suggesting that the upward development of mature wood was progressing at a much slower rate relative to crown recession. The following hypothesis was tested for each tree sampled:

H_{5.1}: the passage along a tree stem, from juvenile wood to mature wood, occurs at the base of the live crown

The shape of the juvenile core, from stump level up to the base of the live crown, has commonly been described as cylindrical (Panshin and de Zeeuw 1980, Krahmer 1985, Jozsa and Middleton 1994, BC Ministry of Forests 1999). Variations have included conical with a slight diameter decrease upward (Zobel and Talbert 1984, Yang *et al.* 1986, Kucera 1994, Yang *et al.* 1994), and conical with a slight diameter decrease downward (BC Ministry of Forests 1999). A third objective was to define the shape of the juvenile core as a function of initial spacing and stem taper. Previously established stemwood relative density profiles suggested a cylindrically-shaped juvenile core within fast-grown, second-growth stems for the three species considered in this study (Jozsa *et al.* 1989, 1998). Whether growth rate, as governed by available growing space, had a subsequent effect on the shape of the juvenile core was unknown. The following hypothesis was tested for each tree sampled:

H_{5.2}: the shape of the juvenile core, in terms of ring number from pith, is cylindrical from stump level up to the base of the live crown

A fourth objective was to profile the shape of an average juvenile core by species and initial spacing interval, and to compare the results obtained with corresponding relative density stem profiles.

5.2 Data Analysis

5.2.1 Juvenile Wood Transition Zone Determination

Various segmented regression models have been used in past studies to define a boundary between juvenile wood and mature wood. A linear version, fitted to individual whole-ring relative density data sets (Di Lucca 1989, Abdel-Gadir and Krahmer 1993, Tasissa and Burkhart 1998), was initially employed in this study:

$$(4) \quad y_i = \beta_0 + \beta_1 x_i + \beta_2 D_i(x_i - x_0) + e_i$$

where

y_i	predicted value (whole-ring relative density)
β 's	regression coefficients
x_i	ring number from pith
x_0	juvenile wood transition age estimate
D_i	1 if $x_i > x_0$, 0 if $x_i \leq x_0$
e_i	independent, normally distributed random error term

Regression segments were chosen to minimise the total residual sum of squares under the constraint that the intersection of the two line segments in the above model would occur between two consecutive data points that split the respective data set. The intersection point obtained was then used to identify the number of growth rings present within the juvenile wood core. An additional constraint involved forcing the slope coefficient of the second line segment to be greater than or equal to zero, and less than or equal to the slope coefficient of the first line segment. A final constraint had the model fitted onto the data set beginning at the lowest value data point.

Unsatisfactory results were obtained by way of this model. The average whole-ring relative density profiles illustrated in Figure 2.1 typically demonstrate an initial decrease in value from the pith for the three species considered in this study. A minimum is eventually reached after which a subsequent increase may, or may not, be observed. The choice of the lowest relative density value as a starting point for segmented linear regression therefore meant that data points closest to the pith would be ignored during analysis.

Use of segmented linear regression in past studies has traditionally been limited to samples bearing a minimum of 50 growth rings. All core samples in this study were collected from relatively young trees, approximating 40 rings at the stump, and as low as 15 near toward the base of the live

crown. The low number of data points available from each core sample often resulted in transition zones too broad to allow hypothesis testing and for making inferences. Transition zones in this study were interpreted as 95 % confidence intervals for the break points in the model. If transition zones did not overlap, then transition age estimates were considered significantly different at the 5 % level (Cook and Barbour 1989).

A segmented quadratic regression model was subsequently proposed, with no restrictions placed for model fitting to be initiated at the lowest value data point. Furthermore, by taking into account all data points, the proposed model more closely mimicked the characteristic whole-ring relative density profiles illustrated in Figure 2.1. The following model was used:

$$(5) \quad \begin{aligned} \hat{Y}_i &= \beta_0 + \beta_1 x_i + \beta_2 x_i^2 + e_i && \text{if } x_i < x_0 \\ \hat{Y}_i &= \beta_0 + \beta_1 x_0 + \beta_2 x_0^2 + e_i && \text{if } x_i \geq x_0 \end{aligned}$$

where

\hat{Y}_i	predicted value (whole-ring relative density)
β 's	regression coefficients
x_i	ring number from pith
x_0	juvenile wood transition age estimate
e_i	independent, normally distributed random error term

Regression segments were once again chosen to minimise the mean squared error under the constraint that the demarcation age would occur between two consecutive data points that split the data set. An assumption was initially made that whole-ring relative density development within the mature wood segment would remain more-or-less constant, hence the slope coefficient equalling zero when $x_i \geq x_0$. A juvenile wood transition age was identified at the intersection point between the quadratic and the linear portions of the model. In turn, the relative density value corresponding to this transition age represented the mean value for all data points dispersed about the horizontal line

segment within the mature wood zone. All estimates of the regression parameters were obtained using SAS NLIN (SAS Inc. 1989).

A F-test was conducted to verify the need for a segmented regression. A simple linear regression model (equation 3) was initially fitted to each data set, from the lowest value onward. A ratio was then calculated between the mean squared error obtained using the simple linear model, and the corresponding value obtained via the segmented quadratic model. Profiles yielding F-values less than or equal to one were classified as exclusively juvenile wood. If only the quadratic portion of Model 1 could be fitted, but a F-value greater than one was nonetheless obtained, then it was likewise assumed that the profile of interest contained juvenile wood only. Profiles yielding F-values greater than one signified the presence of mature wood and the need for a segmented regression analysis.

Three regression models were accordingly fitted to each whole-ring relative density profile. These included Model 1 (segmented quadratic regression), Model 2 (segmented linear regression) and Model 3 (simple linear regression). A comparison of the three regression models, fitted to a common data set, is provided in Figure 5.1.

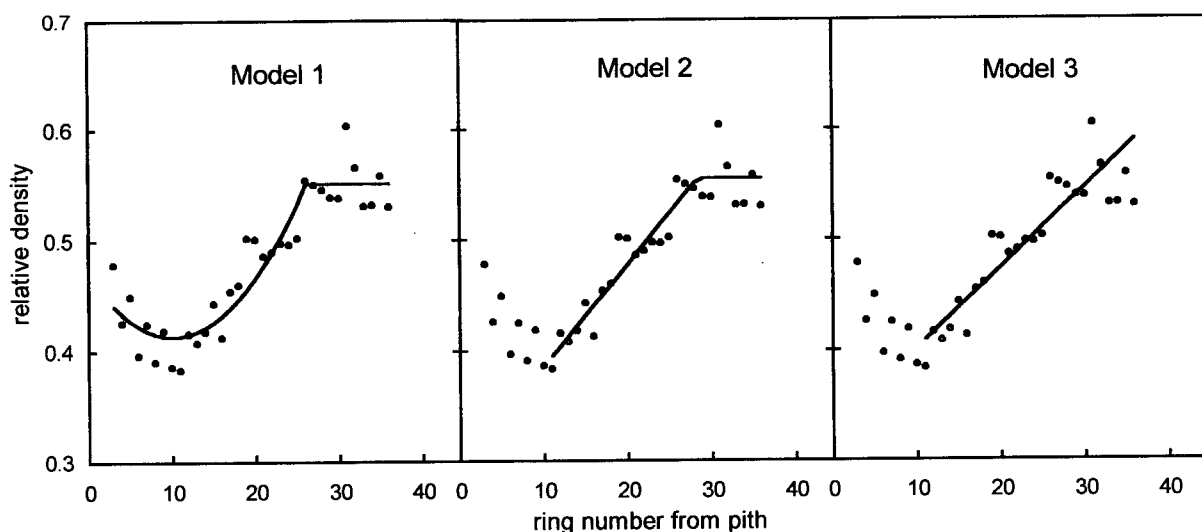


Figure 5.1 Example of juvenile-mature wood transition point determination at breast height (Douglas-fir, 4.57 m spacing, tree # 64) using Model 1 (segmented quadratic regression), Model 2 (segmented linear regression) and Model 3 (linear regression).

5.2.2 Juvenile Wood Taper Modelling

Diameter inside bark along the stem was profiled using Kozak's (1988) variable exponent taper model. The following model was used:

$$(6) \quad \text{dib}_i / \text{dib}_{\text{BH}} = X^C$$

where

$$X = (1 - \sqrt{Z}) / (1 - \sqrt{P})$$

$$Z = h_i / H$$

$$P = 1.3/H$$

$$C = b_1Z + b_2\sqrt{Z} + b_3(D/H) + b_4CL + b_5CR + b_6CB$$

and

dib _i	diameter inside bark (cm) at h _i
dib _{BH}	diameter inside bark (cm) at breast height
P	inflection point
h _i	height from ground (m), 0 ≤ h _i ≤ H
H	total height (m)
D	diameter outside bark (cm) at breast height
CL	live-crown-length
CR	live-crown-ratio
CB	height to the base of the live crown
b's	regression coefficients

Juvenile wood diameter along the stem was described using a modified version of this model, with the diameter inside bark ratio dib/dib_{BH} replaced by the juvenile wood diameter ratio jwd/jwd_{BH}

(jwd_i = juvenile wood diameter (cm) at h_i, jwd_{BH} = juvenile wood diameter (cm) at breast height). Juvenile wood transition ages were transferred into radial distance values using corresponding x-ray densitometry ring width readings. Live-crown-length, live-crown-ratio and height to the base of live crown were all integrated into the revised model. The above modifications (addition of crown variables) were similar to those suggested by Maguire and Batista (1996) for modelling sapwood distribution in coastal Douglas-fir. A 1.3 m inflection point above ground level was retained.

The following formulae were used to calculate mean bias (B) and standard error of estimate (SE_E) by vertical position for both dib_i and jwd_i:

(7)

$$B = \frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)}{n}$$

(8)

$$SE_E = \sqrt{\frac{\sum_{i=1}^n (Y_i - \hat{Y}_i)^2}{n - m}}$$

where

Y_i	actual observation
\hat{Y}_i	predicted value
n	number of observations
m	number of estimated parameters

Data from all spacings were initially pooled to obtain better parameter estimation from a wider range of tree sizes. All models were fitted by ordinary least squares and linearised by logarithmic transformation. The subsequent evaluation of the fitted taper-estimating systems was not attempted due to the insufficient size of the data set. Juvenile wood diameter by height interval was estimated by doubling the corresponding radial width value previously obtained. Diameter inside bark at breast height was estimated directly from core samples. Once defined, the relative proportion of juvenile wood was profiled by initial spacing and species using the calculated estimation parameters.

5.3 Results and Discussion

Sampling along the branch-free bole was impossible within the 1.83 and 2.74 m spacings for Douglas-fir, the 1.83 m spacing for western hemlock and the 0.91 and 1.83 m spacings for western redcedar. All of the above were excluded from this portion of the study. A total of 54 trees were subsequently available for analysis (3 species, 3 spacings/species, 6 trees/spacing). The following tree count subtotals were established as a function of taper class; suppressed taper class (6 Douglas-fir and 11 western hemlock), intermediate taper class (5 Douglas-fir, 4 western hemlock and 3 western redcedar) and dominant taper class (7 Douglas-fir, 3 western hemlock and 15 western redcedar).

5.3.1 Juvenile Wood Transition Zone Analysis

An original objective was to see if a common juvenile wood transition age could be defined at breast height using relative density, tracheid length and microfibril angle data collected from pith to bark. Difficulties were soon encountered during a preliminary analysis with both the tracheid length and microfibril angle data. Sampling for both wood properties, due to its labourious nature, had been conducted starting at the third growth ring from the pith, and on every third growth ring thereafter. Practically all of the core samples collected displayed a maximum of 30 to 35 growth rings. Consequently, only 10 or 11 data points were available per profile for segmented regression analysis. This is much less than the minimum of 50 data points suggested by past studies. The subsequent fitting of Models 1 and 2 became very difficult. Calculated F-values were, for the most part, less than one. Where F-values happened to be greater than one, the low number of degrees of freedom often resulted in very wide juvenile wood transition zones. Making comparisons between relative density, tracheid length and microfibril angle under such conditions would have been meaningless.

Results of the juvenile wood transition zone analysis are presented in Tables 5.1 to 5.9 (Appendix II). All core length and juvenile wood thickness values reflect an equilibrium moisture content of approximately 8 %. Missing height intervals represent cases where a juvenile wood transition age could not be determined due to insufficient data points from damaged cores. Missing

height intervals also identify instances where the mean square error (MSE) obtained using Model 3 was inferior to that obtained using Model 1, resulting in a F-value less than or equal to 1. Cases where only the quadratic portion of Model 1 could be fitted to the data, and where the F-value obtained was greater than 1, are identified by an asterisk (*). A total of 471 core samples were analysed (204 Douglas-fir, 130 western hemlock and 137 western redcedar), with a F-value greater than one obtained from 339 of the profiles considered (168 Douglas-fir, 88 western hemlock and 83 western redcedar). A juvenile wood transition age was, in turn, successfully determined from 281 of the profiles considered (150 Douglas-fir, 69 western hemlock and 62 western redcedar).

The confidence intervals obtained using Model 1 were, for the most part, much narrower in width than those obtained using Model 2. All core samples had been collected from relatively young trees (41 years-of-age for Douglas-fir, 40 years for both western hemlock and western redcedar). A limited number of data points were subsequently available for analysis. The fact that Model 2 was fitted onto the data set beginning at the lowest value data point further reduced the number of degrees of freedom. Moreover, locating a definite minimum whole-ring relative density data point for many of the western redcedar profiles often proved difficult when a subsequent increase in value was not readily observed over time. This difficulty, coupled with the fact that Model 1 more closely mimicked whole-ring relative density development for the three species considered, justified its use over Model 2 throughout the remainder of the study.

Figures 5.2, 5.3 and 5.4 illustrate the juvenile wood transition ages and juvenile wood transition zones estimated by way of Model 1 for Douglas-fir, western hemlock and western redcedar, respectively. The trees sampled within each spacing are arranged from smallest *hdr* (greatest taper) to largest (least taper). Many of the foregoing trees featured confidence intervals which did not overlap with increasing height. Significant differences between transition ages were accordingly identified at the 5 % level. A gradual decrease in the number of growth rings within the juvenile wood core was therefore implied from stump level up to the base of the live crown. An unchanging transition age was assumed for all other trees where confidence bands remained overlapping.

Table 5.10 (Appendix II) summarises the mean juvenile wood transition ages obtained according to species, taper class and height position. A mean breast height value of 21.0 years (data

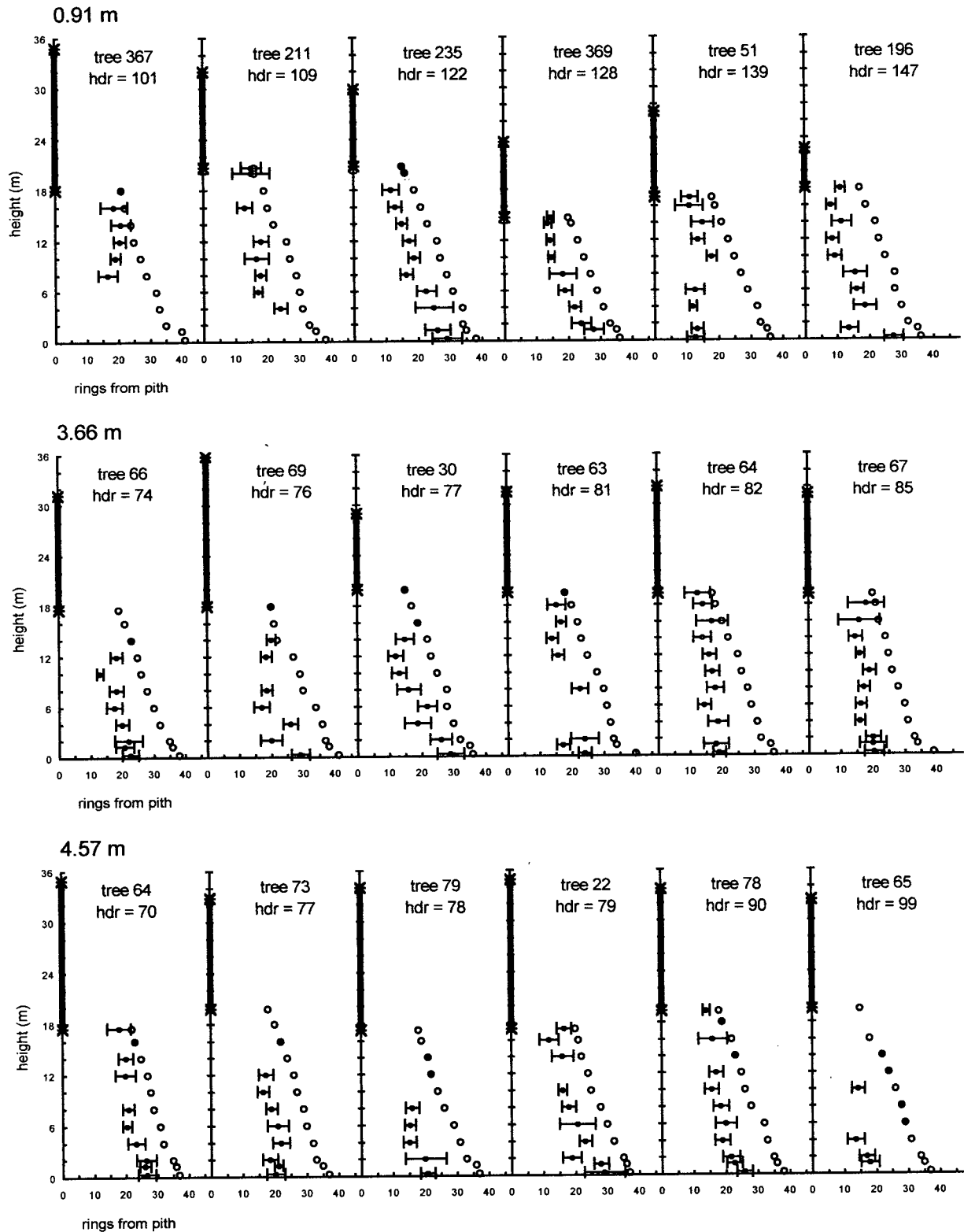


Figure 5.2 Juvenile-mature wood transitional ages (Model 1) illustrated according to sampled tree, height over diameter ratio (hdr) and by initial spacing for Douglas-fir.

—●— : transition age plus confidence interval ○ : total growth rings (pith-to-bark)
 ● : assumed as solely juvenile wood ★ : live-crown-length

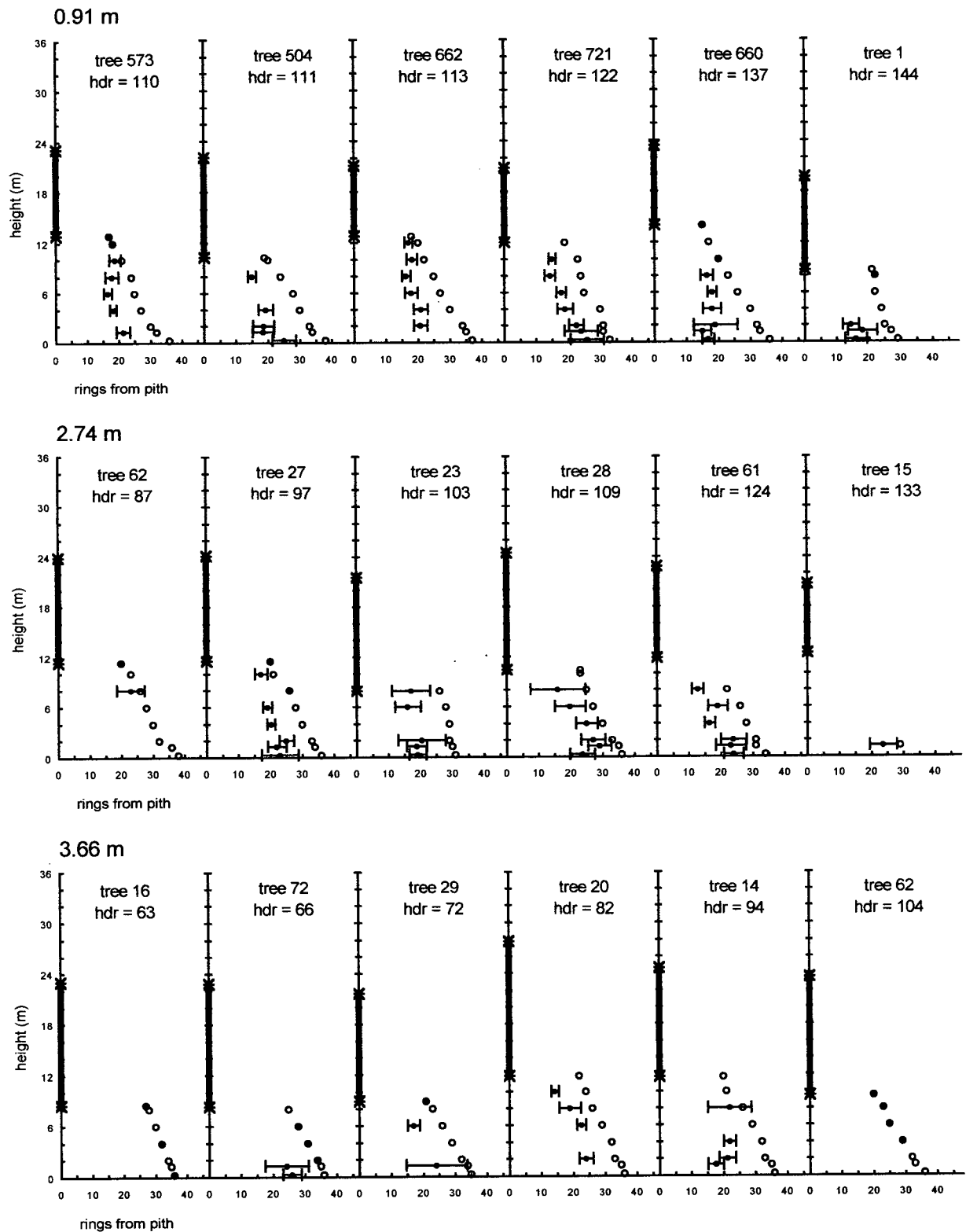


Figure 5.3 Juvenile-mature wood transitional ages (Model 1) illustrated according to sampled tree, height over diameter ratio (hdr) and by initial spacing for western hemlock.

—●— : transition age plus confidence interval ○ : total growth rings (pith-to-bark)
 ● : assumed as solely juvenile wood ★—★ : five-crown-length

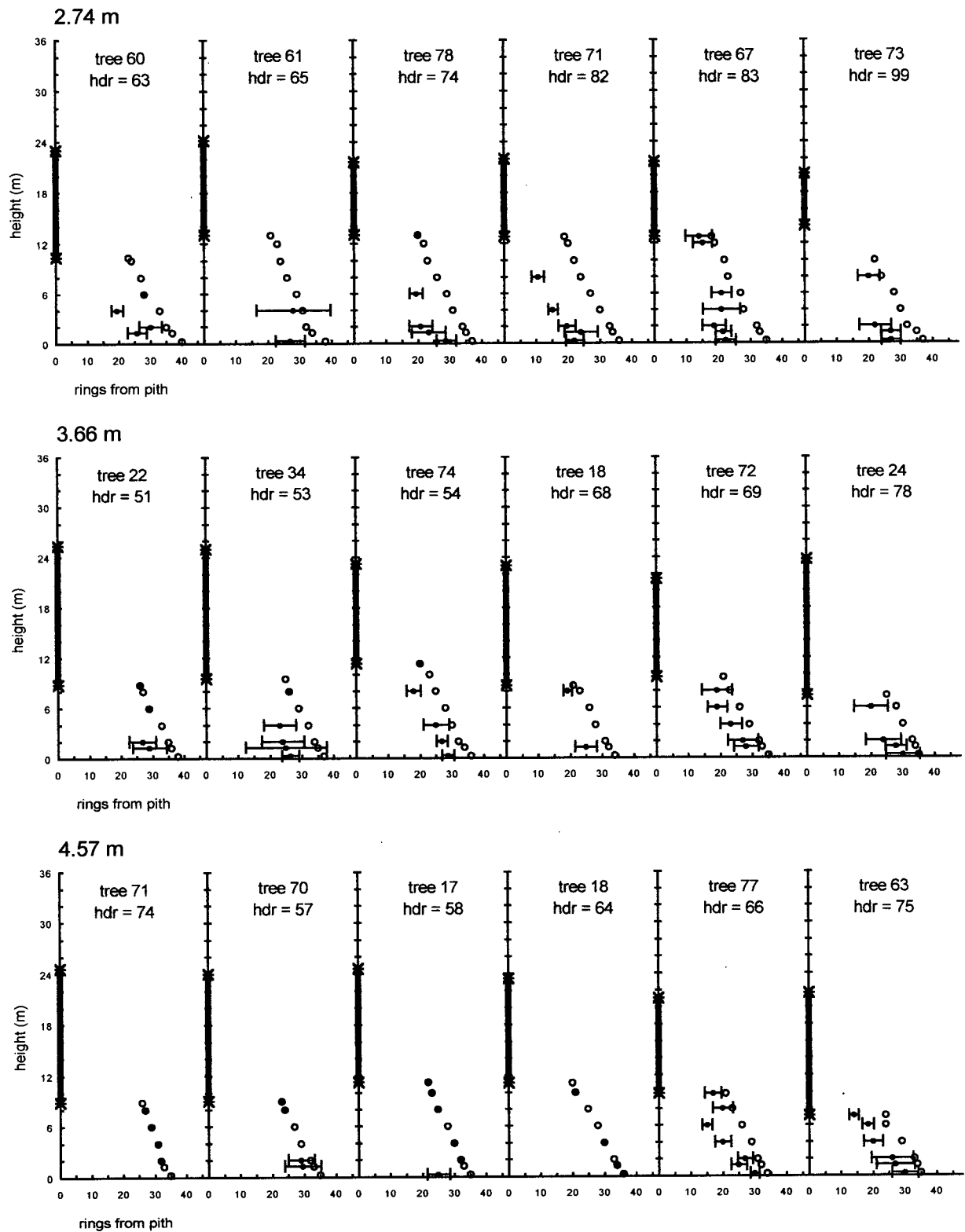


Figure 5.4 Juvenile-mature wood transitional ages (Model 1) illustrated according to sampled tree, height over diameter ratio (hdr) and by initial spacing for western redcedar.

—●— : transition age plus confidence interval ○ : total growth rings (pith-to-bark)
 ● : assumed as solely juvenile wood ★—★ : live-crown-length

from all spacings combined) was identified for Douglas-fir. This compares with 15 years reported by Wellwood and Smith (1962), 22.4 years by Di Lucca (1989) and 26.0 years by Abdel-Gadir and Krahmer (1993). All of the preceding transition ages were likewise established based on whole-ring relative density trends from pith to bark. Mean breast height transition age values of 21.5 years and 26.0 years were obtained for western hemlock and western redcedar, respectively. Very little comparative information exists in the literature relative to these two species.

Only a slight decrease in mean juvenile wood transition age was displayed from the dominant to the suppressed taper class for all species considered (Table 5.10). A more important decrease in transition age was generally displayed with increasing height. Such a trend is contrary to that reported by Di Lucca (1989), who concluded that transition age and sampling height (for Douglas-fir) were independent. The mean transition age values reported by Di Lucca equalled 22.4 years at breast height, 22.9 years at 20 % relative height and 20.9 years at 40 %. Nonetheless, it must be noted that Di Lucca's conclusion was based upon a sampling of nine trees ranging in hdb from 72 to 91 (breast height age ranging from 43 to 63 years). Sampling was restricted to what was defined as dominant and codominant crown class trees of uniform growth rate.

The preceding results can perhaps be interpreted through the following discussion which examines stand dynamics in the context of even-aged, single-species stands established at initial square spacing intervals. A common site-index value by species, along with relatively few micro-site differences, and strong epinastic control, is assumed throughout.

Regardless of spatial arrangement, all trees can initially be classified as open-grown. A similar rate of crown expansion is typically displayed by all stems so long as growing conditions remain uniform throughout. With time, lower branches begin to interlock, thus curbing lateral expansion. As interlocking slowly progresses to overlying branches, the lower branches gradually become shaded, leading to a decrease in photosynthetic activity. Stagnation and branch death eventually occur, the exact timing being intimately related to the shade tolerance of the species in question. Since the upper branches of adjacent trees will continue to expand into their individual growing spaces at similar rates, complete crown cover will invariably be maintained. Provided no competition-induced mortality occurs, the shading of underlying layers of branches will persist, and crown

recession will proceed unabated (Krahmer 1966, Curtis and Reukema 1970, Mitchell 1975, Oliver and Larson 1996).

Crown recession is initiated sooner among closely-spaced trees, but will proceed at about the same rate for all spacings so long as the potential for height growth remains the same for all trees (Oliver and Larson 1996). Since it has been assumed that the passage from juvenile wood to mature wood occurs at, or just below, the base of the live crown (Larson 1969, 1973), the onset of mature wood production at breast height should likewise be initiated sooner at the narrowest spacings.

Height growth for a tree does not proceed at a constant rate. It is initially slow during youth when too little foliage is available to accumulate sufficient energy for rapid terminal growth. As foliage volume expands, height growth increases rapidly and exponentially. At the onset of crown closure, the tree crown becomes restricted in lateral expansion. A constant in gross photosynthate production is soon reached, resulting in practically linear height growth well into maturity. At senescence, height growth slows and eventually levels off. The increased respiration demands at this time, along with stresses created by the extreme height, exposure and crown size, combine to limit the extension of the lateral shoots (Oliver and Larson 1996). Consequent to the above pattern of height development, growth rings counted within a tree stem, from pith to bark and at 2 m intervals from stump to tree top, should observably decrease in number at a non-constant rate.

An equal number of growth rings throughout the juvenile wood core would imply a pattern of crown recession over time that would parallel height growth. In order to maintain a constant number of growth rings, crown recession would have to follow the sigmoidal pattern of being initially slow, followed by a steep increase in activity. A steady rate of progression would ensue, succeeded by a final period of decreasing activity. In effect, crown recession through its first year would have to equal height growth achieved by the tree at age one. Crown recession the following year would have to equal height growth achieved during year two, and so on. No competition-induced mortality that could alter the makeup of the stand and affect the rate of crown recession would be permitted. The above also assumes that the passage along a tree stem, from juvenile wood to mature wood, would always remain at a constant position relative to the base of the live crown.

When all trees in a stand grow in height at an equal rate, all should maintain crown dimensions comparable to those displayed at crown closure (Oliver and Larson 1996). A constant live-crown-length over time would ideally require a pattern of crown recession that would correspond to height growth following crown closure. A constant rate of crown recession would be observed from the onset, followed by a decrease in activity to a final period of very little change. An initial period of arrested crown recession, followed by an exponential increase in activity (as would be the case for height growth from the onset of stand development), would not be observed. Consequent to the above pattern of crown development, a somewhat greater ring count should be displayed within the juvenile wood core at stump level than at successive 2 m intervals above (Figures 5.2, 5.3 and 5.4).

Kucera (1994) suggested that the onset of mature wood development at stump level in Norway spruce monocultures took place at the culmination of the current annual height increment. This hypothesis essentially presumed that the timing of crown closure within a stand was closely linked to the culmination of annual height growth. As crown recession at a narrower spacing is generally initiated at an earlier date, annual height growth may still be within the reach of its culmination point. Accordingly, a short period of brisk crown recession could be observed from the beginning, resulting in a rapid decrease in ring count within the juvenile wood core from stump level upward. Conversely, a very wide initial spacing could see the synchronization of the onset of crown recession with height growth culmination, or possibly even to a subsequent period of time. As the rate of annual height growth would have stabilised at this point, the juvenile wood core should demonstrate a much slower decline in ring count with increasing height.

With continued height growth, increasingly greater levels of photosynthate will be required for maintenance respiration. For trees growing at the narrower spacings, proportionally smaller crowns will have to support growing respiration surface areas. Due to priorities in the allocation of available photosynthates, height growth for such trees should carry on uninterrupted. However, very little corresponding growth in diameter will be observed at breast height, resulting in the development of narrow, cylindrical boles (e.g. hdr greater than or equal to 100). If not subjected to windthrow or snow-related damage, such closely-spaced trees will eventually enter a phase where even height growth could become repressed (Oliver and Larson 1996, Smith *et al.* 1997). This was presumably the case for trees #235, #369, #51 and #196 at the 0.91 m spacing for Douglas-fir (Figure 5.2).

If no significant mortality is incurred, and full crown closure is maintained, crown recession within such narrowly-spaced stands should carry on at a regular pace. However, tree crowns will eventually become flat-topped due to the sharp reduction in height growth (e.g. tree #196), with only the uppermost limbs exposed to direct sunlight (Kozlowski *et al.* 1991, Oliver and Larson 1996, Smith *et al.* 1997). Both live-crown-length and the total number of growth rings identified at the base of the live crown will have decreased. If the argument holds true that the passage from juvenile wood to mature wood occurs at, or just below, the base of the live crown, then a further decrease in the number of growth rings identified within the juvenile wood core should also be observed.

Upon creation of a large-scale opening within a narrowly-spaced stand, or following a commercial thinning operation, remnant trees that were previously suppressed are suddenly released. Oliver and Larson (1996) stated that only rarely will a tree actually rebound from an overtopped crown class position and merge into an upper dominant crown class. The frequency of such an occurrence ultimately depends on the plasticity of the species, the age at time of release, the severity of the suppression and the ability of the tree to withstand further windthrow and snow damage. Upon release, crown recession may slow down significantly or may even cease over a period of time. Both live-crown-length and crown width, and subsequently the overall photosynthetic efficiency of the tree crown, should in turn increase. It is therefore presumable that the juvenile wood ring count at the base of the live crown will likewise increase.

Artificial pruning would likely produce an opposite effect, with a stand-grown tree suddenly created from an open-grown tree. Di Lucca (1989) stated that the pruning of lower branches from a live crown could bring about a decrease in the proportion of juvenile wood by accelerating the occurrence of the juvenile wood to mature wood transition. Due to the sudden reduction in live-crown-length, the number of growth rings identified from pith to bark at the base of the live crown would suddenly decrease. A correspondingly sharp reduction in the number of growth rings identified within the juvenile wood core should therefore also be observed.

Even within stands that have not experienced major losses to competition-induced mortality (e.g. 3.66 m spacing for Douglas-fir, Figure 5.2), the intensification of competition will progressively lead to crown class differentiation (Oliver and Larson 1996). The less vigorous trees (e.g. tree #30)

will eventually display a certain reduction in height growth. If crown closure remains complete, and if a constant rate of crown recession is maintained, then greater variability in juvenile wood ring count should be displayed at the base of the live crown. Dominant trees would presumably demonstrate the greatest number of juvenile wood rings, codominant trees would display fewer, and overtopped trees would show the least. The range in ring count at the base of the live crown would accordingly reflect the intensity of competition, with the most homogenous stands displaying the least variability.

A distance of at least 3.8 m below the base of the live crown was defined by Di Lucca (1989) as the average point along the stem where the passage from juvenile wood to mature wood could be observed for Douglas-fir. Di Lucca concluded that this value apparently decreased with increasing age and tree height, and suggested that it could approach the base of the live crown as a tree became older and taller. The results obtained for Douglas-fir (Figure 5.2) are similar to Di Lucca's with respect to those trees classified within his identified range of *hdr* values (72 to 91). Most points of transition along the stem ranged from zero to several metres below the base of the live crown. However, some of the slower growing trees did demonstrate a transition point that extended well into the live crown. Locating an exact point of transition along the stem was ultimately deemed infeasible in this study. Such an approach would have required a more precise definition than the one employed for locating the base of the live crown.

For a widely-spaced tree possessing a large volume of crown foliage relative to length of branch-free stem, high auxin levels are generally believed to promote the formation of large diameter, thin-walled tracheids over an extended portion of the growing season. Due to stronger auxin gradients within the upper reaches of the branch-free stem, latewood production is tempered, thus leading to the development of mostly transitional-type tracheids over the latter portion of the growing season. Due to weaker auxin gradients further down the stem, latewood tracheids will be produced in somewhat greater quantities over the same time period (Larson 1973). A gradual relative density transition from earlywood to latewood should therefore be displayed at the base of the live crown, resulting in a generally lower whole-ring relative density, and in the subsequent continuation of juvenile wood production. A definite latewood increment should in turn develop toward the stump, resulting in a more abrupt intra-ring transition, a higher whole-ring relative density, and in the subsequent development of mature wood.

For a narrowly-spaced tree undergoing the effects of greater competition, high auxin production would presumably be limited to the upper reaches of the crown where branches are most vigorous and have the shortest translocation pathways to the stem. Underlying branches subject to the effects of shading would, in turn, experience a decrease in photosynthetic activity. Smaller buds would develop each year, further decreasing the potential for photosynthate and auxin production during the following seasons. Auxin gradients would eventually decrease to such a low that large quantities of latewood tracheids would begin to develop in the vicinity of the lower branch unions. The transition from earlywood to latewood within each growth ring would thus become more abrupt. The relative proportion of latewood immediately below the base of the live crown would also increase, resulting in the production of mature wood (Larson 1973). The passage from juvenile wood to mature wood along the stem, relative to that observed for a widely-spaced tree, would therefore have moved upward with respect to the base of the live crown.

A highly suppressed tree can be compared to a branch undergoing senescence. The live crown is generally short, narrow, often has gaps and foliage is sparse. Photosynthetic activity is often severely limited, to the point that only a limited number of earlywood tracheids are produced within very narrow growth rings. Transitional-type tracheids are generally produced into what remains of the live crown. An abrupt earlywood to latewood transition should therefore be observed along the length of the branch-free stem, and the passage from juvenile wood to mature wood should accordingly remain abrupt (Larson 1973). Mature wood production could presumably even extend into the live crown. Such an extension would, in turn, bring about a further decrease in the number of growth rings identified within the juvenile wood core at the base of the live crown. This was presumably the case for trees #369, #51 and #196 at the 0.91 m spacing for Douglas-fir (Figure 5.2).

Height growth and crown recession for western hemlock (Figure 5.3) and western redcedar (Figure 5.4) were both much slower than that observed for Douglas-fir (Figure 5.2). Reukema and Smith (1987) observed very little crown lifting within the 3.66 m spacing for Douglas-fir prior to age 16 (same spacing trial plots sampled as in this study). In turn, very little crown lifting was observed within the 3.66 m spacing for both western hemlock and western redcedar prior to age 20. By age 25, the base of the live crown for Douglas-fir approached 7 m. That for western hemlock and western redcedar approximated 2 m.

