AN ABSTRACT OF THE THESIS OF

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Stem growth, stem form development, and the dynamics of crown recession in young red alder (*Alnus rubra* Bong.) were studied by analyzing annual growth rings of stems and knots, annual height increments, projected crown areas, and branch diameters. Forty-one trees were sampled from three plantation spacing studies, representing ages 1 through 12 years and square spacings from 0.94 × 0.94 m to 8.6 × 8.6 m. Data from the spacing studies were used to develop non-linear functions describing height-age and diameter-age relationships, and one-year stem diameter growth rates, in relation to spacing and site index. Linear functions were developed that describe the variation in responses to spacing of stem taper, live crown ratios, projected crown areas, stem diameters at live crown bases, and mean branch diameters. At age 27 years, nine trees were sampled from a thinning study; naturally established red alder were thinned at age 14 years to square spacings of 4.2 × 4.2 m and 5.8 × 5.8 m, or left unthinned as control. A non-linear function was developed, describing height-age relationships as affected by thinning intensity. Linear functions were developed that describe the variation in responses to thinning of stem taper, projected crown

areas, stem diameters at live crown bases, heights to live crown bases, and mean branch diameters.

Stem diameter growth of planted red alder increased faster and culminated earlier at intermediate (3 to 4 m) spacings than at wider spacings. Total diameter growth of trees planted at spacings closer than 3 × 3 m and wider than 6 × 6 m was markedly reduced. The greatest height growth was attained by trees planted at 2, 3, and 4 m spacings; significant long-term height growth reductions occurred in trees planted at the high and low ends of the density spectrum. Planting density strongly affected crown development; trees planted at high densities developed short, narrow crowns, and small branches, while trees planted at progressively wider spacings had progressively wider and longer crowns, and larger branches. Stem growth patterns were subsequently affected. Trees planted at high densities developed cylindrical form, and widely-spaced trees developed stems with significant taper.

Results from the thinning study showed that in response to thinning, crown recession slowed, crown areas expanded, more branch wood was produced, and height growth was reduced. These effects were more pronounced in trees thinned to the widest spacing. Further, stem taper increased significantly after thinning. With increased growing space, allocation of growth to crown expansion appears to occur at the expense of stem height growth; thus, the capacity to produce large crowns has important implications for lumber recoverability and wood quality in red alder.

Effects of Planting Density and Thinning
on Growth, Stem Form, and Crown Recession
in Young Red Alder

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LIST OF ABBREVIATIONS

Symbol	Definition	Units
A	Total age of a tree.	years
$A1$	Age of a tree at the beginning of a one-year growth interval.	years
$BRDIA$	Diameter of a branch, outside bark, just above the point of insertion into the stem.	mm
CA	Projected area of a living crown.	m^2
CB	Base of a living crown.	n/a
CR	The ratio of live crown length to total tree height.	m/m (dimensionless)
d	Diameter inside bark at any point on the stem above 1.37 m.	cm
DBH	Stem diameter inside bark at 1.37 m above the ground surface.	cm
$DBHINC$	One-year incremental stem growth at 1.37 m above the ground surface.	$cm\ yr^{-1}$
$D1$	DBH at the beginning of a one-year growth interval.	cm
$DBLC$	Stem diameter, outside bark, at the base of a living crown.	cm
h	Height above the ground at any point on the stem.	m
H	Total tree height.	m
HCB	Height from the ground surface to the base of a living crown.	m
S_{20}	Site index based on height of dominant trees at age 20 years.	m
SPC	The average spacing between stems, based on the number of stems per hectare.	m

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INTRODUCTION

Red alder (*Alnus rubra* Bong.) is an early seral, deciduous hardwood species that is fast-growing and shade intolerant. Its natural range extends from latitude 34° N in southern California to 60° N in southeastern Alaska, generally in a narrow zone within 200 km of the Pacific Ocean, and at elevations below 750 meters (Fowells 1965, Harrington et al. 1994). Disturbed sites with exposed mineral soil, full sunlight, and a good supply of water are readily colonized and dominated by red alder (Franklin et al. 1968). It is the most abundant hardwood in the western Pacific Northwest, and natural stands occupy 1.1 to 1.5 million hectares in this region (Atterbury 1978, Hibbs et al. 1989).

The actinomycete *Frankia* forms nitrogen-fixing root nodules in a symbiotic association with red alder; consequently, red alder stands can grow well on soils where productivity is potentially nitrogen-limited (Hilger et al. 1991, Harrington 1994). However, susceptibility of seedlings to damage by frost, extreme cold, heat, and drought limits the range of this species (Ahrens 1994, Harrington et al. 1994, Shainsky et al. 1994). The most productive red alder sites are in Washington and northern Oregon at elevations below 450 meters, on pedogenically young, deep, well-drained loams or sandy loams of alluvial origin, along stream terraces or flood plains (Fowells 1965, Harrington and Courtin 1994).

Red alder growth and yield research has focused primarily on stand density effects (Puettmann 1990), thinning effects (Hibbs et al. 1994), and height-age relationships (Harrington and Curtis 1986) in natural stands. As illustrated in the following sections, much is known about effects of stand density on growth patterns and stem development in forest trees. However, few studies have examined effects of initial planting density on the development of stem and crown dimensions, and stem form of red alder. Furthermore, effects of post-thinning density on stem form and height growth in red alder are not well understood. The goal of this study was to examine the effects of initial planting density and post-thinning density on stem diameter and height growth, stem form (taper), and live crown recession in young red alder trees.

Some Growth Characteristics of Red Alder

In the Pacific Northwest, young red alder is one of the most rapidly-growing species where soil moisture, temperature, and light conditions are favorable. Height increments up to 1.5 meters per year for the first 15 to 20 years are common in this species (Zavitkovski and Stevens 1972); maximum height growth rates of more than 3 meters per year have been documented in 2- to 5-year-old seedlings growing on productive sites (Harrington and Curtis 1986). By 10 years of age, individual trees attain up to one third of their total mature height (Newton and Cole 1994), which commonly varies from 24 to 36 meters by 60 to 90 years of age (Harlow et al. 1979). Mature red alder can reach a diameter at breast height (*DBH* is stem diameter at 1.37 m above the ground surface) of 90 cm or more (Harlow et al. 1979).

Due to its early rapid growth, red alder produces biomass very fast during the first 20 years of stand development; production is at a maximum between 10 and 15 years. This early rapid growth leads to a rapid accumulation of stand volume. In a study of fifty naturally-regenerated red alder stands, the maximum observed aboveground biomass was 240 metric tons per hectare in a closed-canopy, 33-year-old stand (Zavitkovski and Stevens 1972).

Annual shoot growth of red alder is indeterminate (DeBell and Giordano 1994); that is, not all shoot and leaf primordia are formed in the previous year's bud, and growth can be sustained during a growing season while environmental conditions remain favorable (Harrington et al. 1994). Compared to determinate growth in species of the genus *Acer*, indeterminate height growth has been found to give young, suppressed trees of the genus *Acer* a capacity for rapid stem elongation in response to a sudden increase in light (Sakai 1990). Generally, annual height growth is greater in indeterminate species than in determinate species, and indeterminate growth may represent a successful competitive strategy in trees that colonize early successional sites (Sakai 1990).

Branch meristems of trees, which are initiated in the axils of leaves, can either grow immediately to form sylleptic shoots, or they can develop a bud that overwinters and grows the following year (Wilson 1984). Young red alder regularly forms sylleptic shoots initiated in axils along the stem between two successive years of height growth (i.e., between annual nodes). Older trees produce fewer sylleptic branches; this branching pattern enables young trees to display a large leaf area, and probably contributes to early, rapid growth. Branches that develop from overwintered buds are usually longer-lived and attain a greater diameter than the sylleptic shoots (DeBell and Giordano 1994). They are initiated near the

termination point of annual stem elongation (defined as annual nodes throughout this thesis), and provide a means for determining a single year's height growth.

Stand Density Effects: Growth and Stem Development

Inter-tree competition influences the growth, structure, and volume of individual tree crowns (Perry 1985, Kikuzawa et al. 1986). In young, even-aged stands with uniform spacing (e.g., plantations), tree crowns are similar in size and shape; trees growing in the open have full, symmetrical crowns with live limbs and foliage extending almost to the ground. However, as trees grow, crown closure occurs and the lower branches of trees become shaded. Because shaded leaves have lower photosynthetic rates, the lower branches can contribute little or nothing to stem growth. The resulting decrease in net photosynthesis within the lower crown reduces the supply of available carbohydrates, leading to reductions in root growth and to decreased cambial activity along the lower stem (Kramer and Kozlowski 1979). If net photosynthesis of an entire branch is zero, the branch will die because it will not be supported by carbohydrates from the rest of the tree (Millington and Chaney 1973, Wilson 1984).

Crown closure occurs sooner in dense stands than in stands where stems are widely-spaced; competition for light among more closely-spaced trees results in earlier mortality of lower branches and recession of the live crown base. A reduction in crown volume results as productive foliage becomes limited to the upper layers of a crown (Kikuzawa et al. 1986), and a smaller leaf area is maintained per tree (Rook et al. 1985). This reduction in the photosynthetic surface of a tree has a feedback effect; root and stem growth are further decreased, causing reductions in absorption of water and minerals by the roots, and

in the supply of photosynthate from the foliage, thereby accelerating a decline in growth (Kramer and Kozlowski 1979). Thus, in stands where inter-tree competition is intense (e.g., at high stem densities), resource allocation to each tree is limited. Furthermore, as a tree grows taller, and if an equal or smaller amount of carbohydrates are produced by the foliage each year, the photosynthate will be spread in progressively narrower increments over an increasing stem surface area (Bormann 1965). Therefore, compared to widely-spaced stands, competition at close spacings can diminish the average diameter increment and biomass of individual trees (Kikuzawa et al. 1986, Auclair and Bouvarel 1992). In addition to small, unproductive crowns, slow stem diameter growth, and decreased root growth, closely-spaced trees tend to develop small branches relative to more widely-spaced trees.

Trees planted at low stem densities (wide spacings) have larger and longer-lived branches, and individual trees develop with large live crown ratios (crown ratio is total live crown length divided by total tree height). Consequently, leaf area and light capture are greater, allowing large-crowned trees to produce greater amounts of photosynthate than small-crowned trees (Rook et al. 1985). Compared to closely-spaced trees, cambial activity and radial growth are greater toward stem bases in widely-spaced individuals. Ratios of upper to lower stem diameters tend to be smaller in trees grown at wide spacings, as explained below.

Because individual trees growing at different spacings exhibit characteristic differences in the structure of their crowns, stem diameter growth is affected; this leads to the development of predictable differences in the distribution of diameter growth along the stem. The thickness of an annual ring is at a minimum in the topmost internode (an internode is the segment of a stem between two successive annual nodes) of a large-crowned

tree; diameter increment increases in the direction of the stem base, approaching a maximum near the height on the stem where foliar volume or mass is greatest (Farrar 1961, Hall 1965, Fujimori and Kiyono 1986). Below the crown base, diameter increment begins to decrease again. If the base of the live crown has begun to recede, ring width decreases adjacent to the lower crown and below that point along most of the branch-free bole (Figure 1). Increment then becomes thicker at the base of the stem, leading to a characteristic known as butt-swell. Because the crown of an open-grown tree can extend downwards to the stem base, annual ring width can increase downwards along the entire length of the bole (Farrar 1961).

In contrast, in closely-spaced trees, the region of maximum annual diameter growth occurs nearer to a tree's apex (Farrar 1961); that is, at a greater relative height on the stem (where relative height is the ratio of the height at any point on the stem to total tree height). Annual ring thickness narrows rapidly below this point, and butt-swell may be slight or nonexistent (Figure 1). Extremely suppressed trees can even exhibit discontinuous or missing rings in the branch-free bole (Bormann 1965).

Stem form can be defined as the rate of change in stem diameter with increased tree height, relative to some lower stem diameter [generally relative to *DBH* (Larson 1963, Kozak et al. 1969)]. This decrease in stem diameter from the base upwards is also known as taper (Ford-Robertson and Winters 1983); it is controlled by the size and vigor of the crown, its distribution along the stem, and by the growth dynamics associated with branch mortality (Farrar 1961, Larson 1963, Maguire et al. 1990). Because the size of an individual tree is the result of the sum of all annual increments, it follows that the form of a tree stem is determined by the pattern of allocation of successive layers of annual wood. If the width
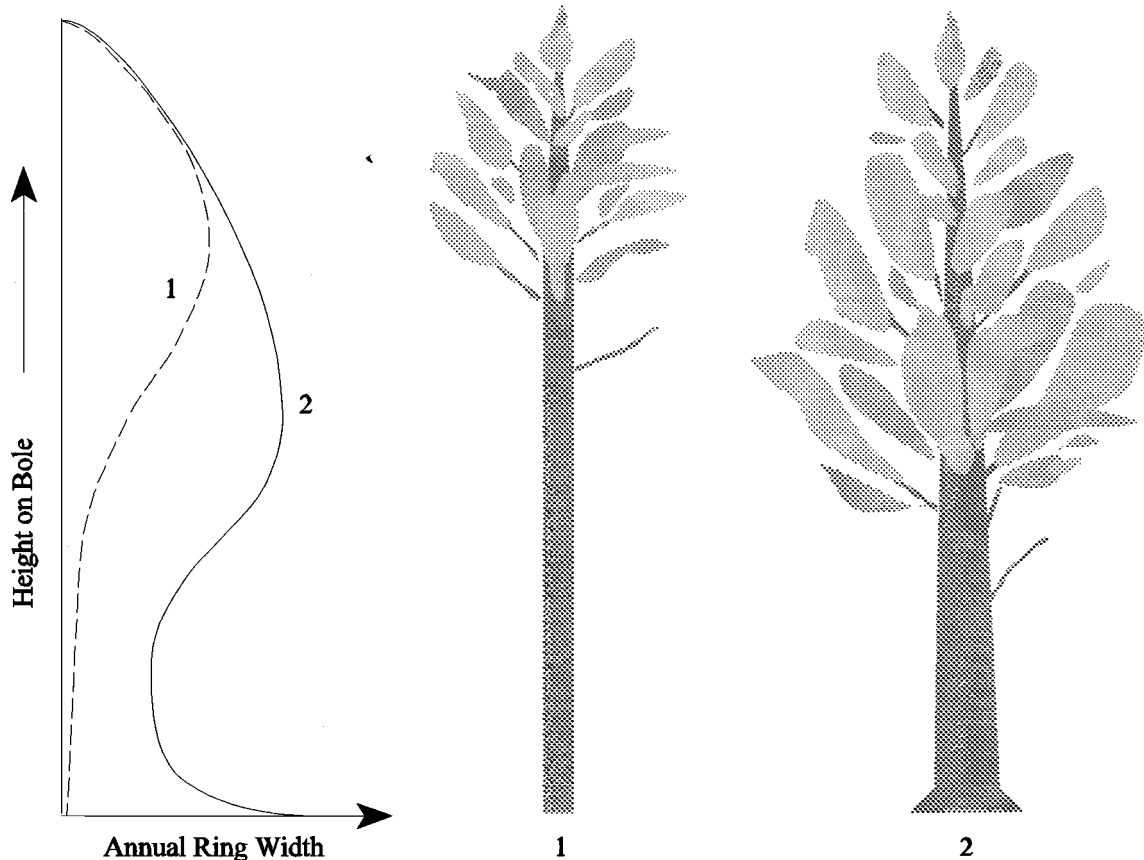
Figure 1. Longitudinal variation in the thickness of the most recent annual sheath of wood in relation to a ring's position in (1) a small-crowned, closely-spaced tree, and (2) a large-crowned, widely-spaced tree. Ring width peaks near the base of a live crown. The horizontal scale of the graph is greatly exaggerated.

of each layer increases from the apex of a tree to its base, as is true for open-grown individuals, or if the width of each layer is uniform from apex to base, then a stem will be tapered (Farrar 1961). Because the point of maximum ring growth shifts continually upwards as lower limbs die and crowns recede, trees with small live crown ratios exhibit a greater decrease in annual ring width below the base of the live crown. Therefore, with increasing stand density and decreasing crown ratio, stems become more cylindrical (less tapered); widely-spaced, long-crowned trees exhibit a greater degree of taper (Figure 1).

The relationship of stem form with stand density and crown ratio is probably most predictable for shade-intolerant species (Larson 1963). For example, at a high stem density (approximately 26,000 stems ha^{-1}), birch trees (*Betula ermanii*, a fast-growing, shade-intolerant species) developed a rapidly ascending, shallow canopy. By age 16 years, suppressed individuals exhibited very little stem diameter growth, but continued to grow in height (Hara et al. 1991). Thus, these trees produced narrow, cylindrical stems. In a true fir (*Abies* spp., shade tolerant and slow-growing) stand of similar density (approximately 30,000 stems ha^{-1}), trees produced wide, deep crowns. By age 25 years, suppressed individuals exhibited little height growth, but continued to grow in diameter (Hara et al. 1991). As illustrated by the contrast in growth patterns of theses two species, patterns of suppressed growth can vary with the shade tolerance and successional status of a species.

Stand respacing (thinning) increases the space available to residual trees for growth and expansion of root systems and crowns. Subsequently, branch longevity, branch size, crown width, and leaf growth can increase. An increase in the leaf area maintained per tree results in greater cambial growth. Because stem diameter increment approaches a maximum near the height on the stem where foliar mass is at a maximum (Farrar 1961, Hall 1965, Fujimori and Kiyono 1986), and because greater branch longevity results in the occurrence of this maximum at a lower relative height on stems of respaced trees, cambial activity and radial growth will be greater toward stem bases in thinned versus closely-spaced trees (Larson 1963). Thus, thinning causes xylem increment to be redistributed along the stem (Larson 1963, Kramer and Kozlowski 1979). Furthermore, cambial activity and radial growth tend to increase more toward stem bases than in the crowns of thinned trees (Kramer

and Kozlowski 1979). It follows that widely-spaced thinning can cause a tree to develop a bole with a high degree of taper (Larson 1963).

In contrast to the well-documented effects of spacing on radial growth, many authors contend that height growth is not affected by stand density, except at very close spacings (e.g., Mitchell 1975, Lanner 1985). In tree species with determinate growth, differences in the responses of height and diameter growth to spacing have been explained by differences in how apical and lateral meristems develop, and by differences in carbohydrate sink strengths of elongating shoots and the active cambium (Lanner 1985).