The larger tree crowns at the wider spacings for both western hemlock and western redcedar, coupled with a shortened translocation pathway, apparently resulted in an extended period of juvenile wood development. A definite juvenile wood transition zone was accordingly difficult to identify for both species. Furthermore, all of the western redcedar trees selected for study originated from the three wider spacings available. Slow growing trees were unavailable for analysis, as no large-scale blowdowns had occurred within the 0.91 and 1.83 m spacings.

The juvenile wood transition zones for both western hemlock and western redcedar, as depicted by the wider confidence bands, tended to be very gradual. Many of the whole-ring relative density profiles established for western hemlock never attained a relatively stable period of development that would otherwise have pinpointed the onset of maturity. Many of the profiles analysed for western redcedar did not display a subsequent rise in whole-ring relative density following the initial decrease in value from the pith. Even though a subsequent increase was displayed by some of the slower growing trees, relatively stable values were seldom achieved. Consequently, a large proportion of the samples analysed for both species supported the assumption that only juvenile wood was present from pith to bark.

5.3.2 Diameter and Shape of Juvenile Wood Core

Figures 5.5, 5.6 and 5.7 illustrate the diameter and shape of the juvenile wood cores identified for Douglas-fir, western hemlock and western redcedar, respectively. All crown profiles correspond to measurements obtained on site (15:1 ratio for crown radius to stem radius at breast height). All stems were profiled by relative height to facilitate comparisons between individual trees and spacings. Each tree was arranged within each spacing from smallest *hdr* value to largest. All data points correspond to those displayed as a function of ring number from pith in Figures 5.2, 5.3 and 5.4.

Allowing the live-crown-ratio to decrease to a level roughly less than 30 % will generally lead to a reduction in diameter growth, whereas a ratio under 20 % will commonly see a reduction in height growth (Smith *et al.* 1997). Most of the trees sampled from the narrowest spacings displayed relatively low live-crown-ratios, along with small amounts of stem taper. The intensification of

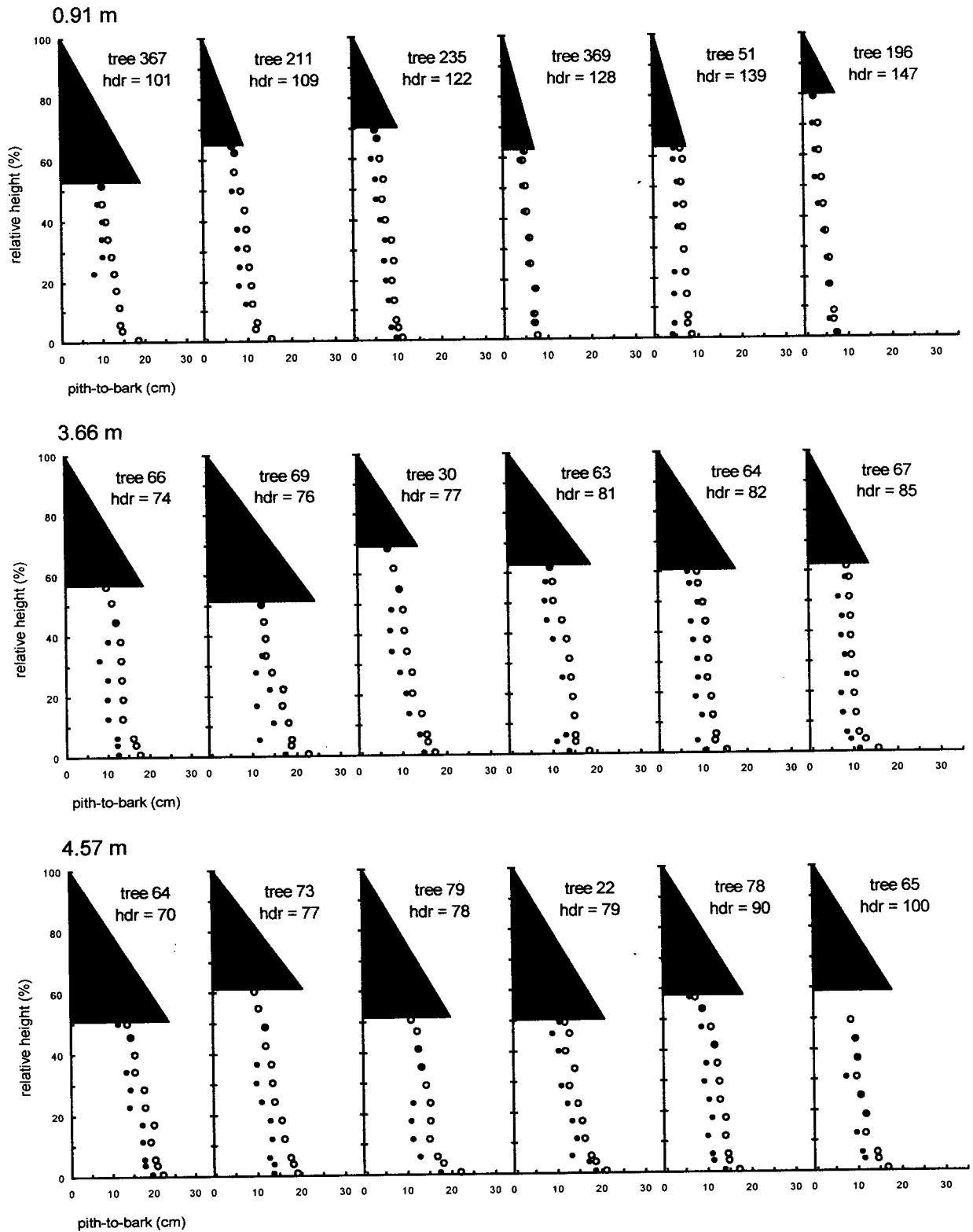


Figure 5.5 Juvenile wood thickness values corresponding to transitional ages obtained using Model 1 and illustrated according to sampled tree, height over diameter ratio (hdr) and by initial spacing for Douglas-fir (15:1 crown-width scale).

● : juvenile wood thickness ○ : pith-to-bark thickness ▲ : crown profile

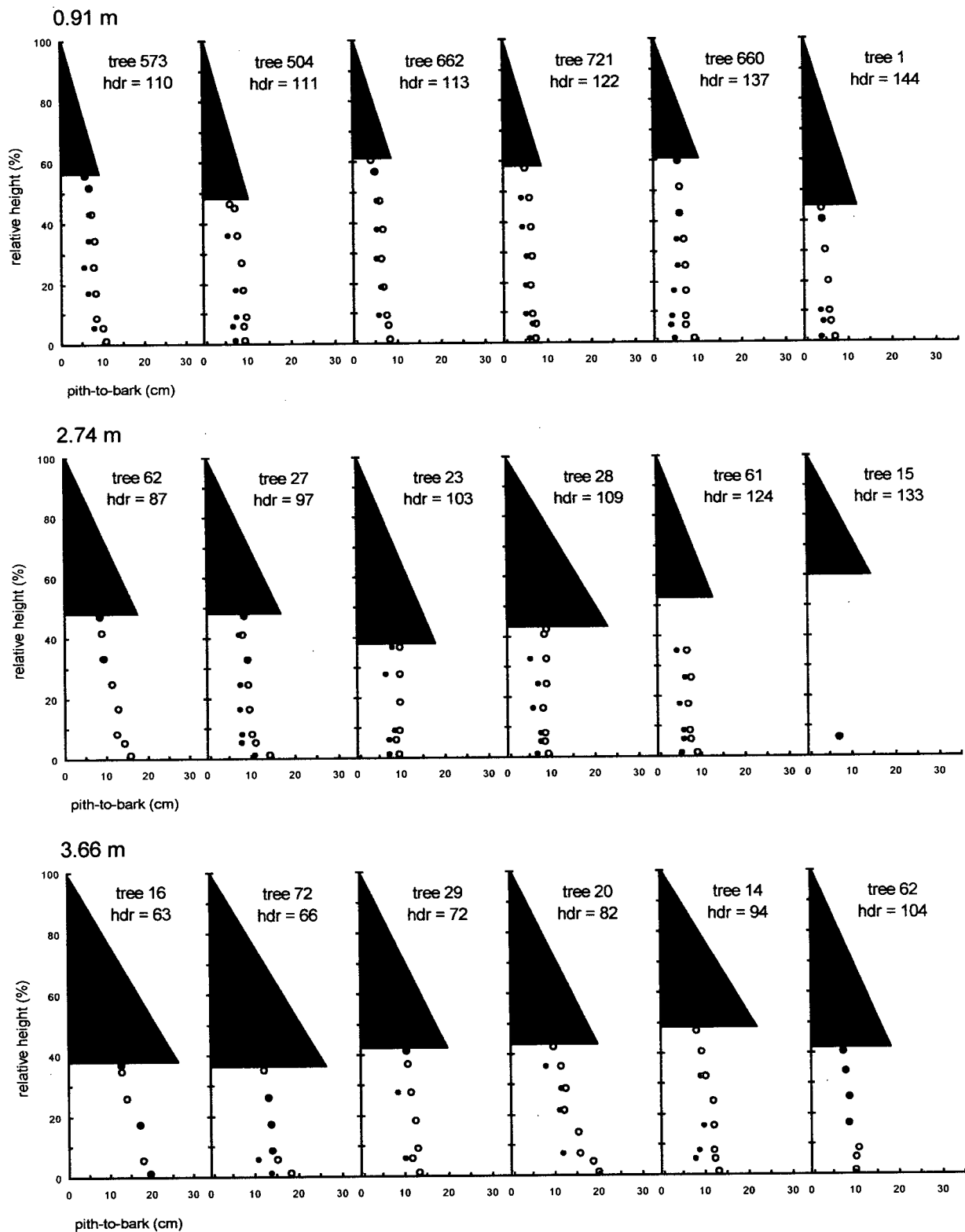


Figure 5.6 Juvenile wood thickness values corresponding to transitional ages obtained using Model 1 and illustrated according to sampled tree, height over diameter ratio (hdr) and by initial spacing for western hemlock (15:1 crown-width scale).

● : juvenile wood thickness ○ : pith-to-bark thickness ▲ : crown profile

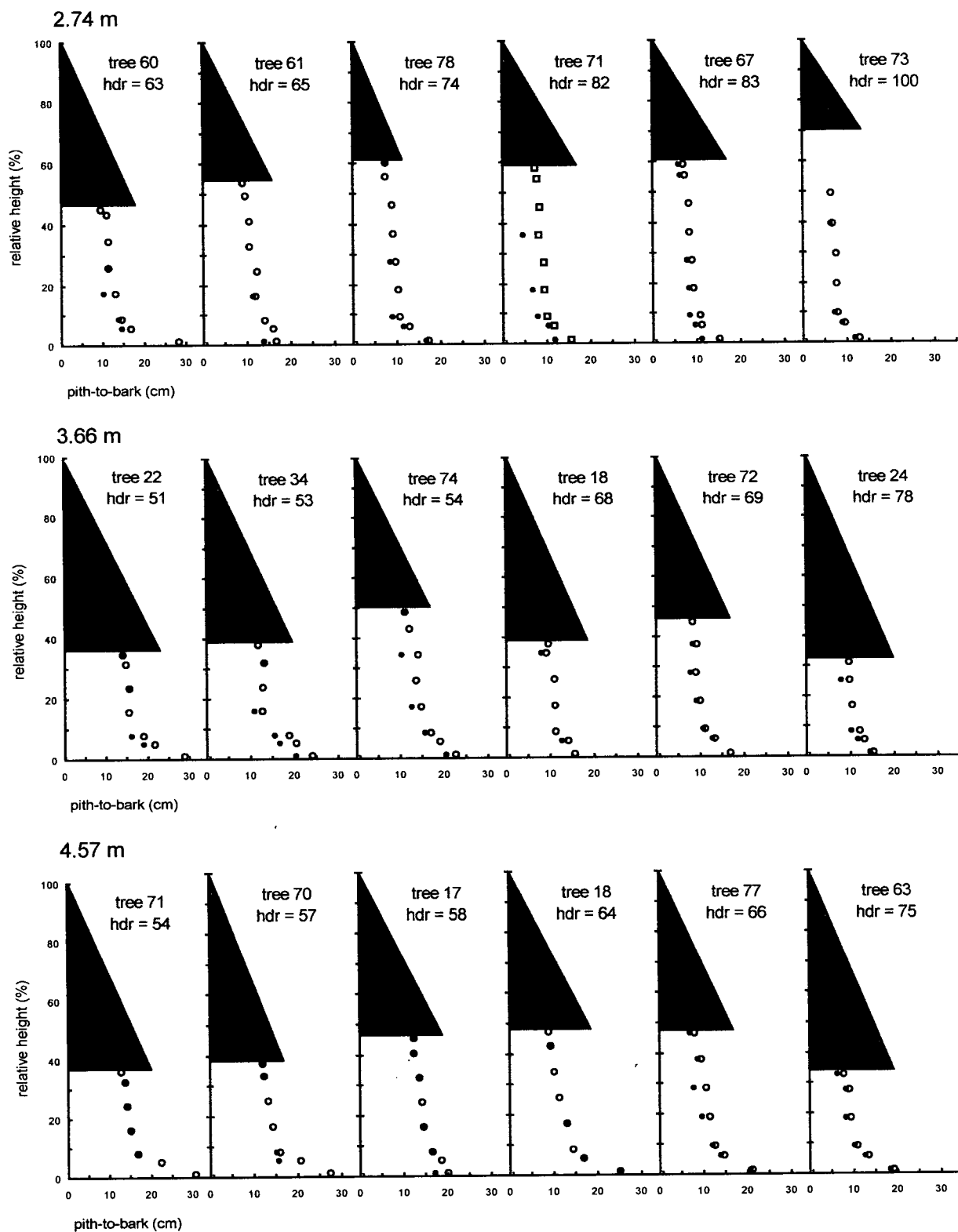


Figure 5.7 Juvenile wood thickness values corresponding to transitional ages obtained using Model 1 and illustrated according to sampled tree, height over diameter ratio (hdr) and by initial spacing for western redcedar (15:1 crown-width scale).

● : juvenile wood thickness ○ : pith-to-bark thickness ▲ : crown profile

competition at these spacings accordingly led to smaller diameter juvenile cores. Even though the development of mature wood was generally initiated at an earlier date, its distribution about the juvenile wood, as a direct consequence of the poorer incremental growth, remained very thin.

The larger juvenile core diameters for each species were generally associated with the larger crown dimensions at the wider spacings. In the case of Douglas-fir (Figure 5.5), the greatest amounts of mature wood were likewise produced at the wider spacings (3.66 and 4.57 m). Given time and assuming superior incremental growth was maintained, one could expect a substantial decrease in the proportion of juvenile wood within such stems. The proportion of juvenile wood could conceivably even, at some point, become lower than for trees growing at the narrower spacings.

Minimal amounts of mature wood were produced at the wider spacings for both western hemlock (Figure 5.6) and western redcedar (Figure 5.7). A transition from juvenile wood to mature wood was consistently difficult to identify for both species. Limited crown recession, coupled with large volumes of crown foliage, often resulted in a very gradual increase in whole-ring relative density below the base of the live crown, and in a subsequent gradual transition from juvenile wood to mature wood. Nonetheless, with further crown recession, one could expect the eventual development of relatively stable whole-ring relative density values. Such values were, on occasion, observed at the narrower spacings for both species. An accelerated pattern of mature wood development at breast height, similar to that displayed by Douglas-fir, could likewise be expected provided that superior incremental growth was maintained over time.

Juvenile wood, when profiled by ring number from pith (Figures 5.2, 5.3 and 5.4), displayed a higher degree of tapering with increasing height than when profiled by radial distance (Figures 5.5, 5.6 and 5.7). Such a trend can be explained by way of Figure 4.1 which illustrates ring width development over time by species and spacing. Ring width development was initially subject to an increase followed by a continual decrease to a point at which more-or-less constant values were maintained. The initial increase in ring width was generally of greater duration at the wider spacings where larger values were also attained. Minimum constant values were reached at an earlier age as spacing decreased, and these values tended to be lower than those observed at the wider spacings. Consequently, the first 15 growth increments considered as a whole for any profile in Figure 4.1 were

significantly wider than the ensuing 15. As a decrease in the number of growth rings within the juvenile wood core would reflect the outer rings only, the actual change in core dimension would be tempered. Only a minor change in core dimension would therefore be displayed by a slow growing tree due to the narrower growth rings produced throughout.

Mature wood, when profiled by ring number from pith, would also appear thicker relative to juvenile wood. Since mature wood is essentially formed during a period of decreasing incremental growth, the growth rings produced are much narrower than those observed within the juvenile wood core. Its distribution about the juvenile core, when profiled as a function of radial distance, should therefore appear very thin.

Juvenile wood, when profiled by radial distance, ranged in shape from highly tapering to more-or-less cylindrical. At 0.91 m, the juvenile cores for Douglas-fir (Figure 5.5) appeared relatively cylindrical. A slight increase in diameter was nonetheless observed toward the stump as spacing increased. The juvenile cores for western hemlock (Figure 5.6) remained more-or-less cylindrical for all spacings, essentially paralleling the contours of the individual stems. Perhaps greater tapering would have been encountered had the 4.57 m spacing been available for sampling. Western redcedar (Figure 5.7) continually demonstrated excessive tapering at stump level. Again, it must be noted that only the wider spacings were available for analysis (2.74, 3.66 and 4.57 m), and that a juvenile wood transition age remained difficult to identify for many of the samples collected.

A rapid decrease in juvenile wood core diameter was generally observed for western redcedar from 0 to 10 % relative height. As previously discussed, crown recession, once initiated, will proceed at a rate faster than height growth immediately following stand establishment. The juvenile ring count at stump level should therefore be greater than that displayed at successive height intervals above. Furthermore, there are stresses created by a tree's weight and from increasingly strong winds in an exposed environment that will generally alter incremental growth at the stump. Excessive ring width swelling will take place, providing greater anchoring support and wind-firmness (Larson 1963). Many of the trees sampled for western redcedar (especially within the 3.66 and 4.57 m spacings) featured large amounts of buttressing. With wider than normal growth rings produced, the effect of a greater number of juvenile growth rings at stump level, in terms of core diameter, was compounded.

5.3.3 Juvenile Wood Taper Modelling

Kozak (1988) proposed a variable-exponent taper equation for modelling the shape of the bole for a standing tree. A single, continuous function incorporating a changing exponent from ground level to tree top was used to describe the neiloid, paraboloid and conic forms inherent to a tree stem. The existence of similar tapering within the juvenile wood cores in this study (all three species previously considered by Kozak) suggested the use of a variable exponent taper equation for describing juvenile wood distribution.

The fitting of the variable-exponent taper equation to data for both dib and jwd produced highly significant results ($p = 0.0001$) for all species. The partial regression coefficients and the multiple coefficients of determination obtained are displayed for dib and jwd in Tables 5.11a and 5.12a, respectively (Appendix II). All coefficient of determination values correspond to estimations based upon the original untransformed independent variable. Average bias and standard error of estimate values are presented for dib and jwd in Tables 5.11b and 5.12, respectively (Appendix II).

The variable-exponent taper equation was most effective at modelling dib for Douglas-fir. Higher coefficient of determination values would most likely have been observed for all species had sampling been conducted within the live crown as well. The suggested model nonetheless provided a very good fit, with average bias values for the most part less than 1 cm. The only exception was for western redcedar, where a bias value of 1.17 cm was obtained at breast height. Due to excessive buttressing in many of the trees sampled, a relatively higher standard error of estimate value (6.32 cm) was recorded for the species at stump level.

The coefficient of determination values obtained for jwd were comparatively lower than those listed for dib. Values of 0.831, 0.811 and 0.923 were obtained for Douglas-fir, western hemlock and western redcedar, respectively. Values of 0.863, 0.831 and 0.898 would have been obtained for jwd had the unmodified version of Kozak's taper equation been used. Choice of the better model would ultimately require a much larger sampling of trees. Average jwd bias, for the most part, did not exceed 1 cm. However, the values obtained were generally greater than those listed at corresponding height intervals for dib. The same applied for the standard error of estimate, with values obtained for

jwd largely greater than those obtained for dib. Missing data, originating from profiles where a juvenile wood transition age could not be determined, was an important contributor to the above.

Variability for all species, in terms of jwd, was greatest at stump level and also as the base of the live crown was approached. Such a trend points to the possibility of the suggested taper model performing more poorly within certain spacings. As previously discussed, the base of the live crown for an overtopped, small-crowned tree does not necessarily represent the full extent of mature wood distribution. Some mature wood development may be observed within the live crown. Conversely, the passage from juvenile wood to mature wood within a dominant, large-crowned tree may occur at a significant distance below the base of the live crown. In either case, the base of the live crown is not synonymous with the passage from juvenile wood to mature wood as was initially assumed.

Missing data were a major problem during the fitting of the jwd data set. Ideally, stem analysis (destructive sampling) conducted on older trees that demonstrate greater amounts of mature wood development would have yielded better results. Sampling above the base of the live crown would, in turn, have been conceivable. Taper equations function best if 6 to 15 measurements are obtained at well spread out intervals from ground level to tree top (Kozak 1988). The samples obtained through stem analysis would also have been of better quality since increment boring, while using climbing gear, would have been avoided. The possibility of repeated sampling at a specific height position would also have eliminated the problem of missing data arising from damaged core samples.

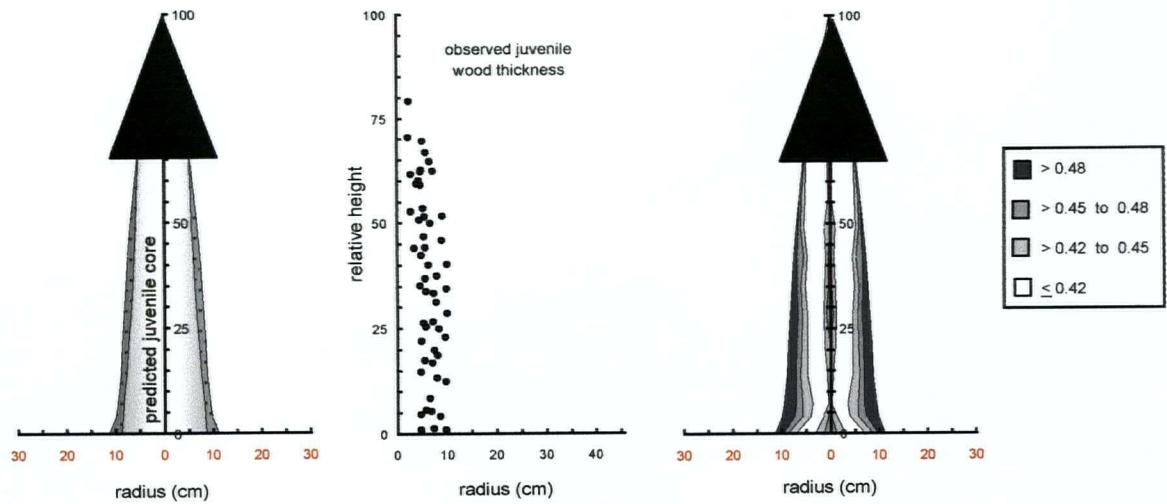
Sampling would likewise have been conducted on a greater number of tree stems. A total of 18 trees per species were available for testing in this study. Kozak (1988) suggested that parameters should be estimated from a minimum of about 60 to 100 trees that cover a wide range of heights and breast height diameters. With more trees available, the performance of the taper model could then have been evaluated as a function of initial spacing. The validation of the taper model would also have been a possibility. The effects of a range of inflection points on the performance of the equation could furthermore have been investigated. Juvenile wood volume calculations would ultimately have been conceivable.

The fitted dib and jwd variable-equation taper models are pictured within the left-hand column of Figures 5.8, 5.9 and 5.10 for Douglas-fir, western hemlock and western redcedar, respectively. A tree of average jwd, dbh, dib, height, crown width and live-crown-length (by spacing) was used to descriptively assess the behaviour of both the modified (jwd) and unmodified (dib) versions of the variable-equation taper model. The partial regression coefficients listed in Tables 5.11a and 5.12a were used for plotting. The mean crown width illustrated for each spacing is scaled to 15:1 (ratio for crown radius to stem radius at breast height). The distribution of observed juvenile wood thickness values are featured within the central column. Average stemwood relative density below the base of the live crown is illustrated within the right-hand column. Stemwood relative density zones equalling 0.03 were arbitrarily selected for gradient mapping. The average profiles illustrated for each spacing, in both the right-hand and left-hand columns, are in direct proportion to one another. All data were profiled by relative height to allow comparisons between the various spacings and species sampled.

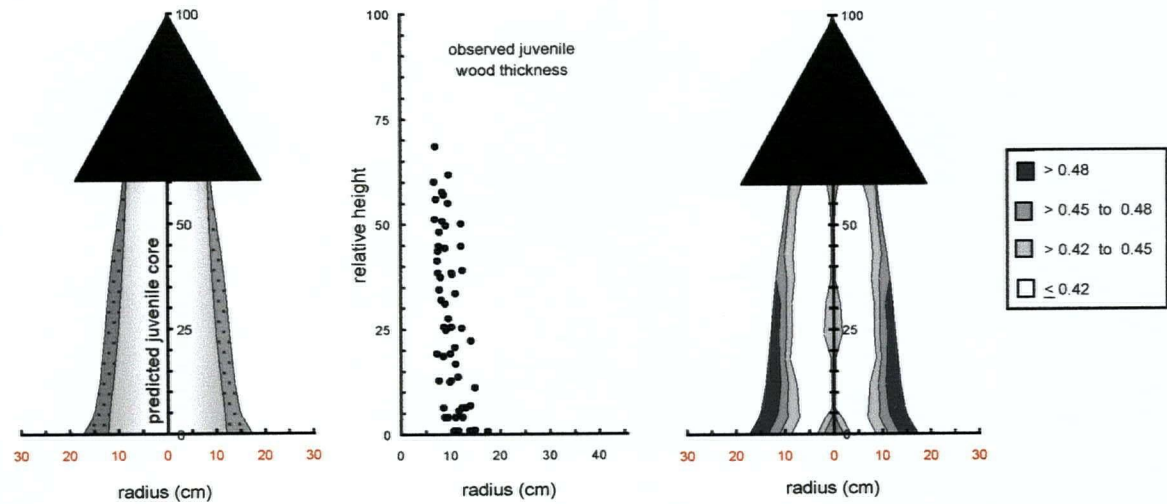
The predicted shapes of the juvenile wood cores compare well with the observed juvenile wood thickness data, and also with each corresponding stemwood relative density profile. However, the predicted profiles remain exploratory in nature. The predicted shapes are each based upon a tree of average dimensions and do not necessarily reflect the variability of measurements observed within each spacing. The possibility exists that the proposed model could perform better within some dbh classes than others. Bias is also a concern, as juvenile wood diameter at each height position was estimated by doubling the radial distance value corresponding to the juvenile wood transition age defined. Sampling on a larger scale (minimum of two transition age estimates obtained per height interval), along with a complete data set, would ultimately be required to establish reliable parameters.

Douglas-fir (Figure 5.8) displayed the most consistent vertical pattern of relative density variation. Medium-density wood (0.42 to 0.48) was associated with the pith at all spacings. A more-or-less cylindrical zone of low-density wood (≤ 0.42) invariably surrounded this higher density core. Greatest widths within this low-density wood zone were achieved at the 4.57 m spacing. High-density wood (> 0.48) was continually displayed next to the bark. Its thickness was greatest at the stump, and gradually tapered off as the base of the live crown was approached. The wider the spacing, the further the point below the base of the live crown at which it faded. The wider spacings

0.91 m



3.66 m



4.57 m

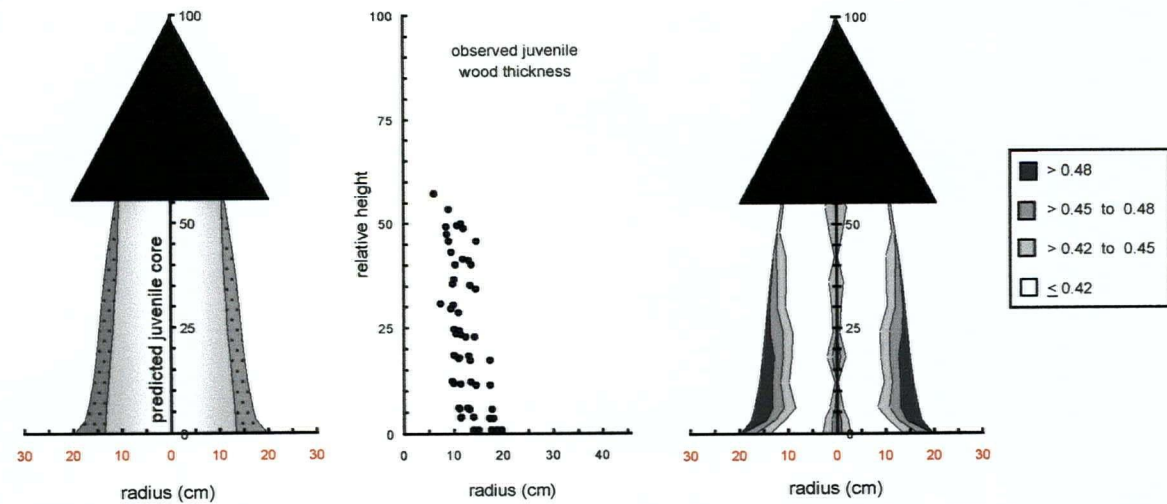
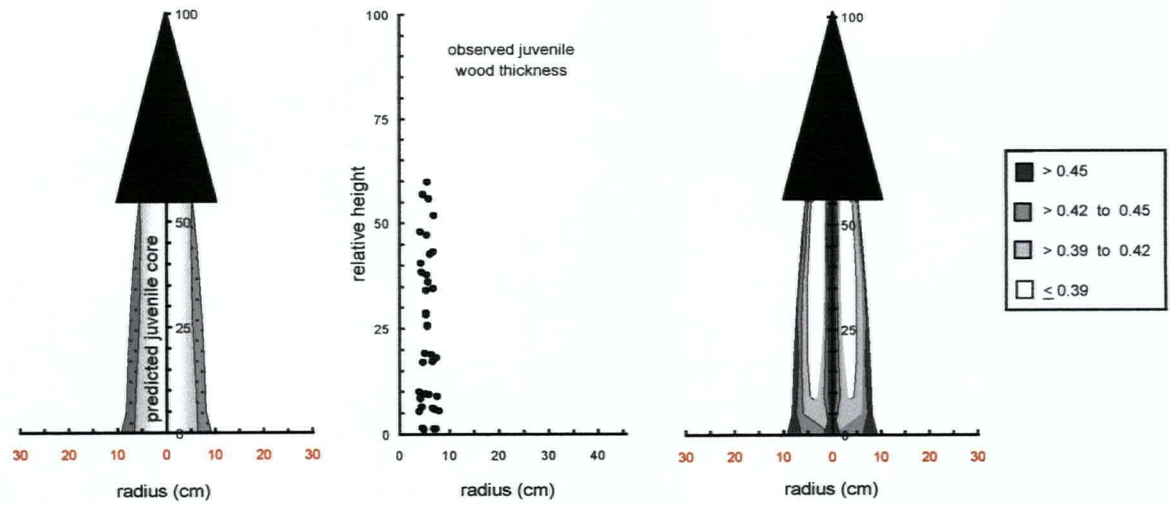
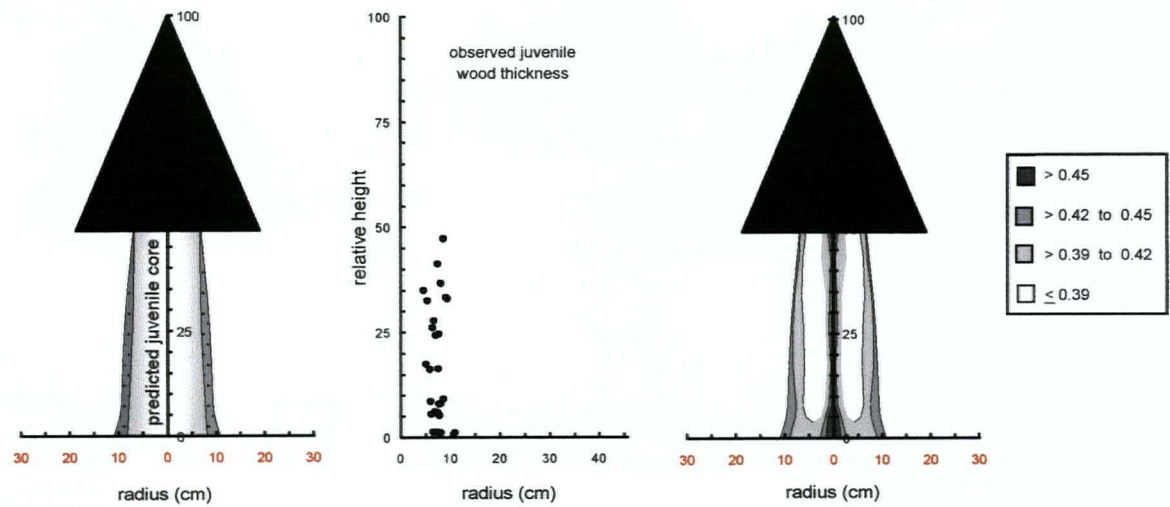


Figure 5.8 Predicted diameter inside bark and juvenile wood taper (left), observed juvenile wood thickness (centre) and mean stemwood relative density distribution (right) by initial spacing for Douglas-fir.

0.91 m



2.74 m



3.66 m

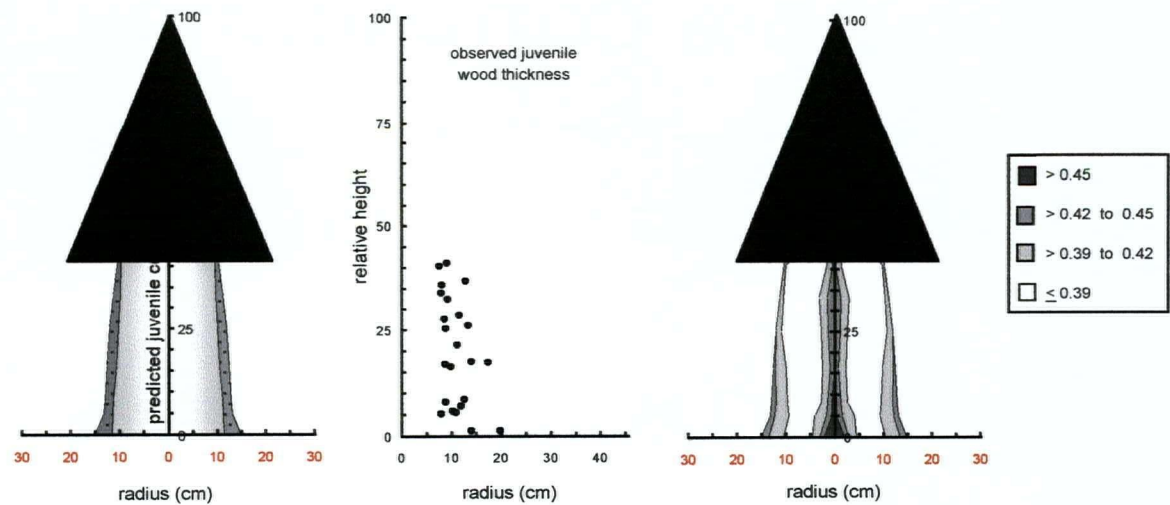
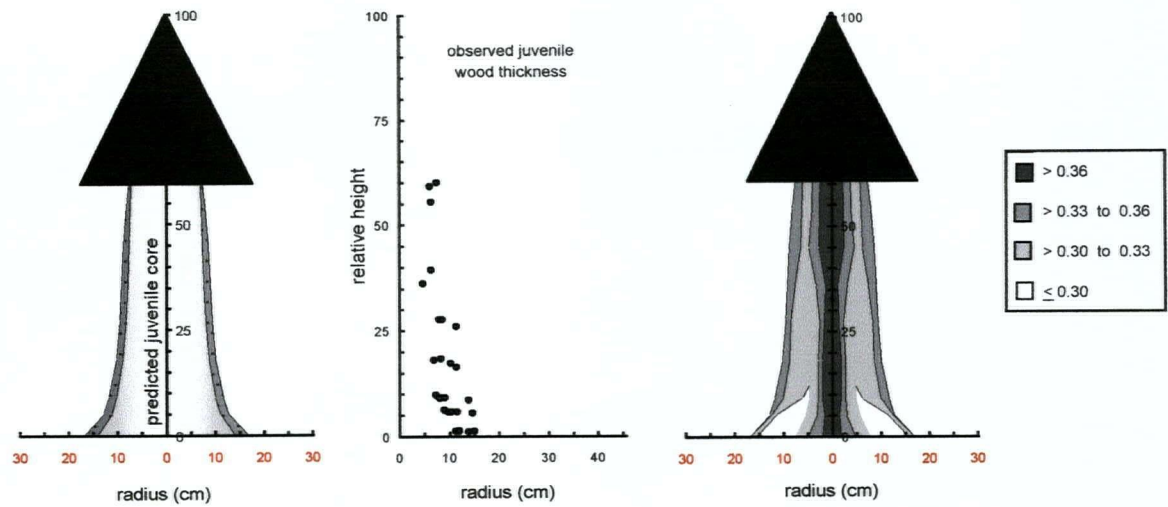
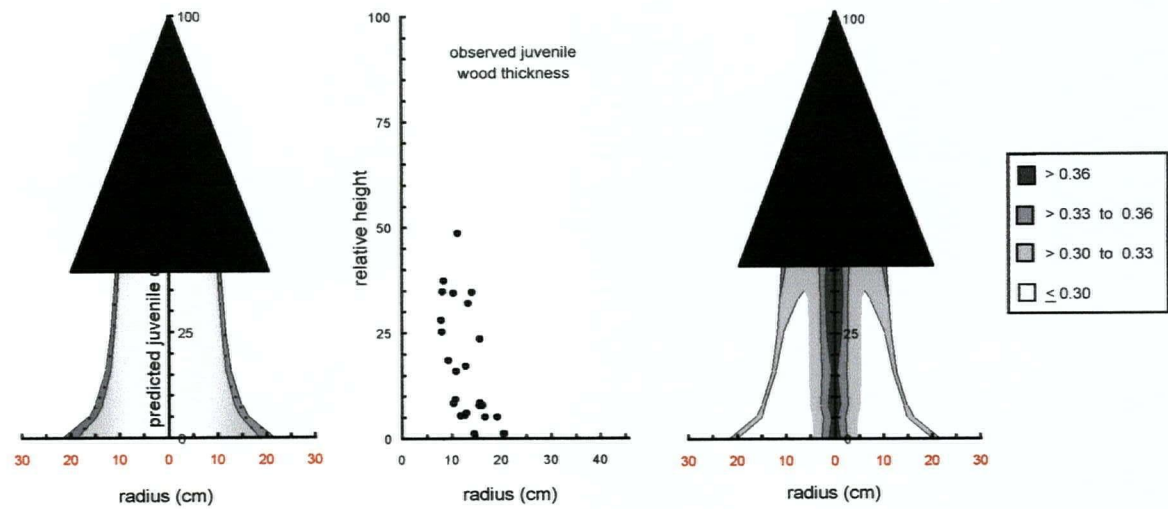


Figure 5.9 Predicted diameter inside bark and juvenile wood taper (left), observed juvenile wood thickness (centre) and mean stemwood relative density distribution (right) by initial spacing for western hemlock.