In determinate species, all shoot primordia that will elongate during a given year are formed in the previous year's terminal bud. Consequently, the theoretical upper limit to annual height growth in determinate species is fixed by environmental factors affecting growth during the previous year (Wilson 1984); if growing conditions are favorable, a large terminal bud will develop containing many stem units. According to Lanner (1985), shoot elongation during the current year is little affected by environmental conditions, because growing shoots have a higher priority for carbohydrate allocation than the active cambium, and are a strong sink for carbohydrates exported by the foliage. Therefore, according to this theory, a terminal shoot in a determinate species gets the photosynthate necessary to achieve its growth potential.

In contrast to apical meristems of determinate species, the numbers of cambial initials in lateral meristems are not fixed (Lanner 1985). Xylem increment (diameter growth) has a low carbon allocation priority; stored carbohydrate is distributed first to stronger carbon sinks such as new foliage and shoots (Waring and Schlesinger 1985). Thus, the availability of resources during a growing season strongly affects diameter growth; if more resources

become available, potential annual shoot growth remains fixed, and diameter growth will increase (Lanner 1985).

I argue that this theory does not adequately explain an insensitivity of height growth to spacing in determinate tree species, though it may account for a greater sensitivity of diameter growth to resource limitations during a growing season. For example, the number of shoot and leaf primordia formed in the terminal bud of a determinate species are influenced by a current year's resources (Cannell et al. 1976), but both the size of leaves and the amount of shoot elongation are influenced by the amount of photosynthate produced during the year of growth itself (Little 1974). Thus, if either close or wide spacings create an unfavorable environment for photosynthetic activity during a growing season, height growth of a determinate species may be negatively affected. If determinate height growth can be affected by spacing, then height growth of an indeterminate species must be sensitive to spacing, because indeterminate species exhibit sustained height growth during periods when environmental conditions are favorable.

Additionally, competition for water among closely-spaced trees can lead to reduced water uptake per tree, resulting in limited rates of leaf expansion (Schulze et al. 1987). Production of new photosynthetic surface is then reduced, limiting bud development and the future growth potential of a determinate species; height growth during a current growing season of both determinate and indeterminate species may also be adversely affected.

Contrary to the common belief that stand density does not affect height growth, Sjolte-Jørgensen (1967) reviewed numerous plantation spacing studies that showed reductions in height growth of 15- to 60-year-old conifers (Pinaceae) at planted spacings closer than 2 meters. Few studies reviewed by Sjolte-Jørgensen (1967) tested effects of

spacings greater than 4 meters, and many trials were established in a narrow range of spacings between about 2 and 4 meters. Within this range of spacings, height growth differences may be small, and can potentially be difficult to detect (Lanner 1985). Furthermore, the magnitude of density effects on growth, and the ages and spacings at which these effects become manifest, vary by species. Spacing effects also will vary with site properties; for example, height growth may be sustained longer at close spacings where soils are fertile and a supply of water is abundant (Sjolte-Jørgensen 1967). However, several other studies appear to contradict Lanner's (1985) argument, and are reviewed below.

Auclair and Bouvarel (1992) described height growth and biomass yield of a hybrid poplar (*Populus trichocarpa* × *deltoides*) coppiced at 1-, 2-, and 3-year rotations. At all coppice intervals, height growth, stem diameter growth and biomass production decreased per shoot across a range of densities from 2000 to 20,000 cuttings per hectare.

Curtis and Reukema (1970) measured stem and crown dimensions in a 43-year old plantation spacing test. *Pseudotsuga menziesii* (Douglas-fir, a determinate species) seedlings had been planted at five square spacings, from 1.22 through 3.66 m, with a 0.61 m increase in spacing distance for each treatment. The trees in this study grew under the influence of competition long enough to differentiate into dominant, codominant, intermediate, and suppressed crown classes. Within a crown class and among treatments, crown width and crown length increased from the narrowest to the widest spacings. Height and stem diameter growth also showed positive trends with decreasing stem density (stems per unit area). Because soil properties and topography show little variation at the study site, changes in tree growth patterns, which occurred after crown closure, were clearly due to the effects of spacing.

In apparent contrast to these results, Scott et al. (1992) found that both total height and *DBH* of seven- to nine-year-old Douglas-fir trees decreased as stem density decreased. They measured trees planted at the following densities: 2965, 1853, 1359, 890, 593, and 296 stems ha^{-1}. However, several studies show that tree height may be positively correlated with increasing stand density during early stages of stand development, and that this trend reverses over time.

For example, Hogg and Nester (1991) studied growth of *Pinus caribaea* in a plantation spacing test and a thinning experiment in coastal Australia. In the spacing test, dominant height (average height of the tallest 50 stems ha^{-1}) and planting density were positively correlated up to age 2.4 years. Tallest trees occurred at the densest spacings in a range of densities from 740 to 3090 stems ha^{-1} (equivalent to a range in spacings from 3.7 to 1.8 m). At age 4.5 years, there was no statistical relationship between height and planting density; from ages 5.5 to 10.3 years the trend reversed, so that a significant negative correlation (at the 5 percent probability level) existed between height and planting density.

In Hogg and Nester's (1991) thinning experiment, trees were thinned at age 3 years to densities ranging from 200 to 1000 stems ha^{-1} (spacings of 7.1 to 3.2 m). As in the plantation test, mean height of dominant trees was positively correlated with stem density for two years following treatment. In three successive remeasurements from four to six years after thinning (ages 7 to 9 years), height was negatively correlated with the number of stems ha^{-1}. Taller trees occurred at wider spacings. The results of this study showed that competition began to negatively affect height growth by age 4.5 years in the plantation spacing study, and that inter-tree competition in the unthinned stand began to depress height growth about three years after thinning. Hogg and Nester attributed the "delayed effect" of

thinning to the amount of time required for nutrients, water, and light to become limiting to growth; a peripheral thinning study (Hogg and Nester 1991) showed that the magnitude of the relationship between height growth depression and stand density was even greater on a site with inherent resource limitations.

Adlard et al. (1992) described effects of planting density on growth of two *Eucalyptus* species. Trees were planted in a square spacing pattern at a range of densities from 400 to 10,000 stems ha^{-1}; heights and stem diameters were measured twice per year for four years. There was a "wave effect" in early growth, where height increase was stimulated at close spacing in the first year; this effect was reversed by the fourth year so that height growth of *Eucalyptus* trees was greatest at the widest spacing. A similar trend was found by Hogg and Nester (1991) in *Pinus caribaea* (see above), and by Knowe and Hibbs (in preparation) in *Alnus rubra* (see the following section). Plots of *Eucalyptus* tree size on stem density showed a sigmoidal distribution; a zone of straight line response occurred only at the closest spacings where trees were very small. However, a trend of increasing tree size with decreasing stand density was apparent at the time of final tree measurements. Heights, stem diameters, and volumes all were greatest at the widest spacing. Ratios of total height to *DBH* were considerably higher at narrow spacings. This suggests a greater degree of stem taper at wide spacings, and imminent density-induced mortality at narrow spacings (Adlard et al. 1992, Waring 1987). Because early height growth stimulus at close spacing is probably a short-term phenomenon, the "wave" effect may not be important for plantation management (Adlard et al. 1992).

To summarize this section, tree growth is highly mediated by competition for available resources, but observed growth patterns result from interrelated effects of site

quality, tree age and stand density. Furthermore, species vary according to their shade tolerance in the way they allocate growth in response to competition. For example, stem height growth may be less suppressed and stem diameter growth may be more suppressed in a fast-growing, shade-intolerant species, than in a slow-growing, shade-tolerant species (Hara et al. 1991).

However, after accounting for differences in site productivity, stand density (spacing) causes the development of predictable morphological responses within a species over time. Following a relatively brief period (perhaps three to nine years) where studies have shown that growth is stimulated at high stem densities, individual trees growing in dense stands often exhibit suppressed height and diameter growth. Small, unproductive crowns develop as competition for light among closely-spaced trees results in mortality of lower branches and recession of the live crown base. This leads to the development of narrow, cylindrical (untapered) stems. Trees grown at wide spacing respond by expanding their root systems and crowns. Branch size and longevity of open-grown trees will be greater, relative to individual trees grown at high stand densities; thus, cambial activity and radial growth will be greater toward stem bases in widely spaced individuals. At extremely wide spacing height growth may be reduced, and stems develop with a high degree of taper.

Results of Some Previous Red Alder Spacing Studies

Plantation spacing studies have shown that early height growth of red alder is, like *Eucalyptus* and *Pinus caribaea*, characterized by a temporal "wave"; annual height growth at high planting densities peaks at a younger age than at wide spacings (DeBell and Giordano 1994, Knowe and Hibbs, in prep.). Up to age 2 to 4 years, height growth is

greater at the highest densities, in a range of spacings from less than 1 meter to about 5 meters (Knowe and Hibbs, in prep.). This is a transient phenomenon; the greatest height growth has been found at increasingly wider spacings, up to 4 or 5 meters, through the first seven years after plantation establishment (Knowe and Hibbs, in prep.). However, relatively poor stem growth has been observed for up to 10 years in trees planted at spacings wider than 4 × 4 m (DeBell and Giordano 1994). Compared with trees at dense spacings, reduced aboveground biomass production has been documented in open-grown, four-year-old red alder (Giordano and Hibbs 1993).

In conjunction with slow height growth, large branches and multiple stems occur with greater frequency in widely-spaced red alder, and may account for a greater proportion of biomass produced by a tree (Giordano and Hibbs 1993). Furthermore, a greater energy investment in nitrogen fixation could partly explain decreased allocation to stem growth at wide spacings (Bormann and Gordon 1984).

Planting density also affects diameter growth of red alder. Knowe and Hibbs (in prep.) described a "wave" or "ripple" effect in diameter growth similar to trends in height growth delineated above; maximum diameter growth was achieved at an earlier age in trees growing at the highest densities, in a range of spacings from less than 1 meter to about 5 meters. However, within this range of spacings, quadratic mean diameter (diameter of the tree of average basal area) was significantly smaller at higher densities. Other studies have shown that stem diameter of red alder increases with increasing distance between stems, within a range of planted spacings from 0.5 to 2.7 meters (Bormann and Gordon 1984, DeBell and Giordano 1994).

Hibbs et al. (1989) reviewed results of seven respacing studies conducted in the Pacific Northwest. Naturally-regenerated red alder stands were thinned to a range of densities from 272 to 1811 stems ha^{-1} (analogous to square spacings from 6.1 to 2.3 meters). These studies consistently showed a positive response in *DBH* increment with thinning (e.g., Smith 1983, Bormann 1985, Hibbs and Emmingham 1994). However, information from these studies had limited applicability to red alder management due to lack of treatment replication, application of thinning treatments long after crown closure, measurements of thinning responses taken many years after treatment, and inconsistencies in the timings of treatments (Hibbs et al. 1989). Two thinning studies warrant further discussion.

In a replicated study (Smith 1983), a 10-year-old red alder stand was thinned to nominal distances of 1, 2, 3, 4, and 5 meters. Three years after treatment, root collar diameter, *DBH*, diameter at 2.7 m, crown width, and live crown ratio all increased across the range of spacings. Ratios of total tree height to *DBH* decreased significantly across the gradient from unthinned control plots to the widest spacing (Smith 1983), suggesting greater stem taper in thinned trees. Although height growth was reduced appreciably at wider spacings, height differences among treatments were not statistically significant (Smith 1983).

Hibbs et al. (1989) thinned a fourteen-year-old red alder stand. Treatment plots were respaced to densities of 4.2 × 4.2 m and 5.8 × 5.8 m, or left unthinned as control plots. Height growth reductions in thinned plots were apparent five years after treatment, with the greatest reductions found at the widest spacing. After five years, stem diameter growth (at 1.3 m) had increased significantly with respacing, and average basal area per tree was greatest at the widest spacing (Hibbs et al. 1989).

Ten years after thinning, height growth increment had recovered in thinned plots, but the trend in reduced height with increasing distance between trees was still evident (Hibbs et al. 1994). However, because height measurements were taken using an indirect trigonometric method, the variance (mean squared deviation) was high, and statistical differences were not apparent (Hibbs et al. 1994). The quadratic mean diameter was still greatest at the widest spacing after ten years. Rates of live crown recession were greatest in unthinned plots, and lowest in widely-spaced trees, averaging 0.45 and 0.1 m yr^{-1}, respectively (Hibbs et al. 1994).

To summarize this section, few studies have examined effects of planting density on development of stem and crown dimensions of red alder. Recent results (Knowe and Hibbs, in prep.) have indicated that total tree height and *DBH* were greater at wider spacings by age 7 years; studies encompassing a wide range of spacings are rare. There is a scarcity of information regarding effects of stem density on changes over time in live crown ratio; this attribute of tree vigor is used extensively as a predictive variable for stem diameter growth in numerous other tree species (Hann and Larsen 1991).

Thinning clearly increases lower stem diameter growth, and the study by Hibbs et al. (1994) suggests that thinning also reduces the rate of live crown recession. Due to high variability associated with indirect measurements of tree heights, documentation of height growth reduction caused by thinning has been inconclusive. Furthermore, little is known of the relationship between either planting density or thinning, and the development of stem form in managed red alder stands.

Objectives

To optimize growth at the stand level, quality constraints must be applied at the individual tree level. The number of stems per unit area (trees ha^{-1}) at which tree and stand growth are optimized depends on silvicultural objectives. If sawlog production is the goal, then a balance needs to be achieved between stem growth rates and factors that affect quality such as size and spacing of branches, branch-free bole length, and stem taper (Hibbs et al. 1992, Plank and Willits 1994). These factors are highly spacing-dependent.

This study was designed to examine effects of a wide range of planting densities and of thinning on stem diameter and height growth, and stem form development in young red alder. Effects of spacing on dynamic attributes of individual tree crowns were also studied. These are: branch mortality and crown recession, projected crown area, and branch diameters. Specific objectives are summarized below:

1. For a range of planted spacings from less than 1 × 1 m to greater than 6 × 6 m, reconstruct height growth, diameter growth, and crown recession for the entire life-history of individual destructively-sampled trees.

2. At a respacing installation with a well-documented record of stem diameter growth and live crown recession, reconstruct height growth for the entire life-history of individual destructively-sampled trees.

3. Develop regression equations to model the components of tree growth (described in objectives 1 and 2) over time, as functions of planted spacing or thinning intensity.

4. Develop taper functions that quantify the effects of planting density and thinning on stem taper.

5. Examine crown and branch size at the time of sampling, to determine effects of spacing on current crown dimensions.

METHODS

A total of fifty red alder trees were measured at four sites in 1993 (Figure 2). Sites were chosen to represent a wide range in ages and controlled spacings. A range in productivity was also represented, as estimated by Harrington and Curtis' (1986) site index (base age 20) equation. Three of these sites are red alder plantation spacing trials; the fourth site is a naturally regenerated, even-aged stand of pure red alder that was thinned 14 years after establishment. All of these sites are ongoing growth studies; because the methods in the current study involved destructive measurements, sample trees were selected from homogeneous portions of plot buffer strips, to avoid disturbance of plot interiors.

Study Area Descriptions

Cascade Head Spacing Study

This study area is located in the central Oregon Coast Range, approximately 5 km northwest of Otis, in Cascade Head Experimental Forest. It is situated at an elevation of 330 m on a headland of basaltic origin (Snavely and MacLeod 1981), in a transitional finger between the Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) zones (Franklin and Dyrness 1973). Average annual precipitation is 250 cm, occurring primarily as rain or cloud condensation between October and May (Giordano and Hibbs 1993).

The spacing trial was established in 1985 by the Department of Forest Science of Oregon State University; one year prior to planting it had been clearcut and burned. One-year-old red alder and Douglas-fir seedlings were planted in 0.073 ha treatment plots

Figure 2. Map of western Washington and western Oregon showing the locations of the three red alder spacing studies and the Olney thinning study.

composed of pure and mixed species. Pure red alder plots are spaced at 3 × 3 m and 4.2 × 4.2 m. The mixed composition plots contain 75, 50, 25, and 12 percent red alder, with all trees planted at 3 × 3 m spacings. Each treatment was replicated three times in a randomized complete block design (Radosevich and Hibbs 1988).

Height growth of Douglas-fir is generally much slower than height growth of red alder for about the first 15 years after establishment (Miller and Murray 1978). At Cascade Head, red alder had dramatically overtopped the Douglas-fir by age 7 years. Thus, plots that contained mixtures of the two species were regarded as representative of a red alder monoculture planted at the following square spacings: 3.46, 4.2, 6, and 8.6 m. Sample trees were in their eighth or ninth growing season at the time of measurement.

Centralia Spacing Study

This plantation spacing trial is approximately 7 km northwest of Centralia in southwestern Washington, at the Centralia Coal Mine, which is managed as an open-pit mine by Washington Irrigation and Development Company. The site is located at the southeastern edge of the Puget Sound area in the western hemlock zone (Franklin and Dyrness 1973); prior to mining, vegetation consisted mostly of second-growth stands of Douglas-fir and red alder (Heilman 1990). Elevation of the study area averages about 150 m, and average annual precipitation is about 120 cm. Most of the precipitation occurs as rainfall, from late October through mid-June (Heilman 1990).

Red alder was planted on reclaimed mining spoils. Considerable variability exists in soil properties; both topsoil and subsoil were used as surface layers during the mine reclamation process. High concentrations of salts in the top 90 cm of spoil caused pockets

of extremely poor growth and mortality in some areas (Heilman 1990); thus, it was necessary to avoid these pockets during the selection of sample trees. However, large blocks appeared unaffected by salt toxicity, and red alder has grown well.

The spacing trial was established in 1982; one-year-old red alder seedlings were planted in fifty-two 0.1 ha treatment plots, established in three randomized blocks at six levels of square spacing: 1 × 1 through 6 × 6 m. The number of plots established per spacing treatment were: 4, 12, 12, 8, 9, and 7, for square spacings of 1, 2, 3, 4, 5, and 6 m, respectively. Sample trees were 12 or 13 years old at the time of measurement.

Apiary Spacing Study

This study area is in the northeastern Oregon Coast Range, about 10 km southwest of Apiary, and 17 km south of the Columbia River. It is located at an average elevation of 550 m on land owned by Stimson Lumber Company, in the western hemlock zone (Franklin and Dyrness 1973). Average annual precipitation is 150 cm, occurring primarily as rain between October and May, and the January mean minimum temperature is 0^0 C (Franklin and Dyrness 1973). Prior to plantation establishment, a second-growth Douglas-fir forest dominated the site (Bormann and Gordon 1984, DeBell and Giordano 1994). The forest was cleared and burned in 1973-1974 due to a root rot (*Phellinus* spp.) infestation, and red alder spacing trials were established during the winter of 1974-1975 (Bormann and Gordon 1984).

Spacing treatments were established in two randomized blocks. Within each block, two or three replications were established at five initial spacings: 0.6 × 1.2 m, 1.2 × 1.2 m, 1.2 × 1.8 m, and 2.7 × 2.7 m. However, by age 7 years, about 5 percent of the alder trees

had died, presumably due to frost damage (Bormann and Gordon 1984) and effects of competition. For the analyses in the present study, initial stem density (stems per unit area) was reduced by 5 percent to account for early mortality, and converted to the following square spacing equivalents: 0.94, 1.26, 1.57, 1.88, and 2.81 meters. Sample trees were 19 years old at the time of measurement, but only the first seven years of growth were analyzed in this study, due to variable spacing caused by high rates of mortality after age 7 years.

Olney Thinning Study

The thinning study is located approximately 20 km southeast of Astoria, in the northwestern Oregon Coast Range at an elevation of 60 m. Vegetation is transitional between the Sitka spruce and western hemlock zones (Franklin and Dyrness 1973). Annual precipitation averages 150 to 200 cm, and occurs as rainfall, primarily during winter months (Hibbs and Emmingham 1994). Although the climate is cool throughout the year, sub-freezing temperatures are not common (Hibbs and Emmingham 1994).

The site was logged in 1965, and a dense, even-aged stand of red alder became established from natural seed after the disturbance (Hibbs et al. 1989). When the average tree age was 14 years, twelve treatment plots and three untreated plots (control) were established as 0.2 ha squares. Treatment plots were thinned to 4.2 × 4.2 m and 5.8 × 5.8 m spacings. Average spacing in the control plots was 2.4 × 2.4 m at the time the study was initiated (Hibbs et al. 1989). Both mechanical and herbicide-injection thinning methods were used; in some of the chemically treated plots, uninjected trees were killed by the herbicide, leading to heterogeneous spacing. During sampling in the current study, these pockets of mortality were avoided. Sample trees averaged 27 years old at the time of measurement.

Selection of Sample Trees

Individual trees, rather than plots, were treated as the experimental units in the analyses presented in this thesis. This sampling method is less conservative than an approach that utilizes mean values of trees within a plot (Mead et al. 1993). It was justified because precision estimates of individual-tree growth patterns are obtained from destructive stem analyses; however, considerable time expenditures in the measurement process limit the total sample size. To avoid confounding effects of spacing with effects of environmental homogeneity within a plot (cf., Sakai et al. 1968), trees were sampled from as many different plots within a treatment and among blocks as logistically possible.

Specific criteria were used to select individual trees for sampling, so that a measure of subjectivity was unavoidable. Trees were selected from within plot peripheries, and where spacing between a sample tree and its neighbors was uniform and equivalent to the spacing representative of a given treatment. To obtain unbiased estimates of stand density effects on growth and stem form, it was necessary to sample trees without injury, damage, or various attributes of impeded growth. Thus, features that caused a tree to be rejected from analysis include: top die-back or top breakage, multiple stems, stem damage caused by rubbing of elk or deer antlers, girdling or damage caused by insects or birds, and any abiotic injuries that might serve as entry points for wood decay fungi.

Data Collection

A total of eighteen trees were sampled at Cascade Head, fourteen trees at Centralia, nine trees at Apiary, and nine trees at Olney (Table 1). Field measurements of stem and crown dimensions were accomplished from May through September 1993. Destructive

Table 1. The range of spacing treatments at the four study sites, and the number of trees sampled per spacing.

Installation	Spacing (m)	Trees Sampled
Cascade Head	3.0	6
	3.46	2
	4.2	5
	6.0	4
	8.6	1
Centralia	1.0	2
	2.0	2
	3.0	3
	4.0	3
	5.0	2
	6.0	2
Apiary	0.94	2
	1.26	1
	1.57	2
	1.88	2
	2.81	2
Olney	2.4	3
	4.2	3
	5.8	3

measurements were completed in the laboratory during autumn 1993. The following variables were measured or calculated:

1.   Annual height growth increments were determined for all sample trees to the nearest cm, from annual branching patterns. During the period of rapid height growth, red alder crowns exhibit an excurrent growth form (Harrington et al. 1994); due to strong apical control, the terminal leader elongates more than the lateral branches below it, producing a tree with a single central stem (Ford 1985, Hashimoto 1990). The largest diameter branches produced by a tree are initiated near annual nodes (the termination point of annual stem

elongation), and the termination of a year's height growth occurs several centimeters above the highest of these proleptic branches (see pages 3-4). Often bud scale scars and a reduction in stem diameter are visible at this point, marked by a reduction in the number of annual rings. Along the branch-free bole, groups of large branch scars indicate the terminus point of annual stem elongation. In all cases, estimates of annual height growth were verified by annual ring counts above and below an annual node.

2. Annual stem diameter growth of all sample trees was measured to the nearest mm (to the nearest 0.5 mm for some extremely narrow-ringed trees) at the following points: stem bases (15 to 20 cm above ground level), 1.37 m (breast height), 3.35 m, 5.35 m, every 1.5 to 2 meters above that point depending on tree height, at the base of the live crown (defined below), and along the stem within the crown at 1.5 to 2 meter intervals.

At Cascade Head, no trees could be felled; two increment cores were taken perpendicular to each other, a few centimeters below and above the points described. At the three other sites, trees were felled, stems were cut cross-sectionally, and four radii measured at each point. Radii were averaged and multiplied by 2, to obtain stem diameters at all points throughout the life of a growing tree.

Annual rings can be indistinct and ring counts need to be made with considerable care. However, false or partial rings are not common in red alder, and missing rings occur very infrequently (DeBell et al. 1978), except, perhaps, in extremely suppressed trees. Increment cores from the Cascade Head trees were sawn into 1.5 mm-thick radial strips, using a densitometry sample saw made by Hubert Pneumatic Instruments (1987). To determine the location of annual rings, a narrow beam of light was projected through each

translucent strip, and a mark was made at each annual ring position to facilitate measurement.

At the three other sites, discs were cut from stems at each measurement point. These discs were then sanded on one side to a smooth, clean surface, to facilitate accurate measurement of ring widths. Generally, no magnification was needed. However, some extremely narrow rings were measured with the aid of a 10-power magnifying lens or a dissecting binocular microscope.

3.   Height to the base of the live crown (*HCB*) in 1993 was measured for all sample trees according to three conventions (cf., Maguire and Hann 1987): (i) Where crowns were symmetrical, *HCB* was measured from the ground to the base of the insertion point of the lowest live limb. (ii) Unproductive branches, below a subjective level of minimum vigor, were not counted as part of the live crown. These branches can be recognized by characteristics such as short second-order (lateral) shoots, and sparse, chlorotic foliage (Farrar 1961). (iii) If a gap wider than about 65 cm occurred near the base of a crown, and if a healthy branch was growing at the base of that gap, the gap was 'filled in' by 'moving' the lower branch upward, to 'create' an even-based, symmetrical crown.

4.   A stem dissection technique was used (Maguire and Hann 1987) to backdate branch mortality in all sample trees from Centralia and Apiary, in order to reconstruct crown lift and past crown ratios. The first seven years of crown lift at Apiary, the first twelve or thirteen years of crown lift at Centralia, and 1993 *HCB*s from Centralia and Cascade Head were included in the dataset.

Heights to branch nodes below the live crown base were measured; segments containing branch nodes were then cut from the bole and sectioned longitudinally through dead branches (knots). The number of growth rings were counted between the stem's inner

bark and the point of discontinuity between stem growth rings and branch growth rings. The point where the branch-stem ring continuity ends corresponds to the year when a given branch has stopped producing rings. The year of branch death can be determined from the point where annual stem rings adjacent to a dead branch begin to bulge toward the center of the tree to encase the dead branch stub (Fujimori 1993). Although the point of ring discontinuity does not correspond specifically with the year of branch death, use of this point in reconstructing crown lift was consistent with the convention of disregarding unproductive branches during measurement of *HCB* (see above).

The maximum possible number of alder knots were sectioned, but, in some instances, knots were so close together that the sectioning process could be implemented only on selected branch stubs. Up to ten branch stubs or knots were sectioned between successive annual nodes; priority was given to all the largest and most recently dead branches, i.e., those branches that had been the most important constituents of crown productivity (cf., Fujimori and Kiyono 1986, Fujimori 1993). Although young red alder has distinct annual nodes, it does not exhibit compact whorls of branches. Thus, criteria used to delineate changes in HCB differed slightly from criteria described for Douglas-fir by Maguire and Hann (1987), as explained below.

The region of a stem between two successive annual nodes is defined here (and on page 5) as an annual internode. Because red alder branches can be initiated throughout the length of an annual internode, their locations do not necessarily coincide with the position of annual nodes (see pages 3-4), i.e., they are not necessarily initiated near the termination point of a single year's height growth. Within an annual internode, a 'whorl' of branches was operationally defined as the point where at least three large branches came together without

substantial gaps (from approximately 65 to 80 cm) between them. Because up to ten knots were sectioned within an annual internode, it was possible for more than one 'whorl' to occur within that segment of a stem between two annual nodes.

To reconstruct past locations of *HCB*, branch mortalities were backdated annually. Backdating began at the base of the live crown measured in 1993, and continued downward to the base of a tree. Within an annual internode, if less than three branches remained alive in a 'whorl', crown base (*CB*) was moved upward to the base of the insertion point of the lowest branch in the next highest whorl, above which all branches remained alive. Red alder branches do not always die in a regular order from the stem base to the crown base, often they die in clusters; thus, *CB* for a given year could occur at a point somewhere between annual nodes. Further, where substantial gaps appeared to have opened in the crown of a tree, *CB* was moved upward to create an even-based crown, consistent with conventions applied during measurement of *HCB* (see above).

For all trees, crown ratio was calculated for each year in the life of a tree, based on measured *HCB*s and tree heights as follows: $CR = \dfrac{H-HCB}{H}$ where *CR* is the ratio (varying from 0 to 1.0) of live crown length to total tree height, *H*, and *HCB* is distance from the ground surface to *CB*.

5.   Branch diameters were measured to the nearest mm outside the bark, just above the swelling at the insertion point. Four to ten live branches were measured on all sample trees; they were selected at evenly-spaced, vertical intervals from the top to the bottom of a living crown. A second criterion was selection of branches whose horizontal projection described the circumference of a crown. These selection criteria were mandated by the requirements

of another study (C. Cluzeau, unpublished) with the objective of describing the geometry and growth of red alder crowns.

6. Four crown radii were measured per tree at Cascade Head, eight radii were measured per tree at the other three sites. All crown radii were measured as the maximum horizontal extension of a crown along the lines between a sample tree and its nearest four or eight competitors (the nearest tree per quadrant at Cascade Head and the nearest two trees per quadrant at the three other sites). Where mortality caused gaps in the canopy, the angle between two neighbors was bisected, and a crown radius measured.

From the measured crown radii, projected crown areas (m^2) were calculated for each sample tree by two methods: (i) as the area of a circle with a radius equal to the geometric mean crown radius, and (ii) as the area of a polygon formed by the sum of the areas of the triangles described by measured radii. A paired-sample t test was used to test whether mean crown areas were different using the two different methods; i.e., to test the two-tailed hypotheses that H_o: $\mu_1 = \mu_2$ and H_A: $\mu_1 \neq \mu_2$ (Zar 1984). The null hypothesis was rejected (two-tailed p $= 1.8 \times 10^{-12}$, $\alpha = 0.05$).

Based on observation, intraspecific competition yields non-circular crown bases in red alder. Because the polygon method better approximates the shape of alder crowns, and based on the t test described above, it seemed evident that the polygon method better represents projected crown areas in red alder. Crown areas obtained from the triangular method were used in analyses of spacing effects. Data from the Apiary site were not used in the final analysis of live crown dimensions because self-thinning had been occurring for several years, so current crown areas are not representative of the area available during recent growth.

7.   Site productivity was estimated from Harrington and Curtis' (1986) equation, which uses a reference age of 20 years, and yields a calculated site index (S_{20}) based on total age (years) and total height (m) of trees. Based on convention (Jones 1969, Carmean 1975, Avery and Burkhart 1983), average S_{20} for an installation was determined from measurements of trees deemed to express the yield potential of a site. Heights and ages at the end of the 1992 growing season were used from the tallest 30 percent of trees measured at an installation.

Site index based on height of dominant trees at a reference age is used extensively to estimate site productivity (Carmean 1975). However, if height growth of trees is impeded by competition in dense stands (Smith 1986) or if it is reduced at very wide spacings, site index cannot be considered an independent measure of a site's productive potential (Curtis and Reukema 1970, Hogg and Nester 1991). Although site index may be only an approximation of site productivity, it is easily measured and may be the best available indicator of the yield potential of a site (Jones 1969). Among the three plantations, the range in S_{20} values was small (see Table 2); however, S_{20} was used as an explanatory variable for comparative analyses of growth at the three plantations. It was not used in analyses of tree growth at Olney because no site-to-site comparisons were made of thinning effects on growth.

Table 2. S_{20} values used as estimates of site productivity at the three plantation spacing trials. Site index was not used in analyses of data from the Olney installation.

Installation	S_{20} (m)
Cascade Head	21.66
Centralia	19.95
Apiary	22.51

Data Analyses

The purpose of the analyses was to develop functions describing growth patterns of red alder in relationship to initial planting density or to post-thinning density. A graphical method was used to select initial models for variables. By analyzing single-density functions (mean values versus age) and scatterplots of the data, various linear and non-linear relationships were initially suggested (see appendix for sample plots of heights, diameters, and live crown ratios). Various model forms were then tested, and compared to the original graphs, to verify the general fit of a model. When the general model fit seemed good, a final model for variables was selected through more rigorous statistical methods, as described below. Data from the three plantation spacing studies were combined; data from the Olney thinning study were analyzed separately. Non-linear regressions were used to model height-age and *DBH*-age relationships, and one-year diameter growth rates for trees from the plantation spacing studies. Height-age relationships at the Olney thinning study were also modelled using a non-linear function. Linear regressions were used to model the following dependent variables for trees from the plantation spacing studies: stem taper, crown ratios, projected crown areas, stem diameters at the base of the live crown, and mean branch diameters. Linear regressions were used to model the following dependent variables for trees from the thinning study: stem taper, projected crown areas, stem diameters at the base of the live crown, and mean branch diameters.

Selection of a final non-linear model for variables began by including terms for all explanatory variables and computing 95 percent confidence intervals for the regression parameters, to test the null hypothesis that a given parameter was equal to zero. A model incorporating terms for all explanatory variables is called a 'full' model; a model containing

a subset of the terms in the full model is a 'reduced' model. Variables were deleted from a full model one at a time, based on the criterion that if the 95 percent confidence interval for that variable included zero, it was not contributing to the fit of the model. At each step, the variable exhibiting the smallest contribution to the model fit was deleted. The selection process continued until all variables included in the final (reduced) model were significantly different from zero.

A stepwise selection method was used (where applicable) to develop linear regression models for variables. This method begins with no variables in the model, and adds them one at a time (SAS Institute, Inc. 1989). For a variable to be added to the model, its F-statistic had to be significant at the 5 percent probability level. After a variable has been added to the model, any variable already in the model that is no longer significant at the 0.05 level is deleted. Other explanatory variables are added in this stepwise manner until all variables in the final model are significant.

Plantation Spacing Studies

A sigmoid growth function (Richards 1959) was selected to describe height-age and *DBH*-age relationships, with the general form $Y = a[1 - \exp(-(bA))]^c$. The parameter a determines an asymptote, i.e., the maximum value that a projected line will attain, b determines the rate at which the asymptote is approached, and c determines the degree of curvature of the line, with values of c greater than 1.0 producing a sigmoid growth pattern and values near 1.0 producing a linear growth pattern at early ages (Knowe 1994). The parameter A is total tree age (years). The parameters a, b, and c are functions of planted

spacing (*SPC*, m) and site index (S_{20}, m), so that the full model (i.e., a model in which *a*, *b*, and *c* are all functions of *SPC* and S_{20}) takes the following form:

$$Y = (\beta_0 + \beta_1 S_{20} + \beta_2 SPC)(1 - \exp(-(\beta_3 S_{20} + \beta_4 SPC)A))^{(\beta_5 + \beta_6 S_{20} + \beta_7 SPC)}$$

The general form of the function described above has been widely applied where the response (*Y*) increases sigmoidally over time (Mead et al. 1993). The 'Richards' function has been shown to give good estimates of height, basal area, and stem volume growth of individual trees and whole stands (Pienaar and Turnbull 1973, Means and Sabin 1989), thus, it was selected for application in this study.

A second non-linear equation form (Hann and Larsen 1991) was used to develop a predictive function for one-year diameter growth rate. The general equation form used in the current analysis was

$$DBHINC = \exp(\beta_0 + \beta_1 \ln(D1 + 1) + \beta_2 D1^2 + \beta_3 A1 + \beta_4 SPC + \beta_5 S_{20})$$

where *DBHINC* is future one-year *DBH* growth rate inside bark (cm); *D1* is *DBH* (inside bark) at the beginning of a one-year growth interval; *A1* is total tree age (years) at the beginning of a one-year growth interval; the other variables (*SPC* and S_{20}) are as previously defined. Although live crown ratio is used as an important predictive variable in this general form of diameter growth-rate equation (Hann and Larsen 1991), it was not incorporated into the *DBHINC* model because it was a dependent variable modelled in the current study.

A simple parabolic taper function was fitted to upper stem diameter data obtained from stem analyses. The function has the general form $\dfrac{d^2}{DBH^2} = a + b\left(\dfrac{h}{H}\right) + c\left(\dfrac{h^2}{H^2}\right)$, where *d* is stem diameter (inside bark) at any height on the stem above breast height, *h* is any height above ground level, and *DBH* and *H* are as previously defined. Thus, the dependent variable, $\dfrac{d^2}{DBH^2}$, is the square of the ratio of *d* to *DBH*, and is a function of $\dfrac{h}{H}$, the relative

height. This parabolic function has been found to give unbiased estimates of upper stem diameters over 85 percent of the length of a tree bole, with bias occurring near breast height and near the apex of a tree (Avery and Burkhart 1983). To avoid biasing upper stem diameter estimates, the least squares solution of the parabolic function was restricted so that $\frac{d^2}{DBH^2} = 0$ when $\frac{h}{H} = 1.0$ (Kozak et al. 1969). Inclusion of spacing coefficients gives the following full model:

$$\frac{d^2}{DBH^2} = (\beta_1 + \beta_2 SPC)(\frac{h}{H} - 1) + (\beta_3 + \beta_4 SPC)(\frac{h^2}{H^2} - 1)$$

The dependent variable, $\frac{d^2}{DBH^2}$, is easily modelled using linear regression, however, it is necessary to restrict the intercept term to zero. Because of this, the stepwise selection procedure (described above) can not be implemented. Thus, it was necessary to test for the significance of the coefficients β_2 and β_4 based on their F-statistics. Upper stem diameter d at any relative height, or height h to any specified diameter d, are easily obtained by rearranging the equation and solving for d or h, respectively.