2.74 m



3.66 m



4.57 m

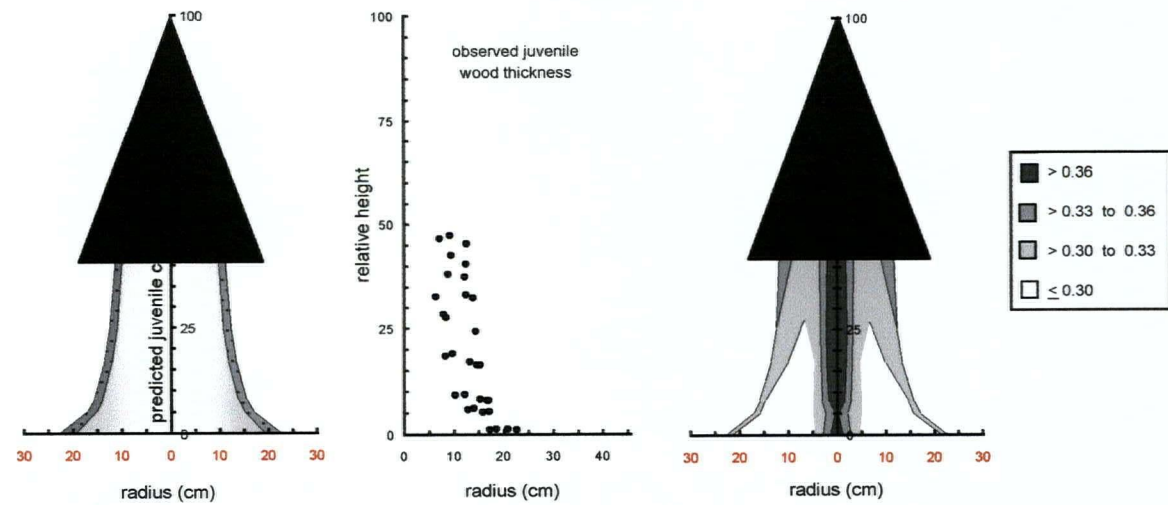


Figure 5.10 Predicted diameter inside bark and juvenile wood taper (left), observed juvenile wood thickness (centre) and mean stemwood relative density distribution (right) by initial spacing for western redcedar.

also displayed the most gradual transition from a low-density wood during early development, to a high-density wood at maturity.

Greater variability was observed for western hemlock (Figure 5.9). Medium-density wood (0.39 to 0.45) was associated with the pith at all spacings. This higher density inner-core was invariably encased by low-density wood (≤ 0.39). The diameter of this low-density cylinder increased as spacing widened, with the transition from a low-density to a high-density wood (> 0.45) becoming more gradual. A relative density exceeding 0.45 was observed next to the bark at the 0.91 m spacing only. The deposition of high-density wood was greatest at the stump, and gradually tapered off with increasing height. The greater the volume of crown foliage, the further below the base of the live crown at which high-density wood blended into the low-density inner-core.

High-density wood (> 0.36) for western redcedar (Figure 5.10) was invariably displayed next to the pith and below the base of the live crown immediately next to the bark. Low-density wood (≤ 0.33) was found mostly at stump level, with the wider spacings displaying the largest volumes. The transition between low and high density wood became more gradual with increased crown size. The smaller the volume of crown foliage relative to length of branch-free stem, the further the downward progression of high-density wood (next to the bark) along the stem.

The mean relative density values obtained for juvenile wood, mature wood, and from pith to bark as a whole (calculated as a mean along the radius), are presented in Tables 5.13, 5.14 and 5.15 for Douglas-fir, western hemlock and western redcedar, respectively (Appendix II). Only common height intervals were listed, with values obtained at the base of the live crown omitted. The mean juvenile wood relative density observed at common heights for Douglas-fir varied little by spacing. Values for both western hemlock and western redcedar tended to decrease as spacing increased. A slight decrease in mean juvenile wood relative density was observed with increasing height for Douglas-fir. A similar decrease in value was observed for western hemlock, whereas a slight increase in value was observed for western redcedar. Generally speaking, the transition from juvenile wood to mature wood occurred at a progressively lower relative density with increasing height for all species considered.

A pattern of decreasing mean stemwood relative density was observed with increasing height for Douglas-fir. A similar trend was reported for the species by Wellwood and Smith (1962), Jozsa and Kellogg (1986), Megraw (1986), Di Lucca (1989) and Jozsa (1989). A pattern of decreasing mean stemwood relative density was also observed for western hemlock, with a similar trend also reported for the species by Krahmer (1966), Jozsa and Kellogg (1986) and Jozsa *et al.* (1998). Mature wood development for both Douglas-fir (Figure 5.8) and western hemlock (Figure 5.9) was initiated at stump level first (where the pith to bark ring count is greatest), and gradually worked its way up along the stem in time with crown recession. The greater the volume of mature wood relative to juvenile wood at any specific height, the greater the stemwood (pith to bark) relative density subsequently recorded.

A pattern of increasing mean stemwood relative density was observed with increasing height for western redcedar. A similar trend was reported for the species by Wellwood and Jurazs (1968) and Jozsa and Kellogg (1986). Heavy stem tapering for western redcedar was displayed at the 3.66 and 4.57 m spacings by many of the faster growing trees sampled. The growth increments produced at stump level were among the widest observed in this study. Less stem tapering was observed at the 2.74 m spacing, with a narrower growth increment produced throughout. Markedly slower radial growth was displayed by all trees toward the base of the live crown.

An increasingly negative relationship over time for western redcedar (from growth ring 13 onward) was previously identified at breast height between ring width and whole-ring relative density (Figure 4.19). If a somewhat similar relationship can be assumed for all height positions along the branch-free stem, then a rapid decrease in ring width with increasing height should logically bring about a corresponding rapid increase in whole-ring relative density. Mature wood development for western redcedar was accordingly initiated at the base of the live crown first, and gradually proceeded in both the upward (in time with crown recession) and downward (in time with slower radial growth) directions (Figure 5.10). Presumably, a certain minimum crown volume and live-crown-ratio had to be attained in order to initiate the development.

A greater whole-ring relative density value, as suggested by the average stemwood relative density profiles in Figures 5.8, 5.9 and 5.10, was definitely associated with the development of mature

wood next to the bark. Jozsa *et al.* (1998) employed such trends to define a juvenile wood transition age in western hemlock. Mature wood was defined as the portion of the outer bole displaying a whole-ring relative density value greater than 0.43. From the perspective of the wood processing industry, such relative density mapping clearly identifies the areas within a tree from which a stronger, and therefore a higher-valued wood product can be obtained. Fundamentally, a demarcation point based on a single whole-ring relative density value is insufficient to differentiate between juvenile wood and mature wood.

The generally accepted definition for mature wood alludes to the development of relatively stable values for a specific wood property (e.g. whole-ring relative density) following an initial period of extreme variability. Yet, the precise level at which a more-or-less stable value is eventually attained by a species may vary with genetic stock and by geographic site (Zobel and Sprague 1998). Variation may also exist within a tree according to height position (Tables 5.13, 5.14 and 5.15). A wood property could presumably stabilise at a level lower than that dictated by an arbitrarily-set transition value. Under these circumstances, mature wood could erroneously be mapped as juvenile wood. The opposite could also happen, with high-density juvenile wood inadvertently mapped as mature wood.

The shape of the juvenile core for very widely-spaced conifers, from stump level up to the base of the live crown, was described by the BC Ministry of Forests (1999) as more-or-less cylindrical. At a narrow spacing, the juvenile wood core gradually increased in diameter with increasing height. A slight buttressing of the core was consistently displayed at stump level. Such patterns of juvenile wood distribution were most likely derived using TASS (Tree and Stand Simulator). Developed by Mitchell (1969, 1975), and upgraded by the BC Ministry of Forests (Mitchell and Cameron 1985), TASS is a biologically oriented spatially explicit individual tree model that assesses the effects of various cultural practises and environmental factors on the potential growth and yield of even-aged, single-species, managed stands. TASS simulates the development and interaction of individual tree crowns over time, and produces summaries of annual volume increment along individual tree stems. TASS can also simulate the production of mature wood, by assuming that its development invariably extends from 3.8 m below the base of the live crown, downward. All incremental growth above this mark is classified as juvenile wood.

Volume estimates for both juvenile wood and mature wood can subsequently be provided with TASS for any period of stand development. In light of the results obtained in this study, such calculations can be considered suspect. None of the trees profiled in Figures 5.5, 5.6 and 5.7 demonstrated a juvenile wood core that noticeably increased in diameter with increasing height. Furthermore, a species difference undoubtedly existed relative to the location of the passage from juvenile wood to mature wood along the stem. TASS consistently employed a value of 3.8 m below the base of the live crown over the range of stocking densities it could process, and for the three species considered in this study. However, a value of 3.8 m mostly corresponded to the faster-growing Douglas-fir trees only. Some of the slower growing Douglas-fir trees in this study demonstrated a transition point extending into the live crown. The faster growing trees for both western hemlock and western redcedar most frequently demonstrated juvenile wood development from pith to bark, and this along much of the branch-free stem. Mature wood development for western redcedar was apparently initiated at the base of the live crown first, and this only after a minimum crown volume and live-crown-ratio had been attained. Its subsequent progression along the branch-free stem seemingly progressed in both the upward and downward directions.

5.4 General Summary

The purpose of this portion of the study was to examine juvenile wood development within second-growth stands established over a range of initial spacing intervals. The following discussion summarises the principal results obtained.

The first objective was to determine a juvenile wood to mature wood transition point based on whole-ring relative density trends from pith to bark:

- Model 1 provided a superior fit ($F > 1$) for 72 % of the profiles considered (82 % for Douglas-fir, 68 % for western hemlock and 61 % for western redcedar).
- The confidence intervals obtained using Model 1 were, for the most part, much narrower in width than those obtained using Model 2.

- The transition to mature wood was mostly abrupt within the slower growing trees, and generally became more gradual as the ratio of crown volume to branch-free stem increased.
- A mean juvenile wood transition age equalling 21.0, 21.5 and 26.0 years was determined at breast height for Douglas-fir, western hemlock and western redcedar, respectively.
- A large proportion of the faster grown samples analysed for both western hemlock and western redcedar supported the assumption that juvenile wood was present from pith to bark.

The second objective was to study the relationship between crown recession and mature wood development along the stem. The following hypothesis was tested for each tree sampled:

$H_{5.1}$: the passage along a tree stem, from juvenile wood to mature wood, occurs at the base of the live crown

Hypothesis 5.1 was not rejected whenever the base of the live crown coincided with the maximum extent of mature wood development along the stem (outer growth increment at the base of the live crown located within the boundary of the juvenile wood transition zone confidence interval). Hypothesis 5.1 was rejected whenever the passage from juvenile wood to mature wood occurred at a point below the base of the live crown, or at a point above it, (outer growth increment at the base of the live crown exceeds the upper juvenile wood transition zone confidence band).

- Generally speaking for both Douglas-fir and western hemlock, the larger the volume of crown foliage relative to length of branch-free stem, the lower the passage from juvenile wood to mature wood below the base of the live crown. In the case of western redcedar, the larger the volume of crown foliage relative to length of branch-free stem, the higher the passage.
- A transition point located at the base of the live crown, and often extending several metres below, was displayed by many of the faster growing Douglas-fir trees. A transition point extending above the live crown base was sometimes displayed by the slower growing trees.

- The transition point for western hemlock was generally situated in the vicinity of the live crown base for the slower growing trees, and ranged from several metres below to stump level for the faster growing trees.
- A transition point along the stem was difficult to identify for western redcedar. Many of the faster growing trees displayed very little subsequent increase in whole-ring relative density following the initial decrease from the pith. Many of the slower growing trees displayed a subsequent increase, but seldom achieved a relatively stable value typical of mature wood.

A third objective was to define the shape of the juvenile wood core as a function of initial spacing and stem taper. The following hypothesis was tested for each tree sampled:

$H_{5.2}$: the shape of the juvenile core, in terms of ring number from pith, is cylindrical from stump level up to the base of the live crown

If the juvenile wood transition zone confidence bands for a tree did not overlap with increasing height, then the identified juvenile wood transition ages were considered significantly different, and Hypothesis 5.2 was rejected. An unchanging transition age was implied when transition zone confidence bands remained overlapping. Hypothesis 5.2 was not rejected when this occurred.

- A gradual decrease in juvenile wood ring count was identified with increasing height. This decrease progressed at a slightly greater rate for the slower growing trees, presumably due to increased levels of crown recession.
- All juvenile cores, when profiled according to ring number from pith, demonstrated a higher degree of tapering with increasing height than when profiled by radial distance.
- The juvenile cores illustrated for the slower growing Douglas-fir (profiled by radial distance) were mostly cylindrical. Greater tapering was displayed toward the stump by the faster growing trees.

- The juvenile cores illustrated for western hemlock (profiled by radial distance) were cylindrical for most trees, except for some of the larger stems which remained highly tapering as they had yet to produce mature wood in any great quantity.
- Since very little mature wood had yet been produced for western redcedar, most juvenile cores (profiled by radial distance) retained a highly tapering shape with excessive buttressing displayed toward the stump.
- The earlier onset of crown recession at the narrower spacings led to a smaller diameter juvenile core. Even though the production of mature wood was likewise initiated at an earlier date, its production about the juvenile core remained thin due to poor incremental growth.
- Overall, the thickest mature wood was produced by the faster growing Douglas-fir. Minimal amounts were produced at the wider spacings for both western hemlock and western redcedar.

A fourth objective was to profile the shape of an average juvenile core by species and initial spacing, and to compare the results obtained with corresponding relative density stem profiles.

- The fitting of the variable-exponent taper equation to data for both dib and jwd produced highly significant results ($p = 0.0001$) for all species.
- Average bias values for dib and jwd were generally less than 1 cm for all height intervals sampled. Average standard error of estimate values for dib and jwd were generally greatest at stump level, and also as the base of the live crown was approached.
- Improving the jwd taper function would ultimately require a wider range of spacings, older trees and a greater number of tree species. A much larger and complete data set (preferably obtained via stem analysis) would be required, as well as a minimum of two juvenile wood transition age estimates per height interval, and sampling above the base of the live crown.

- A medium-density (0.42 to 0.48) inner core for Douglas-fir was commonly surrounded by low-density wood (≤ 0.42). Greatest widths within this zone were achieved by the faster growing trees. High-density wood (> 0.48) was always displayed next to the bark. Its thickness was greatest near the stump, gradually tapering toward the base of the live crown. The wider the spacing, the further the point below the live crown base at which it faded.
- A medium-density (0.39 to 0.45) inner core for western hemlock was generally surrounded by low-density wood (≤ 0.39). Greatest widths within this zone were once again realised by the faster growing trees. High-density wood (> 0.45) next to the bark was mainly displayed at the 0.91 m spacing. The deposition of high-density wood was greatest at the stump, gradually tapering with increasing height. The greater the volume of crown foliage, the further the point below the crown base at which it blended into the low-density inner section.
- High-density wood (> 0.36) for western redcedar was invariably displayed next to the pith. Low-density wood (≤ 0.33) was commonly found in large amounts at the stump. The wider the spacing, the greater the amount of low-density wood produced. The smaller the ratio of crown volume to stem size, the further the downward development of high-density wood below the base of the live crown.
- A pattern of decreasing mean stemwood relative density was observed with increasing height for both Douglas-fir and western hemlock. A pattern of increasing mean stemwood relative density was observed with increasing height for western redcedar.
- Mature wood development for Douglas-fir and western hemlock was initiated at stump level first, and gradually worked its way up the stem in time with crown recession. Mature wood development for western redcedar was initiated at the base of the live crown first, and gradually proceeded in both the upward (in time with crown recession) and downward (in time with slower radial growth) directions.

6. GENERAL CONCLUSIONS

This report describes the results of a non-destructive wood quality study conducted from spacing trials based at the UBC Malcolm Knapp Research Forest in Haney, BC. Established in 1957, these trials are among the oldest in the province from which the effects of cambial ageing, initial spacing, stem taper and growth rate could be evaluated on second-growth wood formation. Initial square spacings of 0.91, 1.83, 2.74, 3.66 and 4.57 m (3, 6, 9, 12 and 15 ft) were sampled, representing initial stocking densities of 12076, 2986, 1332, 747 and 479 stems/ha, respectively. The information obtained pertains to one site only (site-index 39.8 (50) for Douglas-fir, 32.6 (50) for western hemlock and 32.9 (50) for western redcedar), and to trees aged 41 years and less.

Cambial age (ring number from pith) had a highly significant effect on the development of practically each wood property considered. Cambial age was subsequently used as a covariate in all regression and correlation analyses involving growth rate (ring width). Having disregarded cambial age would have resulted in significant relationships for most wood properties, with inflated coefficient of determination values. Highly significant relationships in past studies, when growth rate was related to relative density, tracheid length or microfibril angle development, were frequently obtained as a result of this indiscretion. Cambial age was often overlooked as an important contributor to variation.

6.1 Douglas-fir

The results obtained for Douglas-fir demonstrated that accelerated diameter growth had relatively little impact on whole-ring relative density development. Pith to bark variability was, to a large degree, a function of cambial age. An increasingly non-significant relationship was displayed over time with ring width. A similar pattern of development was observed for trees growing at initial spacings ranging from 0.91 to 4.57 m. Identical profiles were furthermore identified by taper class.

Douglas-fir wood quality can therefore be considered robust in terms of the potential for modification via stand density management. Relatively wide initial spacings could hypothetically be used to produce large diameter sawlogs over a shortened rotation, and this without having an adverse effect on whole-ring relative density development.

Nonetheless, certain differences in wood quality could arise between slow-grown and fast-grown stems, ultimately having an impact on utilisation. A weak, significantly positive relationship between microfibril angle and ring width was identified for Douglas-fir between growth rings 9 and 21. Despite the fact that whole-ring relative density development was not significantly affected by initial spacing, larger microfibril angle values were nonetheless produced over a longer period at the wider spacings. The differences observed could potentially translate into reduced levels of stiffness and increased longitudinal shrinkage for lumber produced from the juvenile wood of these faster-grown trees.

Slightly higher earlywood relative density values and slightly lower latewood relative density values were associated with the wider growth rings during early development. Slightly lower earlywood relative density values and slightly higher latewood relative density values were associated with the wider growth rings toward the bark. In terms of whole-ring relative density, the effects of such peaks were largely cancelled out. In terms of intra-ring relative density, a narrower range of values was being displayed between minimum earlywood and maximum latewood relative density. Greater intra-ring uniformity was subsequently achieved by the faster growing trees ($\text{hdr} \leq 80$) during early development, and by the slower growing trees ($\text{hdr} \geq 100$) toward the bark.

Douglas-fir demonstrated the lowest overall shade tolerance, and the fastest rate for crown recession. The subsequent rapid decrease in live-crown-ratio apparently had an important influence on mature wood development. Generally speaking, the larger the volume of crown foliage relative to length of branch-free stem, the lower the passage from juvenile wood to mature wood below the base of the live crown. A reduction in diameter growth ($\text{hdr} \geq 100$) led to a smaller diameter juvenile core surrounded by a very thin layer of mature wood that seemingly extended into the live crown. Faster diameter growth ($\text{hdr} \leq 80$) typically yielded a larger diameter juvenile core, along with a much thicker layer of mature wood concentrated in the lower branch-free stem.

Given an extended rotation age, and with rapid incremental growth maintained, a substantial decrease in the proportion of juvenile wood at the wider spacings is foreseeable. The proportion could conceivably, at some point, even become lower than that displayed at the narrower spacings. The transition from juvenile wood to mature wood was mostly abrupt for the slow-grown trees, and generally gradual for the fast-grown stems. If lumber was to be produced from juvenile wood, greater relative density uniformity by piece would ultimately be achieved by the fast-grown trees.

6.2 Western Hemlock

Ring width had little impact on whole-ring relative density for western hemlock, save for a minor increase in the strength of the relationship during the mature wood portion of tree development. Slight decreases in earlywood width, with correspondingly little change in latewood width, were being displayed at this time as a function of decreasing ring width. An increasingly negative relationship accordingly emerged for latewood proportion. Very little variability was observed in terms of both earlywood relative density and latewood relative density.

Identical profiles of development, by initial spacing and taper class, were identified for latewood width, earlywood relative density, latewood relative density, whole-ring tracheid length and microfibril angle. Variability in each case was mostly related to ring number from pith. Identical profiles of development for whole-ring relative density were identified by taper class only. Based upon these results, western hemlock could be considered more robust than Douglas-fir in terms of the ability to manipulate via stand density management. Relatively wide initial spacings could hypothetically be used to increase volume production, and this without adversely affecting wood quality. Stem taper could, in turn, be considered a poor indicator of overall wood quality.

However, it must be noted that trees from the 4.57 m spacing interval were unavailable for sampling. Perhaps a more important increase in whole-ring relative density would have been noted had a greater number of fast-growing trees been available for analysis. Most of the trees sampled were representative of the suppressed ($\text{hdr} \geq 100$) and intermediate ($80 < \text{hdr} < 100$) taper classes (as defined in this study). In a forest plantation management scenario, such trees would be likely

candidates for removal during a low-thinning exercise. Trees from the dominant taper class ($hdr \leq 80$) would be representative of the wood quality potentially available at time of harvest if accelerated diameter growth was maintained throughout stand development.

Intra-ring development for western hemlock varied little over time, with a gradual transition invariably displayed from earlywood to latewood. The species demonstrated the greatest overall shade tolerance and consequently, the slowest rate for crown recession. Extensive live-crown-ratios were supported even at high stand densities. The faster the rate for crown recession it was presumed, the greater the extent to which physiological gradients would be modified along the stem, and the greater the variability that would subsequently emerge over time in terms of wood formation. The greatest intra-ring relative density homogeneity, for all species considered, was subsequently displayed from pith to bark over the range of spacings sampled.

Slower diameter growth for the western hemlock led to the production of a small diameter juvenile core surrounded by a very thin layer of mature wood that seemingly extended from stump level upward to the base of the live crown. Faster diameter growth yielded limited amounts of mature wood concentrated at stump level. Generally speaking, the larger the volume of crown foliage relative to length of branch-free stem, the lower the location of the passage from juvenile wood to mature wood below the base of the live crown. A very gradual increase in whole-ring relative density over time was displayed by the faster growing trees, hence the very gradual transition from juvenile wood to mature wood. If lumber was to be produced from the juvenile wood of such trees, greater relative density uniformity by piece would once again be achieved.

6.3 Western Redcedar

Overall, western redcedar presented the greatest potential for modifying wood quality via stand density management. No identical profiles of development were identified for any of the wood properties considered, suggesting great sensitivity in terms of the relationship between available growing space and wood formation. Changes in earlywood width were strongly associated with ring width development. The relationship between latewood width and ring width became somewhat

stronger over time. The relationship between latewood proportion and ring width, in turn, became increasingly negative. Slightly lower latewood relative density values were associated with the wider growth rings during the early years of development. Slightly lower earlywood relative density values were associated with the wider growth rings toward the bark.

Western redcedar accordingly displayed an increasingly negative relationship between whole-ring relative density and ring width that became especially strong as mature wood was produced. Generally speaking, accelerated diameter growth (3.66 and 4.57 m spacings, $\text{hdr} \leq 80$) led to very little subsequent change in whole-ring relative density following the initial decrease in value from the pith. A reduction in diameter growth ($\text{hdr} \geq 100$) led to a gradual increase in value over time. Relatively stable whole-ring relative density values were primarily achieved by trees at the 0.91 m spacing that demonstrated very little earlywood width development.

Heavy stem tapering was displayed by many of the faster growing trees sampled. The growth rings produced at stump level were among the widest observed in this study. Markedly slower radial growth was displayed toward the base of the live crown. Based on the increasingly negative relationship identified between whole-ring relative density and ring width, a pattern of increasing mean stemwood relative density was displayed with increasing height. This is in direct contrast to both Douglas-fir and western hemlock, which both demonstrated greater stem cylindricality, and a much weaker relationship between ring width and whole-ring relative density. In either case, a decreasing mean stemwood relative density was typically displayed with increasing height.

A juvenile wood transition point was frequently difficult to identify for western redcedar. Many of the faster growing trees never displayed a subsequent increase in whole-ring relative density following the initial decrease in value from the pith. Others displayed a subsequent increase in value, but seldom achieved relatively stable values typical of mature wood. Furthermore, slow-growing trees from the two narrower spacing intervals (0.91 and 1.83 m) were unavailable for sampling.

Mature wood development was initiated toward the base of the live crown first, and gradually proceeded in both the upward (in time with crown recession) and downward (in time with slower radial growth) directions. Presumably, a certain minimum crown volume and live-crown-ratio had

to be attained in order to initiate the development. The smaller the volume of crown foliage relative to length of branch-free stem, the further the downward progression of high-density wood (next to the bark) along the stem.

Minimal amounts of mature wood were produced by the faster growing trees at the wider spacings. If the subsequent timber was to be used for aesthetic purposes, or for reasons of dimensional stability, insulation or durability, a relatively low stemwood relative density resulting from a highly tapered stem would not present a serious disadvantage in terms of wood quality. If the principal management goal was to produce timber suitable for structural purposes, an important reduction in stem taper ($hdr > 80$) would be required. In this study, such trees were mainly identified at initial spacings of 2.74 m and less.

6.4 Kajaani FS-200 Optical Fibre Analyser

A precise depiction of mean whole-ring tracheid length development was provided for each species using both image analysis and the Kajaani FS-200 Optical Fibre Analyser. Successive dips and rises in whole-ring tracheid length development were commonly identified using both systems. Significantly shorter tracheid lengths were nonetheless obtained at all sampling points using the Kajaani FS-200 Optical Fibre Analyser. The system was shown to be inadequate for measuring tracheid length variability on the basis of 12 mm increment cores. The length-weighted formula applied to the Kajaani data (Kajaani Electronics Ltd. 1986) was judged ineffective for masking the influence of the large number of folded and/or broken tracheids processed. Image analysis, though extremely tedious, was considered a more reliable option for characterising tracheid length variability.

6.5 Future Work

Little information is available regarding earlywood tracheid diameter development for Douglas-fir, western hemlock and western redcedar. Little concurrent information is available in terms of latewood diameter development, both radially and tangentially. Such information, along

with corresponding data on cell wall thickness and tracheid length, would account for much of the variation in whole-ring relative density existing from pith to bark. This information would, in turn, allow for the establishment of stronger links between the various identified patterns of wood formation, and the various changes in crown morphology and competitive status displayed over time.

Little information is likewise available regarding intra-ring microfibril angle development. Large amounts of variability undoubtedly exist as a function of species, cambial age, and perhaps even growth rate. The limited data that is available most often comes in the form of single mean values generated from a collection of growth rings. Intra-ring profiles are largely unheard of. Such information would allow for the subsequent establishment of relationships between the various patterns of microfibril angle development identified in a tree, with the various changes in crown morphology and competitive status displayed over time.

These data would also allow for the subsequent evaluation of cell wall thickness as an effective predictor of microfibril angle variability. Relationships could in turn be established as a function of overall tracheid morphology by likewise incorporating the corresponding tracheid diameter and tracheid length data into the prediction model. The use of cell wall thickness as a surrogate measure for microfibril angle would be beneficial in future tree breeding programs, and to wood quality research in general. Conducting microfibril angle measurement remains a time consuming procedure when performed using optical means. Scanning technology is readily available for the rapid and inexpensive measurement of cell wall thickness variability.

Further research on a broader scale, from a wider range of spacings and sites, and from slightly older trees, will eventually be required to further the development of the relationships established in this study. Even though the spacing trials at Haney offered the best and only available site for analysing wood quality in an even-aged, evenly-spaced, single-species context, serious limitations were nonetheless encountered in terms of sampling design. A maximum of 18 trees were potentially available for sampling at most spacings. Many trees were missing, including the majority of those originally planted at the 4.57 m spacing for western hemlock. Non-destructive sampling for juvenile wood had to be employed on all standing trees, altogether excluding the 0.91 m spacing for western redcedar, and the 1.83 m spacing for all species.

Certain generalisations were made in this study regarding the location of the passage from juvenile wood to mature wood along the branch-free stem. Mature wood development was found largely traceable to changes in both crown morphology and stem shape over time. Whole-ring relative density development, by species and height position, was generally found to stabilise at a similar time period for trees growing under similar conditions. However, the ability to identify the exact position of the passage from juvenile wood to mature wood was ultimately deemed infeasible. A more precise definition than the one employed for defining and locating the base of the live crown would be needed.

The existence of tapering within the juvenile core implied the use of a variable exponent taper equation for describing juvenile wood distribution. The subsequent fitting of juvenile wood data to a modified version of Kozak's variable exponent taper equation (1988) was deemed exploratory from the onset. A possible long-term objective would be the development of a taper model through which juvenile wood diameter could effectively be predicted along a tree stem. This would enable the modelling of juvenile wood development within uniformly-spaced, single-species, even-aged stands. The only requirement would be obtaining measurements for tree height, height to the base of the live crown, outside bark diameter at breast height and juvenile wood diameter at breast height.

The results of this study demonstrated the potential for incorporating the concept of juvenile wood taper modelling into existing growth and yield models such as TASS. Ultimately, a very large research effort would be required to provide an effective taper function. To date, taper models have seldom been fitted to juvenile wood data. Improving the model proposed in this study would require a greater number of tree species. Ideally, disc samples would be collected from older trees (demonstrating greater amounts of mature wood development) via stem analysis. A minimum of two juvenile wood transition age estimates would be obtained per height position sampled, and from 6 to 15 juvenile wood diameter measurements would be obtained at spread out intervals from ground level to tree top. A complete data set would be required. A minimum of about 60 to 100 trees, covering a wide range of tree heights and breast height diameters, would be sampled (Kozak 1988). With more trees available, the performance of the taper model would then be evaluated as a function of initial spacing. Validation of the taper model would follow. The effects of a range of inflection points on the performance of the equation would also be investigated.

7. LITERATURE CITED

- Abdel-Gadir, A.Y., R.L. Krahmer and M.D. McKimmy. 1993. Relationships between intra-ring variables in mature Douglas-fir trees from provenance plantations. *Wood and Fiber Science*. 25(2):182-191.
- Abdel-Gadir, A.Y. and R.L. Krahmer. 1993. Estimating the age of demarcation of juvenile and mature wood in Douglas-fir. *Wood and Fiber Science*. 25(03):242-249.
- Bailey, I.W. 1923. The cambium and its derivative tissues. IV. The increase in girth of the cambium. *Am. J. Bot.* 10:499-509.
- Baker, G. 1967. Estimating specific gravity of plantation-grown red pine. *For. Prod. J.* 17(8):21-24.
- Bannan, M.W. 1955. The vascular cambium and radial growth in *Thuja occidentalis*. *Can. J. Bot.* 33:113-138.
- Bannan, M.W. 1957. The relative frequency of the different types of anticlinal division in conifer cambium. *Can. J. Bot.* 35:875-884.
- Bannan, M.W. 1962. The vascular cambium and tree-ring development. *In* Tree growth. T.T. Kozlowski (editor). Ronald Press Co., New York. pp. 3-22.
- Bannan, M.W. 1967a. Anticlinal divisions and cell length in conifer cambium. *For. Prod. J.* 17:63-69.

- Bannan, M.W. 1967b. Sequential changes in rate of anticlinal division, cambial cell length, and ring width in the growth of coniferous trees. *Can. J. Bot.* 45:1359-1369.
- Barse, R.C. and P.R. Laidley. 1980. Wood specific gravity of plantation red pine little affected by spacing. USDA For. Serv. Res. Note NC 251.
- BC Ministry of Forests. 1999. Guidelines for developing stand density management regimes. Forest Practices Branch, Victoria.
- Bendtsen, B.A. and J.F. Senft. 1986. Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. *Wood and Fiber Science*. 18(1):23-28.
- Bergqvist, G., U. Bergsten and B. Ahlqvist. 1996. Effect of radial increment core diameter on tracheid length measurement in Norway spruce. *Wood Sci. Technol.* 31:241-250.
- Booker, R.E. and J. Sell. 1998. The nanostructure of the cell wall of softwoods and its functions in a living tree. *Holz Roh Werkstoff*. 56:1-8.
- Briggs, D.G. and W.R. Smith. 1986. Effects of silvicultural practices on wood properties of conifers: a review. *In Douglas-fir: Stand management for the future*. Oliver C.D., D.P. Hanley and J.A. Johnson (editors). College of Forest Resources, Seattle, Wash. pp. 108-117.
- Burns, R.M. and B.H. Honkala. 1990. *Silvics of North America. Vol. I. Conifers*. USDA, For. Serv, Washington, District of Columbia. Agric. Handbook 654.
- Carter, R.E. and K. Klinka. 1992. Variation in shade tolerance of Douglas-fir, western hemlock and western redcedar in coastal British Columbia. *For. Ecol. Manage.* 55:87-105.
- Cave, I.D. and J.C.F. Walker. 1994. Stiffness of wood in fast-grown plantation softwoods: The influence of microfibril angle. *For. Prod. J.* 44(5):43-48.

- Chalk, L. 1953. Variation of density in stems of Douglas-fir. *Forestry*. 26:33-36.
- COFI. 1996. British Columbia forest industry fact book. Council of Forest Industries of British Columbia, Vancouver, BC.
- Cook, J.A. and R.J. Barbour. 1989. The use of segmented regression analysis in the determination of juvenile and mature wood properties. Forintek Canada Corp, Vancouver, BC. CFS Rep. No.31.
- Côté, W.A. 1967. Wood ultrastructure: An atlas of electron micrographs. University of Washington Press, Seattle.
- Cown, D.J. 1981. Comparison of the effects of two thinning regimes on some wood properties of radiata pine. *NZ J. For. Sci.* 11:244-253.
- Curtis, R.O. and D.L. Reukema. 1970. Crown development and site estimates in a Douglas-fir plantation spacing test. *For. Sci.* 16:287-301.
- Dadswell, H.E. 1958. Wood structure variations occurring during tree growth and their influence on properties. *J. Inst. Wood Sci.* 1:11-33.
- DeBell, J.D., J.C. Tappeiner and R.L. Krahmer. 1994. Wood density of western hemlock: Effect of ring width. *Can. J. For. Res.* 24:638-641.
- Di Lucca, C.M. 1989. Juvenile-mature wood transition. *In* Second growth Douglas-fir: Its management and conversion for value. R.M. Kellogg (editor). Forintek Canada Corp., Vancouver, BC. Special Publication No. SP-32. pp. 23-38.
- Duff, G.H. and N.J. Nolan. 1953. Growth and morphogenesis in the Canadian forest species. I. The controls of cambial and apical activity in *Pinus resinosa*. *Can. J. Bot.* 31:471-513.

- Echols, R.M. 1955. Linear relation of fibril angle to tracheid length, and genetic control of tracheid length in slash pine. *Tropical Woods*. 102:11-22.
- Erickson, H.D. and T. Arima. 1974. Douglas-fir wood quality studies. Part 2: Effects of age and stimulated growth on fibril angle and chemical constituents. *Wood Sci. Tech.* 8:255-265.
- Erickson, H.D. and A.T. Harrison. 1974. Douglas-fir wood quality studies. Part 1: Effects of age and stimulated growth on wood density and anatomy. *Wood Sci. Tech.* 8(3):207-226.
- Evans, R., R.P. Kibblewhite and S. Stringer. 1997. Kraft pulp fibre property prediction from wood properties in eleven radiata pine clones. *Appita*. 50(1):25-33.
- Farrar, J.L. 1961. Longitudinal variation in the thickness of the annual ring. *For. Chron.* 38:323-331.
- Fujita, M. and H. Harada. 1991. Ultrastructure and formation of wood cell wall. *In* Wood and cellulosic chemistry. D.N. Hon and N. Shiraishi (editors). Marcel Dekker Inc., New York. pp. 3-58.
- Geyer, W.A. and A.R. Gilmore. 1965. Effect of spacing on wood specific gravity in loblolly pine in southern Illinois. University of Illinois, Urbana, Illinois. *Agr. Expt. Stat. Note* 113.
- Gordon, J.C. and P.R. Larson. 1968. Seasonal course of photosynthesis, respiration and distribution of ^{14}C in young *Pinus resinosa* trees as related to wood formation. *Plant Physiol.* 43:1617-1624.
- Greenhouse, S.W. and S. Geisser. 1959. On methods in the analysis of profile data. *Psychometrika*. 32:95-112.
- Grigal, D.F. and E.I. Sucoff. 1966. Specific gravity variation among thirty jack pine plots. *TAPPI*. 49:497-498.

- Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, Toronto.
- Gumpertz, M.L. and C. Brownie. 1992. Repeated measures in randomized block and split-block experiments. *Can. J. For. Res.* 23:625-639.
- Hamm, E.A. 1989. Fibre length. *In* Second growth Douglas-fir: Its management and conversion for value. R.M. Kellogg (editor). Forintek Canada Corp., Vancouver, BC. Special Publication No. SP-32. pp. 44-49.
- Hansen, J., R. Türk, G. Vogg, R. Heim and E. Beck. 1997. Conifer carbohydrate physiology: updating classical views. *Trees.* 11:97-108.
- Hatton, J.V. and K. Hunt. 1989. Unbleached Kraft pulps. *In* Second growth Douglas-fir: Its management and conversion for value. R.M. Kellogg (editor). Forintek Canada Corp., Vancouver, BC. Special Publication No. SP-32. pp. 87-113.
- Herman, M., P. Dutilleul and T. Avella-Shaw. 1998. Growth rate effects on temporal trajectories of ring width, wood density and mean tracheid length in Norway spruce (*Picea abies*). *Wood and Fiber Science.* 30(1):6-17.
- Herman, M., P. Dutilleul and T. Avella-Shaw. 1999. Growth rate effects on intra-ring and inter-ring trajectories of microfibril angle in Norway spruce (*Picea abies*). *IAWA.* 20(1):3-21.
- Hisashi, A., J. Ohtani and K. Fukazawa. 1994. A scanning electron microscope study of changes in microtubule distributions during secondary wall formation in tracheids. *IAWA.* 15(2):185-189.
- Hoadley, R.B. 1990. Identifying wood: Accurate results with simple tools. The Taunton Press, Newtown, Ct.

- Huynh, H. and L.S. Feldt. 1976. Estimation of the Box correction for degrees of freedom from sample data in the randomized block and split plot designs. *J. Educ. Stat.* 1:69-82.
- Jessome, A.P. 1977. Strength and related properties of woods grown in Canada. *Fish. Env. Can., East. For. Prod. Lab., Ottawa. For. Tech. Rep.* 21.
- Johansson, K. 1993. Influence of initial spacing and tree class on the basic density of *Picea abies*. *Scand. J. For. Res.* 8:18-27.
- Jozsa, L.A. and R.M. Kellogg. 1986. An exploratory study of the density and annual ring weight trends in fast-growth coniferous woods in British Columbia. Forintek Canada Corp., Vancouver, BC.
- Jozsa, L.A. and G.R. Middleton. 1994. A discussion of wood quality attributes and their practical implications. Forintek Canada Corp., Vancouver, BC. Special Publication No. SP-34.
- Jozsa, L.A., B.D. Munro and J.R. Gordon. 1998. Basic wood properties of second-growth western hemlock. Forintek Canada Corp., Vancouver, BC. Special Publication No. SP-38.
- Jozsa, L.A. and R.M. Myronuk. 1986. Direct reading x-ray densitometer. Forintek Canada Corp., Vancouver, BC. Tech. Rep. No. 21.
- Jozsa, L.A., J.E. Richards and S.G. Johnson. 1987. Calibration of Forintek's direct reading x-ray densitometer. Forintek Canada Corp., Vancouver, BC.
- Jozsa, L.A., J.E. Richards and S.G. Johnson. 1989. Relative density. *In* Second growth Douglas-fir: Its management and conversion for value. R.M. Kellogg (editor). Forintek Canada Corp., Vancouver, BC. Special Publication No. SP-32. pp. 5-22.
- Kajaani Electronics Ltd. 1986. User's manual: Kajaani FS-200. Kajaani Electronics Ltd., Kajaani, Finland.

- Kennedy, R.W. 1995. Coniferous wood quality in the future: Concerns and strategies. *Wood Sci. Tech.* 29(5):321-338.
- Kimmins, J.P. 1987. *Forest Ecology*. Macmillan Publishing Company, New York.
- Klem, G.G. 1942. Effect of planting space on the quality of spruce wood and sulphite pulp. *Medd. Nor. Skogforsoksves.* 8:257-293.
- Klem, G.G. 1952. The influence of spacing on spruce quality. *Medd. Nor. Skogforsoksves.* 11:473-506.
- Kozak, A. 1988. A variable-exponent taper equation. *Can. J. For. Res.* 18:1363-1368.
- Kozłowski, T.T. 1971. *Growth and development of trees. Volume II*. Academic Press, New York.
- Kozłowski, T.T. 1992. Carbohydrate sources and sinks in woody plants. *Bot. Rev.* 58:107-122.
- Kozłowski, T.T., P.J. Kramer and S.G. Pallardy. 1991. *The physiological ecology of woody plants*. Academic Press, New York.
- Kozłowski, T.T. and S.G. Pallardy. 1997. *Growth control in woody plants*. Academic Press, San Diego, California.
- Krahmer, R.L. 1966. Variation of specific gravity in western hemlock trees. *Tappi.* 49(5):227-229.
- Krahmer, R.L. 1985. Fundamental anatomy of juvenile and mature wood. *In Juvenile wood: What does it mean to forest management and forest products?* D. Robertson (editor). *For. Prod. Res. Soc. Proc.*, Madison, Wis. pp. 12-16.

- Kramer, H. 1966. Crown development in conifer stands in Scotland as influenced by initial spacing and subsequent thinning treatment. *Forestry*. 39:40-58.
- Krajina, V.J. 1965. Biogeoclimatic zones in British Columbia. *Ecol. West. N. Am.* 1: 1-17.
- Kucera, B. 1994. A hypothesis relating annual height increment to juvenile wood formation in Norway spruce. *Wood and Fiber Science*. 26(1):152-157.
- Kuehl, R.O. 1994. Statistical principles of research design and analysis. Daxbury Press, Belmont, Calif.
- Larcher, W. 1983. Physiological plant ecology. Springer-Verlag, New York.
- Larson, P.R. 1962. Auxin gradients and the regulation of cambial activity. *In* Tree growth. T.T. Kozlowski (editor). The Ronald Press Company, New York. pp. 97-117.
- Larson, P.R. 1963. Stem form development of forest trees. Society of American Foresters, Washington, DC. Forest Science - Monograph 5.
- Larson, P.R. 1964. Some indirect effects of environment on wood formation. *In* The formation of wood in forest trees. M. Zimmermann (editor). Academic Press, New York. pp. 345-365.
- Larson, P.R. 1966. Changes in chemical composition of wood cell walls associated with age in *Pinus resinosa*. *For. Prod. J.* 16(4):37-45.
- Larson, P.R. 1969. Wood formation and the concept of wood quality. Yale University School of Forestry, New Haven, Ct. Bulletin No. 74.
- Larson, P.R. 1973. The physiological basis for wood specific gravity in conifers. IUFRO Proc. Div. 5 Meet. Brisbane, Australia. 2: 672-680.

- Larson, P.R. 1994. The vascular cambium: Development and structure. Springer-Verlag, New York.
- Lindstrom, H. 1995. Basic density of Norway spruce. Part II. Predicted by stem taper, mean growth ring width and factors related to crown development. Wood and Fiber Science. 28(2):240-251.
- Little, C.H.A. and R.P. Pharis. 1995. Hormonal control of radial and longitudinal growth in the tree stem. In Plant stems: Physiology and functional morphology. B. Gartner (editor). Academic Press, San Diego, Calif. pp. 281-319.
- Little, C.H.A. and R.A. Savidge. 1987. The role of plant growth regulators in forest tree cambial growth. Plant Growth Regulators. 6:139-167.
- Little, C.H.A. and P.F. Wareing. 1981. Control of cambial activity and dormancy in *Picea sitchensis* by indole-3-acetic acid and abscisic acid. Can. J. Bot. 59:1480-1493.
- Luukkonen, M., H. Suutari and L. Paavilainen. 1990. Utilization of pulp drainage and fibre length measurements at a TMP mill. Appita. 43(3):213-216.
- Maguire, D.A. and J.L.F. Batista. 1996. Sapwood taper models and implied sapwood volume and foliage profiles for coastal Douglas-fir. Can. J. For. Res. 26:849-863.
- Markstrom, D.C., H.E. Troxell and C.E. Boldt. 1983. Wood properties of immature ponderosa pine after thinning. For. Prod. J. 33(4):33-36.
- McMillin, C.W. 1973. Fibril angle of loblolly pine wood as related to specific gravity, growth rate and distance from pith. Wood Sci. Technol. 7:251-255.
- Megraw, R.A. 1985. Wood quality factors in loblolly pine. Tappi Press, Atlanta.

- Megraw, R.A. 1986. Douglas-fir wood properties. *In* Douglas-fir: Stand management for the future. Oliver C.D., D.P. Hanley and J.A. Johnson (editors). College of Forest Resources, Seattle, Wash. pp. 81-96.
- Meredith, M.P. and S.V. Stehman. 1991. Repeated measures experiments in forestry: Focus on analysis of response curves. *Can. J. For. Res.* 21: 957-965.
- Meylan, B.A. and M.C. Probine. 1969. Microfibril angle as a parameter in timber quality assessment. *For. Prod. J.* 19(4):30-34.
- Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: A literature review. USDA Forest Service, Portland, Oregon. Tech. Rep. PNW-87.
- Mitchell, K.J. 1969. Simulation of the growth of even-aged stands of white spruce. Bull. No. 75. Yale University, School of Forestry. New Haven, CT.
- Mitchell, K.J. 1975. Dynamics and simulated yield of Douglas-fir. *For. Sci. Mono.* 17:1-39.
- Mitchell, K.J. and I.R. Cameron. 1985. Managed stand yield tables for coastal Douglas-fir: Initial density and precommercial thinning. Ministry of Forests, Victoria, BC. Land Management Report No. 31.
- Moser, E.B., A.M. Saxton and S.R. Pezeshki. 1990. Repeated measures analysis of variance: Application to tree research. *Can. J. For. Res.* 20:524-535.
- Muneri, A. and V. Balodis. 1998. Variation in wood density and tracheid length in *Pinus patula* grown in Zimbabwe. *South African Journal.* No 182. 41-50.
- Nemec, A.F.L. 1996. Analysis of repeated measures and time series: An introduction with forestry examples. Biometrics Information Handbook No.6. BC Ministry of Forests Research Branch, Victoria, BC. Work Paper 15/1996.

- Okkonen, E.A., H.E. Wahlgren and R.R. Maeglin. 1972. Relationships of specific gravity to tree height in commercially important species. *For. Prod. J.* 22(7):37-42.
- Olesen, P.O. 1976. The interrelation of between basic density and ring width of Norway spruce. *Det Forstl. Forsøgsv. Danm.* 34(4):340-359.
- Oliver, C.D. 1981. Forest development in North America following major disturbances. *Forest Ecol. Manage.* 3:153-168.
- Oliver, C.D. and B.C. Larson. 1996. Forest stand dynamics: Update edition. John Wiley and Sons, New York.
- Panshin, A.J. and C. de Zeeuw. 1980. Textbook of wood technology. 4th ed. McGraw-Hill Book Co., New York.
- Parker, M.L., R.D. Bruce and L.A. Jozsa. 1980. X-ray densitometry of wood at the W.F.P.L. Forintek Canada Corp., Vancouver, BC. Tech. Rep. No. 10.
- Pearson, R.G. and R.C. Gilmore. 1971. Characterization of the strength of juvenile wood of Loblolly pine (*Pinus taeda* L). *For. Prod. J.* 2(1):23-31.
- Peet, R.K. and N.L. Christensen. 1987. Competition and tree death. *BioScience.* 37:586-595.
- Persson, A. 1975. Wood and pulp of Norway spruce and Scots pine at various spacings. Skogshogsk Stockholm Inst. Skogsprod. Rapp. Uppsala 37.
- Piirainen, R. 1985. Optical method provides quick and accurate analysis of fibre length. *Pulp and Paper.* 59(11):69-71.
- Philipson, W.R. and B.G. Butterfield. 1967. A theory on the causes of size variation in wood elements. *Phytomorphology.* 17:155-159.

- Posey, C.E. 1965. Effect of fertilization upon wood properties of loblolly pine (*Pinus taeda*).
In Proc. 8th Conf. For. Tree Improv., Savannah, Georgia. pp. 126-130.
- Reeve, R.M. 1948. The tunica-corpus concept and development of shoot apices in certain dicotyledons. *Am. J. Bot.* 35:65-75.
- Reukema, D.L. and J.H.G. Smith. 1987. Development over 25 years of Douglas-fir, western hemlock and western redcedar planted at various spacings on a very good site in British Columbia. USDA Forest Service, Portland, Oregon. Research Paper PNW-381.
- Salisbury, F.B. and C.W. Ross. 1992. Plant physiology. Wadsworth Publishing Co., Belmont, Calif.
- SAS Inc. 1989. SAS/STAT User's guide, version 6. SAS Institute Inc., Cary, NC.
- Sauter, U.H., M. Rüdiger and B.D. Munro. 1999. Determining a juvenile-mature wood transition in Scots pine using latewood density. *Wood and Fiber Science.* 31(4):416-425.
- Seagull, R.W. 1989. The role of the cytoskeleton during oriented microfibril orientation. II. Microfibril deposition in cells with disrupted cytoskeletons. *In Cellulose and wood: Chemistry and technology.* C. Schuerch (editor). pp. 811-825.
- Seagull, R.W. 1992. A quantitative electron microscopic study of changes in microtubule arrays and wall microfibril orientation during in vitro cotton fiber development. *J. Cell Sci.* 101:561-577.
- Sheriff, D.W. 1983. Control by indole-3-acetic acid of wood production in *Pinus radiata* segments in culture. *Aust. J. Plant Physiol.* 10:131-135.
- Smith, D.M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. USDA For. Prod. Lab. Rep. No. 2014.

- Smith, D.M., B.C. Larson, M.J. Kelty and P.M. Ashton. 1997. The practice of silviculture. 9th ed. John Wiley and Sons, New York.
- Smith, H.D. 1977. Economically optimum spacing and site preparation for slash pine plantations. NC State University, Raleigh, NC. Tech. Rep. 59.
- Smith, J.H.G. 1980. Influence of spacing on radial growth and percentage latewood of Douglas-fir, western hemlock and western redcedar. *Can. J. For. Res.* 10:169-175.
- Smith, J.H.G., J.W. Ker and J. Csizmazia. 1961. Economics of reforestation of Douglas-fir, western hemlock and western redcedar in the Vancouver Forest District. University of British Columbia, Vancouver, BC. *For. Bull.* 3.
- Sundberg, B. and C.H.A. Little. 1991. Tracheid production in response to changes in the internal level of indole-3-acetic acid in 1-year-old shoots of Scots pine. *Plant Physiol.* 94:1721-1727.
- Tasissa, G. and H.E. Burkhart. 1998. Juvenile-mature wood demarcation in loblolly pine trees. *Wood and Fiber Science.* 30(2):119-127.
- Tilman, G.D. 1988. Plant Strategies and the dynamics and structure of plant communities. Princeton Monographs, New Jersey.
- Tsoumis, G. 1991. Science and technology of wood: Structure, properties, utilization. Van Nostrand Reinhold, New York.
- Walker, J.C.F. and B.G. Butterfield. 1995. The importance of microfibril angle for the processing industries. *For. Prod. J.* 44(5):43-48.
- Walters, J. and J.H.G. Smith. 1973. Review of methods used in establishment and summary of early results from spacing trials on the UBC Research Forest. Faculty of Forestry, University of British Columbia, Vancouver, BC.

- Wardrop, A.B. 1964. Cellular differentiation in xylem. *In* Cellular ultrastructure of woody plants. W.A. Côté (editor). Syracuse University Press, New York.
- Weetman, G.F. and C. Farnden. 1995. Planning stand level silviculture using stand density management diagrams: a student guide to concepts and procedures. Silviculture Institute of Canada, Vancouver, BC.
- Wellwood, R.W. 1962. Tensile testing of small wood samples. *Pulp and Paper Mag. Can.* 63(2):T61-T68.
- Wellwood, R.W. and P.E. Jurazs. 1968. Variation in sapwood thickness, specific gravity, and tracheid length in western redcedar. *For. Prod. J.* 18(12):37-46.
- Wellwood, R.W. and J.H.G. Smith. 1962. Variation in some important qualities of wood from Douglas-fir and hemlock trees. Faculty of Forestry, University of British Columbia, Vancouver, BC. Research Paper No. 50.
- Wenham, M.W. and F. Cusick. 1975. The growth of secondary wood fibers. *New Phytol.* 74:247-271.
- Wilcox, H. 1962. Cambial growth characteristics. *In* Tree growth. T.T. Kozlowski (editor). Ronald Press Co., New York.
- Wilson, J.W. 1964. Wood characteristics III: Intra-increment physical and chemical properties. *Pulp Pap. Res. Inst. Can. Res. Note* 45.
- Yang, K.C., C.A. Benson and J.K. Wong. 1986. Distribution of juvenile wood in two stems of *Larix laricina*. *Can. J. For. Res.* 16:1041-1049.
- Yang, K.C., Y.S. Chen and C. Chiu. 1994. Formation and vertical distribution of juvenile and mature wood in a single stem of *Cryptomeria japonica*. *Can. J. For. Res.* 24:969-975.

- Yang, K.C. 1994. Impact of spacing on tracheid length, relative density, and growth rate of juvenile wood and mature wood in *Picea mariana*. Can. J. For. Res. 24:996-1007.
- Ying, L., D.E. Kretschmann and B.A. Bendtsen. 1994. Longitudinal shrinkage in fast-grown loblolly pine plantation wood. For. Prod. J. 44(1):58-62.
- Youngberg, C.T., L.C. Walker, J.R. Hamilton and R.F. Williams. 1963. Fertilization of slash pine. Georgia Forest Research Council, Atlanta. Res. Pap. 17.
- Zimmermann, M.H. and C.L. Brown. 1971. Trees: Structure and function. Springer-Verlag, New York.
- Zobel, B.J. and J.R. Sprague. 1998. Juvenile wood in forest trees. Springer-Verlag, New York.
- Zobel, B.J. and J.T. Talbert. 1984. Applied forest tree improvement. John Wiley & Sons, New York.
- Zobel, B.J. and J.P. Van Buijtenen. 1989. Wood variation: Its causes and control. Springer-Verlag, New York.

APPENDIX I

SUPPLEMENTARY RESULTS FOR CHAPTER 4.

Table 4.1 Basic tree statistics by species and initial spacing: DBH (diameter at breast height), H (tree height), HBLC (height to the base of the live crown), LCL (live-crown-length), CW (crown width), LCR (live-crown-ratio) and HDR (height over diameter ratio).

species	variable	initial spacing																			
		0.91 m				1.83 m				2.74 m				3.66 m				4.57 m			
		mean	cv	min	max	mean	cv	min	max	mean	cv	min	max	mean	cv	min	max	mean	cv	min	max
Douglas-fir	DBH (cm)	23.6	30.5	15.4	34.4	23.3	34.0	15.7	35.0	33.3	12.6	26.7	38.2	40.3	9.7	36.7	47.2	41.7	14.4	32.5	49.7
	H (m)	28.4	16.9	22.7	34.8	29.8	12.1	25.0	34.5	33.2	4.8	30.9	34.9	31.8	7.0	29.0	35.8	33.8	3.0	32.4	34.9
	HBLC (m)	18.2	12.6	14.7	20.8	20.4	4.9	19.0	21.8	20.6	3.9	19.2	21.4	18.9	4.8	17.6	19.9	18.4	6.5	17.2	19.8
	LCL (m)	10.2	38.2	4.7	16.8	9.4	35.8	6.0	14.7	12.6	15.9	9.7	14.7	12.9	22.1	9.1	17.8	15.0	14.0	12.9	17.6
	CW (m)	3.1	45.2	2.2	5.8	3.3	31.2	2.5	4.9	4.4	18.2	3.2	5.4	5.5	21.3	4.2	7.4	6.2	11.3	5.3	7.2
	LCR	0.35	26.00	0.21	0.48	0.31	24.31	0.22	0.43	0.38	11.67	0.31	0.43	0.40	15.24	0.31	0.50	0.45	11.48	0.40	0.50
western hemlock	HDR	124.4	14.1	101.2	147.4	135.7	20.9	98.6	172.0	100.5	10.1	89.8	118.4	79.2	5.4	73.6	85.0	82.4	12.9	70.2	99.7
	DBH (cm)	17.9	14.5	13.7	21.0	18.8	25.5	15.5	28.2	21.6	19.9	15.6	24.9	30.7	17.7	22.6	36.7	*	*	*	*
	H (m)	21.7	6.6	19.7	23.1	22.4	10.8	19.2	26.0	22.9	7.0	20.7	24.5	23.9	9.0	21.6	27.8	*	*	*	*
	HBLC (m)	11.8	16.5	8.7	14.0	11.0	10.0	10.2	13.1	10.9	14.7	7.9	12.4	9.8	16.1	8.3	11.8	*	*	*	*
	LCL (m)	9.9	13.5	8.3	11.8	11.3	22.8	8.9	15.8	12.1	17.4	8.3	14.1	14.1	8.6	12.7	16.0	*	*	*	*
	CW (m)	3.1	11.3	2.7	3.6	3.4	21.8	2.4	4.4	5.3	19.0	4.0	7.0	6.7	15.2	5.6	8.0	*	*	*	*
western redcedar	LCR	0.459	15.3	0.393	0.558	0.503	13.0	0.441	0.608	0.524	15.1	0.401	0.633	0.592	6.9	0.524	0.636	*	*	*	*
	HDR	98.8	50.1	110.0	143.8	122.2	13.1	92.2	138.6	108.8	15.5	87.2	132.7	80.1	20.5	62.7	104.0	*	*	*	*
	DBH (cm)	12.9	12.4	10.0	14.8	18.5	17.1	14.2	21.3	29.3	21.8	20.3	37.0	39.2	22.0	30.3	49.8	38.0	17.7	28.8	46.0
	H (m)	18.2	9.1	15.9	20.9	19.4	17.2	15.4	22.9	22.1	6.3	20.2	24.2	23.6	6.4	21.4	25.4	23.2	6.5	21.0	24.6
	HBLC (m)	15.1	7.4	13.6	16.2	15.4	14.4	12.8	18.0	12.7	9.4	10.4	14.0	9.2	14.1	7.4	11.3	9.5	15.8	7.1	11.2
	LCL (m)	3.1	30.4	2.3	4.7	4.1	30.1	2.6	5.8	9.4	23.4	6.2	12.6	14.4	14.6	11.8	16.6	13.7	12.4	11.2	15.7
	CW (m)	1.9	9.0	1.7	2.1	2.3	33.2	1.2	2.9	4.7	17.0	3.4	5.4	5.9	11.9	4.9	6.9	5.5	7.3	5.0	6.1
	LCR	0.167	23.2	0.129	0.225	0.206	15.0	0.169	0.257	0.424	18.6	0.307	0.548	0.607	10.7	0.513	0.688	0.590	10.7	0.526	0.671
	HDR	142.6	10.9	116.9	159.0	105.6	9.0	88.7	117.7	77.9	17.2	63.2	99.5	59.8	16.4	51.0	78.2	62.2	12.4	53.5	75.0
	DBH (cm)	12.9	12.4	10.0	14.8	18.5	17.1	14.2	21.3	29.3	21.8	20.3	37.0	39.2	22.0	30.3	49.8	38.0	17.7	28.8	46.0
	H (m)	18.2	9.1	15.9	20.9	19.4	17.2	15.4	22.9	22.1	6.3	20.2	24.2	23.6	6.4	21.4	25.4	23.2	6.5	21.0	24.6
	HBLC (m)	15.1	7.4	13.6	16.2	15.4	14.4	12.8	18.0	12.7	9.4	10.4	14.0	9.2	14.1	7.4	11.3	9.5	15.8	7.1	11.2

Table 4.2 Basic tree statistics by species and taper class: DBH (diameter at breast height), H (tree height), HBLC (height of the base of the live crown), LCL (live-crown-length), CW (crown width), LCR (live-crown-ratio) and HDR (height over diameter ratio).

species	variable	taper class											
		suppressed				intermediate				dominant			
		mean	cv	min	max	mean	cv	min	max	mean	cv	min	max
Douglas-fir	DBH (cm)	23.4	28.0	15.4	31.5	36.1	6.9	31.8	39.1	43.9	8.8	37.5	49.7
	H (m)	29.2	13.3	22.7	34.8	32.9	4.6	30.9	34.9	33.2	7.3	29.0	35.8
	HBLC (m)	19.5	10.6	14.7	21.8	19.8	3.5	19.2	21.2	18.2	6.4	17.2	19.9
	LCL (m)	9.7	32.5	4.7	16.8	13.1	12.2	9.7	14.7	15.0	21.8	9.1	17.8
	CW (m)	3.1	32.1	2.2	5.8	5.1	9.8	4.3	5.9	6.2	16.7	4.2	7.4
	LCR	0.325	22.9	0.207	0.483	0.397	8.6	0.314	0.434	0.449	16.0	0.314	0.504
	HDR	129.7	16.8	101.2	172.0	91.5	7.5	81.2	99.7	75.9	4.0	70.2	79.1
western hemlock	DBH (cm)	18.2	14.3	13.7	22.6	28.1	12.5	24.9	34.0	33.8	9.8	30.2	36.7
	H (m)	22.0	7.0	19.2	24.5	25.3	6.3	23.9	27.8	22.5	3.8	21.6	23.0
	HBLC (m)	11.2	15.1	7.9	14.0	11.3	5.3	10.2	11.8	8.6	3.5	8.3	8.9
	LCL (m)	10.8	18.4	8.3	14.1	14.0	12.1	12.6	16.0	13.9	7.2	12.7	14.5
	CW (m)	3.8	33.0	2.4	7.0	5.5	16.4	4.4	6.8	7.3	15.1	6.0	8.0
	LCR	0.491	15.4	0.393	0.633	0.552	6.9	0.524	0.608	0.618	4.2	0.588	0.636
	HDR	121.9	10.4	102.9	143.8	90.5	6.7	81.8	97.2	66.8	6.7	62.7	71.5
western redcedar	DBH (cm)	15.1	23.1	10.0	21.1	23.6	14.0	20.3	26.8	38.3	16.4	28.8	49.8
	H (m)	18.8	14.5	15.4	22.9	20.7	6.8	18.9	22.0	23.4	5.6	21.0	25.4
	HBLC (m)	15.3	11.5	12.8	18.0	13.6	7.4	12.8	14.9	10.0	18.0	7.1	13.0
	LCL (m)	3.5	34.3	2.3	5.8	7.1	33.8	4.0	9.2	13.4	16.4	8.6	16.6
	CW (m)	2.0	26.1	1.2	2.9	4.3	25.6	2.8	5.2	5.5	14.5	3.4	6.9
	LCR	0.184	21.8	0.129	0.257	0.336	28.9	0.212	0.418	0.570	14.2	0.398	0.688
	HDR	127.3	16.4	105.0	159.0	88.4	9.0	82.1	99.5	62.3	13.3	51.0	78.2

cv : coefficient of variation
min : minimum value observed
max : maximum value observed

Table 4.3a Mean values and variability for ring width (mm) by initial spacing and species.

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 4-33)	mean	2.7		3.1		3.7		4.6		5.3	
	cv (%)	67.5		79.7		72.1		48.8		51.7	
	min max	0.1	8.1	0.2	11.4	0.3	11.5	1.4	9.3	0.5	11.6
western hemlock (rings 4-30)	mean	2.7		2.6		3.2		4.6			
	cv (%)	57.9		63.6		51.0		45.5			
	min max	0.3	8.8	0.2	6.8	0.3	7.8	0.6	9.3		
western redcedar (rings 5-27)	mean	1.7		2.9		4.7		6.1		6.3	
	cv (%)	89.9		68.6		50.8		33.3		37.7	
	min max	0.1	6.1	0.2	8.5	0.8	10.1	1.9	10.3	1.1	12.1

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.3b Repeated measures analysis of variance for ring width (mm) by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	14.60	5.73	0.0024		
	error 1	23	2.55				
	ring	29	7.23	116.86	0.0001	0.0001	0.0001
	spacing * ring	116	0.18	2.84	0.0001	0.0001	0.0001
	error 2	667	0.06			epsGG=0.1889	epsHF=0.2978
western hemlock (rings 4-30)	spacing	3	8.48	5.27	0.0087		
	error 1	18	1.61				
	ring	26	1.68	12.68	0.0001	0.0001	0.0001
	spacing * ring	78	0.12	0.89	0.7429	0.5819	0.6239
	error 2	468	0.13			epsGG=0.1911	epsHF=0.3167
western redcedar (rings 5-27)	spacing	4	38.28	34.24	0.0001		
	error 1	23	1.12				
	ring	22	4.60	66.45	0.0001	0.0001	0.0001
	spacing * ring	88	0.30	4.33	0.0001	0.0001	0.0001
	error 2	506	0.07			epsGG=0.2517	epsHF=0.3983

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.4a Mean values and variability for ring width (mm) by taper class and species.

species		taper class			
		suppressed		intermediate	dominant
Douglas-fir (rings 4-33)	mean	2.9		4.0	5.6
	cv (%)	80.1		59.4	45.0
	min max	0.1	11.5	0.5 10.1	1.3 11.6
western hemlock (rings 4-30)	mean	2.7		4.0	5.1
	cv (%)	54.8		47.9	41.3
	min max	0.2	8.8	0.4 9.3	0.7 9.2
western redcedar (rings 5-27)	mean	2.2		3.6	6.1
	cv (%)	80.7		57.4	37.4
	min max	0.1	7.4	0.2 8.5	1.1 12.1

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.4b Repeated measures analysis of variance for ring width (mm) by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	33.65	16.92	0.0001		
	error 1	25	1.99				
	ring	29	6.67	96.87	0.0001	0.0001	0.0001
	taper class * ring	58	0.20	2.95	0.0001	0.0030	0.0008
	error 2	725	0.07			epsGG=0.1627	epsHF=0.2212
western hemlock (rings 4-30)	taper class	2	15.95	13.48	0.0002		
	error 1	19	1.18				
	ring	26	0.86	6.70	0.0001	0.0001	0.0001
	taper class * ring	52	0.14	1.12	0.2717	0.3551	0.3406
	error 2	494	0.13			epsGG=0.2046	epsHF=0.3235
western redcedar (rings 5-27)	taper class	2	74.01	60.09	0.0001		
	error 1	25	1.23				
	ring	22	4.19	54.92	0.0001	0.0001	0.0001
	taper class * ring	44	0.44	5.80	0.0001	0.0001	0.0001
	error 2	550	0.08			epsGG=0.2305	epsHF=0.3194

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.5a Mean values and variability for earlywood width (mm) by initial spacing and species.

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 4-33)	mean	1.8		2.1		2.6		3.1		3.7	
	cv (%)	80.3		95.7		87.1		60.0		60.9	
	min max	0.0	7.4	0.0	8.5	0.1	8.9	0.8	7.2	0.3	9.3
western hemlock (rings 4-30)	mean	2.1		1.9		2.5		3.9			
	cv (%)	75.0		78.7		62.0		51.6			
	min max	0.3	9.1	0.1	6.2	0.1	8.5	0.3	9.7		
western redcedar (rings 5-27)	mean	1.4		2.4		3.9		5.3		5.1	
	cv (%)	101.4		75.9		54.8		37.9		43.4	
	min max	0.0	5.4	0.1	8.1	0.5	9.3	1.5	9.7	0.0	9.8

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.5b Repeated measures analysis of variance for earlywood width (mm) by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	11.47	5.06	0.0045		
	error 1	23	2.27				
	ring	29	6.88	114.07	0.0001	0.0001	0.0001
	spacing * ring	116	0.17	2.82	0.0001	0.0001	0.0001
	error 2	667	0.06			epsGG=0.2280	epsHF=0.3854
western hemlock (rings 4-30)	spacing	3	11.58	6.47	0.0037		
	error 1	18	1.79				
	ring	26	1.79	11.96	0.0001	0.0001	0.0001
	spacing * ring	78	0.15	1.01	0.4691	0.4553	0.4620
	error 2	468	0.15			epsGG=0.1825	epsHF=0.2972
western redcedar (rings 5-27)	spacing	4	36.63	29.59	0.0001		
	error 1	23	1.24				
	ring	22	4.35	54.03	0.0001	0.0001	0.0001
	spacing * ring	88	0.34	4.18	0.0001	0.0001	0.0001
	error 2	506	0.08			epsGG=0.2683	epsHF=0.4340

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.6a Mean values and variability for earlywood width (mm) by taper class and species.

species	taper class					
			suppressed	intermediate	dominant	
Douglas-fir (rings 4-33)	mean		2.0	2.8	3.9	
	cv (%)		95.1	73.7	53.4	
	min	max	0.0	8.9	0.2	8.6
western hemlock (rings 4-30)	mean		2.0	3.3	4.3	
	cv (%)		67.7	58.5	47.7	
	min	max	0.1	9.1	0.2	9.0
western redcedar (rings 5-27)	mean		1.8	3.0	5.1	
	cv (%)		89.7	62.1	42.0	
	min	max	0.0	6.6	0.1	8.1

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.6b Repeated measures analysis of variance for earlywood width (mm) by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	26.76	15.01	0.0001		
	error 1	25	1.78				
	ring	29	6.41	94.89	0.0001	0.0001	0.0001
	taper class * ring	58	0.19	2.81	0.0001	0.0025	0.0005
	error 2	725	0.07			epsGG=0.1886	epsHF=0.2669
western hemlock (rings 4-30)	taper class	2	18.36	11.54	0.0005		
	error 1	19	1.59				
	ring	26	0.85	5.82	0.0001	0.0001	0.0001
	taper class * ring	52	0.18	1.24	0.1258	0.2727	0.2424
	error 2	494	0.15			epsGG=0.1946	epsHF=0.3016
western redcedar (rings 5-27)	taper class	2	71.31	55.05	0.0001		
	error 1	25	1.30				
	ring	22	3.98	45.47	0.0001	0.0001	0.0001
	taper class * ring	44	0.51	5.78	0.0001	0.0001	0.0001
	error 2	550	0.09			epsGG=0.2493	epsHF=0.3529

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.7 Linear regression equations and correlation coefficients for earlywood width (mm) calculated yearly as a function of ring width (mm) for Douglas-fir.

ring number from pith	n	a	b		r	r ²	SE _E
3	22	-1.1132	1.0067	***	0.95	0.90	0.5334
4	29	-1.6742	1.0451	***	0.94	0.89	0.5595
5	29	-1.2953	0.9333	***	0.92	0.84	0.6607
6	29	-0.9193	0.9140	***	0.96	0.91	0.5364
7	29	-0.7047	0.8732	***	0.96	0.91	0.5858
8	29	-0.8976	0.8711	***	0.99	0.98	0.3446
9	29	-0.8499	0.8297	***	0.97	0.95	0.5002
10	29	-0.6035	0.8323	***	0.98	0.97	0.3598
11	29	-0.3998	0.7870	***	0.97	0.94	0.4728
12	29	-0.5110	0.7920	***	0.98	0.96	0.3743
13	29	-0.5695	0.8028	***	0.98	0.97	0.3259
14	29	-0.5516	0.7880	***	0.98	0.97	0.3187
15	28	-0.3349	0.7694	***	0.98	0.97	0.2933
16	28	-0.3720	0.7791	***	0.99	0.98	0.2272
17	29	-0.2379	0.7323	***	0.98	0.96	0.2866
18	29	-0.1103	0.6803	***	0.99	0.97	0.2331
19	29	-0.1701	0.6762	***	0.98	0.95	0.2718
20	29	-0.1242	0.6545	***	0.97	0.95	0.2700
21	29	-0.0867	0.6212	***	0.99	0.98	0.1578
22	29	-0.1031	0.6394	***	0.99	0.98	0.1337
23	29	-0.1239	0.6441	***	0.98	0.95	0.1998
24	29	-0.2022	0.6931	***	0.97	0.94	0.2185
25	29	-0.0952	0.6686	***	0.99	0.98	0.1149
26	29	-0.1929	0.6807	***	0.97	0.95	0.1753
27	29	-0.1643	0.6727	***	0.98	0.96	0.1358
28	29	-0.0954	0.6110	***	0.98	0.96	0.1213
29	29	-0.1081	0.6303	***	0.97	0.95	0.1351
30	29	-0.0661	0.6132	***	0.97	0.94	0.1558
31	29	-0.1022	0.6197	***	0.97	0.95	0.1625
32	29	-0.1474	0.6565	***	0.98	0.96	0.1583
33	29	-0.0957	0.6152	***	0.97	0.94	0.1929

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.8 Linear regression equations and correlation coefficients for earlywood width (mm) calculated yearly as a function of ring width (mm) for western hemlock.

ring number from pith	n	a	b		r	r ²	SE _E
3	15	-0.8720	0.9324	***	0.90	0.82	0.7216
4	24	-1.0494	0.9420	***	0.91	0.83	0.6477
5	24	-1.2714	1.0513	***	0.95	0.90	0.6726
6	24	-0.6321	0.9388	***	0.94	0.89	0.5212
7	24	-1.7177	1.1694	***	0.98	0.95	0.4147
8	24	-0.7361	0.9775	***	0.98	0.97	0.2543
9	24	-0.8334	1.0308	***	0.96	0.93	0.3168
10	24	-0.2389	0.8916	***	0.97	0.94	0.2862
11	24	-0.3615	0.9036	***	0.98	0.96	0.2956
12	24	-0.4366	0.9264	***	0.97	0.95	0.3807
13	24	-0.4984	0.9355	***	0.98	0.96	0.3384
14	24	-0.4945	0.9581	***	0.98	0.95	0.3616
15	24	-0.3266	0.9375	***	0.99	0.98	0.2277
16	24	-0.2480	0.8725	***	0.98	0.96	0.3178
17	24	-0.1983	0.8531	***	0.98	0.96	0.2740
18	24	-0.5059	0.9471	***	0.98	0.97	0.2645
19	24	-0.5818	0.9671	***	0.98	0.97	0.3468
20	24	-0.6899	0.9831	***	0.98	0.97	0.2902
21	24	-0.5825	0.9543	***	0.99	0.99	0.2107
22	24	-0.4997	0.9561	***	0.99	0.99	0.2210
23	24	-0.4337	0.9326	***	0.98	0.96	0.2505
24	24	-0.4897	0.9236	***	0.98	0.96	0.3310
25	23	-0.5367	0.9848	***	0.99	0.99	0.2425
26	23	-0.4872	0.9397	***	0.99	0.98	0.2055
27	23	-0.4133	0.9288	***	0.99	0.98	0.2262
28	22	-0.4155	0.9251	***	0.99	0.98	0.2328
29	22	-0.4020	0.9258	***	0.99	0.98	0.2699
30	22	-0.4424	0.9199	***	0.99	0.97	0.3040
31	18	-0.4543	0.9423	***	0.98	0.97	0.3635
32	16	-0.3441	0.8933	***	0.98	0.96	0.3092
33	11	-0.1786	0.7985	***	0.94	0.89	0.3690

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.9 Linear regression equations and correlation coefficients for earlywood width (mm) calculated yearly as a function of ring width (mm) for western redcedar.

ring number from pith	n	a	b		r	r ²	SE _E
3	17	-2.4923	1.1677	***	0.83	0.68	0.6939
4	23	-1.0273	0.9712	***	0.92	0.84	0.5472
5	30	-0.4867	0.9117	***	0.95	0.91	0.4276
6	30	-0.5055	0.9279	***	0.97	0.94	0.3904
7	30	-0.3495	0.8870	***	0.98	0.96	0.3405
8	30	-0.6557	0.9620	***	0.99	0.97	0.3409
9	30	-0.2465	0.9055	***	0.98	0.97	0.3230
10	30	-0.6063	0.9537	***	0.99	0.99	0.2563
11	30	-0.1881	0.8671	***	0.99	0.98	0.2777
12	30	-0.3602	0.9266	***	0.99	0.98	0.3064
13	30	-0.5734	0.9576	***	0.99	0.98	0.2664
14	30	-0.3420	0.9292	***	0.99	0.98	0.3272
15	30	-0.2646	0.9410	***	1.00	0.99	0.2004
16	30	-0.1613	0.8945	***	0.99	0.98	0.2846
17	30	-0.2224	0.9182	***	1.00	0.99	0.1820
18	30	-0.2138	0.9204	***	1.00	1.00	0.1684
19	30	-0.2728	0.9428	***	1.00	1.00	0.1733
20	29	-0.3370	0.9554	***	1.00	1.00	0.2068
21	29	-0.2768	0.9416	***	1.00	1.00	0.1977
22	29	-0.3113	0.9546	***	0.99	0.99	0.3005
23	28	-0.2830	0.9256	***	1.00	0.99	0.1813
24	28	-0.2530	0.9129	***	1.00	0.99	0.1739
25	28	-0.1840	0.8780	***	1.00	1.00	0.0955
26	28	-0.1292	0.8482	***	1.00	0.99	0.1043
27	28	-0.2025	0.8990	***	0.99	0.99	0.1517
28	23	-0.2753	0.9215	***	0.99	0.99	0.1571
29	24	-0.2872	0.9410	***	0.99	0.99	0.1780
30	22	-0.3517	0.9490	***	1.00	0.99	0.1475
31	21	-0.2880	0.8981	***	1.00	0.99	0.1395
32	21	-0.2736	0.8910	***	0.99	0.98	0.2237
33	18	-0.2536	0.8726	***	0.99	0.99	0.1746

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.10a Mean values and variability for latewood width (mm) by initial spacing and species.