Crown ratio (CR) was modelled using linear regression. Calculated values of crown ratios were plotted over age for each tree at Centralia and Apiary (see appendix). Based on graphical interpretation, a general trend was clear: crown ratio decreased slowly for the first several years (varying by spacing), then decreased more rapidly, and eventually appeared to reach a quasi-stable value. Due to the shape of the curvilinear trend in the data, and because the response variable (CR) is within a range between 0 and 100 percent, a logit transformation of CR was applied, where $logit\,(CR,\%) = \ln[\frac{(CR,\%)}{(100 - CR,\%)}]$.

To determine the independent variables important in explaining the variation in logit(CR), the stepwise regression technique was used. A 5 percent probability level was

used as a criterion for entry and retention of explanatory variables in the final model. Spacing, tree height, age, site index, and an interaction term (age × spacing) were tested in the model. Calculated crown ratios from all years at Centralia, for the first seven years at Apiary, and measured crown ratios for the current year at Cascade Head were included in the dataset. A simple back-transformation gives crown ratio as follows: $CR,\% = 100\frac{e^{logit}}{(1+e^{logit})}$ (Ramsey and Schafer 1993). Height to crown base (*HCB*) is easily calculated from predicted *CR* and *H* as $HCB = H - (CR \times H)$.

Stem diameters (outside bark) at live crown bases (*DBLC*, cm), projected crown areas (*CA*, m), and mean branch diameters (*BRDIA*, mm) were analyzed using stepwise regressions. Residual plots (residual values plotted over predicted values) were assessed for violations of the assumption of constant variance (Zar 1984), i.e., for the tendency of residuals to have greater variance at larger fitted values. Where the assumption was violated, the natural logarithm of a dependent variable was used to make the residuals normally distributed, with constant variance. In addition to spacing and age, various allometric relationships were tested. Results of these analyses are presented in the 'Results' section of this thesis.

Olney Thinning Study

Stem diameter growth rates (at 1.3 m) and rates of live crown recession were well-documented at the Olney site (Hibbs et al. 1994). Thus, functions were only developed to describe height growth, stem taper, and current crown dimensions. Crown dimensions were analyzed using the stepwise regression technique.

A sigmoid height growth function and a parabolic taper function were developed from the same general equation forms described for use in the plantations. However, two general questions arose that differ from questions that can be put to the plantation data: (i) Were height growth and stem form affected by thinning? (ii) Were the effects of thinning different at different thinning intensities? To address these questions, it was necessary to create two types of indicator variables (designated below by Z) which take on values of zero or one, and to test their significance in four general types of full models. A similar approach has been used (Meng 1981) to detect fertilization and thinning effects on stem form in black spruce (*Picea mariana*).

The general full model forms for height growth are as follows:

$$H = (\beta_1 + \beta_{11}Z)(1 - \exp(-(\beta_2 + \beta_{21}Z)A))^{\beta_3} \qquad a.$$

$$H = (\beta_1 + \beta_{11}Z_1 + \beta_{12}Z_2)(1 - \exp(-(\beta_2 + \beta_{21}Z)A))^{\beta_3} \qquad b.$$

$$H = (\beta_1 + \beta_{11}Z)(1 - \exp(-(\beta_2 + \beta_{21}Z_1 + \beta_{22}Z_2)A))^{\beta_3} \qquad c.$$

$$H = (\beta_1 + \beta_{11}Z_1 + \beta_{12}Z_2)(1 - \exp(-(\beta_2 + \beta_{21}Z_1 + \beta_{22}Z_2)A))^{\beta_3} \qquad d.$$

Model a tests the significance of a thinning effect on height growth, model b tests the significance of thinning intensity on the asymptote parameter, model c tests the effect of thinning intensity on the rate parameter, and model d tests the effect of thinning intensity on the asymptote and rate parameters. Z equals 1 if a plot was thinned, and equals 0 otherwise. Z_1 equals 1 if a plot was thinned to 4.2 × 4.2 m, and is 0 otherwise. Z_2 equals 1 if a plot was thinned to 5.8 × 5.8 m, and is 0 otherwise.

The indicator variables do not enter the model until the year of thinning (1980); if any indicator variables are significant in the model, projected tree heights diverge from a

single mean value after thinning. Given the possibility that thinning had a significant effect on the asymptote parameter, it was clear that the transition point, where heights diverge from a single curve, would not be smooth. Thus, a 'timing' variable (T) was incorporated into the asymptote parameter, where $T = \dfrac{A - Age\,@\,thinning}{Age\,@\,thinning}$. Inclusion of this variable in the model forces a smooth transition from a single mean.

A similar approach, incorporating indicator variables, was used to develop a taper function, resulting in four general full model forms:

$$\frac{d^2}{DBH^2} = (\beta_1 + \beta_{11}Z)(\frac{h}{H} - 1) + (\beta_2 + \beta_{21}Z)(\frac{h^2}{H^2} - 1) \qquad\qquad a.$$

$$\frac{d^2}{DBH^2} = (\beta_1 + \beta_{11}Z_1 + \beta_{12}Z_2)(\frac{h}{H} - 1) + (\beta_2 + \beta_{21}Z)(\frac{h^2}{H^2} - 1) \qquad\qquad b.$$

$$\frac{d^2}{DBH^2} = (\beta_1 + \beta_{11}Z)(\frac{h}{H} - 1) + (\beta_2 + \beta_{21}Z_1 + \beta_{22}Z_2)(\frac{h^2}{H^2} - 1) \qquad\qquad c.$$

$$\frac{d^2}{DBH^2} = (\beta_1 + \beta_{11}Z_1 + \beta_{12}Z_2)(\frac{h}{H} - 1) + (\beta_2 + \beta_{21}Z_1 + \beta_{22}Z_2)(\frac{h^2}{H^2} - 1) \qquad\qquad d.$$

Again, the first model tests for a general thinning effect on the parabolic taper function, the other three models are possible combinations testing the significance of thinning intensity on the parameters in the taper function.

RESULTS

Effects of Planting Density on Stem Diameter and Height Growth

Initial test results showed significant effects of spacing (SPC) and site index (S_{20}) on the asymptote parameter, and significant effects of SPC on the rate and shape parameters in the sigmoid growth function used to describe DBH-age relationships. An initial model was obtained with the form $DBH = (\beta_0 + \beta_1 S_{20} + \beta_2 SPC)(1 - \exp(-(\beta_3 SPC)A))^{(\beta_4 + \beta_5 SPC)}$, accounting for 86 percent of the variation in DBH. However, a graphical comparison of actual versus predicted values of DBH over age revealed a lack of agreement in the pattern of stem diameter growth at spacings of 5 × 5 m and greater. This discrepancy appeared due to the effects of the shape and asymptote parameters on the projected curve; the initial model predicted greater line curvature and earlier attainment of a maximum DBH than was observed in widely-spaced trees. The projected growth pattern was nearly opposite from the observed pattern, where trees at 5 × 5 and 6 × 6 m spacings showed a nearly linear increase in DBH over age (see appendix). Although these widely-spaced trees were initially smaller in diameter than trees planted at 3 × 3 and 4 × 4 m (i.e., at intermediate spacings), trees planted at 5 × 5 and 6 × 6 m appeared to be growing faster in diameter by about age 7 years at the Cascade Head and Centralia sites. The initial model closely matched the actual data as follows: (i) Projected diameters of trees planted at spacings less than 3 × 3 m were smaller at all ages than diameters of more widely-spaced trees. (ii) The projected line for total diameter growth of very widely-spaced trees (i.e., trees planted at spacings greater than 6 × 6 m) appeared to approach an asymptotic value at an early age (i.e., by about age 7 years).

Transformations of the independent variable *SPC* were tested in numerous model runs; the terms SPC^2 and *ln(SPC)* were included in the asymptote, rate, and shape parameters of the sigmoid growth function. Although models were fit using either of the two terms, none of the models including transformations of the independent variable *SPC* resolved the discrepancy between observed and predicted patterns of diameter growth.

These initial results suggested that diameter growth patterns were so different between open-grown trees and trees exhibiting effects of inter-tree competition (i.e.,trees exhibiting crown lift), that either the 'Richards' function was inappropriate for describing *DBH*-age relationships in young red alder, or separate regressions should be used. Separate regressions were tested on two data sets created from: (i) trees grown at spacings greater than or equal to 5 × 5 m, and (ii) trees grown at spacings less than 5 × 5 m. Trees were separated into the two data sets based on whether or not they had exhibited any crown lift at the time of sampling. Use of separate regressions for open- and competition-grown trees is an approach that has been recommended by Adlard et al. (1992).

The final model for trees grown at spacings less than 5 × 5 m (equation 1) accounted for 90 percent of the variation in *DBH* and has a root MSE of 1.32. Spacing *(SPC)* was significant (p < 0.0005), and was the most important explanatory variable in the *DBH*-age function, accounting for 16.4 percent of the variation. Site index (S_{20}) explained only an additional 1.2 percent of the variation in total diameter, but was also significant (p < 0.0005).

The final model for widely-spaced trees (equation 2) explained less variation than either the initial model (all data combined) or the final model for intermediate and close spacings ($R^2 = 0.77$, root MSE = 2.38). Site index was not a significant explanatory variable in this model. The spacing term accounted for only 0.9 percent of the variation in total

diameter (cm), but it was significant at the 5 percent probability level (p = 0.048). Inclusion of a spacing term in the *DBH* model for widely-spaced trees was justified based on projected patterns of total diameter growth; these growth patterns were in closer agreement with reality when two separate *DBH*-age models were used, and when a spacing term was included in the model for widely-spaced trees. Figures 3 and 4 show predicted *DBH* (cm) over age (years). An average site index (S_{20}) of 21.37 m was used to predict *DBH* from equation 1. Based on these analyses, the final *DBH*-age functions for young red alder plantations are:

$$DBH = (20.8487 - 1.37252\ SPC)(1 - \exp(-(0.089368\ SPC)A))^{(5.44639 - 0.203111 S_{20} + 0.7172305 SPC)} \quad (1)$$

$$DBH = (27.4755 - 1.78793\ SPC)(1 - \exp(-(0.047469\ SPC)A))^{3.609397} \quad (2)$$

In the non-linear, annual *DBH* increment model, all five independent variables [$ln(D1 + 1)$, $D1^2$ ($D1$ is *DBH* at the beginning of a one-year growth interval), $A1$, *SPC*, and S_{20}] tested in the full model differed significantly from zero (at the 5 percent probability level). The spacing term was highly significant (p < 0.0005), and accounted for 6.9 percent of the explained variation. The site index term (S_{20}) was also important in the model (p < 0.0005), although it accounted for only 1.6 percent of the variation in diameter increment. The final model explained only 55 percent of the variation in future one-year diameter increment (root MSE = 0.48). However, residual plot analysis indicated that mean residual values were centered around zero, with constant variance. Further, a plot of predicted versus actual values of *DBH* increment revealed a linear relationship. From this analysis, the final model of future one-year diameter increment (cm yr^{-1}) is:

$$DBHINC = \exp(-1.22310 + 0.790729\ \ln(D1 + 1) - 0.001287\ D1^2 + 0.0620115\ S_{20} \quad (3)$$
$$-0.237821\ A1 + 0.074078\ SPC)$$
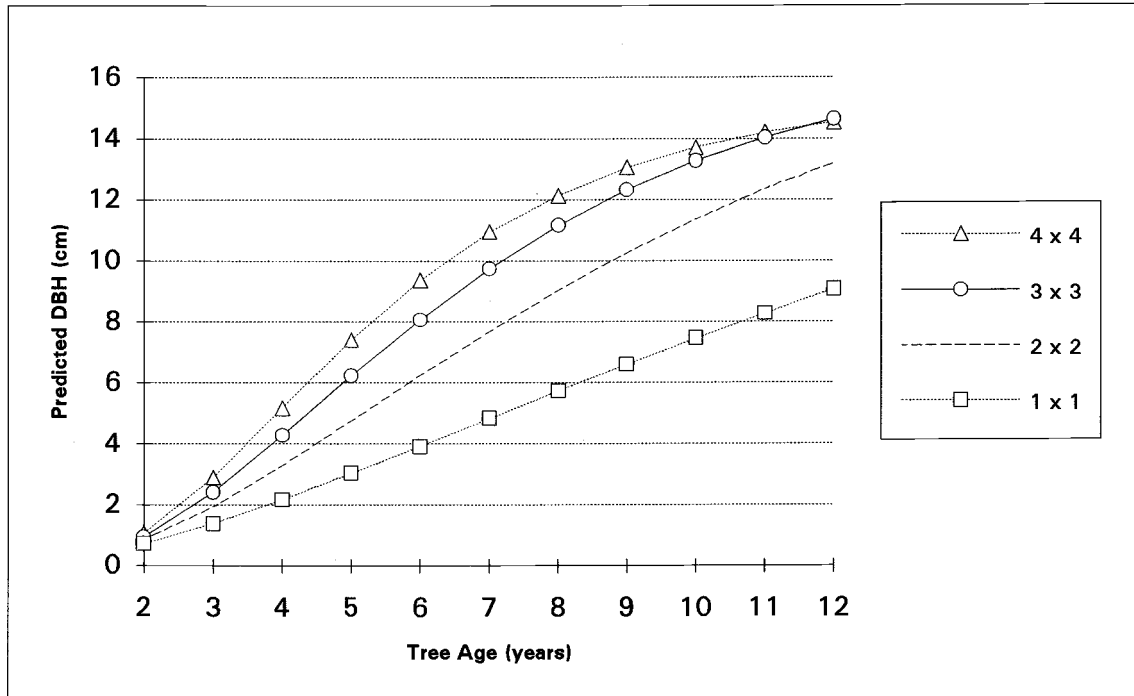
Figure 3. DBH-age relationships for trees planted at spacings less than 5 x 5 m. Diameters were predicted from equation 1.
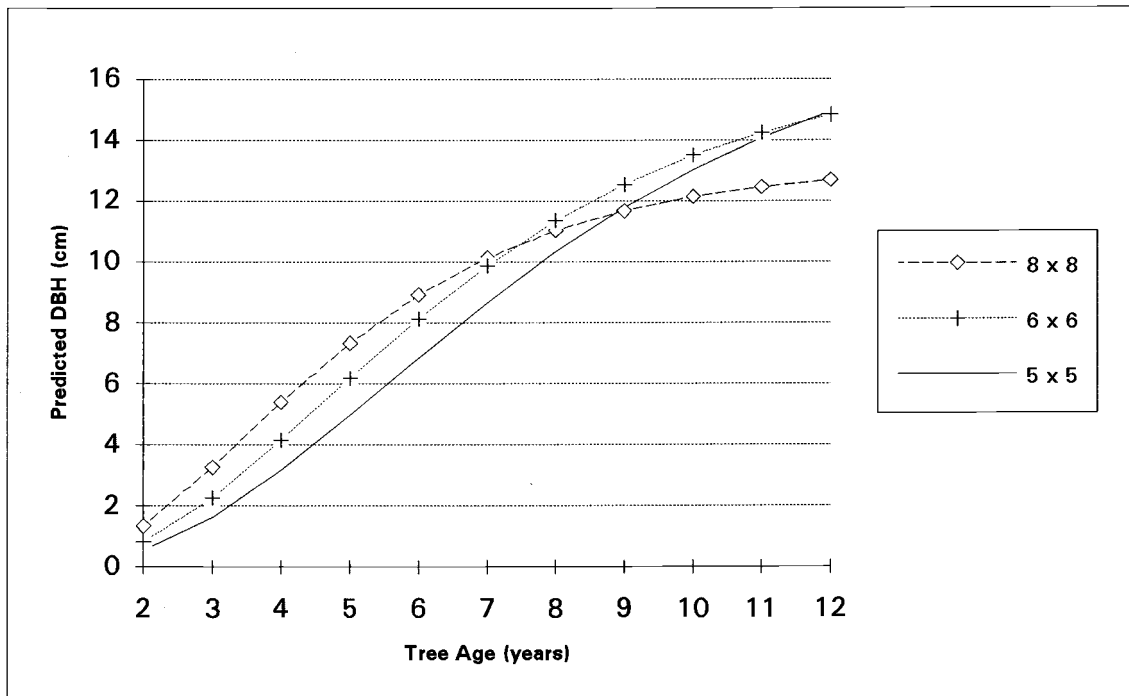

Figure 4. DBH-age relationships for trees planted at spacings of 5 x 5 m and greater. Diameters were predicted from equation 2.

Equation 3 can be separated into two components (Hann and Larsen 1991), a maximum predicted growth rate for a given site index represented by $\exp(\beta_0 + \beta_1 \ln(D1 + 1) + \beta_2 D1^2 + \beta_3 S_{20})$, and a component that shows how that maximum rate is modified, represented by $\exp(\beta_4 A1 + \beta_5 SPC)$. Separation of equation 3 into these two components enables graphical interpretation of how spacing affects diameter growth over time. Figure 5 graphically depicts maximum diameter growth rate plotted over $D1$ at an average site index ($S_{20} = 21.37$ m), and Figure 6 shows effects of age and spacing on the proportion of the maximum growth rate attained by a tree.

The total diameter growth functions (equations 1 and 2) can be conceptually integrated with the diameter increment function (equation 3) by considering the graphical comparison of predicted stem diameters with predicted diameter increments, for trees planted at 4 × 4 and 6 × 6 m. Predicted stem diameters of trees planted at 4 × 4 m are greater for the first 10 years of growth (Figures 3 and 4). However, holding $D1$ and $A1$ constant, the greatest diameter growth rate (increment) is attained at the widest spacing (Figures 5 and 6). This means that current annual increment (cm yr^{-1}) reaches a maximum at a later age in trees planted at the widest spacing. This spacing effect diminishes over time (Figure 6), so that by age 8 or 9 years, current annual increment for all spacings is similar, holding $D1$ constant.