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 4-33)	mean	0.9		1.0		1.1		1.5		1.6	
	cv (%)	57.4		59.5		49.8		36.8		43.1	
	min max	0.1	2.6	0.1	3.0	0.2	2.7	0.5	3.0	0.2	3.6
western hemlock (rings 4-30)	mean	0.7		0.8		0.7		0.7			
	cv (%)	39.2		54.2		57.4		50.6			
	min max	0.2	1.4	0.1	2.0	0.1	2.5	0.2	2.3		
western redcedar (rings 5-27)	mean	0.3		0.5		0.8		0.8		0.9	
	cv (%)	56.2		49.8		48.7		41.9		39.2	
	min max	0.1	0.8	0.1	1.2	0.3	1.9	0.3	1.9	0.3	1.8

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.10b Repeated measures analysis of variance for latewood width (mm) by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	3.61	5.95	0.0019		
	error 1	23	0.61				
	ring	29	0.91	32.51	0.0001	0.0001	0.0001
	spacing * ring	116	0.03	1.21	0.0761	0.2454	0.2020
	error 2	667	0.03			epsGG=0.1937	epsHF=0.3080
western hemlock (rings 4-30)	spacing	3	0.43	2.00	0.1498		
	error 1	18	0.21				
	ring	26	0.16	5.16	0.0001	0.0001	0.0001
	spacing * ring	78	0.03	0.82	0.8651	0.6930	0.7763
	error 2	468	0.03			epsGG=0.2630	epsHF=0.5115
western redcedar (rings 5-27)	spacing	4	2.96	22.36	0.0001		
	error 1	23	0.13				
	ring	22	0.44	35.77	0.0001	0.0001	0.0001
	spacing * ring	88	0.02	1.36	0.0239	0.0912	0.0304
	error 2	506	0.01			epsGG=0.4335	epsHF=0.8950

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.11a Mean values and variability for latewood width (mm) by taper class and species.

species	taper class					
			suppressed	intermediate	dominant	
Douglas-fir (rings 4-33)	mean		0.9	1.3	1.7	
	cv (%)		60.8	43.4	37.9	
	min	max	0.1	3.0	0.2	3.6
western hemlock (rings 4-30)	mean		0.7	0.8	0.8	
	cv (%)		52.1	53.4	49.8	
	min	max	0.1	2.0	0.1	2.3
western redcedar (rings 5-27)	mean		0.4	0.7	0.8	
	cv (%)		55.9	53.3	42.4	
	min	max	0.1	1.2	0.1	1.9

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.11b Repeated measures analysis of variance for latewood width (mm) by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	7.97	15.62	0.0001		
	error 1	25	0.51				
	ring	29	0.81	29.99	0.0001	0.0001	0.0001
	taper class * ring	58	0.05	1.93	0.0001	0.0553	0.0294
	error 2	725	0.03			epsGG=0.2114	epsHF=0.3110
western hemlock (rings 4-30)	taper class	2	0.32	1.38	0.2767		
	error 1	19	0.24				
	ring	26	0.13	3.95	0.0001	0.0007	0.0001
	taper class * ring	52	0.02	0.64	0.9753	0.8219	0.9034
	error 2	494	0.03			epsGG=0.2632	epsHF=0.4699
western redcedar (rings 5-27)	taper class	2	5.18	28.63	0.0001		
	error 1	25	0.18				
	ring	22	0.39	29.71	0.0001	0.0001	0.0001
	taper class * ring	44	0.01	1.01	0.4525	0.4472	0.4518
	error 2	550	0.01			epsGG=0.4341	epsHF=0.7807

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.12 Linear regression equations and correlation coefficients for latewood width (mm) calculated yearly as a function of ring width (mm) for Douglas-fir.

ring number from pith	n	a	b		r	r ²	SE _E
3	22	0.8225	0.0260	ns	0.11	0.01	0.3723
4	29	1.6742	-0.0451	ns	-0.12	0.02	0.5595
5	29	1.2952	0.0667	ns	0.16	0.03	0.6607
6	29	0.8019	0.0939	*	0.39	0.15	0.4335
7	29	0.8135	0.1209	**	0.47	0.22	0.4911
8	29	0.8976	0.1288	***	0.69	0.47	0.3445
9	29	0.6256	0.1953	***	0.79	0.62	0.4049
10	29	0.6036	0.1677	***	0.78	0.60	0.3598
11	29	0.3998	0.2130	***	0.74	0.54	0.4728
12	29	0.5110	0.2080	***	0.79	0.63	0.3743
13	29	0.5695	0.1972	***	0.79	0.63	0.3260
14	29	0.3689	0.2586	***	0.93	0.86	0.2121
15	28	0.2702	0.2531	***	0.92	0.85	0.2244
16	28	0.3720	0.2209	***	0.90	0.81	0.2272
17	29	0.2217	0.2601	***	0.95	0.91	0.1664
18	29	0.1103	0.3197	***	0.94	0.88	0.2331
19	29	0.0913	0.3603	***	0.95	0.90	0.2115
20	29	0.1242	0.3455	***	0.92	0.84	0.2700
21	29	0.0727	0.3898	***	0.98	0.96	0.1309
22	29	0.1031	0.3606	***	0.97	0.94	0.1337
23	29	0.1240	0.3559	***	0.93	0.87	0.1998
24	29	0.2022	0.3069	***	0.87	0.76	0.2185
25	29	0.0952	0.3314	***	0.96	0.92	0.1149
26	29	0.1929	0.3193	***	0.89	0.80	0.1752
27	29	0.1643	0.3273	***	0.93	0.86	0.1358
28	29	0.0954	0.3890	***	0.95	0.91	0.1213
29	29	0.1081	0.3697	***	0.93	0.86	0.1351
30	29	0.0661	0.3868	***	0.93	0.87	0.1558
31	29	0.1022	0.3803	***	0.93	0.87	0.1625
32	29	0.1474	0.3435	***	0.93	0.86	0.1583
33	29	0.0795	0.4025	***	0.95	0.90	0.1590

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.13 Linear regression equations and correlation coefficients for latewood width (mm) calculated yearly as a function of ring width (mm) for western hemlock.

ring number from pith	n	a	b		r	r ²	SE _E
3	15	0.8720	0.0676	ns	0.15	0.02	0.7216
4	24	1.0396	0.0554	ns	0.14	0.02	0.5946
5	24	0.8391	0.0468	ns	0.16	0.03	0.5566
6	24	0.4391	0.0861	ns	0.32	0.10	0.4098
7	24	1.4206	-0.1022	ns	-0.39	0.15	0.3838
8	24	0.7361	0.0225	ns	0.12	0.01	0.2543
9	24	0.8334	-0.0308	ns	-0.10	0.01	0.3168
10	24	0.2389	0.1085	*	0.42	0.18	0.2862
11	24	0.2920	0.1044	**	0.60	0.36	0.2276
12	24	0.5662	0.0271	ns	0.16	0.02	0.2918
13	24	0.4984	0.0645	ns	0.31	0.10	0.3384
14	24	0.5565	0.0093	ns	0.06	0.00	0.2568
15	24	0.3266	0.0625	*	0.41	0.17	0.2277
16	24	0.2480	0.1275	**	0.56	0.31	0.3178
17	24	0.1966	0.1474	***	0.67	0.45	0.2677
18	24	0.5059	0.0529	ns	0.29	0.08	0.2645
19	24	0.5899	0.0287	ns	0.16	0.03	0.3523
20	24	0.6899	0.0169	ns	0.10	0.01	0.2902
21	24	0.5825	0.0457	ns	0.38	0.15	0.2107
22	24	0.4997	0.0439	ns	0.35	0.12	0.2210
23	24	0.3848	0.0924	**	0.54	0.29	0.2492
24	24	0.3695	0.1444	***	0.71	0.50	0.2656
25	23	0.4264	0.0769	**	0.52	0.27	0.2554
26	23	0.4872	0.0603	*	0.46	0.21	0.2055
27	23	0.4133	0.0712	*	0.49	0.24	0.2262
28	22	0.4155	0.0749	*	0.50	0.25	0.2328
29	22	0.4020	0.0742	*	0.51	0.26	0.2698
30	22	0.4424	0.0801	*	0.45	0.20	0.3040
31	18	0.4543	0.0577	ns	0.32	0.11	0.3635
32	16	0.2619	0.1687	*	0.57	0.33	0.4402
33	11	0.1698	0.3434	*	0.58	0.33	0.7023

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.14 Linear regression equations and correlation coefficients for latewood width (mm) calculated yearly as a function of ring width (mm) for western redcedar.

ring number from pith	n	a	b		r	r ²	SE _E
3	17	2.4923	-0.1677	ns	0.21	0.04	0.6939
4	23	1.0273	0.0288	ns	0.07	0.00	0.5472
5	30	0.4867	0.0883	ns	0.29	0.08	0.4258
6	30	0.5402	0.0718	ns	0.30	0.09	0.3837
7	30	0.3495	0.1130	**	0.53	0.29	0.3405
8	30	0.6557	0.0380	ns	0.24	0.06	0.3409
9	30	0.2465	0.0945	**	0.51	0.26	0.3230
10	30	0.6063	0.0463	*	0.37	0.14	0.2563
11	30	0.1881	0.1329	***	0.73	0.53	0.2777
12	30	0.3880	0.0617	**	0.47	0.23	0.2562
13	30	0.6144	0.0313	ns	0.30	0.09	0.2682
14	30	0.3256	0.0666	***	0.59	0.35	0.2456
15	30	0.2646	0.0590	***	0.60	0.36	0.2004
16	30	0.1613	0.1055	***	0.69	0.47	0.2846
17	30	0.2224	0.0818	***	0.77	0.60	0.1820
18	30	0.2138	0.0796	***	0.81	0.65	0.1684
19	30	0.2613	0.0556	***	0.79	0.62	0.1429
20	29	0.3535	0.0379	***	0.58	0.34	0.2027
21	29	0.3016	0.0502	***	0.64	0.41	0.2006
22	29	0.2637	0.0698	***	0.71	0.51	0.1851
23	28	0.2830	0.0744	***	0.70	0.49	0.1813
24	28	0.1889	0.1245	***	0.87	0.75	0.1269
25	28	0.1869	0.1215	***	0.92	0.84	0.0939
26	28	0.1302	0.1516	***	0.90	0.80	0.1039
27	28	0.1905	0.0966	***	0.83	0.69	0.1083
28	23	0.2753	0.0785	**	0.61	0.37	0.1571
29	24	0.2872	0.0590	**	0.53	0.28	0.1780
30	22	0.3517	0.0510	**	0.55	0.30	0.1475
31	21	0.2880	0.1019	***	0.82	0.67	0.1395
32	21	0.2369	0.1096	***	0.83	0.68	0.1496
33	18	0.2192	0.1307	***	0.89	0.80	0.1276

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.15a Mean values and variability for latewood proportion (%) by initial spacing and species.

species	initial spacing					
		0.91 m	1.83 m	2.74 m	3.66 m	4.57 m
Douglas-fir (rings 4-33)	mean	41.5	42.4	37.4	36.4	34.3
	cv (%)	41.1	35.5	32.2	26.3	29.4
	min max	6.7 93.0	10.8 91.1	13.0 75.8	13.6 59.2	13.6 78.1
western hemlock (rings 4-30)	mean	31.1	38.8	28.5	19.3	
	cv (%)	55.1	51.0	57.2	50.6	
	min max	6.4 67.3	9.5 78.0	5.5 78.4	5.5 57.3	
western redcedar (rings 5-27)	mean	29.6	23.2	20.1	14.8	16.3
	cv (%)	50.0	51.6	39.7	47.8	46.7
	min max	6.4 65.3	6.4 56.7	6.8 47.4	4.0 40.8	4.3 39.4

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.15b Repeated measures analysis of variance for latewood proportion (%) by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	0.11	1.21	0.3354		
	error 1	23	0.09				
	ring	29	0.11	24.40	0.0001	0.0001	0.0001
	spacing * ring	116	0.00	0.84	0.8780	0.7014	0.7702
	error 2	667	0.00			epsGG=0.2484	epsHF=0.4359
western hemlock (rings 4-30)	spacing	3	0.80	7.87	0.0015		
	error 1	18	0.10				
	ring	26	0.08	6.73	0.0001	0.0001	0.0001
	spacing * ring	78	0.01	1.12	0.2352	0.3377	0.3016
	error 2	468	0.01			epsGG=0.2446	epsHF=0.4556
western redcedar (rings 5-27)	spacing	4	0.46	8.24	0.0003		
	error 1	23	0.06				
	ring	22	0.07	12.33	0.0001	0.0001	0.0001
	spacing * ring	88	0.02	3.41	0.0001	0.0001	0.0001
	error 2	506	0.01			epsGG=0.4124	epsHF=0.8227

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.16a Mean values and variability for latewood proportion (%) by taper class and species.

species	taper class					
			suppressed	intermediate	dominant	
Douglas-fir (rings 4-33)	mean		41.8	37.1	33.6	
	cv (%)		38.6	29.2	26.8	
	min	max	6.7	93.0	10.8	57.4
western hemlock (rings 4-30)	mean		32.3	25.6	18.8	
	cv (%)		56.2	62.1	48.6	
	min	max	6.1	78.4	5.5	57.3
western redcedar (rings 5-27)	mean		26.8	22.5	16.0	
	cv (%)		51.0	44.2	46.6	
	min	max	6.4	65.3	6.4	44.3

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.16b Repeated measures analysis of variance for latewood proportion (%) by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	0.24	2.97	0.0694		
	error 1	25	0.08				
	ring	29	0.10	21.84	0.0001	0.0001	0.0001
	taper class * ring	58	0.00	0.79	0.8741	0.6862	0.7441
	error 2	725	0.00			epsGG=0.2479	epsHF=0.3858
western hemlock (rings 4-30)	taper class	2	0.53	3.18	0.0464		
	error 1	19	0.17				
	ring	26	0.04	3.13	0.0001	0.0047	0.0004
	taper class * ring	52	0.02	1.32	0.0760	0.2088	0.1537
	error 2	494	0.01			epsGG=0.2620	epsHF=0.4667
western redcedar (rings 5-27)	taper class	2	0.84	14.75	0.0001		
	error 1	25	0.06				
	ring	22	0.07	12.60	0.0001	0.0001	0.0001
	taper class * ring	44	0.03	5.57	0.0001	0.0001	0.0001
	error 2	550	0.01			epsGG=0.4129	epsHF=0.7208

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.17 Linear regression equations and correlation coefficients for latewood proportion (%) calculated yearly as a function of ring width (mm) for Douglas-fir.

ring number from pith	n	a	b		r	r ²	SE _E
3	22	33.9460	-0.0218	*	-0.46	0.21	6.8240
4	29	54.3700	-0.0438	**	-0.55	0.30	10.1880
5	29	36.9700	-0.0123	ns	-0.17	0.03	11.3800
6	29	37.4500	-0.0192	**	-0.50	0.25	6.3800
7	29	38.8090	-0.0181	*	-0.40	0.16	8.9480
8	29	48.8150	-0.0281	***	-0.76	0.57	6.1370
9	29	49.1840	-0.0243	***	-0.66	0.43	7.3430
10	29	39.8740	-0.0157	**	-0.50	0.25	7.2590
11	29	41.5390	-0.0185	*	-0.40	0.16	10.1300
12	29	41.7990	-0.0169	**	-0.57	0.32	5.8570
13	29	45.9750	-0.0241	***	-0.60	0.36	6.8410
14	29	47.2290	-0.0242	***	-0.67	0.45	5.8660
15	28	42.5770	-0.0210	**	-0.57	0.32	6.6050
16	28	42.8290	-0.0222	***	-0.68	0.46	4.9180
17	29	45.4830	-0.0277	***	-0.63	0.39	7.0240
18	29	44.8650	-0.0182	ns	-0.32	0.10	10.6430
19	29	48.2000	-0.0244	*	-0.45	0.21	8.6200
20	29	45.3550	-0.0160	ns	-0.31	0.10	8.0960
21	29	48.3000	-0.0188	*	-0.41	0.17	6.8310
22	29	49.3700	-0.0272	**	-0.51	0.26	6.3000
23	29	58.6000	-0.0498	**	-0.51	0.26	12.1450
24	29	59.1199	-0.0660	**	-0.55	0.30	12.6370
25	29	48.0190	-0.0371	**	-0.49	0.24	7.7450
26	29	54.3840	-0.0495	**	-0.57	0.32	7.5190
27	29	59.0816	-0.0728	***	-0.74	0.55	6.4310
28	29	57.2680	-0.0558	**	-0.55	0.30	8.1980
29	29	52.4140	-0.0417	ns	-0.34	0.12	9.5690
30	29	57.2600	-0.0638	*	-0.42	0.18	14.0040
31	29	59.6470	-0.0645	**	-0.48	0.23	12.9960
32	29	64.1460	-0.0850	***	-0.66	0.44	11.0500
33	29	61.3520	-0.0656	**	-0.55	0.30	12.0090

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.18 Linear regression equations and correlation coefficients for latewood proportion (%) calculated yearly as a function of ring width (mm) for western hemlock.

ring number from pith	n	a	b		r	r ²	SE _E
3	15	63.9330	-0.0636	ns	-0.36	0.13	22.7800
4	24	52.2189	-0.0312	ns	-0.27	0.07	17.0660
5	24	37.1900	-0.0252	*	-0.44	0.19	10.3530
6	24	28.0870	-0.0159	ns	-0.30	0.09	8.2560
7	24	45.0300	-0.0469	***	-0.71	0.50	7.5700
8	24	35.6030	-0.0322	**	-0.58	0.34	6.1460
9	24	40.0192	-0.0494	*	-0.47	0.22	10.1170
10	24	19.1820	-0.0054	ns	-0.11	0.01	6.1630
11	24	26.4880	-0.0173	*	-0.42	0.18	5.9740
12	24	31.0950	-0.0257	*	-0.43	0.19	9.4390
13	24	31.8700	-0.0253	*	-0.46	0.21	8.4330
14	24	38.5170	-0.0463	***	-0.65	0.42	9.3220
15	24	34.5000	-0.0444	***	-0.63	0.40	8.9000
16	24	39.2700	-0.0420	*	-0.44	0.19	14.5380
17	24	30.1500	-0.0226	ns	-0.35	0.12	10.0380
18	24	47.7300	-0.0669	**	-0.58	0.34	14.1240
19	24	46.4500	-0.0519	**	-0.53	0.28	16.6310
20	24	57.1030	-0.0799	***	-0.72	0.52	12.6580
21	24	58.3000	-0.0820	***	-0.78	0.61	12.4970
22	24	54.8550	-0.0818	***	-0.77	0.59	12.8300
23	24	52.8400	-0.0794	***	-0.70	0.48	14.2760
24	24	50.2680	-0.0551	*	-0.50	0.25	17.1130
25	23	47.4110	-0.0470	*	-0.52	0.27	15.5220
26	23	55.6600	-0.0800	***	-0.72	0.52	13.5320
27	23	55.4530	-0.0831	***	-0.70	0.49	15.0760
28	22	55.1690	-0.0814	***	-0.69	0.47	15.7780
29	22	48.0140	-0.0582	***	-0.67	0.45	14.0950
30	22	48.9480	-0.0588	***	-0.70	0.48	12.1000
31	18	48.1910	-0.0540	**	-0.60	0.36	15.4390
32	16	50.3420	-0.0714	**	-0.73	0.53	11.9650
33	11	37.1100	0.0191	ns	0.11	0.01	24.1490

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.19 Linear regression equations and correlation coefficients for latewood proportion (%) calculated yearly as a function of ring width (mm) for western redcedar.

ring number from pith	n	a	b		r	r ²	SE _E
3	17	98.9440	-0.1171	*	-0.50	0.25	17.8800
4	23	39.6330	-0.0231	ns	-0.21	0.04	13.9910
5	30	25.2580	-0.0087	ns	-0.13	0.02	9.3230
6	30	24.6500	-0.0094	ns	-0.18	0.03	8.7920
7	30	22.2177	-0.0046	ns	-0.13	0.02	6.5810
8	30	27.2860	-0.0173	**	-0.56	0.31	5.7140
9	30	23.4800	-0.0140	*	-0.42	0.17	6.2200
10	30	28.6540	-0.0197	***	-0.65	0.42	4.9720
11	30	21.1800	-0.0064	ns	-0.27	0.07	5.0310
12	30	24.0210	-0.0152	**	-0.54	0.29	5.2550
13	30	35.1500	-0.0302	***	-0.79	0.62	6.3140
14	30	30.1600	-0.0252	***	-0.67	0.44	7.4650
15	30	23.7530	-0.0200	***	-0.62	0.38	6.3530
16	30	20.1050	-0.0098	*	-0.41	0.17	5.5570
17	30	30.0300	-0.0281	***	-0.70	0.49	7.7670
18	30	28.7840	-0.0255	***	-0.77	0.59	6.1710
19	30	33.8667	-0.0330	***	-0.85	0.72	6.6100
20	29	36.3170	-0.0322	***	-0.82	0.67	8.6220
21	29	36.3800	-0.0361	***	-0.83	0.69	8.0150
22	29	40.5860	-0.0477	***	-0.81	0.66	9.1610
23	28	33.3850	-0.0337	***	-0.82	0.67	5.5850
24	28	39.3960	-0.0485	***	-0.73	0.53	9.6790
25	28	42.0290	-0.0599	***	-0.78	0.61	8.6060
26	28	40.9430	-0.0659	***	-0.72	0.52	8.7190
27	28	43.1170	-0.0687	***	-0.80	0.64	8.5290
28	23	42.0280	-0.0681	***	-0.65	0.43	12.0000
29	24	38.1980	-0.0524	***	-0.80	0.63	7.5390
30	22	37.2540	-0.0457	***	-0.84	0.70	5.7420
31	21	36.7740	-0.0378	***	-0.68	0.46	7.9860
32	21	36.0820	-0.0354	**	-0.55	0.30	10.4510
33	18	34.2600	-0.0293	*	-0.53	0.28	8.7800

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.20a Mean values and variability for earlywood relative density by initial spacing and species.

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 4-33)	mean	0.3		0.3		0.3		0.3		0.3	
	cv (%)	15.4		13.7		9.7		10.1		8.9	
	min	max	0.23	0.44	0.24	0.45	0.25	0.40	0.25	0.41	0.27
western hemlock (rings 4-30)	mean	0.4		0.4		0.4		0.4			
	cv (%)	8.5		9.1		10.0		9.1			
	min	max	0.29	0.44	0.30	0.48	0.29	0.45	0.28	0.43	
western redcedar (rings 5-27)	mean	0.3		0.3		0.3		0.3		0.3	
	cv (%)	11.9		9.5		9.9		9.8		8.0	
	min	max	0.20	0.34	0.22	0.32	0.19	0.31	0.20	0.32	0.20

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.20b Repeated measures analysis of variance for earlywood relative density by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	0.09	0.63	0.6492		
	error 1	23	0.14				
	ring	29	0.07	10.17	0.0001	0.0001	0.0001
	spacing * ring	116	0.01	1.65	0.0001	0.0332	0.0094
	error 2	667	0.01			epsGG=0.2268	epsHF=0.3825
western hemlock (rings 4-30)	spacing	3	0.24	2.77	0.0714		
	error 1	18	0.08				
	ring	26	0.04	6.91	0.0001	0.0001	0.0001
	spacing * ring	78	0.01	1.19	0.1469	0.2554	0.1704
	error 2	468	0.01			epsGG=0.3401	epsHF=0.8085
western redcedar (rings 5-27)	spacing	4	0.13	1.44	0.2530		
	error 1	23	0.09				
	ring	22	0.03	7.55	0.0001	0.0001	0.0001
	spacing * ring	88	0.01	3.35	0.0001	0.0001	0.0001
	error 2	506	0.00			epsGG=0.3285	epsHF=0.5773

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.21a Mean values and variability for earlywood relative density by taper class and species.

species	taper class				
			suppressed	intermediate	dominant
Douglas-fir (rings 4-33)	mean		0.31	0.31	0.31
	cv (%)		14.4	9.8	9.3
	min	max	0.23 0.45	0.25 0.41	0.25 0.42
western hemlock (rings 4-30)	mean		0.37	0.36	0.36
	cv (%)		10.1	9.5	7.6
	min	max	0.28 0.48	0.29 0.46	0.30 0.42
western redcedar (rings 5-27)	mean		0.27	0.26	0.25
	cv (%)		11.3	7.5	9.5
	min	max	0.20 0.34	0.22 0.30	0.19 0.32

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.21b Repeated measures analysis of variance for earlywood relative density by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	0.02	0.15	0.8652		
	error 1	25	0.14				
	ring	29	0.06	8.42	0.0001	0.0001	0.0001
	taper class * ring	58	0.01	2.18	0.0001	0.0094	0.0024
	error 2	725	0.01			epsGG=0.2406	epsHF=0.3700
western hemlock (rings 4-30)	taper class	2	0.01	0.05	0.9514		
	error 1	19	0.12				
	ring	26	0.02	4.64	0.0001	0.0001	0.0001
	taper class * ring	52	0.00	0.79	0.8484	0.6997	0.7973
	error 2	494	0.01			epsGG=0.3296	epsHF=0.6878
western redcedar (rings 5-27)	taper class	2	0.24	2.88	0.0748		
	error 1	25	0.08				
	ring	22	0.02	5.45	0.0001	0.0001	0.0001
	taper class * ring	44	0.02	5.70	0.0001	0.0001	0.0001
	error 2	550	0.00			epsGG=0.3357	epsHF=0.5285

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.22 Linear regression equations and correlation coefficients for earlywood relative density calculated yearly as a function of ring width (mm) for Douglas-fir.

ring number from pith	n	a	b		r	r ²	SE _E
3	22	0.4238	-0.0098	*	-0.47	0.23	0.0280
4	29	0.3738	-0.0045	ns	-0.26	0.07	0.0257
5	29	0.3516	-0.0039	ns	-0.17	0.03	0.0374
6	29	0.2523	0.0068	*	0.41	0.17	0.0286
7	29	0.2355	0.0082	***	0.60	0.36	0.0239
8	29	0.2594	0.0058	**	0.54	0.29	0.0229
9	29	0.2632	0.0040	*	0.39	0.15	0.0253
10	29	0.2776	0.0016	ns	0.20	0.04	0.0215
11	29	0.2820	0.0007	ns	0.06	0.00	0.0248
12	29	0.2789	0.0021	ns	0.10	0.01	0.0211
13	29	0.2957	-0.0010	ns	-0.10	0.01	0.0211
14	29	0.2963	0.0000	ns	0.00	0.00	0.0293
15	28	0.3129	-0.0031	ns	-0.27	0.07	0.0244
16	28	0.3177	-0.0038	ns	-0.28	0.08	0.0273
17	29	0.3072	0.0002	ns	0.01	0.00	0.0336
18	29	0.3273	-0.0049	ns	-0.25	0.06	0.0372
19	29	0.3385	-0.0080	*	-0.40	0.16	0.0324
20	29	0.3245	-0.0042	ns	-0.23	0.05	0.0319
21	29	0.3415	-0.0072	ns	-0.32	0.11	0.0352
22	29	0.3169	-0.0029	ns	-0.18	0.03	0.0236
23	29	0.3578	-0.0159	**	-0.58	0.34	0.0322
24	29	0.3390	-0.0106	ns	-0.36	0.13	0.0349
25	29	0.3428	-0.0143	**	-0.50	0.25	0.0299
26	29	0.3677	-0.0225	***	-0.62	0.39	0.0310
27	29	0.3635	-0.0203	**	-0.53	0.28	0.0325
28	29	0.3799	-0.0267	***	-0.58	0.34	0.0370
29	29	0.3624	-0.0226	**	-0.51	0.26	0.0343
30	29	0.3765	-0.0286	***	-0.67	0.45	0.0321
31	29	0.3774	-0.0270	***	-0.62	0.38	0.0381
32	29	0.3617	-0.0157	*	-0.44	0.20	0.0364
33	29	0.3574	-0.0170	**	-0.54	0.29	0.0318

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.23 Linear regression equations and correlation coefficients for earlywood relative density calculated yearly as a function of ring width (mm) for western hemlock.

ring number from pith	n	a	b		r	r ²	SE _E
3	15	0.4349	-0.0070	ns	-0.29	0.09	0.0375
4	24	0.4505	-0.0081	ns	-0.37	0.14	0.0306
5	24	0.4124	-0.0042	ns	-0.31	0.10	0.0249
6	24	0.4012	-0.0040	ns	-0.22	0.05	0.0288
7	24	0.4209	-0.0068	ns	-0.37	0.13	0.0276
8	24	0.3922	-0.0044	ns	-0.22	0.05	0.0269
9	24	0.3732	-0.0034	ns	-0.14	0.02	0.0257
10	24	0.3745	-0.0063	ns	-0.35	0.12	0.0206
11	24	0.3703	-0.0036	ns	-0.17	0.03	0.0330
12	24	0.3570	0.0003	ns	0.02	0.00	0.0362
13	24	0.3558	-0.0023	ns	-0.14	0.02	0.0285
14	24	0.3602	-0.0001	ns	0.00	0.00	0.0307
15	24	0.3528	0.0012	ns	0.05	0.00	0.0398
16	24	0.3934	-0.0093	ns	-0.34	0.12	0.0427
17	24	0.3650	-0.0046	ns	-0.19	0.04	0.0378
18	24	0.3775	-0.0091	ns	-0.39	0.16	0.0322
19	24	0.3711	-0.0050	ns	-0.26	0.07	0.0366
20	24	0.3688	-0.0059	ns	-0.26	0.07	0.0367
21	24	0.3989	-0.0081	*	-0.44	0.19	0.0316
22	24	0.3776	-0.0065	ns	-0.29	0.08	0.0407
23	24	0.3818	-0.0108	ns	-0.40	0.16	0.0419
24	24	0.3779	-0.0049	ns	-0.19	0.04	0.0450
25	23	0.3688	-0.0005	ns	-0.03	0.00	0.0376
26	23	0.3738	-0.0049	ns	-0.24	0.06	0.0341
27	23	0.3696	-0.0019	ns	-0.10	0.01	0.0328
28	22	0.3813	-0.0066	ns	-0.30	0.09	0.0379
29	22	0.3689	-0.0040	ns	-0.23	0.05	0.0375
30	22	0.3575	0.0000	ns	0.00	0.00	0.0337
31	18	0.3508	0.0027	ns	0.19	0.04	0.0300
32	16	0.3632	0.0025	ns	0.09	0.01	0.0499
33	11	0.3727	-0.0008	ns	-0.03	0.00	0.0373

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.24 Linear regression equations and correlation coefficients for earlywood relative density calculated yearly as a function of ring width (mm) for western redcedar.

ring number from pith	n	a	b		r	r ²	SE _E
3	17	0.3988	-0.0117	ns	-0.33	0.11	0.0292
4	23	0.3602	-0.0079	ns	-0.36	0.13	0.0268
5	30	0.2667	0.0020	ns	0.14	0.02	0.0212
6	30	0.2652	0.0019	ns	0.17	0.03	0.0188
7	30	0.2545	0.0029	ns	0.28	0.08	0.0188
8	30	0.2565	0.0012	ns	0.15	0.02	0.0184
9	30	0.2609	0.0006	ns	0.06	0.00	0.0228
10	30	0.2582	0.0007	ns	0.08	0.01	0.0196
11	30	0.2680	-0.0014	ns	-0.18	0.03	0.0169
12	30	0.2501	0.0009	ns	0.12	0.01	0.0171
13	30	0.2657	-0.0013	ns	-0.17	0.03	0.0203
14	30	0.2890	-0.0050	**	-0.49	0.24	0.0238
15	30	0.2896	-0.0053	*	-0.46	0.21	0.0267
16	30	0.2731	-0.0032	*	-0.38	0.15	0.0198
17	30	0.2736	-0.0038	ns	-0.33	0.11	0.0290
18	30	0.2678	-0.0036	*	-0.45	0.20	0.0208
19	30	0.2607	-0.0026	ns	-0.32	0.10	0.0249
20	29	0.2631	-0.0025	ns	-0.36	0.13	0.0246
21	29	0.2777	-0.0051	**	-0.50	0.25	0.0290
22	29	0.2770	-0.0075	**	-0.58	0.34	0.0283
23	28	0.2516	-0.0022	ns	-0.18	0.03	0.0284
24	28	0.2612	-0.0048	ns	-0.32	0.10	0.0303
25	28	0.2665	-0.0079	*	-0.47	0.22	0.0265
26	28	0.2778	-0.0146	**	-0.56	0.31	0.0304
27	28	0.2861	-0.0167	***	-0.65	0.43	0.0319
28	23	0.2645	-0.0099	*	-0.45	0.20	0.0303
29	24	0.2549	-0.0056	ns	-0.33	0.11	0.0308
30	22	0.2472	-0.0029	ns	-0.23	0.05	0.0239
31	21	0.2464	-0.0022	ns	-0.15	0.02	0.0293
32	21	0.2512	-0.0045	ns	-0.29	0.08	0.0264
33	18	0.2520	-0.0034	ns	-0.14	0.02	0.0298

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.25a Mean values and variability for latewood relative density by initial spacing and species.

species		initial spacing				
		0.91 m	1.83 m	2.74 m	3.66 m	4.57 m
Douglas-fir (rings 4-33)	mean	0.7	0.7	0.7	0.7	0.7
	cv (%)	9.8	8.1	7.6	8.0	8.8
	min max	0.53 0.83	0.53 0.82	0.57 0.85	0.55 0.81	0.52 0.83
western hemlock (rings 4-30)	mean	0.6	0.6	0.6	0.6	
	cv (%)	5.9	7.1	7.4	6.0	
	min max	0.49 0.68	0.46 0.70	0.47 0.70	0.47 0.66	
western redcedar (rings 5-27)	mean	0.5	0.5	0.5	0.5	0.5
	cv (%)	10.6	7.0	7.6	9.1	9.1
	min max	0.39 0.62	0.44 0.64	0.41 0.62	0.42 0.63	0.42 0.64

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.25b Repeated measures analysis of variance for latewood relative density by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	0.02	0.77	0.5550		
	error 1	23	0.03				
	ring	29	0.03	13.49	0.0001	0.0001	0.0001
	spacing * ring	116	0.00	1.09	0.2591	0.3746	0.3620
	error 2	667	0.00			epsGG=0.1442	epsHF=0.2108
western hemlock (rings 4-30)	spacing	3	0.05	1.60	0.2251		
	error 1	18	0.03				
	ring	26	0.01	2.72	0.0001	0.0069	0.0002
	spacing * ring	78	0.00	1.21	0.1227	0.2391	0.1559
	error 2	468	0.00			epsGG=0.3250	epsHF=0.7407
western redcedar (rings 5-27)	spacing	4	0.04	1.02	0.4186		
	error 1	23	0.04				
	ring	22	0.02	3.18	0.0001	0.0009	0.0001
	spacing * ring	88	0.01	2.60	0.0001	0.0001	0.0001
	error 2	506	0.00			epsGG=0.4410	epsHF=0.9218

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.26a Mean values and variability for latewood relative density by taper class and species.

species	taper class					
			suppressed	intermediate	dominant	
Douglas-fir (rings 4-33)	mean		0.68	0.71	0.69	
	cv (%)		8.9	8.2	8.3	
	min	max	0.53	0.83	0.52	0.85
western hemlock (rings 4-30)	mean		0.60	0.58	0.57	
	cv (%)		6.5	7.8	5.0	
	min	max	0.46	0.70	0.47	0.70
western redcedar (rings 5-27)	mean		0.51	0.53	0.52	
	cv (%)		9.2	6.7	9.0	
	min	max	0.39	0.62	0.43	0.64

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.26b Repeated measures analysis of variance for latewood relative density by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	0.04	1.48	0.2477		
	error 1	25	0.03				
	ring	29	0.03	14.71	0.0001	0.0001	0.0001
	taper class * ring	58	0.00	2.16	0.0001	0.0240	0.0111
	error 2	725	0.00			epsGG=0.1733	epsHF=0.2394
western hemlock (rings 4-30)	taper class	2	0.07	2.34	0.1236		
	error 1	19	0.03				
	ring	26	0.01	1.77	0.0116	0.0767	0.0226
	taper class * ring	52	0.00	0.93	0.6197	0.5467	0.5989
	error 2	494	0.00			epsGG=0.3479	epsHF=0.7609
western redcedar (rings 5-27)	taper class	2	0.06	1.53	0.2355		
	error 1	25	0.04				
	ring	22	0.01	2.13	0.0021	0.0262	0.0061
	taper class * ring	44	0.01	2.73	0.0001	0.0002	0.0001
	error 2	550	0.01			epsGG=0.4231	epsHF=0.7492