Initial test results showed significant effects of spacing and site index (SPC and S_{20}) on the asymptote and rate parameters, and significant effects of SPC on the shape parameter in the sigmoid growth function used to describe height-age relationships. An initial model was obtained with the form $H = (\beta_0 + \beta_1 S_{20} + \beta_2 SPC)(1 - \exp(-(\beta_3 S_{20} + B_4 SPC)A))^{(\beta_5 + \beta_6 SPC)}$, accounting for 87 percent of the variation in height. However, a graphical comparison of
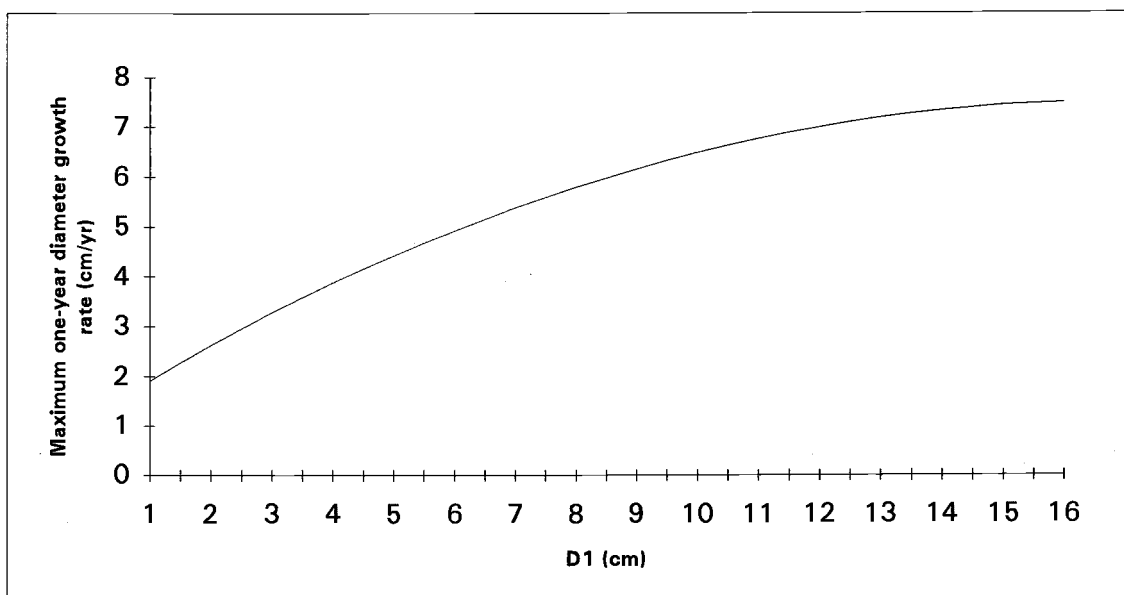
Figure 5. Maximum predicted one-year diameter growth rate (cm/yr) plotted over D1 (DBH at the beginning of a one-year growth interval). Values were calculated from equation 3, using an average site index of 21.37 m.
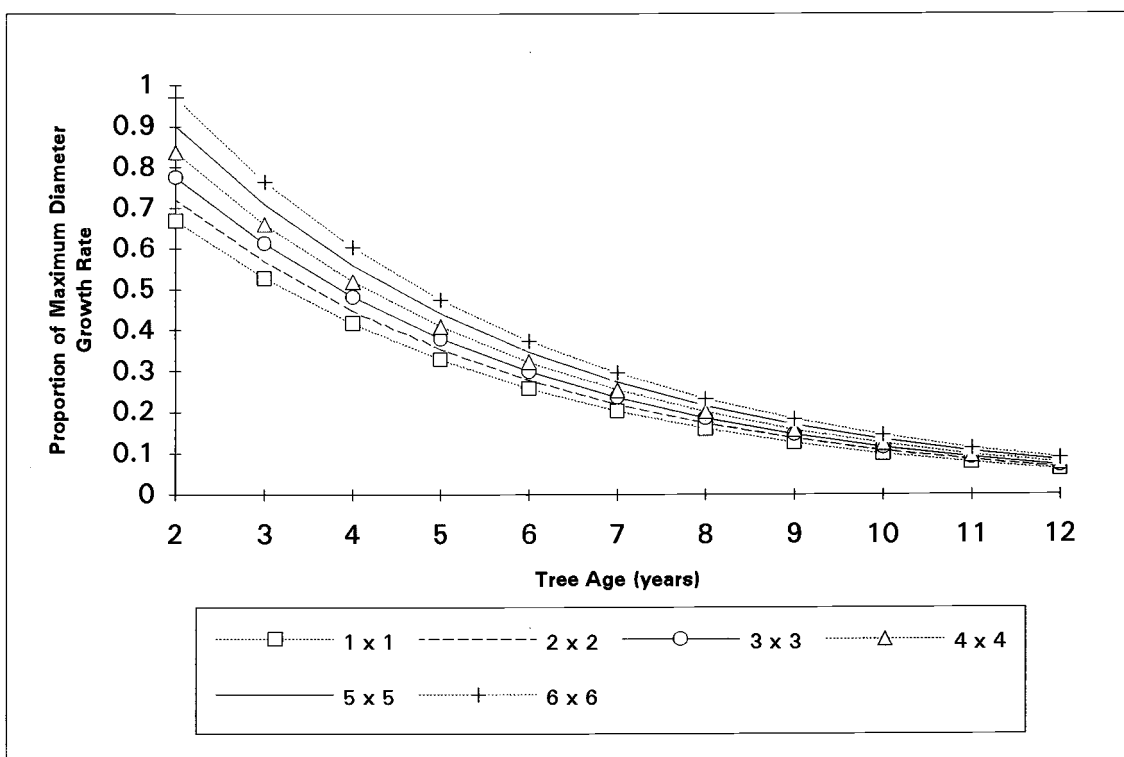
Figure 6. Proportion of maximum diameter growth rate attained by trees planted at six spacings (m). Values were calculated from equation 3.

actual versus predicted values of height over age showed that total tree heights were underestimated by the model.

A natural logarithmic transformation of the independent variable *SPC* was used in the rate parameter of the sigmoid height growth function, resulting in a closer agreement between predicted and actual values of height. Site index and spacing were significant (p-values < 0.0005) explanatory variables in the model, accounting for 2.9 percent, and 3.1 percent of the explained variation in height, respectively. The resulting model accounted for 88 percent of the variation in height, and has a root MSE of 1.2. Based on these analyses, the final height-age function for red alder plantations is:

$$H = (-11.02736 + 1.57552\ S_{20} - 1.38478\ SPC)$$
$$\times (1 - \exp(-((0.004335\ S_{20} + 0.051053\ \ln(SPC))A)))^{(1.46656 + 0.027768SPC)} \tag{4}$$

From this analysis, the greatest height is attained at 2, 3, and 4 m spacings, at all ages. Height growth is reduced at both closer and wider spacings, as shown for an average site index ($S_{20} = 21.37$ m) in Figures 7 and 8.

Effects of Planting Density on Stem Taper

Planting density (*SPC*) was a significant (p < 0.0001) explanatory variable in the parabolic taper function. Ninety-two percent of the variation in relative diameter squared, $\frac{d^2}{DBH^2}$, was explained by the final model (root MSE = 0.078). The spacing term accounted for only 1.52 percent more variation in $\frac{d^2}{DBH^2}$ than a reduced model (a model without a spacing coefficient); however, reduction in the mean square error was highly significant (p < 0.0001). The final parabolic taper function for red alder plantations is:

$$\frac{d^2}{DBH^2} = -2.07966\ (\frac{h}{H} - 1) + ((0.762466 + 0.036788\ SPC)(\frac{h^2}{H^2} - 1)) \tag{5}$$
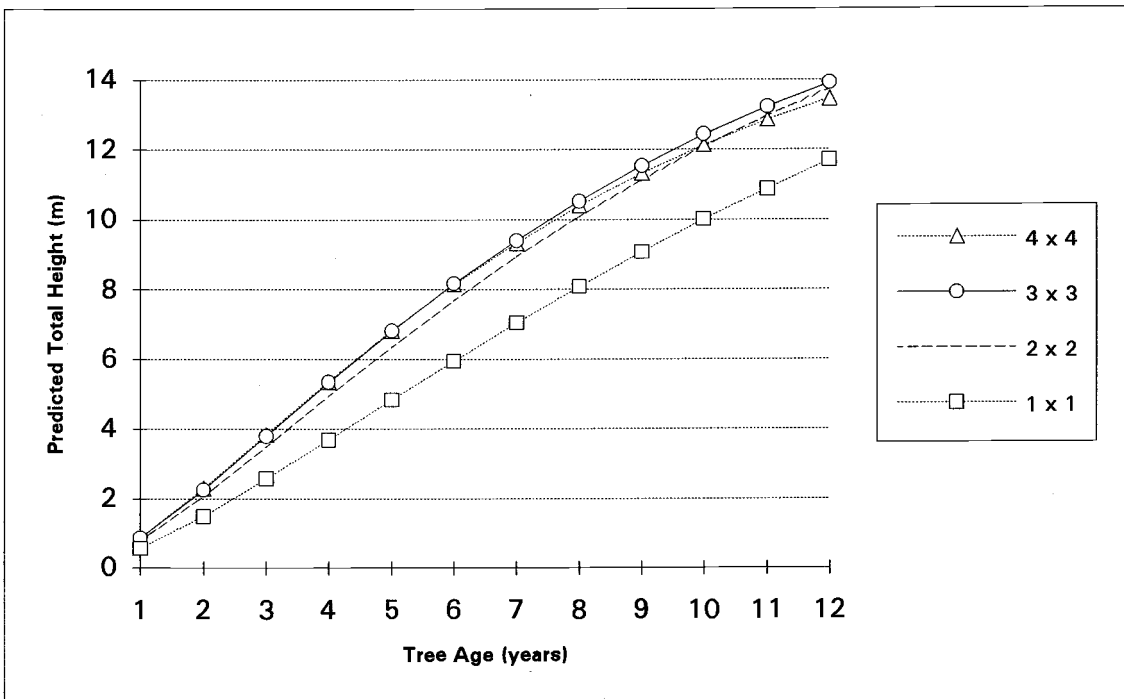
Figure 7. Height-age relationships for trees planted at spacings less than 5 x 5 m. Heights were predicted from equation 4.
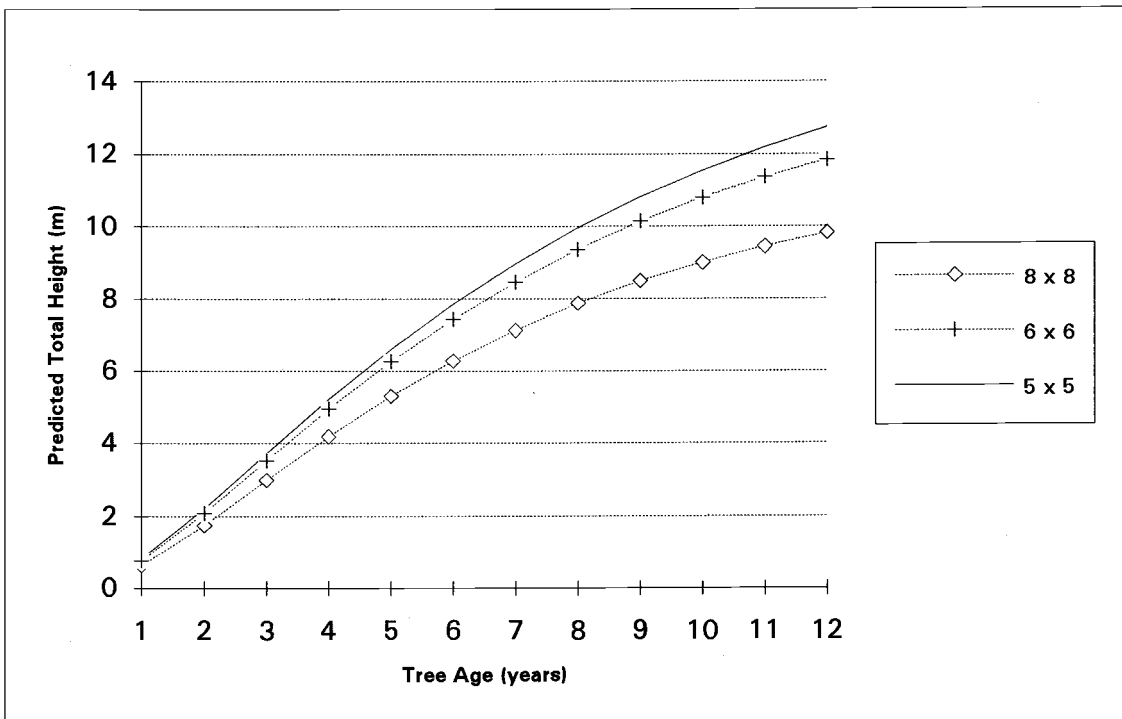
Figure 8. Height-age relationships for trees planted at spacings of 5 x 5 m and greater. Heights were predicted from equation 4.

From this analysis, as stem density decreases (as spacing gets wider), the ratio $\dfrac{d^2}{DBH^2}$ also decreases, holding relative height, $\dfrac{h}{H}$, constant. This can be understood by considering the effects of 2 and 6 m spacings on the second term in the model, $(\beta_2 + \beta_3 SPC)(\dfrac{h^2}{H^2} - 1)$, for a fixed relative height of 0.5. In this example, $(\beta_2 + (\beta_3 \times 6)) = 0.98$, and $(\beta_2 + (\beta_3 \times 2)) = 0.84$. Thus, at a spacing of 6×6 m, $(\beta_2 + \beta_3 SPC)(\dfrac{h^2}{H^2} - 1) = -0.735$. At a spacing of 2×2 m, $(\beta_2 + \beta_3 SPC)(\dfrac{h^2}{H^2} - 1) = -0.63$, a less negative value.

The results of this model show that stem taper increases with increasing spacing between stems. This does not necessarily imply smaller upper stem diameters at wider spacings. It does, however, directly imply that for a given relative height and *DBH*, the ratios $\dfrac{d^2}{DBH^2}$ and $\dfrac{d}{DBH}$ will be smaller at wider spacing.

The parabolic function gave small overestimates (≈ 2 %) of stem diameters at relative heights near 0.1, which is breast height for a 13.7 m tall tree. This function, however, has been shown to fit well over 85 percent of the length of a stem (Avery and Burkhart 1983), and data used in analyses of taper were limited to observations where $\dfrac{d^2}{DBH^2}$ was less than 1.0, i.e., to stem diameters at heights above breast height. Thus, Figure 9 shows predicted ratios of upper stem diameters to *DBH*, $\dfrac{d}{DBH}$, plotted over relative heights greater than or equal to 0.15.

Effects of Planting Density on Crown Recession and Crown Dimensions

Planting density (*SPC*), tree height (*H*), site index (S_{20}), and the interaction term, age by spacing (*ASPC*), were all significant (all p-values < 0.0001) explanatory variables in the model of live crown ratio [*logit(CR)*]. Eighty-five percent of the variation in *logit(CR)* was explained by the variation in the explanatory variables (root MSE = 0.66). Spacing, as
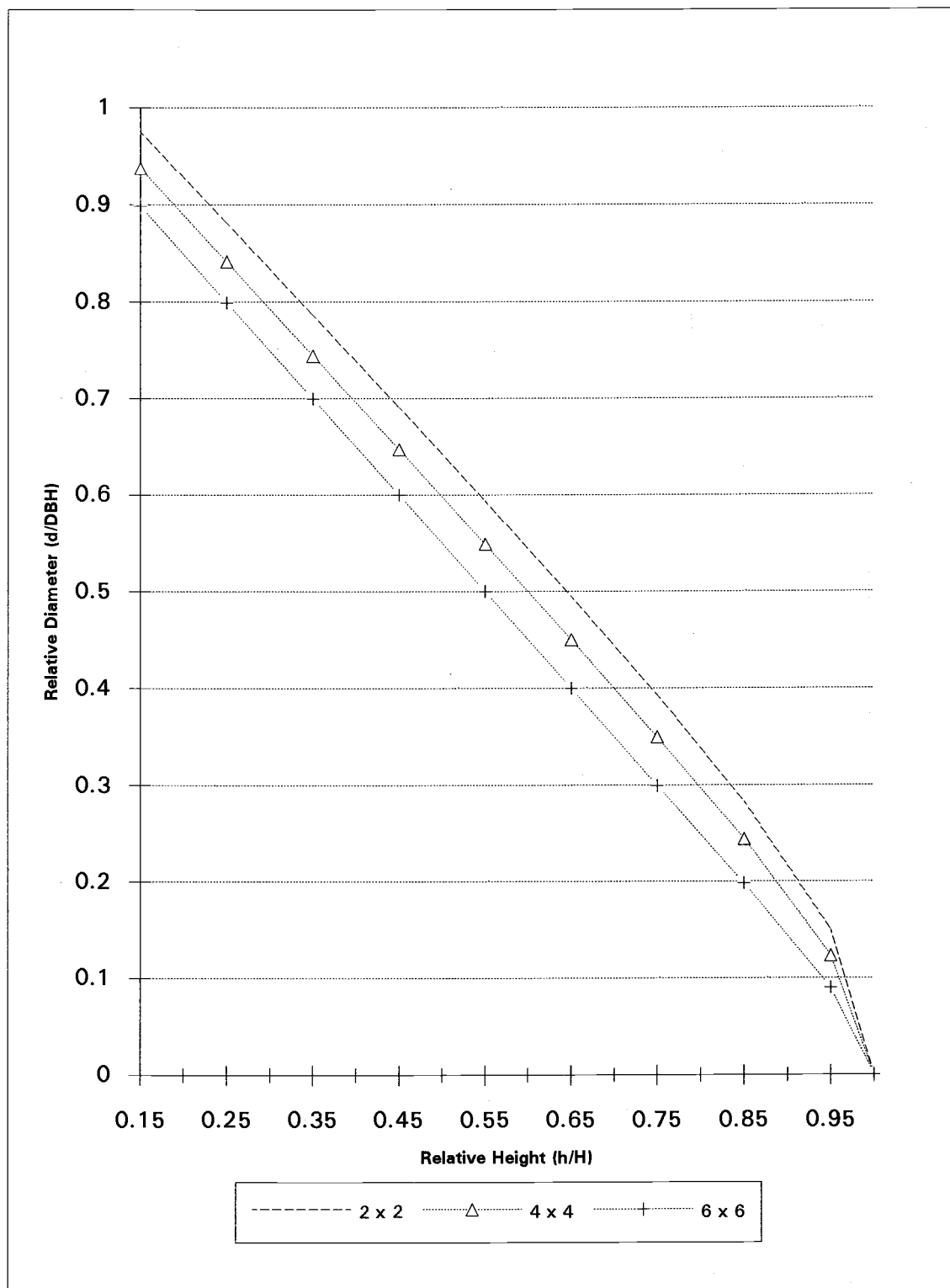
Figure 9. Predicted ratios of upper stem diameters to DBH, plotted over relative heights, for three planting densities. Values were calculated as the square root of predicted values from equation 5.

expected, was the most important term in the model, accounting for 73 percent of the variation in *logit(CR)*. The final model of crown ratios in red alder plantations is:
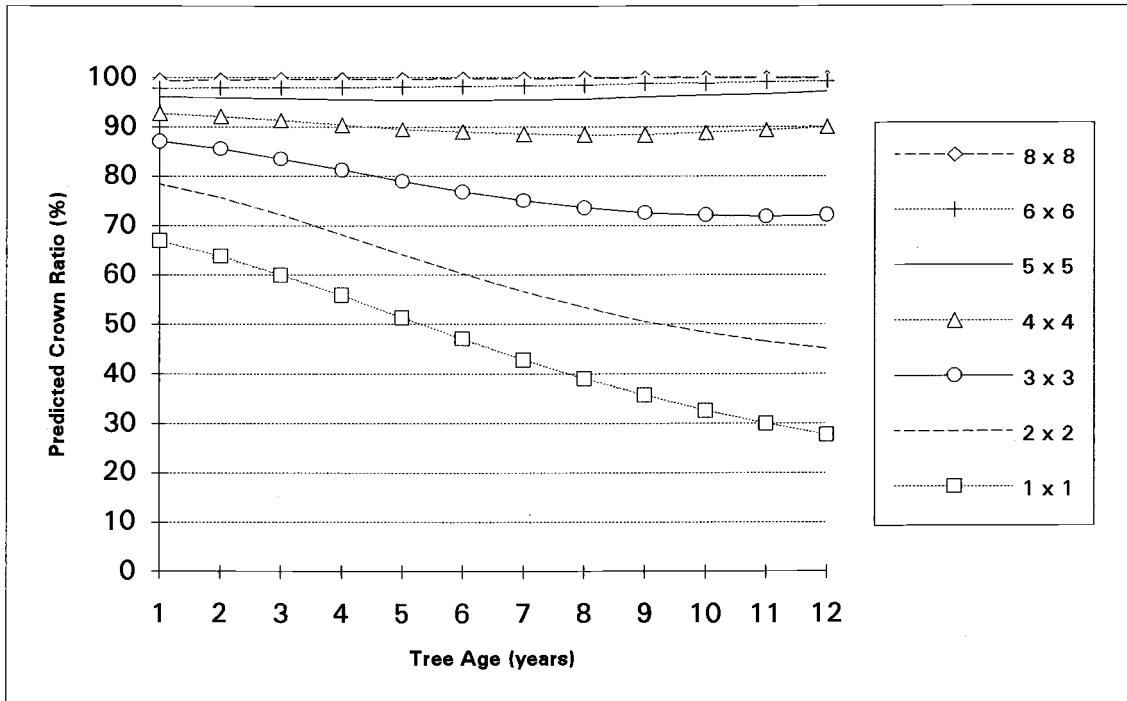
$$logit\,(CR) = -9.847 + 0.585\,SPC - 0.198\,H + 0.469\,S20 + 0.049\,ASPC \qquad (6)$$

From this analysis, as planting density decreases, live crown ratio increases, when all other variables are held constant (Figure 10 shows predicted crown ratios at an average S_{20} of 21.37 m). Similarly, greater crown ratios are predicted at higher site index values. There is also a trend for height to have a negative effect on predicted live crown ratios, because as trees grow taller their crowns generally recede. This, however, is not the whole story.

The interaction term (*ASPC*) accounted for only 3.1 percent of the variation in *logit(CR)*, but the importance of its *positive* effect on predicted values of crown ratio can be understood by holding all variables constant except spacing and age. Across a range in spacing, a one year increase in age causes a greater *increase* in predicted crown ratios of trees grown at wider spacings. The positive algebraic sign of the coefficient for *ASPC* may initially appear to be counterintuitive. However, no crown lift was measured in trees planted at spacings greater than 4 × 4 m. Thus, if height to crown base does not change appreciably over time (Figure 11), crown ratio can increase slightly as a tree grows taller.

Spacing, heights to live crown bases, and tree ages were entered as independent variables in the stepwise regression to predict diameter at the base of the live crown (*DBLC*, cm). All three variables were significant (all p-values < 0.028) in the final model ($R^2 = 0.69$, root MSE = 3.86). As expected, spacing explained the greatest proportion of the variation in *DBLC* (partial $R^2 = 0.49$, p=0.0001). The following linear equation was obtained:

Figure 10. Crown ratios predicted for seven planted spacings, calculated by back-transformation of predicted values from equation 6.
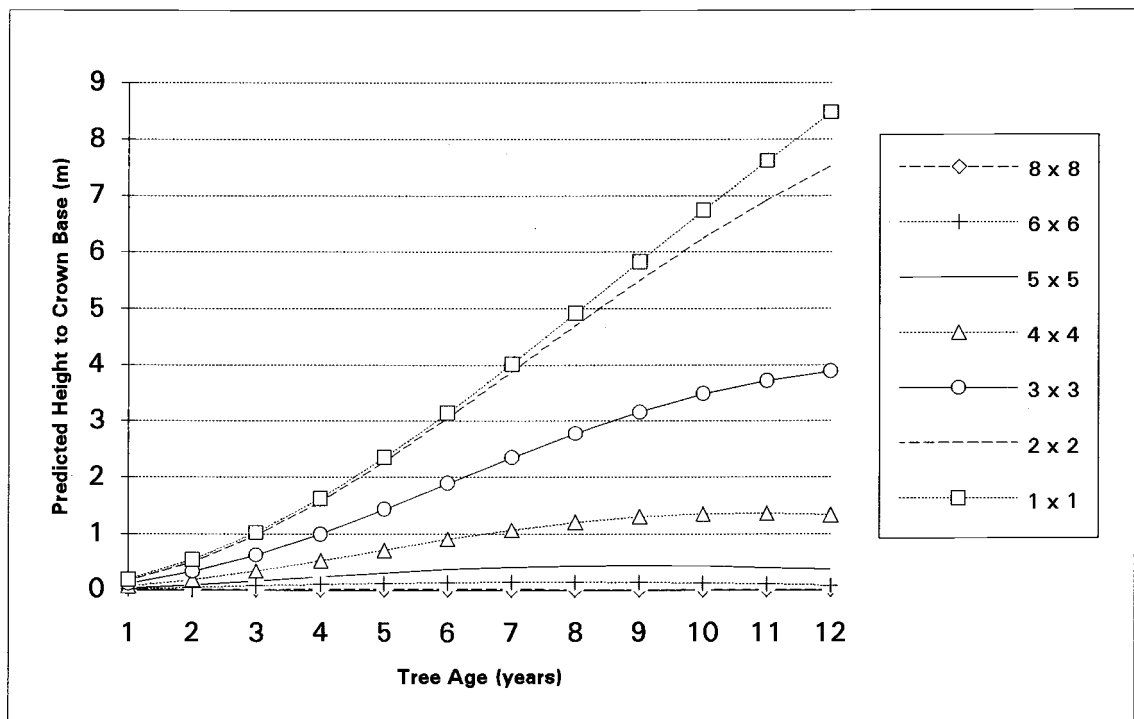
Figure 11. Heights to live crown bases for seven spacings. Values were calculated from predicted tree heights and crown ratios (HCB=H-(CR*H).

$$DBLC = -0.205 - 1.674\,HCB + 1.517\,SPC + 1.284\,A \tag{7}$$

From this analysis, as height to crown base (*HCB*) increases, *DBLC* decreases, when all other variables are held constant. Similarly, as planting density decreases, *DBLC* increases. The age variable shows that *DBLC* also increases with age. Because crown ratios are greater at wider spacings, *HCB* is necessarily closer to ground level at wider spacing; because stem diameters of trees increase from the apex to the base, it is not surprising that diameter at crown bases showed a strong tendency to increase linearly with spacing.

SPC, *A*, *HCB*, S_{20}, and *DBLC* were tested as explanatory variables for projected crown areas (*CA*, m^2) using the stepwise variable selection method. Due to increased variation at greater fitted values, a natural logarithmic transformation of the dependent variable *CA* was necessary. *DBLC* was highly significant (p < 0.0001), and was the only explanatory variable retained in the final model for *ln*(*CA*), resulting in the following allometric relationship ($R^2 = 0.77$, root MSE = 0.32):

$$\ln(CA) = 1.332 + 0.087\,DBLC \tag{8}$$

Because *DBLC* is greater at wider spacings, greater projected crown areas are directly implied, and greater branch lengths are indirectly implied, at wider spacings.

SPC, *A*, *HCB*, S_{20}, and *DBLC* were tested as explanatory variables for average branch diameters (*BRDIA*, mm) using the stepwise variable selection method. Due to increased variation at greater fitted values, a natural logarithmic transformation of the dependent variable, *BRDIA*, was necessary. *DBLC* was highly significant (p < 0.0001), and was the only explanatory variable retained in the final model for *ln*(*BRDIA*), resulting in the following allometric relationship ($R^2 = 0.58$, root MSE = 0.17):

$$\ln(BRDIA) = 2.858 + 0.031\,DBLC \tag{9}$$

Results of this study show that greater diameters at live crown bases result from lower heights to live crown bases (equation 7), which, in turn, result from wider spacings (Figure 11). Extension of the live crown toward ground level directly implies that trees grown at wider spacings have longer lived, and therefore larger diameter, branches growing from their lower stems. The positive coefficient for *DBLC*, as an explanatory variable for *ln*(*BRDIA*), strongly supports this reasoning.

Effects of Thinning on Height Growth

Initial test results showed significant effects of thinning (at the 0.05 probability level) on the asymptote parameter in the sigmoid growth function used to describe height-age relationships. To determine whether effects of thinning were different at different thinning intensities, the indicator variables Z_1 and Z_2 were substituted for Z in the asymptote parameter. These indicator variables take on values of zero or one, and enter the model at the time of thinning. Both thinning intensity variables (Z_1 and Z_2) were significant at the 0.05 probability level. The model including indicator variables for thinning intensity accounted for only 0.1 percent more of the explained variation in the height-age function than the model including only a Z term, but this difference was significant (p = 0.048). The resulting model accounted for 95 percent of the variation in height and has a root MSE of 1.3. Based on these analyses, the final height-age function for the thinning study is:

$$H = (25.8924 - 2.65472\ Z_1 T - 4.520725\ Z_2 T)(1 - \exp(-(0.079403 \times A)))^{1.23730} \qquad (10)$$

The timing variable T forces a smooth transition from a single mean projected height curve after thinning, where $T = \dfrac{A - Age\ @thinning}{Age\ @thinning}$.

From this analysis, height growth was reduced for trees thinned to 4.2 × 4.2 and 5.8 × 5.8 m. The greatest reduction in height growth after thinning occurred at the widest respacing distance (Figure 12).

Effects of Thinning on Stem Taper

Initial test results showed that the indicator variable Z was highly significant (p < 0.0001) in the parabolic function used to describe stem form change after thinning. Ninety-five percent of the variation in $\dfrac{d^2}{DBH^2}$ was explained by this model (root MSE = 0.063). Adding the variable for thinning effects (Z) accounted for only 0.23 percent more variation than a reduced model, where $\dfrac{d^2}{DBH^2}$ was only a function of relative height. However, by including the thinning term Z, the reduction in the mean square error was highly significant (p < 0.0001). To determine whether effects of thinning were different at different thinning intensities, the indicator variables Z_1 and Z_2 were substituted for Z in the model. These variables accounted for slightly more variation in $\dfrac{d^2}{DBH^2}$, but they were not significant at the 5 percent probability level. Based on these analyses, the final parabolic taper function for the thinning study is:

$$\frac{d^2}{DBH^2} = (-1.78284 + 0.058894\ Z)(\frac{h}{H} - 1) + 0.559483\ (\frac{h^2}{H^2} - 1) \qquad (11)$$

From this analysis, the ratio $\dfrac{d^2}{DBH^2}$ decreases with thinning, when relative height is held constant. These results show that stem taper is greater in thinned than in unthinned red alder; within the range of respacing densities analyzed in this study, differences in stem taper did not arise among the two thinning treatments. These results do not imply smaller upper stem diameters in thinned trees. For a given relative height and DBH, however, the ratio $\dfrac{d}{DBH}$ will be smaller in thinned trees.
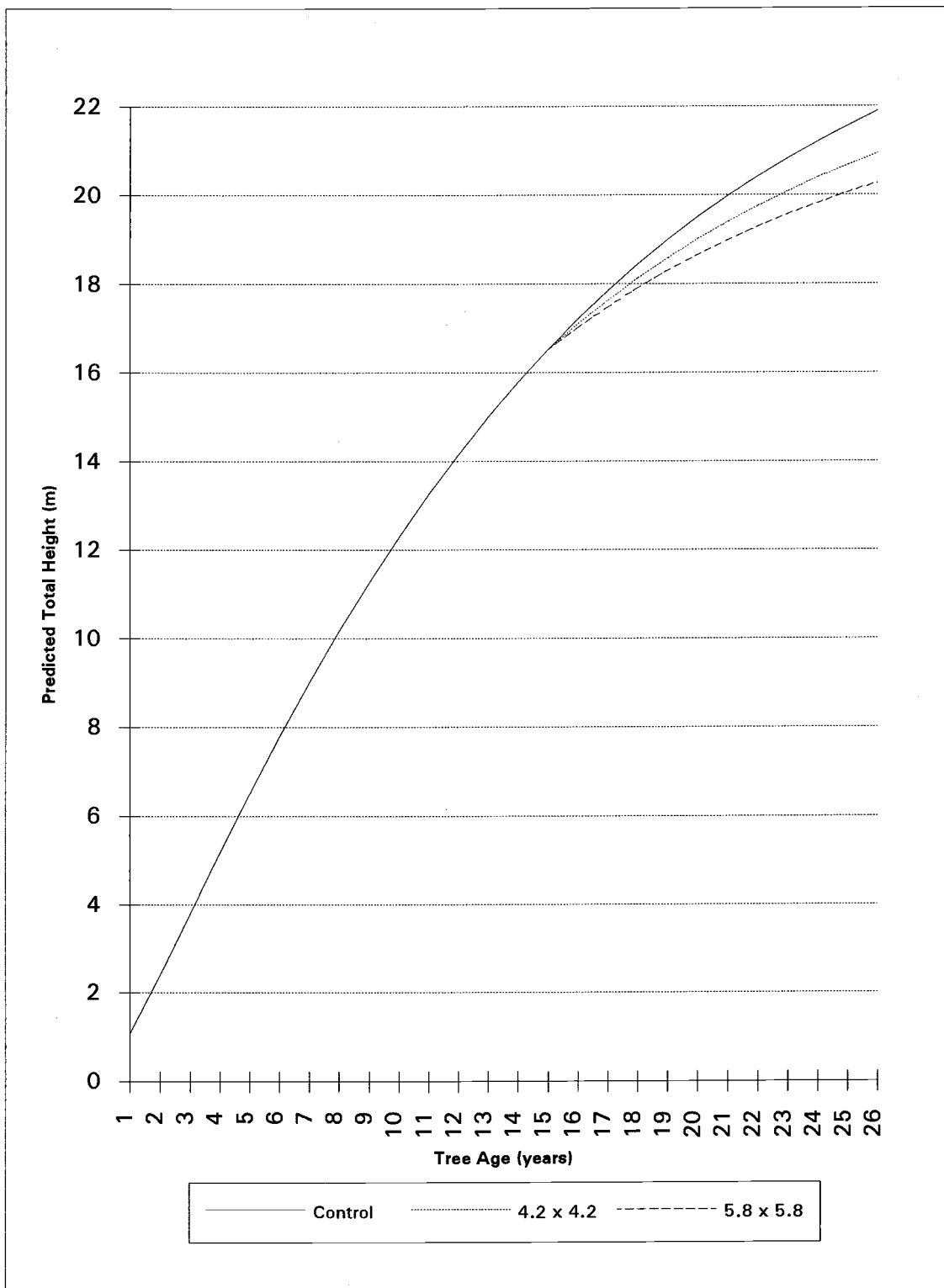
Figure 12. Height-age relationships for trees at the Olney thinning study.
Heights were predicted from equation 10. Trees were thinned to spacings
of 4.2 x 4.2 and 5.8 x 5.8 m, or left unthinned as a control.

The parabolic taper function gave slight overestimates ($\approx 1\%$) of stem diameters at relative heights near 0.1. As with the plantations, however, data were limited to observations of stem diameters at heights greater than breast height. Figure 13 shows predicted ratios of upper stem diameters, d, to DBH, plotted over relative heights ≥ 0.15 (greater than or equal to 3.0 m for a 20 m tall tree).

Effects of Thinning on Crown Dimensions

Spacing (SPC), heights to live crown bases (HCB), and tree ages (A) were entered in the stepwise regression to predict diameter at the base of the live crown ($DBLC$, cm). HCB was the only significant ($p = 0.01$) explanatory variable remaining in the final model, and it accounted for 64 percent of the variation in $DBLC$ (root MSE = 2.99). The following allometric relationship was obtained:

$$DBLC = 30.484 - 1.204\,HCB \tag{12}$$

From this analysis, $DBLC$ decreases as HCB increases. Rates of live crown recession were greatest in the unthinned trees in the Olney thinning study, and were lowest in the most widely-spaced trees (Hibbs et al. 1994). This implies greater mean values of HCB, and smaller predicted values of $DBLC$ for unthinned trees.