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.27 Linear regression equations and correlation coefficients for latewood relative density calculated yearly as a function of ring width (mm) for Douglas-fir.

ring number from pith	n	a	b		r	r ²	SE _E
3	22	0.6507	-0.0075	ns	-0.38	0.14	0.0295
4	29	0.6161	-0.0009	ns	-0.04	0.00	0.0336
5	29	0.6563	-0.0044	ns	-0.21	0.04	0.0332
6	29	0.7112	-0.0089	*	-0.40	0.16	0.0388
7	29	0.6245	0.0030	ns	0.17	0.03	0.0390
8	29	0.6889	-0.0048	ns	-0.23	0.05	0.0506
9	29	0.7627	-0.0134	***	-0.72	0.51	0.0344
10	29	0.7446	-0.0107	***	-0.62	0.38	0.0361
11	29	0.7352	-0.0082	**	-0.48	0.23	0.0368
12	29	0.7493	-0.0104	**	-0.50	0.25	0.0424
13	29	0.7406	-0.0079	*	-0.44	0.20	0.0346
14	29	0.7297	-0.0075	*	-0.39	0.15	0.0392
15	28	0.7162	-0.0081	*	-0.39	0.15	0.0407
16	28	0.7150	-0.0056	ns	-0.26	0.07	0.0444
17	29	0.7189	-0.0068	ns	-0.31	0.09	0.0416
18	29	0.7272	-0.0040	ns	-0.16	0.02	0.0502
19	29	0.7034	0.0050	ns	0.16	0.03	0.0541
20	29	0.6868	0.0075	ns	0.21	0.04	0.0619
21	29	0.6757	0.0121	*	0.42	0.18	0.0434
22	29	0.6861	0.0060	ns	0.19	0.04	0.0440
23	29	0.6846	0.0085	ns	0.21	0.04	0.0572
24	29	0.6875	0.0171	*	0.42	0.18	0.0465
25	29	0.6814	0.0243	**	0.47	0.23	0.0548
26	29	0.6803	0.0266	**	0.58	0.34	0.0403
27	29	0.6461	0.0439	***	0.69	0.48	0.0465
28	29	0.6541	0.0365	***	0.61	0.37	0.0478
29	29	0.6361	0.0492	***	0.65	0.42	0.0513
30	29	0.6041	0.0543	***	0.66	0.43	0.0636
31	29	0.6040	0.0473	***	0.68	0.47	0.0557
32	29	0.6596	0.0295	**	0.52	0.27	0.0552
33	29	0.6610	0.0234	*	0.41	0.17	0.0623

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.28 Linear regression equations and correlation coefficients for latewood relative density calculated yearly as a function of ring width (mm) for western hemlock.

ring number from pith	n	a	b		r	r ²	SE _E
3	15	0.5978	-0.0074	ns	-0.31	0.10	0.0367
4	24	0.6023	-0.0066	*	-0.46	0.21	0.0199
5	24	0.6264	-0.0096	**	-0.52	0.27	0.0316
6	24	0.6057	-0.0051	ns	-0.33	0.11	0.0232
7	24	0.6485	-0.0136	**	-0.63	0.39	0.0267
8	24	0.6336	-0.0126	**	-0.55	0.30	0.0266
9	24	0.6269	-0.0104	ns	-0.34	0.12	0.0308
10	24	0.5863	0.0010	ns	0.04	0.00	0.0348
11	24	0.6127	-0.0075	ns	-0.38	0.15	0.0292
12	24	0.6474	-0.0157	***	-0.66	0.44	0.0312
13	24	0.6176	-0.0061	ns	-0.31	0.09	0.0325
14	24	0.6259	-0.0123	*	-0.46	0.21	0.0403
15	24	0.5669	-0.0022	ns	-0.08	0.01	0.0464
16	24	0.5564	0.0027	ns	0.10	0.01	0.0468
17	24	0.6066	-0.0055	ns	-0.21	0.04	0.0417
18	24	0.6354	-0.0114	*	-0.45	0.20	0.0343
19	24	0.6061	-0.0096	ns	-0.40	0.16	0.0432
20	24	0.6201	-0.0100	ns	-0.39	0.15	0.0394
21	24	0.6099	-0.0043	ns	-0.26	0.07	0.0300
22	24	0.6261	-0.0101	ns	-0.38	0.14	0.0470
23	24	0.6247	-0.0100	ns	-0.34	0.11	0.0479
24	24	0.6024	-0.0068	ns	-0.26	0.07	0.0447
25	23	0.6193	-0.0058	ns	-0.29	0.09	0.0381
26	23	0.6276	-0.0105	*	-0.51	0.26	0.0307
27	23	0.6089	-0.0053	ns	-0.26	0.07	0.0349
28	22	0.6162	-0.0056	ns	-0.20	0.04	0.0511
29	22	0.5929	-0.0028	ns	-0.16	0.02	0.0397
30	22	0.5994	-0.0027	ns	-0.13	0.02	0.0404
31	18	0.5842	0.0048	ns	0.15	0.02	0.0690
32	16	0.5983	0.0000	ns	0.00	0.00	0.0365
33	11	0.6200	-0.0049	ns	-0.13	0.02	0.0492

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.29 Linear regression equations and correlation coefficients for latewood relative density calculated yearly as a function of ring width (mm) for western redcedar.

ring number from pith	n	a	b		r	r ²	SE _E
3	17	0.5455	-0.0075	ns	-0.20	0.04	0.0326
4	23	0.4840	0.0006	ns	0.03	0.00	0.0332
5	30	0.5872	-0.0146	**	-0.57	0.32	0.0309
6	30	0.6052	-0.0162	**	-0.55	0.30	0.0418
7	30	0.6121	-0.0166	***	-0.61	0.38	0.0406
8	30	0.5887	-0.0122	**	-0.55	0.30	0.0411
9	30	0.6027	-0.0125	*	-0.42	0.18	0.0542
10	30	0.6102	-0.0142	***	-0.64	0.41	0.0376
11	30	0.5784	-0.0100	**	-0.53	0.28	0.0357
12	30	0.5252	0.0001	ns	0.00	0.00	0.0460
13	30	0.5354	-0.0007	ns	-0.05	0.00	0.0382
14	30	0.5141	-0.0001	ns	-0.01	0.00	0.0350
15	30	0.4652	0.0106	**	0.52	0.27	0.0445
16	30	0.4841	0.0094	**	0.48	0.23	0.0438
17	30	0.5041	0.0077	*	0.41	0.17	0.0459
18	30	0.4998	0.0038	ns	0.21	0.04	0.0525
19	30	0.5030	0.0027	ns	0.19	0.04	0.0449
20	29	0.5109	-0.0022	ns	-0.17	0.03	0.0465
21	29	0.5145	0.0009	ns	0.06	0.00	0.0496
22	29	0.5122	0.0019	ns	0.11	0.01	0.0457
23	28	0.5206	0.0013	ns	0.07	0.00	0.0451
24	28	0.5143	0.0017	ns	0.10	0.01	0.0366
25	28	0.5309	0.0014	ns	0.06	0.00	0.0395
26	28	0.5278	0.0026	ns	0.09	0.01	0.0376
27	28	0.5375	0.0006	ns	0.03	0.00	0.0396
28	23	0.5323	0.0072	ns	0.27	0.07	0.0390
29	24	0.5331	0.0054	ns	0.22	0.05	0.0459
30	22	0.5400	0.0005	ns	0.03	0.00	0.0340
31	21	0.5377	0.0011	ns	0.04	0.00	0.0479
32	21	0.5447	0.0030	ns	0.12	0.01	0.0441
33	18	0.5313	-0.0025	ns	-0.07	0.00	0.0451

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.30a Mean values and variability for whole-ring relative density by initial spacing and species.

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 4-33)	mean	0.4		0.5		0.5		0.5		0.4	
	cv (%)	13.4		16.4		13.7		13.4		12.8	
	min	max	0.32	0.58	0.33	0.66	0.33	0.61	0.34	0.60	0.34
western hemlock (rings 4-30)	mean	0.4		0.5		0.4		0.4			
	cv (%)	11.7		10.7		12.1		10.3			
	min	max	0.33	0.56	0.36	0.60	0.31	0.58	0.32	0.50	
western redcedar (rings 5-27)	mean	0.3		0.3		0.3		0.3		0.3	
	cv (%)	14.3		12.4		10.3		10.2		9.2	
	min	max	0.23	0.43	0.25	0.42	0.23	0.39	0.23	0.38	0.23

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.30b Repeated measures analysis of variance for whole-ring relative density by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	spacing	4	0.05	0.31	0.8704		
	error 1	23	0.18				
	ring	29	0.23	34.15	0.0001	0.0001	0.0001
	spacing * ring	116	0.01	1.17	0.1271	0.2572	0.1961
	error 2	667	0.01			epsGG=0.2849	epsHF=0.5366
western hemlock (rings 4-30)	spacing	3	0.70	5.21	0.0091		
	error 1	18	0.13				
	ring	26	0.05	6.55	0.0001	0.0001	0.0001
	spacing * ring	78	0.01	1.31	0.0486	0.1846	0.1167
	error 2	468	0.01			epsGG=0.2569	epsHF=0.4924
western redcedar (rings 5-27)	spacing	4	0.41	3.71	0.0179		
	error 1	23	0.11				
	ring	22	0.03	5.56	0.0001	0.0001	0.0001
	spacing * ring	88	0.02	3.59	0.0001	0.0001	0.0001
	error 2	506	0.01			epsGG=0.3709	epsHF=0.6938

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.31a Mean values and variability for whole-ring relative density by taper class and species.

species	taper class					
			suppressed	intermediate	dominant	
Douglas-fir (rings 4-33)	mean		0.46	0.46	0.44	
	cv (%)		14.9	13.5	12.7	
	min	max	0.32	0.66	0.33	0.61
western hemlock (rings 4-30)	mean		0.44	0.41	0.40	
	cv (%)		12.7	12.1	8.6	
	min	max	0.31	0.60	0.33	0.56
western redcedar (rings 5-27)	mean		0.33	0.32	0.29	
	cv (%)		13.7	9.2	9.9	
	min	max	0.23	0.43	0.26	0.42

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.31b Repeated measures analysis of variance for whole-ring relative density by taper class and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 4-33)	taper class	2	0.10	0.59	0.5595		
	error 1	25	0.16				
	ring	29	0.21	30.70	0.0001	0.0001	0.0001
	taper class * ring	58	0.01	1.10	0.2866	0.3532	0.3311
	error 2	725	0.01			epsGG=0.2959	epsHF=0.5004
western hemlock (rings 4-30)	taper class	2	0.26	1.25	0.3094		
	error 1	19	0.21				
	ring	26	0.02	3.35	0.0001	0.0030	0.0002
	taper class * ring	52	0.01	1.08	0.3299	0.3804	0.3661
	error 2	494	0.01			epsGG=0.2588	epsHF=0.4578
western redcedar (rings 5-27)	taper class	2	0.93	9.84	0.0007		
	error 1	25	0.09				
	ring	22	0.04	6.15	0.0001	0.0001	0.0001
	taper class * ring	44	0.03	5.69	0.0001	0.0001	0.0001
	error 2	550	0.01			epsGG=0.3758	epsHF=0.6234

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.32 Linear regression equations and correlation coefficients for whole-ring relative density calculated yearly as a function of ring width (mm) for Douglas-fir.

ring number from pith	n	a	b		r	r ²	SE _E
3	22	0.4952	-0.0145	**	-0.56	0.31	0.0345
4	29	0.5111	-0.0160	**	-0.56	0.31	0.0366
5	29	0.4900	-0.0121	*	-0.41	0.16	0.0440
6	29	0.4123	-0.0044	ns	-0.20	0.04	0.0403
7	29	0.3929	-0.0018	ns	-0.13	0.02	0.0312
8	29	0.4664	-0.0092	**	-0.48	0.23	0.0430
9	29	0.4941	-0.0119	***	-0.60	0.36	0.0424
10	29	0.4498	-0.0077	*	-0.45	0.21	0.0407
11	29	0.4635	-0.0097	*	-0.43	0.19	0.0494
12	29	0.4646	-0.0083	**	-0.52	0.27	0.0320
13	29	0.4940	-0.0133	***	-0.59	0.35	0.0390
14	29	0.4914	-0.0115	**	-0.56	0.31	0.0375
15	28	0.4804	-0.0125	***	-0.59	0.35	0.0367
16	28	0.4927	-0.0143	***	-0.63	0.40	0.0365
17	29	0.4900	-0.0119	*	-0.41	0.17	0.0524
18	29	0.5009	-0.0110	ns	-0.32	0.10	0.0643
19	29	0.5133	-0.0121	*	-0.39	0.15	0.0513
20	29	0.4951	-0.0073	ns	-0.24	0.06	0.0528
21	29	0.5122	-0.0085	ns	-0.34	0.12	0.0391
22	29	0.5183	-0.0153	*	-0.44	0.20	0.0442
23	29	0.5320	-0.0173	*	-0.46	0.21	0.0478
24	29	0.5203	-0.0151	ns	-0.35	0.12	0.0505
25	29	0.5122	-0.0156	*	-0.39	0.15	0.0444
26	29	0.5440	-0.0216	*	-0.47	0.22	0.0444
27	29	0.5387	-0.0188	*	-0.39	0.15	0.0444
28	29	0.5357	-0.0151	ns	-0.28	0.08	0.0508
29	29	0.5077	-0.0043	ns	-0.06	0.00	0.0618
30	29	0.5004	-0.0056	ns	-0.09	0.01	0.0630
31	29	0.5026	-0.0060	ns	-0.12	0.01	0.0556
32	29	0.5306	-0.0144	ns	-0.32	0.10	0.0488
33	29	0.5280	-0.0142	ns	-0.28	0.08	0.0585

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.33 Linear regression equations and correlation coefficients for whole-ring relative density calculated yearly as a function of ring width (mm) for western hemlock.

ring number from pith	n	a	b		r	r ²	SE _E
3	15	0.5231	-0.0173	*	-0.56	0.31	0.0421
4	24	0.5225	-0.0124	ns	-0.38	0.15	0.0454
5	24	0.4910	-0.0112	*	-0.45	0.21	0.0423
6	24	0.4620	-0.0085	ns	-0.30	0.09	0.0435
7	24	0.5140	-0.0174	**	-0.57	0.32	0.0401
8	24	0.4683	-0.0123	*	-0.45	0.21	0.0331
9	24	0.4607	-0.0145	*	-0.43	0.19	0.0329
10	24	0.4182	0.0071	ns	-0.30	0.09	0.0279
11	24	0.4341	-0.0086	ns	-0.34	0.11	0.0391
12	24	0.4378	-0.0085	ns	-0.31	0.10	0.0460
13	24	0.4387	-0.0099	*	-0.40	0.16	0.0385
14	24	0.4560	-0.0135	*	-0.50	0.25	0.0401
15	24	0.4249	-0.0085	ns	-0.30	0.09	0.0438
16	24	0.4561	-0.0142	*	-0.42	0.18	0.0513
17	24	0.4673	-0.0179	*	-0.51	0.26	0.0491
18	24	0.4860	-0.0232	**	-0.59	0.35	0.0484
19	24	0.4712	-0.0175	**	-0.58	0.33	0.0492
20	24	0.4996	-0.0252	***	-0.64	0.41	0.0497
21	24	0.5128	-0.0227	***	-0.74	0.55	0.0392
22	24	0.4980	-0.0238	***	-0.68	0.47	0.0481
23	24	0.4899	-0.0250	***	-0.69	0.47	0.0452
24	24	0.4841	-0.016508	*	-0.48	0.23	0.0536
25	23	0.4689	-0.0100	ns	-0.37	0.14	0.0505
26	23	0.5054	-0.0235	***	-0.69	0.47	0.0435
27	23	0.4959	-0.0208	**	-0.57	0.33	0.0524
28	22	0.5070	-0.0248	**	-0.59	0.35	0.0625
29	22	0.4754	-0.0163	**	-0.59	0.35	0.0490
30	22	0.4695	-0.0130	*	-0.45	0.20	0.0505
31	18	0.4654	-0.0104	ns	-0.31	0.10	0.0695
32	16	0.4714	-0.0078	ns	-0.19	0.04	0.0694
33	11	0.4722	-0.0053	ns	-0.14	0.02	0.0515

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.34 Linear regression equations and correlation coefficients for whole-ring relative density calculated yearly as a function of ring width (mm) for western redcedar.

ring number from pith	n	a	b		r	r ²	SE _E
3	17	0.5483	-0.0302	*	-0.53	0.28	0.0421
4	23	0.4045	-0.0093	ns	-0.35	0.12	0.0324
5	30	0.3329	-0.0025	ns	-0.12	0.01	0.0304
6	30	0.3334	-0.0030	ns	-0.18	0.03	0.0274
7	30	0.3280	-0.0021	ns	-0.15	0.02	0.0252
8	30	0.3347	-0.0050	*	-0.44	0.19	0.0225
9	30	0.3338	-0.0054	ns	-0.35	0.12	0.0298
10	30	0.3598	-0.0088	**	-0.54	0.29	0.0301
11	30	0.3310	-0.0048	*	-0.46	0.21	0.0198
12	30	0.3138	-0.0034	ns	-0.33	0.11	0.0215
13	30	0.3585	-0.0094	***	-0.68	0.46	0.0276
14	30	0.3553	-0.0101	***	-0.64	0.41	0.0321
15	30	0.3425	-0.0092	***	-0.60	0.37	0.0311
16	30	0.3242	-0.0052	*	-0.40	0.16	0.0300
17	30	0.3521	-0.0105	***	-0.69	0.48	0.0296
18	30	0.3383	-0.0093	***	-0.73	0.53	0.0254
19	30	0.3379	-0.0094	***	-0.72	0.52	0.0290
20	29	0.3473	-0.0096	***	-0.76	0.58	0.0313
21	29	0.3608	-0.0125	***	-0.76	0.58	0.0352
22	29	0.3616	-0.0156	***	-0.79	0.62	0.0326
23	28	0.3407	-0.0104	***	-0.61	0.38	0.0320
24	28	0.3568	-0.0149	***	-0.65	0.42	0.0372
25	28	0.3735	-0.0211	***	-0.76	0.58	0.0324
26	28	0.3754	-0.0263	***	-0.75	0.56	0.0322
27	28	0.3921	-0.0307	***	-0.82	0.68	0.0347
28	23	0.3740	-0.0247	**	-0.64	0.41	0.0454
29	24	0.3632	-0.0193	***	-0.69	0.47	0.0386
30	22	0.3546	-0.0154	***	-0.71	0.51	0.0291
31	21	0.3487	-0.0119	*	-0.52	0.27	0.0386
32	21	0.3573	-0.0153	**	-0.56	0.31	0.0403
33	18	0.3454	-0.0125	ns	-0.30	0.09	0.0476

n : number of observations
 a : intercept estimate
 b : slope estimate
 r : correlation coefficient
 r² : coefficient of determination
 SE_E : standard error of estimate
 ns : non-significant relationship
 * : relationship significant at P < 0.05
 ** : relationship significant at P < 0.01
 *** : relationship significant at P < 0.001

Table 4.35 Mean earlywood and latewood tracheid length (mm) and standard deviation values obtained for Douglas-fir at breast height, by initial spacing, and on every third growth increment from the pith, via image analysis.

spacing	tracheid		ring number from pith										
			3	6	9	12	15	18	21	24	27	30	33
0.91 m	earlywood	mean	1.81	2.14	2.57	2.92	3.19	3.44	3.29	3.58	3.71	3.86	3.83
		std	0.18	0.23	0.25	0.33	0.27	0.32	0.32	0.27	0.29	0.31	0.37
	latewood	mean	1.89	2.53	3.04	3.25	3.35	3.50	3.57	3.62	3.71	3.95	4.05
		std	0.19	0.27	0.25	0.29	0.29	0.34	0.35	0.19	0.33	0.33	0.36
	%	4.2	15.3	15.5	10.3	4.6	1.8	7.9	1.1	0.0	2.3	5.4	
	n	240	240	240	240	200	200	160	120	160	120	120	
		***	***	***	***	***	ns	***	ns	ns	*	***	
3.66 m	earlywood	mean	1.93	2.23	2.56	2.81	3.03	3.33	3.48	3.69	3.80	3.91	3.97
		std	0.13	0.19	0.22	0.36	0.32	0.36	0.31	0.33	0.34	0.26	0.23
	latewood	mean	1.68	2.19	2.69	2.92	3.13	3.35	3.43	3.64	3.74	3.90	4.01
		std	0.18	0.28	0.28	0.26	0.31	0.28	0.30	0.27	0.30	0.28	0.27
	%	-14.5	-1.9	4.9	3.7	3.2	0.3	-1.2	-1.5	-1.6	-0.3	0.9	
	n	240	240	240	240	240	240	240	240	240	240	240	
		***	ns	***	***	***	ns	ns	ns	*	ns	ns	
4.57 m	earlywood	mean	2.04	2.32	2.60	2.94	3.13	3.40	3.47	3.76	3.61	4.01	3.96
		std	0.23	0.32	0.27	0.36	0.40	0.31	0.36	0.32	0.36	0.34	0.31
	latewood	mean	1.88	2.20	2.53	2.92	3.05	3.46	3.52	3.78	3.97	4.11	4.22
		std	0.22	0.24	0.21	0.27	0.40	0.42	0.35	0.35	0.27	0.30	0.33
	%	-8.3	-5.3	-2.4	-0.9	-2.8	1.9	1.5	0.5	9.1	2.3	6.3	
	n	240	240	240	240	240	240	240	240	200	200	200	
		***	***	**	ns	*	ns	ns	ns	***	**	***	

std : standard deviation

n : number of tracheids sampled (same value for both earlywood and latewood at respective growth increment)

% : percentage tracheid length difference from earlywood to latewood

ns : non-significant difference in tracheid length

* : significant difference in tracheid length at $P < 0.05$

** : significant difference in tracheid length at $P < 0.01$

*** : significant difference in tracheid length at $P < 0.001$

Table 4.36 Mean earlywood and latewood tracheid length (mm) and standard deviation values obtained for western hemlock at breast height, by initial spacing, and on every third growth increment from the pith, via image analysis.

spacing	tracheid		ring number from pith										
			3	6	9	12	15	18	21	24	27	30	33
0.91 m	earlywood	mean	1.70	1.97	2.35	2.64	2.88	2.91	3.06	3.09	2.88	3.01	3.13
		std	0.15	0.19	0.23	0.23	0.29	0.27	0.43	0.34	0.18	0.21	0.42
	latewood	mean	1.75	2.04	2.50	2.71	2.92	2.99	3.15	3.15	3.20	3.08	3.16
		std	0.15	0.18	0.23	0.30	0.36	0.30	0.30	0.35	0.18	0.23	0.29
	%	2.6	3.5	5.9	2.4	1.4	2.8	2.9	1.8	10.2	2.5	0.9	
	n	240	240	240	240	240	160	120	120	40	40	120	
		***	***	***	**	ns	*	ns	ns	***	ns	ns	
2.74 m	earlywood	mean	1.61	1.95	2.39	2.64	2.85	3.02	3.03	3.01	3.19	3.15	2.83
		std	0.13	0.29	0.22	0.25	0.21	0.19	0.37	0.55	0.33	0.34	0.64
	latewood	mean	1.75	2.17	2.42	2.66	2.85	3.10	3.25	3.07	3.23	3.24	3.43
		std	0.18	0.23	0.19	0.26	0.22	0.22	0.31	0.43	0.28	0.33	0.25
	%	7.9	10.3	1.3	0.7	-0.1	2.8	6.8	1.7	1.1	2.7	17.3	
	n	240	240	240	240	200	120	160	120	80	80	80	
		***	***	ns	ns	ns	**	***	ns	ns	ns	***	
3.66 m	earlywood	mean	1.54	1.78	2.10	2.49	2.62	2.82	3.07	3.16	3.17	2.98	3.19
		std	0.16	0.15	0.20	0.21	0.25	0.23	0.28	0.25	0.25	0.45	0.36
	latewood	mean	1.65	2.04	2.37	2.59	2.66	2.89	3.07	3.17	3.22	3.10	3.28
		std	0.14	0.20	0.24	0.25	0.27	0.26	0.29	0.28	0.36	0.35	0.32
	%	7.1	13.1	11.2	4.0	1.2	2.5	-0.1	0.3	1.8	4.0	2.7	
	n	240	240	240	240	240	200	200	200	200	200	200	
		***	***	***	***	ns	**	ns	ns	ns	**	*	

std : standard deviation

n : number of tracheids sampled (same value for both earlywood and latewood at respective growth increment)

% : percentage tracheid length difference from earlywood to latewood

ns : non-significant relationship

* : relationship significant at $P < 0.05$

** : relationship significant at $P < 0.01$

*** : relationship significant at $P < 0.001$

Table 4.37 Mean earlywood and latewood tracheid length (mm) and standard deviation values obtained for western redcedar at breast height, by initial spacing, and on every third growth increment from the pith, via image analysis.

spacing	tracheid		ring number from pith										
			3	6	9	12	15	18	21	24	27	30	33
2.74 m	earlywood	mean	1.46	1.90	2.16	2.31	2.43	2.55	2.67	2.72	2.86	2.94	2.95
		std	0.19	0.17	0.20	0.27	0.25	0.26	0.24	0.27	0.28	0.24	0.33
	latewood	mean	1.55	1.94	2.25	2.38	2.52	2.67	2.80	2.77	2.84	2.94	3.05
		std	0.16	0.25	0.20	0.25	0.22	0.25	0.25	0.21	0.25	0.22	0.27
		%	6.2	2.5	3.6	2.8	3.3	4.3	4.7	1.9	-0.6	0.2	3.2
		n	240	240	240	240	240	240	200	120	120	80	80
			***	*	***	**	***	***	***	ns	ns	ns	*
3.66 m	earlywood	mean	1.50	1.79	2.06	2.23	2.36	2.49	2.52	2.57	2.73	2.75	2.76
		std	0.18	0.26	0.20	0.22	0.24	0.25	0.24	0.20	0.24	0.23	0.25
	latewood	mean	1.60	1.93	2.16	2.36	2.46	2.56	2.57	2.65	2.81	2.88	2.92
		std	0.14	0.21	0.17	0.22	0.24	0.28	0.26	0.29	0.28	0.32	0.29
		%	6.1	7.3	4.7	5.7	4.2	2.8	1.6	3.1	3.1	4.6	5.3
		n	240	240	240	240	240	240	240	240	240	240	120
			***	***	***	***	***	**	ns	***	***	***	***
4.57 m	earlywood	mean	1.54	1.76	2.01	2.20	2.34	2.39	2.39	2.56	2.73	2.73	2.60
		std	0.28	0.18	0.17	0.24	0.22	0.20	0.24	0.31	0.27	0.27	0.19
	latewood	mean	1.60	1.86	2.11	2.21	2.34	2.41	2.48	2.62	2.82	2.87	2.77
		std	0.21	0.21	0.24	0.21	0.22	0.21	0.20	0.31	0.28	0.28	0.21
		%	3.2	5.3	4.9	0.4	-0.3	0.6	3.6	2.1	3.3	4.8	6.2
		n	240	240	240	240	240	240	240	200	160	200	80
			*	***	***	ns	ns	ns	***	ns	**	***	***

std : standard deviation

n : number of tracheids sampled (same value for both earlywood and latewood at respective growth increment)

% : percentage tracheid length difference from earlywood to latewood

ns : non-significant relationship

* : relationship significant at $P < 0.05$

** : relationship significant at $P < 0.01$

*** : relationship significant at $P < 0.001$

Table 4.38 Mean earlywood and latewood tracheid length (mm) and standard deviation values obtained for Douglas-fir at breast height, by initial spacing, and on every third growth increment from the pith, via the Kajaani FS-200 Optical Fibre Analyser.

spacing	tracheid		ring number from pith										
			3	6	9	12	15	18	21	24	27	30	33
0.91 m	earlywood	mean	1.46	1.81	2.06	2.18	2.36	2.43	2.34	2.36	2.46	2.56	2.45
		std	0.15	0.13	0.16	0.21	0.12	0.26	0.28	0.09	0.25	0.25	0.42
	latewood	mean	1.51	2.11	2.35	2.38	2.45	2.51	2.48	2.38	2.40	2.48	2.59
		std	0.12	0.12	0.12	0.12	0.11	0.16	0.16	0.11	0.17	0.15	0.27
		n	3	6	6	6	5	5	4	3	4	3	3
3.66 m	earlywood	mean	1.53	1.91	2.13	2.14	2.22	2.32	2.36	2.38	2.46	2.45	2.45
		std	0.14	0.22	0.16	0.18	0.21	0.14	0.17	0.15	0.18	0.10	0.15
	latewood	mean	1.40	1.91	2.11	2.25	2.17	2.26	2.34	2.39	2.36	2.52	2.43
		std	0.07	0.13	0.13	0.19	0.11	0.07	0.10	0.04	0.22	0.08	0.10
		n	3	5	5	5	5	6	6	6	6	6	6
4.57 m	earlywood	mean	1.48	1.76	1.99	2.13	2.03	2.30	2.23	2.35	2.22	2.43	2.32
		std	0.09	0.27	0.17	0.23	0.33	0.24	0.26	0.25	0.18	0.10	0.31
	latewood	mean	1.50	1.82	2.05	2.20	2.23	2.32	2.28	2.35	2.35	2.37	2.33
		std	0.22	0.12	0.11	0.16	0.28	0.17	0.15	0.23	0.21	0.06	0.27
		n	6	6	6	6	6	6	6	6	5	5	5

std : standard deviation

n : number of trees sampled (same value for both earlywood and latewood at respective growth increment)

Table 4.39 Mean earlywood and latewood tracheid length (mm) and standard deviation values obtained for western hemlock at breast height, by initial spacing, and on every third growth increment from the pith, via the Kajaani FS-200 Optical Fibre Analyser.

spacing	tracheid		ring number from pith										
			3	6	9	12	15	18	21	24	27	30	33
0.91 m	earlywood	mean	1.44	1.55	1.96	2.13	2.30	2.26	2.38	2.32	2.25	2.22	2.17
		std	0.07	0.17	0.10	0.19	0.26	0.21	0.38	0.09			0.45
	latewood	mean	1.59	1.76	1.97	2.11	2.22	2.30	2.37	2.36	2.43	2.17	2.41
		std	0.13	0.13	0.18	0.26	0.35	0.30	0.34	0.29			0.35
		n	4	6	6	6	6	4	3	3	1	1	2
2.74 m	earlywood	mean	1.31	1.47	1.76	1.89	1.97	2.12	2.26	1.99	2.40	2.24	1.82
		std	0.07	0.20	0.14	0.31	0.22	0.21	0.42	0.55	0.25	0.28	0.35
	latewood	mean	1.41	1.73	1.93	1.99	2.02	2.10	2.28	2.26	2.39	2.28	2.30
		std	0.09	0.12	0.09	0.13	0.18	0.16	0.30	0.40	0.33	0.11	0.13
		n	4	6	6	6	5	3	4	3	2	2	2
3.66 m	earlywood	mean	1.26	1.40	1.67	1.81	1.75	1.95	2.02	2.09	2.06	1.80	2.05
		std	0.18	0.08	0.13	0.21	0.29	0.20	0.19	0.12	0.34	0.33	0.27
	latewood	mean	1.32	1.62	1.91	1.92	1.76	1.92	1.97	2.14	2.04	2.00	2.03
		std	0.24	0.17	0.18	0.16	0.30	0.06	0.17	0.16	0.27	0.27	0.26
		n	3	6	6	6	6	5	5	5	5	5	5

std : standard deviation

n : number of trees sampled (same value for both earlywood and latewood at respective growth increment)

Table 4.40 Mean earlywood and latewood tracheid length (mm) and standard deviation values obtained for western redcedar at breast height, by initial spacing, and on every third growth increment from the pith, via the Kajaani FS-200 Optical Fibre Analyser.

spacing	tracheid		ring number from pith										
			3	6	9	12	15	18	21	24	27	30	33
2.74 m	earlywood	mean	1.29	1.49	1.63	1.73	1.80	2.05	2.15	1.97	2.10	2.20	2.05
		std		0.13	0.17	0.21	0.20	0.10	0.19	0.25	0.31	0.23	0.30
	latewood	mean	1.39	1.64	1.89	1.96	2.04	2.15	2.18	2.30	2.35	2.24	2.37
		std		0.11	0.13	0.21	0.23	0.14	0.17	0.19	0.24	0.18	0.22
		n	1	6	6	6	6	6	5	3	3	2	2
3.66 m	earlywood	mean	0.89	1.43	1.55	1.72	1.74	1.85	1.79	1.80	1.97	2.04	1.97
		std	0.23	0.11	0.04	0.17	0.18	0.29	0.27	0.22	0.27	0.27	0.18
	latewood	mean	1.33	1.63	1.78	1.91	1.86	1.97	1.99	2.08	2.20	2.18	2.18
		std	0.09	0.11	0.12	0.22	0.31	0.26	0.24	0.19	0.27	0.23	0.12
		n	4	6	6	6	6	6	6	6	6	6	3
4.57 m	earlywood	mean	0.64	1.31	1.56	1.58	1.70	1.75	1.70	1.83	1.98	1.96	1.96
		std		0.20	0.14	0.17	0.14	0.15	0.19	0.23	0.06	0.11	0.02
	latewood	mean	1.04	1.56	1.77	1.76	1.94	1.89	1.87	2.02	2.17	2.18	2.14
		std		0.12	0.17	0.18	0.11	0.17	0.19	0.29	0.26	0.20	0.04
		n	1	6	6	6	6	6	6	5	4	5	2

std : standard deviation

n : number of trees sampled (same value for both earlywood and latewood at respective growth increment)

Table 4.41a Mean values and variability for whole-ring tracheid length (mm) by initial spacing and species (image analysis).

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 3-33)	mean	3.24						3.16		3.22	
	cv (%)	20.0						22.0		22.5	
	min	max	1.73	4.24					1.65	4.06	1.69
western hemlock (rings 3-33)	mean	2.74				2.84		2.66			
	cv (%)	19.1				20.3		21.9			
	min	max	1.66	3.69			1.62	3.80	1.42	3.55	
western redcedar (rings 3-33)	mean					2.50		2.37		2.33	
	cv (%)					20.0		18.1		17.9	
	min	max					1.27	3.21	1.37	3.08	1.19

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.41b Repeated measures analysis of variance for whole-ring tracheid length (mm) by initial spacing and species (image analysis).

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 3-33)	spacing	2	0.11	0.50	0.6151		
	error a	15	0.23				
	ring	10	8.63	579.41	0.0001	0.0001	0.0001
	spacing * ring	20	0.06	3.89	0.0001	0.0003	0.0001
	error b	150	0.01			epsGG=0.4890	epsHF=0.8509
western hemlock (rings 3-33)	spacing	2	0.55	2.34	0.1307		
	error a	15	0.24				
	ring	10	5.30	207.44	0.0001	0.0001	0.0001
	spacing * ring	20	0.04	1.49	0.0930	0.1839	0.1427
	error b	150	0.03			epsGG=0.3848	epsHF=0.6031
western redcedar (rings 3-33)	spacing	2	0.55	3.91	0.0431		
	error a	15	0.14				
	ring	10	3.43	195.58	0.0001	0.0001	0.0001
	spacing * ring	20	0.03	1.47	0.1004	0.2067	0.1749
	error b	150	0.02			epsGG=0.3161	epsHF=0.4638

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.42 Linear regression equations and correlation coefficients for whole-ring tracheid length (mm, image analysis) calculated on every third growth ring from the pith as a function of ring width (mm) for Douglas-fir, western hemlock and western redcedar.

species	ring number from pith	n	a	b		r	r ²	SE _E
Douglas-fir	3	13	1.93	-0.0051	ns	-0.06	0.00	0.15
	6	17	2.36	-0.0142	ns	-0.17	0.03	0.15
	9	17	2.98	-0.0463	**	-0.68	0.46	0.15
	12	17	3.28	-0.0479	*	-0.56	0.32	0.19
	15	17	3.47	-0.0594	ns	-0.47	0.22	0.24
	18	18	3.54	-0.0283	ns	-0.27	0.07	0.21
	21	18	3.64	-0.0420	ns	-0.32	0.11	0.21
	24	18	3.71	-0.0050	ns	-0.04	0.00	0.18
	27	18	3.69	0.0353	ns	0.22	0.05	0.17
	30	18	3.82	0.0507	ns	0.29	0.09	0.18
	33	18	3.88	0.0414	ns	0.28	0.08	0.18
western hemlock	3	11	1.86	-0.0368	ns	-0.52	0.27	0.09
	6	18	2.28	-0.0591	*	-0.54	0.29	0.15
	9	18	2.56	-0.0605	*	-0.48	0.23	0.13
	12	18	2.80	-0.0475	*	-0.49	0.24	0.14
	15	18	2.98	-0.0576	ns	-0.45	0.20	0.18
	18	18	3.09	-0.0450	ns	-0.36	0.13	0.19
	21	18	3.19	-0.0372	ns	-0.31	0.10	0.23
	24	18	3.25	-0.0474	ns	-0.34	0.12	0.26
	27	18	3.30	-0.0249	ns	-0.21	0.05	0.22
	30	18	3.49	-0.1234	***	-0.72	0.51	0.25
	33	13	3.38	-0.0817	ns	-0.37	0.14	0.28
western redcedar	3	6	1.69	-0.0511	ns	-0.35	0.12	0.15
	6	18	2.00	-0.0207	ns	-0.18	0.03	0.16
	9	18	2.23	-0.0194	ns	-0.22	0.05	0.13
	12	18	2.47	-0.0332	ns	-0.36	0.13	0.16
	15	18	2.68	-0.0476	ns	-0.46	0.21	0.15
	18	18	2.75	-0.0421	ns	-0.44	0.19	0.17
	21	18	2.67	-0.0196	ns	-0.26	0.07	0.20
	24	18	2.93	-0.0700	**	-0.60	0.36	0.19
	27	18	2.95	-0.0561	ns	-0.44	0.19	0.19
	30	18	2.96	-0.0376	ns	-0.39	0.15	0.18
	33	18	3.00	-0.0391	ns	-0.34	0.12	0.21

n : number of observations

a : intercept estimate

b : slope estimate

r : correlation coefficient

r² : coefficient of determination

SE_E : standard error of estimate

ns : non-significant relationship

* : relationship significant at P < 0.05

** : relationship significant at P < 0.01

*** : relationship significant at P < 0.001

Table 4.43 Mean earlywood microfibril angle and standard deviation values observed by species and initial spacing, at breast height, and on every third growth increment from the pith.