To verify the preceding statement, HCB was regressed on SPC. A significant ($p = 0.03$) negative linear trend was revealed, as expected, resulting in the following relationship:

$$HCB = 18.862 - 1.505\,SPC \tag{13}$$

This model shows substantial variation about the mean ($R^2 = 0.51$, root MSE = 2.30); however, these results are consistent with results from the plantation spacing studies. Thus, HCB decreases at decreased thinning density due to decreased rates of live crown recession.
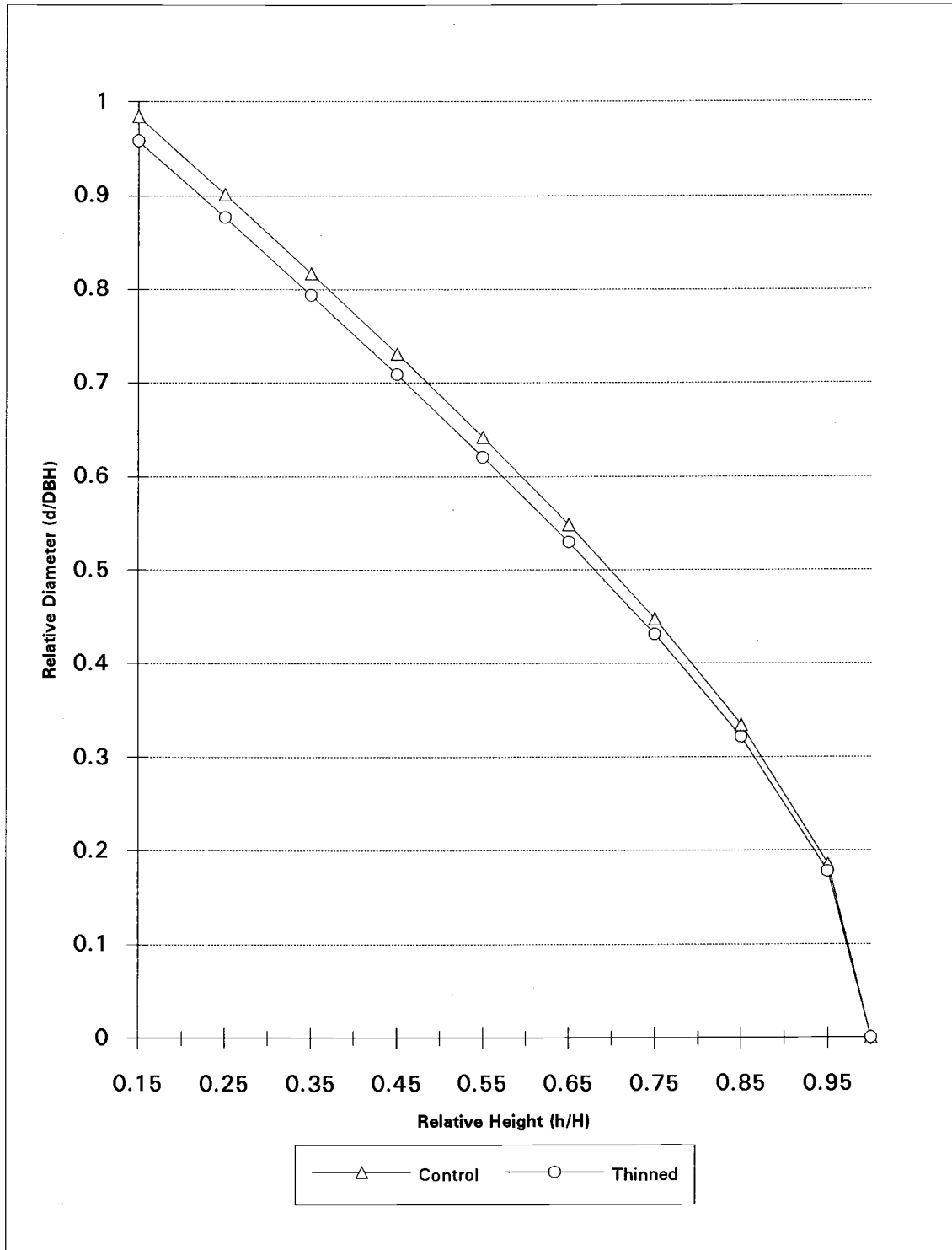
Figure 13. Predicted ratios of upper stem diameters to DBH, plotted over relative heights, for unthinned (control) and thinned trees at the Olney site. Values were calculated as the square root of predicted values from equation 11.

SPC, HCB, and DBLC were tested as explanatory variables for projected crown areas (CA, m^2) using the stepwise variable selection method. No logarithmic transformation of the dependent variable CA was necessary, as it was for the plantations. SPC and DBLC were significant explanatory variables (p-values = 0.002 and 0.04, respectively) in the model, accounting for 89 percent of the variation in CA (root MSE = 3.34); spacing was the most important term in the model, accounting for 76 percent of the explained variation. Based on this analysis, the final model for crown areas in the thinning study is:

$$CA = -6.678 + 3.365 SPC + 0.859 DBLC \qquad (14)$$

From this analysis, projected crown areas increase at wider respacing distances (i.e., with thinning intensity). Thus, red alder trees in this study exhibited an increase in the amount of growth allocated to branch elongation after release from competition by thinning. Because smaller predicted values of DBLC are implied for unthinned trees, it is not surprising that crown area increases with increasing diameter at the base of the live crown.

SPC, A, HCB, and DBLC were tested as explanatory variables for average branch diameters (BRDIA, mm) using the stepwise variable selection method. No logarithmic transformation of the dependent variable BRDIA was necessary, as it was for the plantations. DBLC was highly significant (p < 0.0005), and was the only explanatory variable retained in the final model for BRDIA, resulting in the following allometric relationship (R^2 = 0.84, root MSE = 3.62):

$$BRDIA = 8.476 + 1.673 DBLC \qquad (15)$$

Results of this study show that greater diameters at live crown bases result from lower heights to live crown bases (equation 10), which, in turn, result from wider spacings (equation 11). This directly implies that larger mean branch diameters occur on trees

thinned to wider spacings. The positive coefficient for *DBLC*, as an explanatory variable for

BRDIA, strongly supports this reasoning.

Table 3. Summary table of regression equations developed for the spacing studies. See List of Abbreviations (page x) for variable definitions and units of measurement.

Model	$\sqrt{MSE}$, R^2

(1)
$$DBH = (20.8487 - 1.37252\ SPC)(1 - \exp(-(0.089368\ SPC)A))^{(5.44639 - 0.203111 S_{20} + 0.7172305 SPC)}$$

$$(\sqrt{MSE} = 1.32,\ R^2 = 0.90)$$

(2) $$DBH = (27.4755 - 1.78793\ SPC)(1 - \exp(-(0.047469\ SPC)A))^{3.609397}$$

$$(\sqrt{MSE} = 2.38,\ R^2 = 0.77)$$

(3)
$$DBHINC = \exp(-1.22310 + 0.790729\ \ln(DI + 1) - 0.001287\ DI^2 + 0.0620115\ S_{20}$$
$$-0.237821\ AI + 0.074078\ SPC)$$

$$(\sqrt{MSE} = 0.48,\ R^2 = 0.55)$$

(4)
$$H = (-11.02736 + 1.57552\ S_{20} - 1.38478\ SPC)$$
$$\times (1 - \exp(-((0.004335\ S_{20} + 0.051053\ \ln(SPC))A)))^{(1.46656 + 0.027768 SPC)}$$

$$(\sqrt{MSE} = 1.20,\ R^2 = 0.88)$$

(5) $$\frac{d^2}{DBH^2} = -2.07966\ (\frac{h}{H} - 1) + ((0.762466 + 0.036788\ SPC)(\frac{h^2}{H^2} - 1))$$

$$(\sqrt{MSE} = 0.078,\ R^2 = 0.92)$$

(6) $$logit\ (CR) = -9.847 + 0.585\ SPC - 0.198\ H + 0.469\ S20 + 0.049\ ASPC$$

$$(\sqrt{MSE} = 0.66,\ R^2 = 0.85)$$

(7) $$DBLC = -0.205 - 1.674\ HCB + 1.517\ SPC + 1.284\ A \qquad (\sqrt{MSE} = 3.86,\ R^2 = 0.69)$$

(8) $$\ln(CA) = 1.332 + 0.087\ DBLC \qquad (\sqrt{MSE} = 0.32,\ R^2 = 0.77)$$

(9) $$\ln(BRDIA) = 2.858 + 0.031\ DBLC \qquad (\sqrt{MSE} = 0.17,\ R^2 = 0.58)$$

Table 4. Summary table of regression equations developed for the thinning study. See List of Abbreviations (page x) for variable definitions and units of measurement.

Model	$\sqrt{MSE},\ R^2$

$$(10) \quad H = (25.8924 - 2.65472\ Z_1 T - 4.520725\ Z_2 T)(1 - \exp(-(0.079403 \times A)))^{1.23730}$$

$$(\sqrt{MSE} = 1.30,\ R^2 = 0.95)$$

$$(11) \quad \frac{d^2}{DBH^2} = (-1.78284 + 0.058894\ Z)(\frac{h}{H} - 1) + 0.559483\ (\frac{h^2}{H^2} - 1)$$

$$(\sqrt{MSE} = 0.063,\ R^2 = 0.95)$$

$$(12) \quad DBLC = 30.484 - 1.204\ HCB \qquad (\sqrt{MSE} = 2.99,\ R^2 = 0.64)$$

$$(13) \quad HCB = 18.862 - 1.505\ SPC \qquad (\sqrt{MSE} = 2.30,\ R^2 = 0.51)$$

$$(14) \quad CA = -6.678 + 3.365\ SPC + 0.859\ DBLC \qquad (\sqrt{MSE} = 3.34,\ R^2 = 0.89)$$

$$(15) \quad BRDIA = 8.476 + 1.673\ DBLC \qquad (\sqrt{MSE} = 3.62,\ R^2 = 0.84)$$

DISCUSSION

<u>Crown Dynamics and Stem Growth in Red Alder Plantations</u>

Figures 14 and 15 show predicted crown areas and predicted mean branch diameters

plotted over spacing, at ages 4, 8, and 12 years. Data plotted in these two figures were

derived from the allometric relationships of crown areas and branch diameters with *DBLC*

(equations 8 and 9). Assuming that these allometric relationships remain valid back through

time, they can be integrated with predicted trends in live crown recession (Figures 10 and

11), revealing a dynamic relationship between spacing and crown structure over time.

Studies have shown that red alder seedlings planted at spacings of 3 m close crown

within three to five years on productive sites (DeBell and Giordano 1994). Those results

are consistent with predicted crown areas presented in Figure 14, which show little or no

horizontal crown expansion beyond age 4 years at planted spacings closer than 3 m. Though

measurable crown overlap can occur in young red alder plantations (personal observation),

the space available for horizontal expansion of a crown is restricted in a closed canopy stand

(Fujimori and Kiyono 1986). Physical crowding causes intercrown abrasion as trees scrape

against each other in the wind, resulting in bud loss and decreased foliage production (Putz

et al. 1984). Further, earlier crown closure at closer spacings results in more rapid mortality

of lower branches and greater rates of crown recession. Thus, besides exhibiting short

crowns and small live crown ratios, trees planted at close spacings probably experienced

horizontally restricted crown growth within the first few years after establishment. Trees

planted at wide spacings not only had greater live crown ratios throughout the eight to

twelve years of growth analyzed in this study, but also developed significantly larger mean
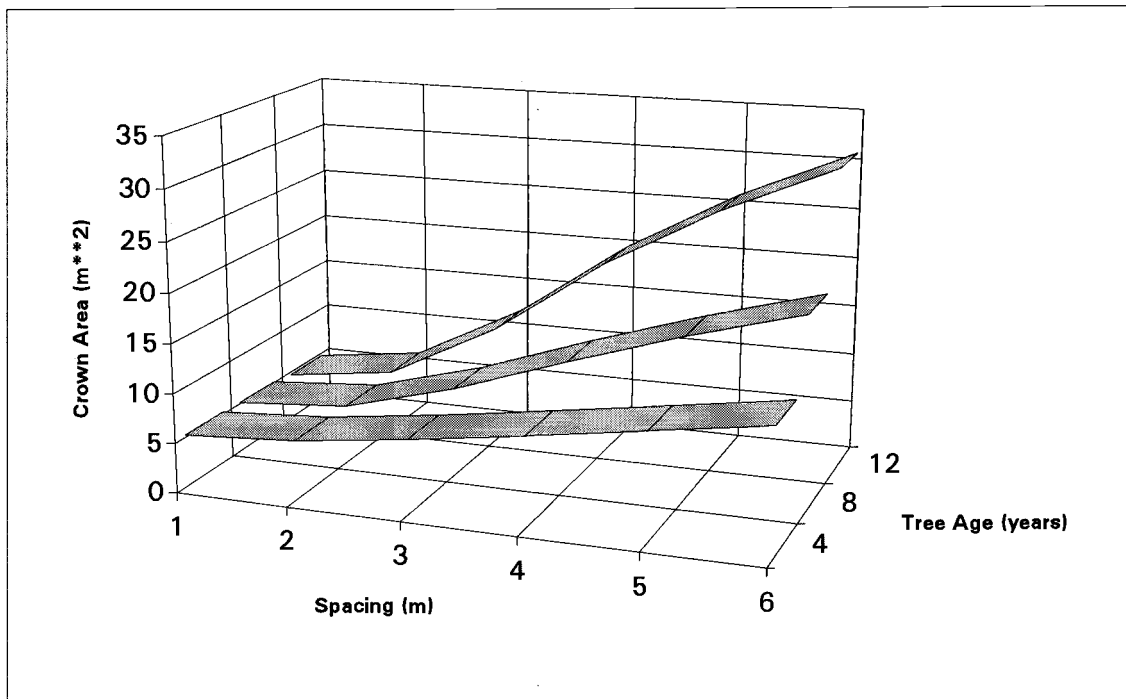
Figure 14. Crown areas at six planting densities and three ages. Crown areas were calculated from equation 8, using predicted values of DBLC (equation 7).
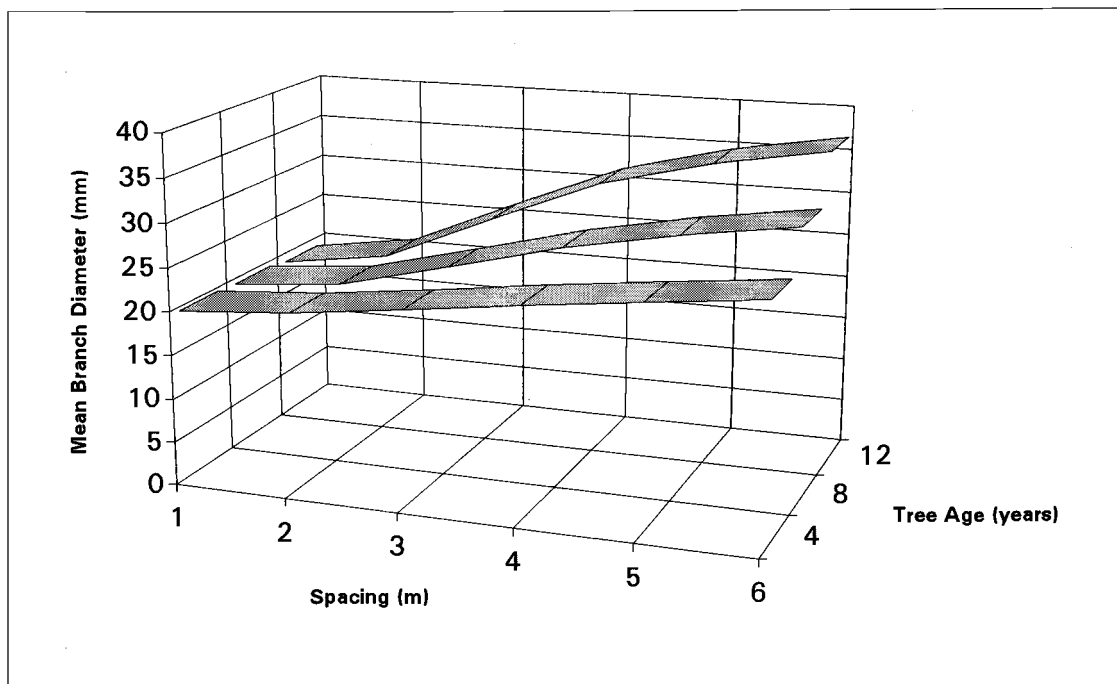
Figure 15. Mean branch diameters at six planting densities and three ages. Diameters were calculated from equation 9, with predicted values of DBLC (eq. 7).

branch diameters (Figure 15). Therefore, planting density strongly affected branch growth and longevity, resulting in differences among spacing treatments in the development of crown volumes and leaf areas maintained by individual trees through time; these differences among spacings resulted in the characteristic differences observed in patterns of stem growth.

Results of the diameter growth analyses (equations 1, 2, and 3) were consistent with results presented by DeBell and Giordano (1994), and Knowe and Hibbs (in prep.). Maximum diameter growth increment (at breast height) culminated earlier in trees growing at high planting densities; this earlier decrease in radial stem growth undoubtedly resulted from effects of earlier crown closure and more intense competition at closer spacings.

Relatively poor diameter growth was observed in trees planted at spacings wider than 4 × 4 m for the first 5 to 11 years of stand development. Predicted diameters of trees planted at 5 × 5 m were smaller than predicted diameters of trees planted at 3 × 3 m (based on an average site index of 21.37 m) for the first 10 years of growth, and smaller than predicted diameters of trees planted at 4 × 4 m for the first 11 years of growth (Figures 3 and 4). Predicted diameters of trees planted at 6 × 6 m were smaller than predicted diameters of trees planted at 3 × 3 m for the first 5 years of growth, and smaller than predicted diameters of trees planted at 4 × 4 m for the first 10 years of growth. However, by age 12 years, the greatest stem diameters were predicted for trees planted at 5 and 6 m spacings. Trees planted at spacings closer than 3 m, and at spacings wider than 6 m, had smaller predicted diameters throughout the analysis period of this study.

Based on the results of the annual diameter increment model developed in this study (equation 3), greater one-year diameter growth is attained by larger trees at an early age.

Although red alder planted at 5 and 6 m spacings initially had smaller stem diameters than

trees planted at 3 and 4 m spacings, their predicted diameters were greatest by age 12 years;

therefore, future annual diameter growth should be greatest in these trees. These widely-

spaced individuals did not begin to close crown until age 10 to 12 years (Figure 14); thus,

increased shading of their lower branches is imminent, and their crown bases should soon

begin to recede as their lower branches senesce and die. In many tree species, it has been

found that a 40 percent crown ratio represents a threshold value, below which production

becomes extremely limited (Kramer and Kozlowski 1979). Until their crowns have receded

to a threshold ratio of perhaps 40 percent, thereby limiting future growth potential, trees

planted at 5 and 6 m spacings should continue to exhibit greater annual diameter increments

than trees planted at closer spacings.

Studies have shown that early height growth of trees is often characterized by a

temporal "wave," with annual height growth peaking earlier at high planting densities

(Adlard et al. 1992, Knowe and Hibbs in prep.). This trend was not evident in heights

predicted by the sigmoid height-age function developed in this study (Figures 7 and 8); the

greatest heights, at all ages, were predicted for trees planted at spacings of 2, 3, and 4 m.