Douglas-fir

spacing		ring number from pith										
		3	6	9	12	15	18	21	24	27	30	33
0.91 m	mean	26.6	23.3	20.0	18.2	17.8	17.3	16.6	17.1	16.6	16.9	16.2
	std	3.8	4.1	3.7	4.2	4.5	4.0	3.9	4.5	3.9	3.7	3.9
3.66 m	mean	24.5	21.5	22.0	20.7	22.0	21.0	21.1	20.4	20.0	20.0	19.8
	std	4.2	3.6	3.9	3.7	4.1	3.8	3.9	3.5	3.5	3.9	3.7
4.57 m	mean	24.3	23.1	23.0	23.7	23.7	21.9	22.5	20.5	20.0	18.7	17.8
	std	4.4	4.1	4.6	4.5	5.0	4.3	4.5	4.4	4.1	3.9	4.2

western hemlock

spacing		ring number from pith										
		3	6	9	12	15	18	21	24	27	30	33
0.91 m	mean	30.0	29.2	23.4	21.4	20.5	20.9	19.3	20.2	19.0	18.2	16.9
	std	4.5	3.4	4.2	3.7	3.8	6.1	4.3	4.2	5.0	4.5	3.1
2.74 m	mean	29.9	28.3	26.0	23.3	22.9	21.1	20.1	18.8	20.3	19.0	17.7
	std	4.5	4.1	4.4	5.7	5.5	4.2	5.3	5.7	5.1	4.6	2.8
3.66 m	mean	29.6	28.0	24.9	22.5	23.7	20.6	19.7	19.8	19.0	17.8	18.9
	std	4.4	5.0	4.6	4.3	4.8	4.2	4.6	4.8	5.1	5.1	5.7

western redcedar

spacing		ring number from pith										
		3	6	9	12	15	18	21	24	27	30	33
2.74 m	mean	36.5	33.9	34.2	30.9	29.3	26.0	26.0	26.0	26.1	25.7	26.2
	std	5.1	5.1	5.5	6.3	5.4	5.8	6.5	6.0	7.0	6.8	7.9
3.66 m	mean	38.0	38.6	36.6	36.2	35.3	34.6	32.4	34.7	33.4	31.0	34.4
	std	5.9	4.7	5.6	6.2	5.0	7.2	7.1	7.5	7.9	6.4	7.0
4.57 m	mean	37.7	38.5	37.0	34.0	33.3	33.2	34.0	31.7	32.1	30.4	30.3
	std	4.7	6.1	4.6	5.3	5.2	4.7	6.0	5.8	5.0	6.2	4.3

std : standard deviation

Table 4.44a Mean values and variability for microfibril angle by initial spacing and species.

species		initial spacing									
		0.91 m		1.83 m		2.74 m		3.66 m		4.57 m	
Douglas-fir (rings 3-33)	mean	18.7						21.2		21.8	
	cv (%)	20.3						9.7		13.9	
	min max	12.3	29.8					17.9 26.4		13.9 29.9	
western hemlock (rings 3-33)	mean	22.2				22.5		22.2			
	cv (%)	22.3				23.0		23.3			
	min max	14.0	33.2			12.2 32.8		13.6 32.9			
western redcedar (rings 3-33)	mean					29.1		34.9		34.0	
	cv (%)					20.4		15.1		14.3	
	min max					20.1 42.5		22.0 43.1		23.4 44.3	

cv : coefficient of variation

min max : minimum and maximum values observed

Table 4.44b Repeated measures analysis of variance for microfibril angle by initial spacing and species.

species	source	df	MSE	F	P>F	adjusted P>F	
						G-G	H-F
Douglas-fir (rings 3-33)	spacing	2	171.44	10.75	0.0013		
	error 1	15	15.95				
	ring	10	80.05	24.36	0.0001	0.0001	0.0001
	spacing * ring	20	13.71	4.17	0.0001	0.0002	0.0001
	error 2	150	3.29			epsGG=0.4654	epsHF=0.7904
western hemlock (rings 3-33)	spacing	2	9.79	0.11	0.9000		
	error 1	15	92.26				
	ring	10	289.82	59.84	0.0001	0.0001	0.0001
	spacing * ring	20	4.06	0.84	0.6647	0.5993	0.6601
	error 2	150	4.84			epsGG=0.5286	epsHF=0.9590
western redcedar (rings 3-33)	spacing	2	635.34	3.87	0.0441		
	error 1	15	164.09				
	ring	10	172.31	20.80	0.0001	0.0001	0.0001
	spacing * ring	20	10.68	1.29	0.1964	0.2634	0.2289
	error 2	150	8.28			epsGG=0.4174	epsHF=0.6755

df : degrees of freedom

MSE : mean square error

F : F statistic for testing the hypothesis that all parameters are zero except for the intercept

P>F : probability of getting a greater F statistic than that observed if the hypothesis is true

epsGG : Greenhouse and Geisser epsilon correction factor

epsHF : Huynh and Feldt epsilon correction factor

Table 4.45 Linear regression equations and correlation coefficients for microfibril angle calculated on every third growth ring from the pith as a function of ring width (mm) for Douglas-fir, western hemlock and western redcedar.

species	ring number from pith	n	a	b		r	r ²	SE _E
Douglas-fir	3	13	24.06	0.1659	ns	0.10	0.01	2.65
	6	17	21.03	0.2607	ns	0.28	0.08	1.65
	9	17	18.66	0.4751	*	0.52	0.27	2.24
	12	17	16.39	0.7319	*	0.58	0.34	2.73
	15	17	14.92	1.2006	***	0.73	0.53	2.48
	18	18	17.33	0.7124	*	0.57	0.32	2.19
	21	18	16.60	1.0320	**	0.55	0.30	2.82
	24	18	17.22	0.8114	ns	0.43	0.19	2.33
	27	18	17.15	0.7525	ns	0.33	0.11	2.27
	30	18	16.36	1.0345	ns	0.42	0.18	2.37
	33	18	15.57	0.9093	ns	0.40	0.16	2.66
western hemlock	3	11	30.17	0.0227	ns	0.01	0.00	2.31
	6	18	28.95	-0.0809	ns	-0.05	0.00	2.93
	9	18	25.95	-0.3070	ns	-0.12	0.01	3.12
	12	18	19.48	0.7653	ns	0.37	0.14	3.12
	15	18	21.41	0.3133	ns	0.13	0.02	3.78
	18	18	22.32	-0.4885	ns	-0.21	0.04	3.68
	21	18	17.83	0.6192	ns	0.36	0.13	3.23
	24	18	18.88	0.2653	ns	0.13	0.02	3.95
	27	18	18.85	0.2561	ns	0.12	0.02	3.96
	30	18	17.85	0.2014	ns	0.08	0.01	3.88
	33	13	19.74	-0.4392	ns	-0.13	0.02	4.06
western redcedar	3	6	27.76	1.5840	ns	0.47	0.22	3.40
	6	18	26.14	1.4983	*	0.49	0.24	3.92
	9	18	27.05	1.2881	*	0.48	0.23	3.54
	12	18	29.34	0.6846	ns	0.26	0.07	4.68
	15	18	25.81	1.1069	ns	0.41	0.17	4.03
	18	18	20.37	1.7967	**	0.62	0.38	4.57
	21	18	26.24	0.7813	ns	0.34	0.11	6.11
	24	18	23.86	1.9692	**	0.61	0.37	5.21
	27	18	25.61	1.8693	ns	0.46	0.21	5.85
	30	18	27.61	0.5266	ns	0.18	0.03	5.74
	33	18	27.70	0.7770	ns	0.26	0.07	5.41

n : number of observations

a : intercept estimate

b : slope estimate

r : correlation coefficient

r² : coefficient of determination

SE_E : standard error of estimate

ns : non-significant relationship

* : relationship significant at P < 0.05

** : relationship significant at P < 0.01

*** : relationship significant at P < 0.001

APPENDIX II

SUPPLEMENTARY RESULTS FOR CHAPTER 5.

Table 5.1 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (0.91 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C.I.		df	transition ring	SE _E	C.I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
51	0.3	36	8.5	17	12.6	4.7	0.59	1.3	9.9	15.4	12	13.4	3.2	6.4	20.4	14	0.75	1.28
	1.3	35	7.6	25	13.2	4.6	0.72	0.9	11.3	15.1	22	16.0	1.9	12.2	19.8	24	0.86	1.19
	4.0	32	7.5	16	11.9	4.6	0.17	0.6	10.7	13.1	12	14.1	1.7	10.3	17.8	14	0.54	3.26
	6.0	29	7.3	23	12.6	4.7	0.73	1.4	9.7	15.5	18	14.0	2.7	8.3	19.7	20	0.92	1.26
	10.0	25	6.7	17	17.8	5.5	0.24	0.8	16.2	19.5	14	19.6	1.6	16.1	23.0	16	0.32	1.33
	12.0	23	6.9	16	13.6	5.2	0.68	1.0	11.6	15.6	12	14.5	2.4	9.3	19.6	14	1.06	1.56
	14.0	21	6.3	15	15.0	5.4	0.62	1.6	11.5	18.5	7	14.5	2.4	8.7	20.3	9	0.74	1.20
	16.0	19	6.8	13	10.9	4.6	0.88	2.0	6.5	15.2	7	10.7	6.5	0.0	26.0	9	1.45	1.66
	17.0	18	6.2	12	11.0	4.8	0.70	1.2	8.3	13.7	7	11.0	2.1	6.0	16.0	9	1.03	1.47
196	0.3	36	7.4	31	27.5	7.2	1.53	1.5	24.5	30.4	27	30.9	5.3	20.0	41.9	29	1.98	1.30
	1.3	35	6.6	23	13.7	5.7	2.00	1.3	11.0	16.4	19	16.8	2.8	10.8	22.7	21	3.44	1.72
	4.0	30	5.7	25	18.6	5.5	1.71	1.7	15.1	22.1	20	18.0	4.3	9.0	27.0	22	2.85	1.67
	6.0	28	5.7	24	16.1	5.2	2.26	1.0	14.2	18.1	19	21.1	4.4	12.0	30.3	21	3.28	1.45
	8.0	28	5.0	22	15.6	4.5	4.06	1.8	11.9	19.3	18	15.5	5.6	3.7	27.4	20	6.01	1.48
	10.0	25	4.5	17	9.3	3.4	3.28	1.0	7.2	11.4	12	11.6	7.9	0.0	28.9	14	4.88	1.49
	12.0	23	4.1	14	8.6	2.7	2.81	0.9	6.7	10.5	11	11.6	4.8	1.0	22.1	13	5.09	1.81
	14.0	22	3.6	11	11.4	2.7	1.19	1.4	8.4	14.5	9	11.1	2.2	6.1	16.1	11	1.45	1.22
	16.0	19	3.4	11	8.1	2.2	1.73	0.7	6.6	9.6	8	8.5	4.8	0.0	19.5	10	2.15	1.24
18.0	17	2.5	7	11.0	2.4	0.52	0.6	9.5	12.5	2	12.0	6.2	0.0	38.5	4	1.58	3.05	

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.1 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (0.91 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 x10 ⁻³	MSE-3 / MSE-1
									lower	upper				lower	upper			
211	4.0	31	11.2	24	24.0	9.7	0.58	1.0	22.0	26.0	21	25.4	3.0	19.1	31.7	23	0.71	1.23
	6.0	30	10.9	23	17.0	8.0	1.03	0.6	15.7	18.4	14	15.1	0.8	13.4	16.8	16	1.64	1.60
	8.0	29	10.5	21	17.9	8.3	0.70	0.8	16.1	19.6	14	19.9	2.4	14.8	25.1	16	1.55	2.23
	10.0	27	10.1	20	16.6	7.8	2.13	1.8	12.8	20.4	15	18.8	4.8	8.8	28.8	17	2.57	1.20
	12.0	26	9.9	16	18.0	7.8	0.68	1.1	15.6	20.4	11	18.1	3.1	11.2	24.9	13	0.89	1.32
	16.0	20	8.6	14	13.0	6.6	0.84	1.1	10.6	15.4	10	13.0	5.8	0.2	25.8	12	0.85	1.02
	20.0	16	7.3	11	15.0	7.1	0.72	2.7	9.1	20.9	7	14.8	6.5	0.0	30.1	9	0.86	1.19
	20.7	16	6.7	10	15.0	6.5	0.75	1.4	11.8	18.2	8	*	*	*	*	9	0.96	1.29
235	0.3	38	11.1	29	29.0	9.7	0.88	2.3	24.3	33.7	28	*	*	*	*	28	1.00	1.13
	1.3	35	10.2	28	26.0	8.5	0.99	1.9	22.1	30.0	14	27.5	4.0	18.9	36.0	16	1.12	1.13
	4.0	34	9.3	28	25.0	7.9	1.10	2.9	19.1	30.9	25	25.1	5.3	14.2	36.0	27	1.29	1.17
	6.0	31	8.8	25	22.6	7.4	1.09	1.5	19.6	25.7	21	23.6	3.1	17.2	30.0	23	1.30	1.20
	8.0	29	9.2	23	16.5	7.0	1.28	1.0	14.5	18.5	14	18.6	3.6	10.8	26.3	16	2.03	1.58
	10.0	27	8.7	22	18.8	7.2	0.98	0.9	17.0	20.7	15	19.3	2.5	13.9	24.6	17	1.38	1.42
	12.0	26	7.3	20	17.3	6.2	1.21	1.0	15.3	19.3	14	18.0	3.1	11.4	24.6	16	1.73	1.42
	14.0	23	6.7	17	15.0	5.3	1.08	0.8	13.3	16.7	11	15.0	2.0	10.5	19.5	13	1.91	1.76
	16.0	21	7.0	14	12.9	5.2	0.81	0.9	10.9	14.9	10	13.0	3.1	6.0	20.0	12	1.07	1.32
	18.0	19	6.2	13	11.6	4.2	1.67	1.2	9.0	14.2	8	11.0	4.5	0.5	21.5	10	1.79	1.07
	20.0	16	5.7	11	*	*	0.93	*	*	*	3	*	*	*	*	4	1.64	1.76
	20.8	15	5.1	10	*	*	1.97	*	*	*	2	*	*	*	*	2	2.83	1.44

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.1 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (0.91 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic					model 2 - segmented linear				model 3 - linear		F-value				
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 $\times 10^{-3}$	MSE-3 / MSE-1	
									lower	upper				lower					upper
367	8.0	29	12.7	21	16.7	7.9	0.68	1.5	13.7	19.8	18	21.1	5.6	9.4	32.8	20	0.70	1.03	
	10.0	27	12.1	20	19.0	10.0	0.34	0.8	17.4	20.6	16	20.3	2.7	14.6	25.9	18	0.66	1.97	
	12.0	25	11.3	15	20.5	9.9	0.28	0.9	18.6	22.4	14	*	*	*	*	14	0.49	1.74	
	14.0	24	10.9	17	20.9	10.0	0.30	1.5	17.8	24.0	9	12.0	6.4	0.0	26.6	11	0.33	1.12	
	16.0	22	10.0	16	18.6	8.9	0.73	2.0	14.3	22.8	7	*	*	*	*	7	0.92	1.26	
	18.0	21	9.9	14	*	*	0.34	*	*	*	4	*	*	*	*	4	0.34	1.01	
369	1.3	35	7.0	28	27.9	6.7	1.02	1.5	24.9	30.9	20	28.0	12.6	1.8	54.2	22	1.04	1.02	
	2.0	33	6.9	27	24.0	6.5	1.03	1.5	20.9	27.1	24	24.8	16.7	0.0	59.2	26	1.17	1.13	
	4.0	31	7.3	24	22.0	6.9	0.68	0.9	20.2	23.8	19	23.0	3.6	15.4	30.6	21	1.08	1.58	
	6.0	29	6.1	22	19.0	5.7	1.68	1.0	16.8	21.2	19	20.1	3.8	12.1	28.2	21	2.91	1.74	
	8.0	27	6.0	17	18.4	5.7	0.49	2.3	14.1	22.7	6	17.7	3.2	9.9	25.5	8	0.70	1.42	
	10.0	25	5.3	17	14.8	4.7	0.37	0.5	13.8	15.8	12	18.1	2.9	11.9	24.4	14	1.49	4.06	
	12.0	23	5.1	17	14.4	4.4	0.76	0.6	13.2	15.6	11	13.5	0.9	11.4	15.5	13	1.99	2.61	
	14.0	21	4.5	14	13.6	3.9	0.46	0.5	12.4	14.8	9	12.1	1.0	9.8	14.5	11	0.69	1.50	
	14.7	20	4.9	14	14.5	4.6	0.53	0.5	13.5	15.5	10	16.7	1.3	13.9	19.5	12	0.77	1.46	

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.2 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic					model 2 - segmented linear			model 3 - linear		F-value				
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E		MSE-3 $\times 10^{-3}$	df	MSE-3 $\times 10^{-3}$	
									lower	upper								lower
30	0.3	36	17.4	29	29.0	14.9	1.75	2.1	24.8	33.2	24	32.9	8.0	16.4	49.4	26	1.81	1.03
	2.0	32	15.5	25	26.0	13.9	0.88	1.6	22.6	29.4	18	26.5	4.4	17.3	35.7	20	1.16	1.32
	4.0	30	14.4	24	18.8	11.5	1.45	2.0	14.6	22.9	19	18.0	12.1	0.0	43.3	21	1.51	1.04
	6.0	28	12.3	21	21.8	10.9	0.53	1.4	18.8	24.8	12	21.2	4.2	11.9	30.4	14	0.68	1.29
	8.0	28	12.3	21	16.0	9.6	1.45	1.8	12.3	19.7	20	16.0	3.0	9.7	22.3	22	1.69	1.17
	10.0	25	11.2	17	13.1	7.7	0.64	1.1	10.8	15.4	11	10.8	2.4	5.5	16.0	13	0.86	1.34
	12.0	23	10.6	16	12.0	7.4	0.41	1.1	9.6	14.4	12	11.7	2.0	7.4	16.0	14	0.57	1.39
	14.0	22	10.4	14	14.8	7.7	0.36	1.3	12.0	17.7	8	15.0	3.6	6.8	23.2	10	0.45	1.27
	16.0	19	9.6	13	*	*	0.62	*	*	*	4	11.0	3.2	2.2	19.8	6	0.68	1.10
	19.9	15	6.9	10	*	*	0.58	*	*	*	2	*	*	*	*	2	0.59	1.02
63	0.3	40	18.3	27	24.0	13.7	0.70	1.0	22.0	26.0	23	28.0	3.8	20.1	35.9	25	1.15	1.65
	1.3	34	15.2	28	17.2	10.9	0.57	1.0	15.2	19.3	24	17.0	3.1	10.5	23.5	26	1.11	1.94
	2.0	33	15.2	28	23.9	13.0	0.88	2.1	19.6	28.3	25	24.0	4.9	14.0	34.0	27	1.06	1.20
	8.0	30	14.3	22	22.5	12.3	0.93	1.3	19.9	25.2	11	21.0	7.5	4.4	37.6	13	1.04	1.12
	12.0	25	13.4	18	15.8	10.3	0.55	0.9	13.8	17.8	10	15.0	6.2	1.1	28.9	12	0.69	1.24
	14.0	23	12.3	16	13.9	8.9	0.48	0.8	12.2	15.7	11	14.0	1.6	10.6	17.4	13	0.96	2.00
	16.0	22	10.4	12	16.8	8.4	0.23	0.7	15.2	18.4	6	13.0	3.4	4.7	21.3	8	0.24	1.07
	18.0	20	10.3	13	15.3	8.6	0.37	1.3	12.4	18.2	2	14.1	1.3	8.6	19.7	4	0.70	1.88
	19.5	18	9.6	12	*	*	0.13	*	*	*	10	*	*	*	*	10	0.15	1.13

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.2 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 $\times 10^{-3}$	MSE-3 / MSE-1
									lower	upper				lower	upper			
64	0.3	36	15.3	30	19.0	10.7	0.75	1.0	17.0	21.0	23	22.8	3.2	16.2	29.5	25	1.18	1.58
	1.3	35	12.7	29	18.0	8.8	1.15	2.0	14.0	22.0	29	19.0	3.2	12.4	25.6	31	1.39	1.21
	4.0	31	12.2	25	18.6	9.8	1.30	1.5	15.5	21.8	25	21.3	2.9	15.2	27.3	27	1.74	1.34
	6.0	29	11.9	22	14.4	8.4	1.36	1.0	12.3	16.4	22	16.1	2.4	11.2	21.0	24	2.16	1.59
	8.0	28	11.1	21	17.9	9.0	1.22	1.3	15.2	20.5	21	18.1	2.8	12.4	23.9	23	2.24	1.83
	10.0	26	11.2	19	16.8	8.9	1.38	1.1	14.6	19.0	19	18.1	2.9	12.0	24.3	21	2.49	1.80
	12.0	25	11.0	18	16.0	8.0	0.73	1.0	13.9	18.1	11	16.0	1.7	12.3	19.7	13	1.74	2.38
	14.0	22	10.7	16	13.8	7.5	0.98	1.3	11.1	16.6	16	16.7	2.5	11.5	21.9	18	1.11	1.13
	16.0	20	10.1	14	16.9	9.0	0.86	2.3	11.9	21.9	9	10.4	1.6	6.8	14.0	11	1.19	1.38
	18.0	18	9.1	11	14.0	7.1	0.27	1.3	11.1	16.9	11	13.9	2.2	9.0	18.8	13	0.38	1.43
	19.3	17	8.9	10	12.4	6.7	0.68	1.8	8.4	16.4	8	13.8	5.4	1.2	26.3	10	0.72	1.06
66	0.3	38	17.8	29	22.5	12.5	0.69	1.3	20.0	25.1	16	22.0	7.7	5.6	38.4	18	1.34	1.94
	1.3	36	16.8	29	20.8	12.3	0.78	1.4	17.9	23.6	22	23.4	3.9	15.3	31.6	24	1.24	1.59
	2.0	35	16.2	26	22.0	12.3	1.22	2.2	17.6	26.4	25	22.6	4.5	13.3	31.8	27	1.42	1.17
	4.0	32	13.7	25	20.0	10.1	0.60	1.0	17.9	22.1	24	23.6	4.3	14.7	32.5	26	0.91	1.52
	6.0	30	13.7	15	17.6	10.0	0.76	1.2	15.1	20.0	9	17.6	5.1	6.1	29.1	11	0.79	1.04
	8.0	28	13.5	16	18.2	10.1	0.74	1.1	15.9	20.6	12	18.0	6.1	4.8	31.2	14	0.86	1.17
	10.0	26	13.4	15	13.0	8.1	0.28	0.5	11.9	14.1	12	13.0	2.7	7.1	18.9	14	0.43	1.56
	12.0	25	13.3	16	18.2	10.2	0.23	0.9	16.3	20.1	15	22.5	5.2	11.5	33.6	17	0.27	1.17
	14.0	23	12.1	15	*	*	0.35	*	*	*	13	*	*	*	*	13	0.41	1.16

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.2 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic					model 2 - segmented linear			model 3 - linear		F-value				
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	MSE-3 $\times 10^{-3}$	df	MSE-3 $\times 10^{-3}$	MSE-3 / MSE-1	
									lower	upper								lower
67	0.3	39	15.7	30	20.3	11.4	1.30	1.5	17.3	23.3	22	22.1	4.5	12.8	31.3	24	1.55	1.20
	1.3	34	12.8	27	20.0	9.4	0.93	2.0	15.8	24.2	20	20.0	2.0	15.8	24.2	22	1.40	1.50
	2.0	33	11.3	24	20.0	8.5	1.75	1.2	17.6	22.4	22	23.3	4.2	14.5	32.0	24	2.87	1.64
	4.0	31	10.6	20	16.0	7.6	1.10	0.8	14.4	17.6	18	16.8	2.3	12.0	21.7	20	1.44	1.31
	6.0	30	10.3	19	16.3	7.3	1.21	0.8	14.6	18.0	19	18.0	4.3	9.1	26.9	21	1.56	1.29
	8.0	28	10.5	18	17.2	8.7	1.09	0.9	15.4	19.0	13	19.0	3.1	12.2	25.8	15	1.48	1.36
	10.0	26	9.7	16	19.0	8.2	0.59	1.0	16.8	21.1	15	21.4	3.1	14.6	28.1	17	0.74	1.25
	12.0	25	9.5	12	16.0	7.4	0.34	0.6	14.7	17.3	8	*	*	*	*	8	0.51	1.51
	14.0	24	9.6	11	14.6	7.6	0.40	1.0	12.5	16.7	4	13.0	2.1	7.3	18.7	6	0.61	1.51
	16.0	22	9.3	8	15.8	6.8	0.55	2.8	9.3	22.3	3	14.8	3.4	4.1	25.5	5	0.75	1.36
18.0	21	9.3	13	18.0	8.4	0.53	2.7	12.2	23.8	2	17.1	2.4	6.9	27.2	4	0.82	1.55	
69	0.3	41	22.7	30	29.0	17.4	0.74	1.4	26.1	31.9	22	31.9	4.9	21.6	42.1	24	0.92	1.25
	2.0	37	18.9	29	20.0	11.6	1.44	1.7	16.6	23.4	22	16.0	2.4	11.0	21.0	24	1.61	1.12
	4.0	36	18.2	24	26.0	14.8	0.62	1.1	23.7	28.3	20	26.2	2.7	20.5	31.9	22	0.90	1.45
	6.0	34	16.8	22	17.0	11.0	1.26	1.2	14.6	19.4	14	17.0	3.0	10.6	23.4	16	1.64	1.30
	8.0	30	17.0	22	18.7	14.1	0.67	0.8	17.0	20.4	15	21.0	2.4	16.0	26.1	17	0.86	1.29
	12.0	27	14.5	16	18.4	11.0	0.34	0.8	16.7	20.2	9	18.0	2.8	11.7	24.3	11	0.45	1.34
	14.0	22	13.2	14	20.0	12.3	0.19	0.7	18.6	21.5	10	*	*	*	*	11	0.24	1.28
	18.0	20	12.2	14	*	*	0.61	*	*	*	5	*	*	*	*	5	0.63	1.03

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.3 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (4.57 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
22	0.3	37	21.1	29	29.0	18.7	0.60	3.1	22.7	35.3	23	29.8	8.0	13.2	46.4	25	0.63	1.05
	1.3	36	18.7	28	28.0	17.1	0.93	1.1	25.7	30.3	19	29.4	4.0	21.2	37.7	21	1.32	1.42
	2.0	35	17.6	26	18.9	13.2	0.85	1.4	15.9	21.8	20	18.6	3.3	11.7	25.5	22	0.96	1.13
	4.0	32	16.3	26	23.1	14.4	0.96	1.0	21.1	25.2	20	25.3	6.1	12.6	38.0	22	1.70	1.76
	6.0	30	15.7	24	20.6	13.3	2.00	2.7	15.0	26.3	22	20.5	3.6	13.0	28.0	24	2.30	1.15
	8.0	28	14.7	21	18.0	12.3	0.71	1.1	15.8	20.2	14	18.0	4.0	9.3	26.7	16	0.90	1.26
	10.0	25	12.8	19	16.0	10.9	0.72	0.7	14.7	17.4	13	17.0	2.3	12.1	22.0	15	1.44	2.00
	14.0	22	12.0	17	16.0	10.4	0.76	1.6	12.6	19.4	16	16.0	4.5	6.4	25.6	18	0.95	1.26
	16.0	21	12.9	15	11.9	9.0	0.53	1.4	8.9	14.9	12	14.0	5.2	2.7	25.3	14	0.56	1.06
	17.3	20	11.9	16	16.5	10.6	0.41	1.1	14.3	18.8	15	*	*	*	*	15	0.45	1.10
64	0.3	37	22.1	30	26.7	19.6	0.69	1.4	23.9	29.5	22	27.8	2.9	21.8	33.8	24	0.81	1.18
	1.3	36	20.9	29	26.1	17.9	0.52	0.9	24.3	27.9	21	28.5	2.0	24.3	32.6	23	0.56	1.08
	2.0	35	20.3	29	26.5	17.7	0.83	1.5	23.4	29.6	21	26.2	2.8	20.3	32.1	23	1.04	1.25
	4.0	32	19.2	26	23.4	17.3	0.48	1.3	20.7	26.0	21	23.0	4.4	13.8	32.2	23	0.54	1.11
	6.0	31	20.1	23	20.5	17.2	0.45	0.7	19.0	22.0	13	17.4	3.1	10.8	24.0	15	0.47	1.04
	8.0	29	18.0	18	20.9	14.2	0.30	0.9	19.1	22.7	12	21.1	2.2	16.2	26.0	14	0.40	1.33
	12.0	27	17.7	19	20.0	14.4	0.48	1.5	16.8	23.2	11	19.6	2.2	14.7	24.4	13	0.50	1.04
	14.0	25	15.5	17	20.1	13.5	0.20	1.1	17.8	22.4	11	20.5	2.8	14.4	26.7	13	0.28	1.43
	16.0	23	14.5	18	*	*	0.50	*	*	*	12	*	*	*	*	12	0.56	1.13
	17.5	22	13.7	16	18.0	11.5	0.23	1.7	14.3	21.7	9	15.5	5.6	2.8	28.3	11	0.33	1.43

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.3 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (4.57 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
65	1.3	35	14.6	26	18.0	11.5	0.76	1.4	15.1	20.9	21	19.0	3.0	12.7	25.3	23	1.21	1.58
	2.0	34	14.4	14	17.0	11.0	0.47	1.1	14.5	19.5	8	17.2	3.8	8.5	26.0	10	0.48	1.03
	4.0	31	11.8	11	13.6	9.7	1.38	1.2	10.9	16.3	13	*	*	*	*	13	1.69	1.22
	6.0	29	11.9	9	*	*	0.56	*	*	*	10	*	*	*	*	10	0.86	1.54
	8.0	28	10.7	10	*	*	0.19	*	*	*	8	*	*	*	*	8	0.20	1.03
	10.0	26	9.8	10	14.4	7.4	0.48	0.9	12.4	16.4	10	*	*	*	*	10	0.73	1.51
	14.0	22	9.5	18	*	*	0.43	*	*	*	17	*	*	*	*	18	0.53	1.22
	16.0	18	8.5	10	*	*	0.33	*	*	*	6	*	*	*	*	6	0.44	1.32
73	0.3	37	19.1	29	20.2	13.7	0.56	1.4	17.3	23.0	17	20.0	1.8	16.2	23.8	19	0.65	1.15
	1.3	35	18.2	24	21.1	13.9	0.28	0.6	19.8	22.4	20	23.5	2.6	18.2	28.9	22	0.48	1.73
	2.0	33	17.6	17	18.4	12.7	0.64	1.1	16.0	20.8	11	17.9	5.5	5.7	30.0	13	0.73	1.14
	4.0	32	16.3	26	22.0	13.4	0.61	1.3	19.2	24.7	17	23.3	2.9	17.1	29.5	19	1.11	1.83
	6.0	30	15.7	24	21.0	13.0	0.63	1.6	17.7	24.3	21	21.0	7.8	4.8	37.2	23	0.74	1.18
	8.0	29	14.1	23	19.0	11.1	0.29	0.9	17.2	20.8	16	19.2	2.1	14.7	23.6	18	0.50	1.72
	10.0	27	13.5	20	16.3	10.0	0.33	0.9	14.5	18.1	12	16.0	2.1	11.4	20.5	14	0.78	2.36
	12.0	26	13.3	17	17.2	10.0	0.23	1.1	15.0	19.5	9	16.8	3.8	8.2	25.3	11	0.25	1.10
16.0	22	12.0	14	*	*	0.24	*	*	*	9	*	*	*	*	9	0.26	1.09	

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.3 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for Douglas-fir (4.57 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 $\times 10^{-3}$
									lower	upper				lower	upper			
78	0.3	38	17.2	26	25.8	13.9	0.51	1.2	23.4	28.2	22	29.0	8.3	11.9	46.1	24	0.52	1.02
	1.3	36	14.9	28	22.7	11.4	1.12	1.2	20.2	25.2	24	23.0	5.1	12.5	33.5	26	1.32	1.18
	2.0	35	14.6	28	21.6	11.0	1.04	1.3	18.9	24.3	23	26.1	3.7	18.5	33.7	25	1.11	1.06
	4.0	33	14.0	22	19.0	10.0	0.55	1.1	16.6	21.4	21	19.0	3.5	11.7	26.3	23	0.75	1.37
	6.0	32	14.2	25	20.0	11.1	2.57	1.6	16.7	23.3	25	22.9	6.4	9.8	36.1	27	3.33	1.29
	8.0	28	12.9	21	18.5	10.4	0.78	1.2	16.1	21.0	15	18.9	2.9	12.8	25.0	17	1.77	2.26
	10.0	26	12.8	19	15.6	9.4	0.49	1.1	13.4	17.9	17	19.4	3.2	12.7	26.2	19	0.61	1.24
	12.0	25	12.3	18	17.1	9.8	0.65	1.1	14.8	19.3	12	16.4	3.2	9.4	23.4	14	0.88	1.36
	14.0	23	11.8	17	*	*	0.50	*	*	*	13	*	*	*	*	13	0.51	1.02
	16.0	22	10.9	16	16.0	8.7	0.56	2.1	11.5	20.5	14	16.0	4.6	6.1	25.9	16	0.63	1.13
	18.0	19	9.0	12	*	*	0.34	*	*	*	3	*	*	*	*	4	0.60	1.78
	19.3	18	7.4	9	14.0	6.1	0.28	0.5	12.9	15.1	7	*	*	*	*	7	0.56	2.02
79	0.3	37	22.1	27	20.8	17.5	0.51	1.1	18.5	23.1	23	21.3	3.1	14.8	27.8	25	0.57	1.12
	2.0	33	16.8	25	20.1	12.9	0.65	3.1	13.7	26.5	24	16.3	2.7	10.7	21.8	26	0.83	1.27
	4.0	31	15.1	13	15.1	11.3	0.29	0.9	13.1	17.2	6	0.3	2.1	9.4	19.6	8	0.34	1.18
	6.0	29	15.3	22	15.3	11.0	0.65	0.8	13.6	17.1	17	14.4	1.2	11.9	16.9	19	1.18	1.81
	8.0	26	15.3	12	16.0	11.4	0.37	1.0	13.9	18.1	5	12.7	1.1	9.8	15.6	7	0.40	1.09
	12.0	22	13.3	9	*	*	0.10	*	*	*	9	*	*	*	*	9	0.12	1.26
	14.0	21	12.7	12	*	*	0.32	*	*	*	4	*	*	*	*	5	0.34	1.07

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.4 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western hemlock (0.91 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	MSE-3 $\times 10^{-3}$	df		MSE-3 $\times 10^{-3}$	
									lower	upper								lower
1	0.3	29	7.0	19	16.0	4.0	0.62	1.6	12.6	19.4	15	16.0	2.8	9.9	22.1	17	0.80	1.28
	1.3	27	6.1	20	18.0	4.4	1.78	2.2	13.4	22.6	15	18.0	10.7	0.0	40.8	17	2.05	1.15
	2.0	25	5.7	20	14.4	3.8	1.25	1.2	11.9	16.9	16	15.1	4.6	5.4	24.9	18	1.52	1.21
	8.0	22	4.2	16	*	*	1.69	*	*	*	12	*	*	*	*	13	1.74	1.03
504	0.3	38	9.4	25	25.0	7.3	0.42	1.8	21.3	28.7	17	22.8	2.3	17.9	27.8	19	0.50	1.18
	1.3	34	9.2	25	18.5	6.7	1.77	1.6	15.1	21.9	21	14.0	3.3	7.2	20.8	23	1.78	1.01
	2.0	33	9.7	26	18.6	7.5	0.72	1.6	15.3	22.0	20	17.3	2.4	12.2	22.4	22	0.86	1.20
	4.0	30	9.1	19	19.3	7.4	0.57	1.1	17.1	21.6	8	17.0	4.8	6.0	28.0	10	0.60	1.05
	8.0	24	7.8	17	15.0	5.6	0.30	0.6	13.7	16.3	13	15.0	3.2	8.2	21.8	15	0.36	1.21
573	1.3	32	10.1	25	21.4	7.9	1.58	1.0	19.3	23.5	17	20.0	4.8	9.8	30.2	19	2.11	1.33
	4.0	27	8.4	18	18.2	6.5	0.34	0.5	17.1	19.2	13	19.0	1.7	15.2	22.8	15	0.35	1.03
	6.0	25	7.9	17	16.4	5.6	0.35	0.6	15.2	17.7	10	16.3	0.8	14.5	18.1	12	0.47	1.33
	8.0	24	8.1	16	17.8	6.7	0.40	1.0	15.8	19.8	10	21.9	4.4	12.1	31.6	12	0.42	1.04
	10.0	21	7.4	14	18.8	6.8	0.50	0.9	16.9	20.6	5	18.8	3.2	10.5	27.2	7	1.11	2.23
	12.0	18	6.8	14	*	*	1.57	*	*	*	4	*	*	*	*	4	5.29	3.37
	12.9	17	5.8	12	*	*	0.85	*	*	*	4	*	*	*	*	4	1.64	1.93

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.4 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western hemlock (0.91 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value			
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 $\times 10^{-3}$	MSE-3 / MSE-1	
									lower	upper				lower	upper				
660	0.3	36	9.2	29	16.8	4.7	0.25	0.9	14.9	18.7	20	16.2	2.9	10.1	22.3	22	0.37	1.50	
	1.3	33	7.2	26	15.0	3.9	0.42	1.3	12.4	17.6	18	14.0	1.5	10.8	17.2	20	0.61	1.46	
	2.0	32	7.3	22	19.0	4.2	0.36	3.3	12.1	25.9	17	10.0	1.2	7.5	12.5	19	0.40	1.12	
	4.0	30	7.4	22	18.0	4.6	0.30	1.3	15.2	20.8	12	17.6	3.2	10.9	24.6	14	0.41	1.37	
	6.0	26	7.2	19	18.0	5.5	0.27	0.7	16.6	19.4	10	18.0	2.9	11.5	2.5	12	0.35	1.29	
	8.0	23	6.9	17	16.3	5.3	0.60	0.9	14.4	18.3	10	16.8	3.4	0.1	24.5	12	0.94	1.56	
	10.0	20	6.0	16	*	*	0.94	*	*	*	4	*	*	*	*	4	2.18	2.31	
	14.0	15	5.5	11	*	*	0.35	*	*	*	3	*	*	*	*	3	0.36	1.02	
662	2.0	34	7.6	28	20.8	5.8	0.98	1.0	18.7	22.8	22	25.0	3.1	18.7	31.3	24	1.02	1.04	
	4.0	30	7.0	23	20.8	6.3	1.07	1.0	18.7	23.0	19	22.0	3.5	14.7	29.3	21	1.72	1.62	
	6.0	27	6.5	22	17.9	5.3	0.81	0.9	16.0	19.9	13	18.8	3.0	12.2	25.4	15	1.33	1.64	
	8.0	25	6.8	19	16.3	5.4	0.69	0.6	15.0	17.6	12	16.7	2.0	12.3	21.2	14	0.99	1.43	
	10.0	22	6.1	17	18.1	5.5	1.55	0.8	16.5	19.7	8	18.8	3.6	10.6	27.1	10	2.46	1.59	
	12.0	20	5.1	12	17.0	4.7	0.46	0.6	15.7	18.3	7	17.0	3.0	9.9	24.1	9	0.49	1.07	
	721	0.3	33	7.2	26	25.9	5.8	1.38	2.5	20.7	31.1	21	26.8	5.1	16.3	37.3	23	1.41	1.02
		1.3	31	7.4	23	24.0	6.6	1.61	2.5	18.8	29.2	16	24.0	4.9	13.7	34.3	18	1.93	1.20
2.0		31	6.6	22	22.5	5.1	0.88	1.1	20.2	24.8	9	25.4	4.2	15.9	35.0	11	1.27	1.45	
4.0		30	6.2	23	19.0	5.0	1.31	1.2	16.6	21.4	17	19.0	3.2	12.2	25.8	19	1.45	1.11	
6.0		25	6.5	18	17.8	5.3	0.57	0.7	16.2	19.3	12	18.7	2.3	13.7	23.7	14	1.20	2.09	
8.0		24	6.4	19	14.3	4.4	0.69	0.8	12.6	16.0	12	14.0	1.6	19.5	17.6	14	1.12	1.62	
10.0		23	6.0	14	15.0	4.2	0.35	0.5	13.8	16.2	6	15.4	1.7	11.2	19.6	8	0.89	2.57	

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.5 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western hemlock (2.74 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
15	1.3	29	7.0	25	23.6	6.8	2.31	2.1	19.3	27.9	10	24.1	4.8	13.3	34.9	12	3.88	1.68
23	0.3	31	9.6	21	19.1	7.3	0.66	1.3	16.5	21.7	7	18.0	0.7	16.4	19.6	9	1.17	1.78
	1.3	30	8.9	24	18.8	7.3	0.98	1.5	15.6	22.0	11	18.1	2.6	12.5	23.8	13	1.45	1.47
	2.0	29	9.7	22	20.4	8.5	2.27	3.6	13.0	27.8	12	19.0	12.6	0.0	46.4	14	3.45	1.52
	6.0	28	9.8	13	16.0	6.6	0.85	2.1	11.5	20.0	11	16.0	6.0	2.8	29.1	13	0.99	1.16
	7.9	26	9.8	18	17.0	8.0	1.29	2.9	11.0	23.0	12	17.0	4.3	7.7	26.3	14	1.86	1.45
27	0.3	36	14.3	26	23.0	10.8	0.36	2.8	17.2	28.8	15	18.0	6.2	5.7	32.3	17	0.41	1.15
	1.3	34	11.0	27	22.0	7.8	0.50	1.4	19.0	24.9	15	19.6	1.7	16.1	23.2	17	1.01	2.02
	2.0	33	10.3	27	25.0	8.0	0.29	1.1	22.7	27.3	17	*	*	*	*	17	0.33	1.13
	4.0	30	9.7	21	20.2	7.5	0.27	0.6	19.0	21.5	13	21.0	2.0	16.8	25.2	15	0.35	1.28
	6.0	28	9.4	18	19.1	7.6	0.22	0.7	17.7	20.5	11	19.0	5.8	6.2	31.8	13	0.23	1.03
	8.0	26	9.3	7	*	*	0.38	*	*	*	2	*	*	*	*	3	0.55	1.46
	10.0	21	8.2	12	17.1	7.4	0.45	0.9	15.2	19.0	2	17.3	1.4	11.3	23.2	4	1.00	2.22
	11.5	20	8.5	10	*	*	0.08	*	*	*	4	*	*	*	*	4	0.11	1.38

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.5 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western hemlock (2.74 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic					model 2 - segmented linear				model 3 - linear		F-value				
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 $\times 10^{-3}$	MSE-3 / MSE-1	
									lower	upper				lower					upper
28	0.3	36	9.295	30	23.6199	6.82	1.147	1.919	19.7	27.54	19	23	7.591	7.111	38.89	21	1.32	1.15083	
	1.3	35	8.6	25	29.0	7.6	1.07	1.8	25.4	32.6	11	30.3	9.6	9.3	51.4	13	2.06	1.93	
	2.0	33	8.6	21	27.0	7.6	1.31	1.8	23.3	30.7	15	27.9	6.7	13.7	42.1	17	2.02	1.54	
	4.0	30	8.2	21	25.0	5.8	0.79	1.7	21.6	28.4	11	24.1	2.5	18.5	29.7	13	0.91	1.15	
	6.0	27	8.9	18	19.8	7.0	0.42	2.3	15.0	24.6	11	17.0	8.9	0.0	36.6	13	0.50	1.19	
	8.0	25	9.0	18	16.0	5.3	0.75	4.1	7.4	24.6	8	16.0	4.1	6.5	25.5	10	1.14	1.52	
61	0.3	34	9.1	26	24.0	5.5	0.53	1.5	20.9	27.1	12	23.5	1.8	19.5	27.4	14	0.57	1.08	
	1.3	31	7.6	23	23.0	6.0	0.88	2.3	18.3	27.7	15	24.0	9.7	3.4	44.6	17	0.95	1.08	
	2.0	31	7.4	24	23.9	5.9	1.01	1.9	19.9	27.9	12	24.0	5.9	11.1	36.9	14	1.31	1.30	
	4.0	28	7.0	12	16.5	5.1	0.29	0.7	14.9	18.1	*	*	*	*	*	10	0.57	1.95	
	6.0	26	7.7	20	19.0	6.3	1.76	1.5	15.9	22.1	14	17.0	5.4	5.4	28.6	16	2.01	1.14	
	8.0	22	6.8	15	12.8	4.5	0.76	0.8	11.0	14.6	12	14.0	2.3	8.9	19.1	14	1.10	1.45	
62	8.0	26	9.5	15	23.0	9.1	0.67	2.0	18.6	27.4	11	*	*	*	*	12	0.69	1.03	
	11.3	20	8.5	7	*	*	0.14	*	*	*	1	*	*	*	*	1	0.29	2.07	

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.6 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western hemlock (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
14	1.3	35	12.3	21	17.6	7.8	0.91	1.2	15.2	20.1	16	20.3	4.1	11.5	29.1	18	0.96	1.06
	2.0	33	12.1	19	21.3	8.7	0.61	1.2	18.7	23.9	12	22.6	3.6	14.8	30.5	14	0.69	1.13
	4.0	32	12.1	26	22.0	9.8	1.02	0.9	20.1	23.9	14	22.2	2.1	17.6	26.7	16	2.50	2.45
	8.0	26	10.3	20	22.0	9.1	0.51	3.3	15.2	28.8	4	21.0	4.0	10.0	32.0	6	0.68	1.34
16	0.3	36	19.7	27	*	*	0.57	*	*	*	19	*	*	*	*	19	0.57	1.01
	4.0	32	17.3	26	*	*	1.05	*	*	*	14	*	*	*	*	14	1.27	1.21
	8.5	27	12.8	20	*	*	0.78	*	*	*	9	*	*	*	*	9	0.98	1.26
20	2.0	33	15.8	25	24.0	11.8	0.36	1.1	21.7	26.3	10	22.5	1.4	19.4	25.7	12	0.55	1.52
	6.0	29	12.3	20	22.6	11.1	0.16	0.7	21.2	23.9	8	22.0	1.2	19.2	24.8	10	0.33	2.08
	8.0	26	12.5	14	19.0	11.5	0.17	1.6	15.6	22.4	4	16.0	4.4	3.7	28.3	6	0.24	1.45
	10.0	24	11.5	16	14.3	8.0	0.19	0.5	13.1	15.4	11	14.0	1.7	10.2	17.8	13	0.20	1.06

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.6 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western hemlock (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 $\times 10^{-3}$
									lower	upper				lower	upper			
29	1.3	34	11.8	28	24.218	10.17	0.763	4.635	14.72	33.71	12	24.113	6.636	9.656	38.57	14	1.06	1.38925
	6.0	26	11.6	18	17.0	8.6	0.31	0.9	15.1	18.9	12	*	*	*	*	14	0.32	1.02
	8.9	21	10.5	12	*	*	0.46	*	*	*	5	*	*	*	*	5	0.48	1.05
62	4.0	29	8.6	22	*	*	1.19	*	*	*	7	*	*	*	*	8	1.58	1.33
	6.0	25	8.8	9	*	*	0.22	*	*	*	3	*	*	*	*	3	0.29	1.35
	8.0	23	7.9	16	*	*	0.91	*	*	*	11	*	*	*	*	12	1.28	1.41
	9.5	20	7.4	15	*	*	0.56	*	*	*	3	*	*	*	*	3	0.92	1.65
72	0.3	36	18.3	25	26.0	13.9	0.18	1.4	23.1	28.9	15	26.0	5.2	15.0	37.0	17	0.19	1.08
	1.3	35	15.2	27	24.4	10.9	0.84	3.3	17.5	31.2	14	24.0	3.8	15.8	32.2	16	0.95	1.14
	2.0	34	14.0	26	*	*	0.61	*	*	*	1	*	*	*	*	3	1.73	2.83
	4.0	31	13.9	23	*	*	0.38	*	*	*	15	*	*	*	*	15	0.42	1.11
	6.0	28	13.3	21	*	*	0.42	*	*	*	15	*	*	*	*	15	0.47	1.12

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.7 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western redcedar (2.74 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 $\times 10^{-3}$
									lower	upper				lower	upper			
60	1.3	37	16.8	26	25.7	14.6	0.22	1.5	22.7	28.7	14	23.0	33.1	16.3	29.7	16	0.23	1.03
	2.0	35	14.6	25	30.0	13.8	0.20	1.8	26.4	33.6	14	29.2	5.3	17.9	40.6	16	0.24	1.20
	4.0	33	13.2	24	19.4	10.2	0.20	0.9	17.6	21.2	15	21.0	5.5	9.2	32.8	17	0.21	1.05
	6.0	28	11.4	10	*	*	0.11	*	*	*	1	*	*	*	*	3	0.20	1.79
61	0.3	38	16.7	27	27.0	13.9	0.25	2.2	22.4	31.6	11	24.0	1.7	20.2	27.8	13	0.38	1.50
	4.0	31	12.0	22	28.0	11.4	0.15	5.6	16.4	39.6	10	*	*	*	*	10	0.21	1.42
67	0.3	35	15.3	27	22.3	11.2	0.59	1.5	19.2	25.4	12	23.9	8.5	5.4	42.5	14	1.11	1.90
	1.3	33	11.2	20	21.5	9.6	0.14	1.2	19.1	23.9	7	19.0	5.0	7.3	30.7	9	0.15	1.08
	2.0	32	10.9	24	18.6	8.4	0.35	1.8	15.0	22.2	15	19.1	3.4	11.8	26.3	17	0.53	1.50
	4.0	28	9.3	18	21.0	8.3	0.27	2.8	15.2	26.8	7	21.0	4.4	10.5	31.5	9	0.46	1.68
	6.0	27	9.0	21	21.0	7.8	0.45	1.5	17.9	24.1	8	21.1	5.3	8.9	33.3	10	0.69	1.53
	12.0	19	7.3	13	15.2	6.4	0.12	1.4	12.2	18.2	4	*	*	*	*	4	0.17	1.37
	12.8	18	7.0	13	14.0	6.0	0.21	1.9	9.8	18.2	3	14.0	7.2	0.0	36.9	5	0.38	1.84

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.7 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western redcedar (2.74 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic					model 2 - segmented linear				model 3 - linear		F-value			
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 $\times 10^{-3}$	
									lower	upper				lower				upper
71	0.3	36	15.65	25	22	11.86	0.167	1.328	19.26	24.74	11	24	4.021	15.15	32.85	13	0.33	1.97605
	1.3	34	11.8	25	24.0	10.3	0.27	2.6	18.7	29.3	11	20.0	6.3	6.1	33.9	13	0.44	
	2.0	33	10.2	24	19.6	8.0	0.29	1.3	16.8	22.3	13	17.6	3.1	10.9	24.3	15	0.38	
	4.0	30	9.6	22	15.2	6.8	0.18	0.7	13.7	16.7	14	14.3	1.6	10.7	17.8	16	0.24	
	8.0	24	8.3	16	10.5	4.6	0.30	0.9	8.6	12.4	11	12.3	2.5	6.8	17.8	13	0.47	
73	0.3	37	12.9	27	27.0	11.8	0.78	1.4	24.0	30.0	16	27.0	3.9	18.7	35.3	18	1.02	1.31
	1.3	35	9.6	25	26.9	8.9	0.64	1.5	23.8	29.9	15	25.0	8.2	7.5	42.5	17	0.80	
	2.0	32	7.9	22	22.0	7.3	0.50	2.4	17.0	27.0	22	*	*	*	*	22	0.52	
	8.0	24	6.8	16	20.0	6.4	0.40	1.6	16.6	23.4	7	20.2	3.8	11.3	29.1	9	0.45	
78	0.3	37	17.3	30	28.8	16.8	1.23	1.5	25.8	31.9	11	27.7	1.9	23.5	32.0	13	1.72	1.40
	1.3	35	13.0	27	23.3	11.5	0.53	2.6	18.1	28.6	14	22.9	3.3	15.9	29.9	16	0.56	
	2.0	34	10.7	27	20.8	9.0	0.38	1.8	17.2	24.4	18	21.0	4.9	10.6	31.4	20	0.46	
	6.0	29	9.8	23	19.5	8.5	0.49	1.0	17.4	21.5	15	22.2	4.0	13.8	30.7	17	0.67	
	13.0	20	7.5	15	16.1	*	0.52	*	*	*	9	*	*	*	*	10	0.57	

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.8 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western redcedar (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 $\times 10^{-3}$	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 $\times 10^{-3}$
									lower	upper				lower	upper			
18	1.3	32	14.1	26	24.9	12.7	0.27	1.7	21.4	28.3	8	24.1	2.9	17.4	30.8	10	0.45	1.65
	8.0	23	9.2	17	19.2	8.1	0.09	0.7	17.8	20.5	4	18.8	1.2	15.3	22.2	6	0.11	1.21
22	1.3	36	21.8	26	29.0	19.1	0.43	2.6	23.6	34.4	7	28.1	3.8	19.2	37.1	9	0.76	1.76
	2.0	35	19.1	23	26.8	16.1	0.11	2.1	22.6	31.0	5	24.2	1.3	21.0	27.4	7	0.12	1.12
	6.0	29	15.7	22	*	*	0.12	*	*	*	5	*	*	*	*	5	0.17	1.37
	8.8	26	14.0	19	*	*	0.12	*	*	*	3	*	*	*	*	3	0.18	1.56
24	0.3	35	15.4	27	30.0	14.5	0.45	2.7	24.6	35.4	8	29.2	4.7	18.4	40.1	10	0.62	1.38
	1.3	34	13.3	28	27.7	11.7	0.51	1.6	24.4	31.1	11	30.1	6.5	15.8	44.3	13	0.56	1.10
	2.0	33	12.2	22	23.8	10.3	0.54	2.7	18.3	29.4	9	*	*	*	*	9	0.65	1.20
	6.0	28	9.9	19	20.0	8.0	0.21	2.5	14.7	25.3	7	21.0	7.6	3.0	39.0	9	0.30	1.40

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.8 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western redcedar (3.66 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic					model 2 - segmented linear				model 3 - linear		F-value			
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.		df	MSE-3 x10 ⁻³	
									lower	upper				lower				upper
34	0.3	37	24.2	28	26.4	20.4	0.24	1.3	23.7	29.1	21	29.0	8.5	11.4	46.6	23	0.26	1.07
	1.3	35	20.5	26	25.0	16.7	0.18	6.2	12.3	37.7	9	25.0	7.3	8.5	41.5	11	0.25	1.41
	2.0	34	18.9	27	24.0	15.5	0.37	3.2	17.4	30.6	8	25.0	8.9	4.6	45.5	10	0.40	1.08
	4.0	32	12.8	21	23.0	10.9	0.20	2.4	18.0	28.0	8	23.9	6.9	8.1	39.7	10	0.26	1.28
	8.0	29	13.2	23	*	*	0.15	*	*	*	4	*	*	*	*	6	0.20	1.36
72	1.3	33	13.3	26	28.0	12.8	0.35	1.9	24.2	31.8	5	26.4	1.0	23.7	29.1	7	0.36	1.03
	2.0	32	11.2	25	27.0	10.7	0.28	2.3	22.3	31.7	11	27.0	7.2	11.1	42.9	13	0.41	1.47
	4.0	29	10.0	21	23.2	9.2	0.17	1.6	19.8	26.6	7	23.6	5.4	10.8	36.3	9	0.32	1.91
	6.0	26	9.1	18	19.0	7.9	0.26	1.5	15.9	22.1	8	18.8	2.4	13.4	24.3	10	0.51	1.96
	8.0	23	9.4	15	19.0	8.4	0.59	2.2	14.3	23.7	11	18.0	5.1	6.7	29.3	13	0.61	1.03
74	0.3	36	22.7	31	28.8	20.5	0.21	0.9	26.9	30.7	12	28.8	4.7	18.6	39.1	14	0.24	1.13
	2.0	32	17.0	24	26.9	15.6	0.09	0.8	25.2	28.6	9	26.6	1.6	23.0	30.2	11	0.10	1.12
	4.0	30	14.9	22	25.0	12.7	0.24	2.0	21.0	29.0	4	25.2	6.1	8.2	42.1	6	0.80	3.36
	8.0	25	14.2	15	18.0	10.3	0.12	1.1	15.8	20.2	6	*	*	*	*	6	0.24	1.95
	11.3	20	11.2	14	*	*	0.43	*	*	*	3	*	*	*	*	3	0.93	2.17

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.9 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western redcedar (4.57m spacing). Comparison of segmented quadratic, segmented linear and simple linear models.

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
17	0.3	35	20.1	24	25.0	17.2	0.32	1.7	21.4	28.6	9	*	*	*	11	0.50	1.57	
	2.0	32	16.6	26	*	*	0.29	*	*	*	9	*	*	*	11	0.32	1.11	
	4.0	30	14.6	23	*	*	0.33	*	*	*	11	*	*	*	13	0.40	1.21	
	8.0	25	13.7	19	*	*	0.08	*	*	*	2	*	*	*	4	0.14	1.70	
	10.0	23	12.4	17	*	*	0.11	*	*	*	5	*	*	*	7	0.18	1.70	
	11.2	22	12.4	15	*	*	0.11	*	*	*	3	*	*	*	3	0.12	1.10	
18	0.3	36	25.2	30	*	*	0.15	*	*	*	9	*	*	*	11	0.16	1.04	
	1.3	34	17.0	27	*	*	0.18	*	*	*	9	*	*	*	11	0.19	1.06	
	4.0	30	13.1	21	*	*	0.11	*	*	*	10	*	*	*	11	0.13	1.20	
	10.0	21	9.4	15	*	*	0.24	*	*	*	5	*	*	*	7	0.28	1.16	
63	0.3	35	19.2	27	30.0	18.4	0.91	2.0	25.8	34.2	9	30.0	12.1	2.6	57.4	11	1.90	2.08
	1.3	34	13.5	26	27.0	12.7	0.58	2.9	21.1	32.9	9	26.5	4.2	17.1	35.9	11	0.84	1.45
	2.0	33	10.9	25	26.0	10.2	0.35	3.2	19.4	32.6	7	24.2	3.8	15.3	33.2	9	0.54	1.55
	4.0	29	9.5	24	20.0	8.3	0.78	1.4	17.0	23.0	8	20.5	7.5	3.2	37.9	10	1.22	1.57
	6.0	24	9.1	17	18.4	8.3	0.16	0.8	16.6	20.2	9	17.1	3.8	8.5	25.7	11	0.20	1.22
	7.1	24	7.9	17	14.0	6.4	0.37	0.7	12.5	15.5	9	16.0	3.1	8.9	23.1	11	0.73	1.99

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.9 Juvenile-mature wood transition zone expressed as number of growth rings and distance from pith (cm) for western redcedar (4.57 m spacing). Comparison of segmented quadratic, segmented linear and simple linear models (continued).

tree	height from ground (m)	total growth rings	core length (cm)	model 1 - segmented quadratic						model 2 - segmented linear				model 3 - linear		F-value		
				df	transition ring	distance from pith (cm)	MSE-1 x10 ⁻³	SE _E	C. I.		df	transition ring	SE _E	C. I.			df	MSE-3 x10 ⁻³
									lower	upper				lower	upper			
70	1.3	33	20.7	26	29.5	15.7	0.18	2.7	24.0	35.1	9	23.0	1.0	20.7	25.3	11	0.18	1.03
	2.0	32	16.0	25	29.0	15.2	0.11	2.0	24.9	33.1	4	26.5	2.3	20.1	32.9	6	0.22	2.06
	8.0	24	12.4	19	*	*	0.09	*	*	*	2	*	*	*	*	4	0.10	1.06
	9.0	23	12.1	17	*	*	0.18	*	*	*	1	*	*	*	*	2	0.39	2.12
71	2.0	32	16.9	26	*	*	0.15	*	*	*	2	*	*	*	*	4	0.35	2.29
	4.0	31	15.2	24	*	*	0.15	*	*	*	2	*	*	*	*	4	0.26	1.73
	6.0	29	14.4	24	*	*	0.18	*	*	*	8	*	*	*	*	10	0.22	1.21
	8.0	27	13.8	22	*	*	0.12	*	*	*	3	*	*	*	*	5	0.13	1.07
77	0.3	34	21.2	22	30.0	20.7	0.19	0.7	28.5	31.4	9	30.0	2.2	25.0	34.9	11	0.33	1.77
	1.3	32	14.7	24	25.0	13.9	0.61	1.2	22.6	27.4	10	22.5	1.9	18.3	26.6	12	1.25	2.05
	2.0	31	12.6	24	27.0	12.1	0.30	1.1	24.7	29.3	11	27.6	5.1	16.5	38.8	13	0.51	1.71
	4.0	29	11.5	21	20.0	9.6	0.33	1.2	17.5	22.5	11	19.4	4.6	9.2	29.6	13	0.44	1.34
	6.0	26	10.7	20	15.2	7.9	0.21	0.8	13.6	16.8	12	15.0	2.5	9.5	20.5	14	0.27	1.26
	8.0	23	9.5	15	20.0	8.8	0.30	1.5	16.9	23.1	4	20.0	6.7	1.3	38.7	6	0.48	1.59
	9.8	21	8.0	15	17.0	7.1	0.61	1.2	14.4	19.6	2	*	*	*	*	4	1.21	2.00

df : degrees of freedom

MSE : mean square error

SE_E : standard error of estimate

C.I. : 95 % confidence interval

Note : missing height intervals denote cases where F value ≤ 1

* : transition point between juvenile and mature wood could not be determined

Table 5.10 Mean juvenile wood transition age (ring number from pith) observed by height, taper class and species.

Douglas-fir

height from ground (m)	suppressed			intermediate			dominant			combined		
	n	mean	std	n	mean	std	n	mean	std	n	mean	std
0.3	3	23.0	9.0	4	22.3	3.2	7	25.3	4.0	14	23.6	4.9
1.3	4	20.2	7.9	5	19.2	2.2	4	24.0	3.6	13	21.0	5.0
2.0	1	24.0		4	20.6	2.9	7	21.7	3.3	12	21.7	3.0
4.0	5	20.3	5.3	4	16.8	2.5	7	21.2	3.6	16	19.4	4.2
6.0	5	17.5	3.7	3	16.9	2.9	7	19.1	2.5	15	18.2	2.9
8.0	5	17.0	1.1	4	19.0	2.4	7	18.1	1.7	16	18.0	1.8
10.0	6	16.1	3.7	4	16.5	1.9	4	14.6	1.8	14	15.8	2.7
12.0	6	15.4	4.2	4	16.2	0.6	5	17.2	3.1	15	16.1	3.1
14.0	5	15.2	3.5	3	14.1	0.4	4	17.7	2.7	12	15.4	3.0
16.0	5	12.7	3.8	4	16.4	0.6				9	14.3	3.3
18.0	3	11.2	0.4	3	15.8	2.0				6	13.5	2.8

western hemlock

height from ground (m)	suppressed			intermediate			dominant			combined		
	n	mean	std	n	mean	std	n	mean	std	n	mean	std
0.3	7	21.5	4.1	1	23.0		1	26.0		9	22.1	3.9
1.3	9	21.3	4.2	2	19.8	3.1	2	24.3	0.1	13	21.5	3.8
2.0	8	20.8	3.8	3	23.4	1.9				11	21.5	3.5
4.0	7	19.5	2.8	2	21.1	1.2				9	19.9	2.5
6.0	7	17.8	1.3	2	20.8	2.5	1	17.0		10	18.3	1.9
8.0	8	15.7	1.6	3	21.3	2.1				11	17.2	3.1
10.0	3	17.3	2.0	2	15.7	2.0				5	16.6	2.0

western redcedar

height from ground (m)	suppressed			intermediate			dominant			combined		
	n	mean	std	n	mean	std	n	mean	std	n	mean	std
0.3				3	23.8	2.8	8	28.2	1.9	11	27.0	2.9
1.3				3	24.1	2.7	10	26.5	2.0	13	26.0	2.3
2.0				3	20.1	1.7	10	26.1	2.7	13	24.7	3.6
4.0				2	18.1	4.1	7	22.7	3.1	9	21.6	3.7
6.0				1	21.0		5	18.4	1.9	6	18.8	2.0
8.0				2	15.3	6.7	4	19.0	0.8	6	17.8	3.6
10.0							1	17.0		1	17.0	

n : number of observations

std : standard deviation

Table 5.11a Partial regression coefficients and coefficients of determination (R^2) for diameter inside bark taper equation.

parameter	Douglas-fir		western hemlock		western redcedar	
	estimate	SE _E	estimate	SE _E	estimate	SE _E
a ₀	0.18169	0.07246	0.44104	0.12900	0.22976	0.12125
a ₁	0.94793	0.02185	0.85198	0.04248	0.92345	0.03517
b ₁	0.37849	1.18303	4.26188	4.22820	-1.73458	2.51465
b ₂	0.37015	0.61950	-1.82199	2.75348	1.73358	1.66909
b ₃	-0.21308	0.04226	-0.21025	0.09195	-0.35108	0.05622
b ₄	-0.09303	0.66537	-2.13113	2.13867	0.51664	1.26327
b ₅	0.01969	0.04719	0.04556	0.13145	0.20141	0.07179
n	204		130		136	
R ²	0.961		0.884		0.937	

SE_E : standard error of estimate

n : number of observations

R² : coefficient of determination, values are in terms of ln(dib_i)

Table 5.11b Biases and standard errors of estimate (SE_E), by height interval sampled, for diameter inside bark taper equation.

height from ground (m)	Douglas-fir			western hemlock			western redcedar		
	n	bias (cm)	SE _E (cm)	n	bias (cm)	SE _E (cm)	n	bias (cm)	SE _E (cm)
0.3	18	0.43	2.70	17	0.40	2.68	18	0.79	6.32
1.3	18	-0.15	0.45	18	0.35	1.62	18	1.17	1.75
2.0	18	0.10	1.15	17	0.20	2.54	18	-0.78	2.42
4.0	18	0.04	2.10	17	0.17	2.83	18	-0.25	1.89
6.0	18	0.28	2.12	17	0.11	3.58	18	0.40	1.84
8.0	18	0.13	1.93	16	-0.15	3.03	16	0.34	2.05
10.0	18	-0.14	2.54	10	-0.25	3.76	9	0.50	2.41
12.0	18	0.15	2.21						
14.0	18	-0.20	2.11						
16.0	17	0.23	1.89						
18.0	11	0.11	2.17						
Total *	204	0.09	1.68	130	0.13	2.36	136	0.18	2.451

n : number of observations

SE_E : standard error of estimate

* : includes samples obtained at, or near, the base of the live crown

Table 5.12a Partial regression coefficients and coefficients of determination (R^2) for juvenile wood taper equation.

parameter	Douglas-fir		western hemlock		western redcedar	
	estimate	SE _E	estimate	SE _E	estimate	SE _E
a ₀	0.72701	0.14129	0.38228	0.17929	-0.03754	0.18940
a ₁	0.77221	0.04504	0.87232	0.06664	1.00415	0.05745
b ₁	-1.22396	0.79279	-1.66965	1.82610	1.78990	1.06852
b ₂	1.25841	0.95224	1.46438	1.96350	-3.42994	1.11219
b ₃	0.01710	0.10986	0.03743	0.27480	0.03227	0.17239
b ₄	-0.05222	0.02033	-0.04082	0.04976	-0.29456	0.04221
b ₅	0.61966	0.88919	0.83858	1.48295	9.20110	0.99620
b ₆	0.02322	0.01060	-0.00080	0.02571	0.06059	0.01505
n	168		88		83	
R ²	0.831		0.811		0.923	

SE_E : standard error of estimate

n : number of observations

R² : coefficient of determination, values are in terms of ln(jwd_i)

Table 5.12b Biases and standard errors of estimate (SE_E), by height interval sampled, for juvenile wood taper equation.

height from ground (m)	Douglas-fir			western hemlock			western redcedar		
	n	bias (cm)	SE _E (cm)	n	bias (cm)	SE _E (cm)	n	bias (cm)	SE _E (cm)
0.3	14	3.53	6.84	10	1.35	5.51	12	-0.08	4.70
1.3	13	-0.39	2.44	13	-0.54	0.95	14	0.63	0.90
2.0	12	-0.45	3.71	12	0.08	2.79	15	-0.09	2.62
4.0	16	-0.34	3.07	12	0.74	4.98	12	-0.42	3.66
6.0	16	-0.60	2.46	12	0.61	4.14	9	0.80	3.72
8.0	17	0.11	3.25	13	0.15	3.52	10	0.36	4.54
10.0	14	-1.34	4.29						
12.0	16	0.35	2.84						
14.0	16	0.54	4.46						
16.0	14	-0.09	5.01						
18.0	8	0.48	5.39						
Total *	168	0.09	2.97	88	0.27	2.59	84	0.03	2.22

n : number of observations

SE_E : standard error of estimate

* : includes samples obtained at, or near, the base of the live crown

Table 5.13 Mean juvenile wood, mature wood and pith to bark relative density observed by initial spacing and height for Douglas-fir.

spacing	height from ground (m)	juvenile wood			mature wood			pith-to-bark		
		n	rd	cv	n	rd	cv	n	rd	cv
0.91 m	0.3	3	0.412	3.9	3	0.465	10.5	5	0.424	5.5
	1.3	4	0.418	3.2	4	0.494	6.6	6	0.442	4.4
	2.0	1	0.427		1	0.501		5	0.460	5.7
	4.0	5	0.410	6.2	5	0.491	6.7	6	0.441	5.5
	6.0	5	0.407	4.6	5	0.496	5.6	6	0.445	3.1
	8.0	5	0.402	2.7	5	0.471	4.0	6	0.439	3.8
	10.0	6	0.397	5.7	6	0.481	7.4	6	0.431	4.4
	12.0	6	0.392	6.3	6	0.478	6.8	6	0.427	5.9
	14.0	5	0.404	4.1	5	0.478	8.4	6	0.425	6.4
	16.0	5	0.387	4.4	5	0.433	6.3	5	0.405	3.5
	18.0	3	0.404	5.3	2	0.455	3.0	4	0.408	5.5
3.66 m	0.3	6	0.431	6.5	6	0.496	6.5	6	0.456	6.0
	1.3	4	0.430	9.2	4	0.497	8.8	6	0.466	10.7
	2.0	5	0.416	6.4	5	0.502	10.5	6	0.460	9.1
	4.0	5	0.428	7.0	5	0.518	8.2	6	0.457	9.6
	6.0	5	0.414	11.9	5	0.502	12.5	6	0.444	12.0
	8.0	6	0.402	7.9	6	0.490	10.4	6	0.434	9.4
	10.0	4	0.409	11.4	4	0.499	16.8	6	0.426	12.5
	12.0	6	0.391	9.2	6	0.458	11.7	6	0.412	10.2
	14.0	6	0.393	8.3	5	0.466	9.6	6	0.411	10.4
	16.0	4	0.419	11.0	3	0.460	13.9	6	0.411	10.8
	18.0	4	0.405	10.0	3	0.450	15.6	5	0.421	11.1
4.57 m	0.3	5	0.419	7.4	5	0.468	8.1	6	0.432	6.9
	1.3	5	0.418	7.9	5	0.511	10.0	6	0.449	6.3
	2.0	6	0.417	6.7	6	0.491	6.5	6	0.444	7.8
	4.0	6	0.411	5.6	6	0.499	8.0	6	0.436	6.1
	6.0	6	0.417	5.6	5	0.497	7.5	6	0.442	7.2
	8.0	6	0.400	6.4	5	0.481	8.6	6	0.421	9.1
	10.0	4	0.391	6.5	4	0.474	11.9	6	0.415	6.4
	12.0	4	0.398	6.1	3	0.440	10.4	5	0.417	7.3
	14.0	5	0.408	3.5	2	0.472	4.6	6	0.407	6.7
	16.0	5	0.393	8.6	2	0.436	3.5	6	0.398	8.2

n : number of observations

rd : relative density

cv : coefficient of variation

Table 5.14 Mean juvenile wood, mature wood and pith to bark relative density observed by initial spacing and height for western hemlock.

spacing	height from ground (m)	juvenile wood			mature wood			pith-to-bark		
		n	rd	cv	n	rd	cv	n	rd	cv
0.91 m	0.3	4	0.436	8.4	4	0.470	14.0	6	0.460	8.5
	1.3	5	0.404	6.8	5	0.460	11.7	6	0.425	7.1
	2.0	5	0.404	3.4	5	0.446	6.3	6	0.420	3.0
	4.0	5	0.392	6.9	5	0.452	12.6	6	0.416	7.6
	6.0	4	0.376	7.7	4	0.431	10.9	6	0.409	8.1
	8.0	6	0.387	8.2	5	0.423	10.6	6	0.400	8.7
	10.0	4	0.393	5.0	3	0.456	2.0	5	0.404	5.7
	12.0	3	0.382	3.8	1	0.428		3	0.387	1.6
2.74 m	0.3	4	0.415	6.7	4	0.433	5.6	5	0.418	5.9
	1.3	5	0.409	7.2	5	0.451	9.6	6	0.421	6.8
	2.0	4	0.391	3.1	4	0.447	6.0	5	0.406	2.9
	4.0	3	0.388	3.4	3	0.452	4.1	5	0.395	4.5
	6.0	4	0.383	5.1	4	0.427	8.3	4	0.395	5.6
	8.0	4	0.382	3.2	3	0.416	6.1	4	0.392	2.2
	10.0	1	0.410		1	0.432		3	0.389	5.7
3.66 m	0.3	2	0.379	10.5	1	0.412		6	0.402	7.5
	1.3	3	0.412	3.0	3	0.430	6.3	6	0.395	7.3
	2.0	3	0.358	3.5	2	0.386	5.5	5	0.372	3.4
	4.0	4	0.385	6.7	1	0.532		6	0.385	11.4
	6.0	4	0.353	5.8	2	0.393	6.3	6	0.366	6.8
	8.0	3	0.377	12.4	2	0.379	16.9	6	0.372	8.0
	10.0	1	0.339		1	0.381		2	0.368	3.9

n : number of observations
rd : relative density
c.v. : coefficient of variation

Table 5.15 Mean juvenile wood, mature wood and pith to bark relative density observed by initial spacing and height for western redcedar.

spacing	height from ground (m)	juvenile wood			mature wood			pith-to-bark		
		n	rd	cv	n	rd	cv	n	rd	cv
2.74 m	0.3	5	0.295	6.8	5	0.318	10.1	6	0.302	6.1
	1.3	5	0.312	3.8	5	0.334	6.5	6	0.309	8.6
	2.0	5	0.323	2.1	5	0.346	4.8	6	0.323	6.9
	4.0	4	0.327	7.0	4	0.331	6.2	6	0.326	5.4
	6.0	3	0.329	4.3	2	0.358	1.1	6	0.325	6.9
	8.0	2	0.325	6.6	2	0.355	3.7	6	0.333	5.6
	10.0							6	0.340	5.2
	12.0	1	0.352		1	0.328		4	0.346	0.8
3.66 m	0.3	3	0.303	8.3	3	0.321	11.3	6	0.303	7.8
	1.3	5	0.303	6.6	5	0.317	7.7	6	0.303	6.9
	2.0	5	0.299	5.7	5	0.305	4.9	6	0.300	4.8
	4.0	3	0.308	4.9	3	0.319	4.7	6	0.308	5.9
	6.0	3	0.318	3.9	2	0.342	6.5	6	0.312	4.7
	8.0	4	0.317	9.7	3	0.341	13.3	5	0.320	8.9
4.57 m	0.3	4	0.277	5.6	3	0.324	5.8	6	0.284	4.5
	1.3	4	0.294	4.8	3	0.319	7.4	6	0.299	3.4
	2.0	5	0.298	3.9	3	0.306	8.0	6	0.300	3.5
	4.0	5	0.305	4.7	2	0.316	5.5	6	0.307	3.8
	6.0	3	0.306	1.5	2	0.324	0.6	6	0.316	3.5
	8.0	4	0.310	2.5	1	0.329		5	0.316	4.0

n : number of observations
rd : relative density
c.v. : coefficient of variation