Height growth stimulus at dense spacings is, however, a short-term phenomenon (Hogg and

Nester 1991, Adlard et al. 1992, Knowe and Hibbs in prep.). Thus, results of this study are

not inconsistent with results presented by Bormann and Gordon (1984), DeBell and

Giordano (1994), and Knowe and Hibbs (in prep.), which show that by age 7 years,

optimum height growth in red alder occurs at intermediate (2 to 4 m) spacings. More rapid

height growth of closely-spaced trees during the first few years after planting, therefore, will

not have a substantial impact on silvicultural objectives directed toward timber production

in red alder plantations. Significant long-term height growth reductions in trees planted at the high and low ends of the density spectrum, however, may be of far greater importance.

Height growth reduction at high stand densities can be attributed to competition effects. The concept of competition, in the classic sense, assumes that a dominance hierarchy becomes established among trees (Perry 1985), causing some individuals to be favored while other individuals become suppressed (Sakai et al. 1968). Red alder trees analyzed in this study showed no observable stratification into crown classes (except at the Apiary site, presumably beginning before the onset of self-thinning), yet effects of competition were evident, particularly in very dense plots (spacings less than 2 × 2 m), where average live crown ratios had decreased to less than 40 percent by age 8 years (Figure 10).

Differences in stand microclimates, in understory competition, and in patterns of growth allocation probably contributed to reduced height growth and slow, early diameter growth at spacings wider than 4 × 4 m. For instance, the microclimate of a stand is strongly affected by the size and structure (height and aerodynamic roughness) of that stand (Jones 1992). Before crown closure, trees grow as isolated individuals; leaf-to-air vapor pressure gradients, and rates of heat and water vapor transfer to the air tend to be greater for widely-spaced trees than for trees growing in closed stands (Jones 1992). To compensate for a greater evaporative demand, partial stomatal closure occurs and can limit rates of photosynthesis in open-grown trees (Waring and Schlesinger 1985). For example, Cochrane and Ford (1978) found that annual height growth of plantation-grown Sitka spruce (*Picea sitchensis*) was slow until the stand developed a uniform, closed canopy; rates of annual height growth then increased rapidly for several years until productivity of individual trees

became limited by the effects of intertree competition. Although photosynthetic rates and changes in stand microclimate were not precisely monitored through time, accelerated height growth in the Sitka spruce plantation coincided with environmental changes, such as increased humidity, commonly associated with closed canopy stands (Cochrane and Ford 1978). Thus, differences across spacing treatments in microclimatological factors such as wind, humidity, and temperature may partly explain poor early growth of widely-planted red alder (Giordano and Hibbs 1993).

During the early stages of plantation development, effects on alder growth due to competition from an understory may last longer where trees are widely-spaced. At denser spacings, earlier crown closure will cause competing understory vegetation to become shaded and die sooner (DeBell and Giordano 1994). At the Cascade Head site, this trend was apparent. Trees planted at 3 × 3 m spacings were growing at relatively low levels of understory competition; at wider spacings, a dense shrub understory, dominated by salmonberry (*Rubus spectabilis* Pursh), was prevalent.

Results of this study strongly suggest that widely-spaced alder trees maintained greater branch and foliar biomass throughout their development (Figures 10, 11, 14, and 15). Because early diameter and height growth were reduced at wide spacings relative to intermediate spacings, it is probable that allocation of growth to crowns of widely-spaced trees occurred at the expense of stem growth. In a 5-year-old red alder plantation, Bormann and Gordon (1984) found a strong linear relationship between the rate at which a tree fixed atmospheric nitrogen and the mass of foliage supported by that tree. They also found that root biomass of alder trees was greater at wider spacings. Thus, a greater investment of

photosynthetic energy into N_2-fixation and belowground growth probably also contributes to decreased allocation to stem growth at wide spacings.

Stem Form Development in Red Alder Plantations

Wind sway can be an important factor affecting the distribution of radial growth and, therefore, stem taper in trees. In trees stayed with wires, studies have shown that stem diameter growth is promoted at the point on the stem where wind-forces cause maximum sway and the greatest bending stresses (Jacobs 1954, Valinger 1992). In trees that are not stayed with wires, the point of maximum sway corresponds to the point on the stem where crown weight is at a maximum (Valinger 1992); Figure 1 shows that foliar volume or mass is greatest near the base of the live crown. The current study showed that crown closure occurred sooner at closer spacings, resulting in significantly greater rates of live crown recession at higher planting densities. Thus, the point of maximum sway would shift upwards more rapidly in a closely-spaced tree as the point of maximum crown weight receded with the receding crown base. However, in closed canopy stands trees are more sheltered and are less subject to bending by the wind (Valinger 1992). In the current study, only trees planted at 5 × 5 m or wider were growing without substantial shelter from surrounding trees at the time of sampling. Thus the 'wind sway' theory may explain only partially the observed differences among treatments in patterns of stem taper.

It has been emphasized throughout this thesis that the crown regulates wood formation throughout the life of a tree; spacing affects crown dimensions, crown vigor, and the vertical distribution of foliage, thus influencing rates and patterns of stem growth (Larson 1969). Trees planted at spacings less than 5 × 5 m developed longer branch-free

boles (Figure 11), and had smaller crowns, with the smallest crowns occurring soonest at the closest spacings (Figure 10). Because stemwood formation is dependent on photosynthate produced in the crown, the point of maximum ring growth recedes upwards with the receding crown base as less foliage becomes available for production of wood along the lower stem of a tree (Farrar 1961, Larson 1963), probably irrespective of the influence of wind. In closely-spaced, plantation-grown alder, maximum ring widths occurred at progressively greater relative heights as crowns receded, and the narrowing of the annual sheath below the point of maximum width became more pronounced. The summation of these xylem increments resulted in the development of less tapered stems in red alder trees planted at closer spacings, so that by age 12 years, trees planted at 2 × 2 and 1 × 1 m had markedly cylindrical form.

Trees planted at spacings greater than 4 × 4 m had large, symmetric and relatively vigorous crowns extending to their stem bases throughout the period of growth analyzed in this study. Therefore, more foliage was available for production of wood along the lower stems of widely-spaced trees, and, as they grew, each successive annual layer of wood that formed was thickened from a tree's apex to its base. The summation of these tapered xylem increments resulted in the development of highly tapered stems by age 12 years in red alder trees planted at wide spacings. Because these trees also exhibited poor height growth relative to trees planted at intermediate spacings, development of stem taper was augmented.

Although trees planted at 3 × 3 and 4 × 4 m spacings exhibited significant live crown recession, they maintained relatively large crowns throughout the period of growth analyzed in this study. Clearly crown productivity in these intermediate-spaced trees was not limited, because they sustained rapid rates of height and diameter growth for up to 12 years.

However, for a given stem diameter, taller trees will have more cylindrical form (Larson 1963; also, equation 5).

Growth and Stem Form Change after Thinning

Thinning provides more growing space for both roots and crowns, leading to gradual changes in crown size and structure; greater leaf areas are supported per tree as crowns expand, and wood production per tree often increases (Larson 1969). Results of this study showed that following thinning, crown recession slowed (equation 13), crowns broadened (equation 14), and more branch wood was produced (equation 15). These effects on crowns were more pronounced in trees thinned to the widest spacing. Thus, the intensity of thinning determined the degree of response. As a result of thinning effects on crowns, stemwood production per tree also increased. Ten years after thinning the Olney site, Hibbs et al. (1994) found that stem diameter growth rates were nearly double the rates found in unthinned trees, although differences among the two spacing treatments were not apparent.

Ten years after thinning, Hibbs et al. (1994) found that annual height increments of thinned trees had increased from an initial post-thinning growth reduction. However, results of the current study showed that twelve years after thinning, total heights of thinned trees were still significantly reduced, with the greatest height reduction occurring at the lowest post-thinning density (Figure 12). Thus, thinning can negatively influence height growth in red alder for prolonged periods.

Because post-thinning patterns of height and diameter growth followed opposite trends, thinned trees developed stems with significantly smaller relative diameters, $\frac{d}{DBH}$ (Figure 13). Therefore, in young red alder, the effects of thinning on stem form

development are counter to effects produced by extreme stand density. Thinned trees developed greater crown ratios, shorter branch-free boles, larger absolute diameters, and developed more tapered stems.

Hara et al. (1991) pointed out that tree species exhibit two extreme types of growth strategies which correspond to the shade-tolerance and successional status of a species. Early-successional, shade-intolerant species often are characterized by rapid and indeterminate shoot extension growth, and develop relatively short, narrow crowns. Species that exhibit this kind of growth pattern are called the "height-growth type" (Hara et al. 1991). Late-successional, shade-tolerant species generally have determinate and relatively slow shoot extension growth, and maintain long, wide crowns. These species are called the "crown-growth type" (Hara et al. 1991).

Although red alder corresponds more closely to a "height-growth type," results of this study suggest that red alder has sufficient morphogenetic plasticity to change its allocation patterns after thinning from a "height-growth type" to an intermediate form resembling a "crown-growth type." Thinned trees developed greater branch and foliar biomass, and it seems probable that allocation of growth to crown expansion occurred at the expense of height growth.

Spacing Effects: Implications for Wood Quality

Red alder wood quality, lumber value, and lumber recoverability are affected by size and spacing of branches, knotty core diameters, branch-free bole lengths, and stem taper (Hibbs et al. 1992, Plank and Willits 1994). Results of this study have shown that annual

internode lengths, mean branch diameters, crown-wood volumes, clear bole lengths, and stem taper all are influenced by planting density and by thinning.

Compared to more widely-spaced trees, red alder established at high planting densities (from 2500 to 10,000 trees ha^{-1}) develop high relative lengths of clear stem, have smaller branches, and form lower percentages of crown wood. These trees also develop cylindrical stem form. Therefore, closely-spaced alder attain some characteristics associated with high lumber value. Individual tree growth, however, is not optimal at these spacings; stem diameter growth is reduced within three to five years after establishment. Because height growth is reduced at very high densities, the distance between annual nodes is reduced. Because the largest diameter branches produced by a tree grow near annual nodes, the largest diameter knots will be more closely-spaced at high planting densities. Additionally, mortality will be high at close spacings (Puettmann 1990), and lumber volume per tree will be small.

At planting densities of 400 trees ha^{-1} and lower (spacings of 5×5 m and greater), both height growth and stem form development are poor. Twelve years after establishment, essentially the entire stem volume consists of crown-formed wood. Following crown closure and the onset of crown recession, stem form should gradually improve in these widely-spaced trees (Larson 1963). However, compared to more closely-spaced trees, stems will be more tapered, clear bole lengths will be shorter, knotty core diameters will be greater, distances between large branches will be shorter, and the average knot diameter will be greater. Although they should become diminished over time, it is likely that these attributes will significantly affect wood quality to the end of a rotation [age 25-30 years (Hibbs and DeBell 1994)].

For at least twelve years after planting, the best balance between growth and wood-quality characteristics is exhibited by trees growing at intermediate densities; i.e., at densities from approximately 600 to 1100 stems ha^{-1} (spacings of 4 × 4 and 3 × 3 m, respectively). Among these two spacings, trees planted at 3 × 3 m are slightly taller and are less tapered (have better form) by age 10 years. For example, based on an average site index (S_{20} = 21.37), 10-year-old trees planted at 3 × 3 m have predicted total heights and diameters (at breast height) of 12.4 m and 13.3 cm (Figures 16 and 17). At the same age, trees planted at 4 × 4 m have predicted heights and diameters of 12.1 m and 13.7 cm. Using these values, and a height, h, of 5.3 m, relative diameters ($\frac{d}{DBH}$ calculated from equation 5) of trees planted at 3 and 4 m are 0.69 and 0.66, respectively. In addition, predicted heights-to-crown-bases at age 10 years are 3.5 m and 1.4 m, for trees planted at 3 and 4 m spacings, respectively (Figure 11).

Thus, characteristics associated with good lumber recoverability and high quality stemwood develop sooner in trees planted at 3 × 3 m. Compared to trees planted at 4 × 4 m, mean branch diameters are smaller, distances between annual nodes are slightly greater, crown-wood volumes are smaller, clear bole lengths are greater, and stems are more cylindrical. However, at an average stem diameter of 13.3 cm, an expected diameter growth rate of approximately 0.8 cm yr^{-1} (equation 3), and a density of 1100 stems ha^{-1}, trees planted at 3 m are rapidly approaching the upper limit of growing stock in managed stands (Puettmann 1990) by age 10 years. This means that to avoid substantial mortality losses, stands planted at 3 × 3 m on a fairly productive site (e.g., S_{20} = 21 m) must be thinned by approximately age 12 years.
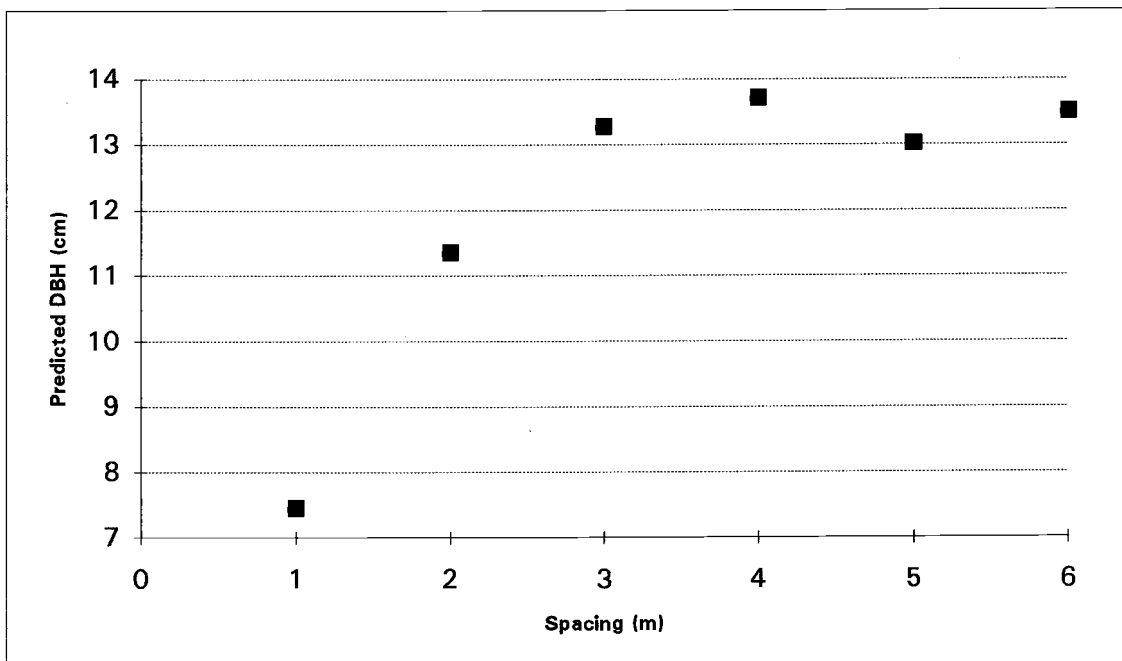
Figure 16. DBH (cm) predicted at age 10 years, for six planted spacings (m). Diameters of trees planted at spacings of 1 x 1 through 4 x 4 m were predicted from equation 1; equation 2 predicts diameters of trees planted at spacings of 5 x 5 m and greater.
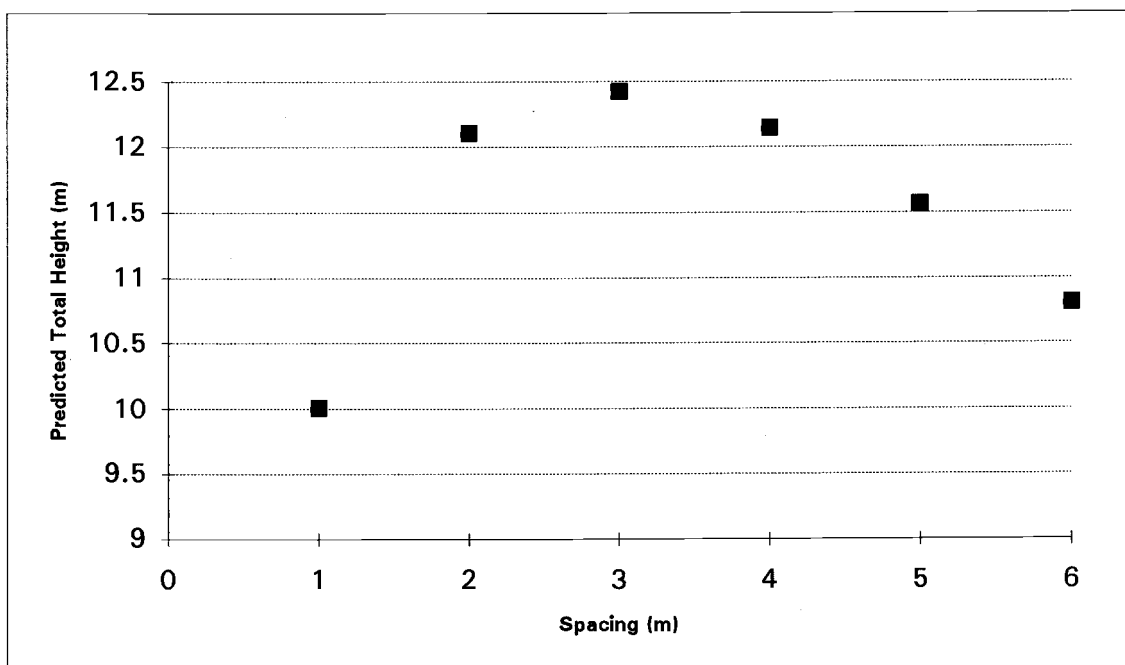
Figure 17. Total heights (m) predicted by equation 4 at age 10 years, for six planted spacings (m).

In contrast, at age 10 years, effects of competition are just beginning to become manifest in trees planted at 4 × 4 m. Density-induced mortality may not become important until these trees grow to a diameter of approximately 24 cm (Puettmann 1990). By this time, stem form should be improved, because crowns will have receded considerably (Larson 1963). However, due to initial spacing effects, red alder planted at 3 and 4 m spacings may exhibit significant differences in wood quality throughout a rotation. Trees planted at 4 × 4 m will have greater knotty core diameters, and larger knots encased within their lower boles. The choice of a silvicultural strategy will depend on a tradeoff between diminished wood quality at the wider spacing, and economic benefits associated with a lower intensity management regime.

In natural stands, by the time red alder trees are 25 to 30 years old (rotation age) lumber value per board foot is about 30 percent greater from butt logs than from logs higher up the bole (Ahrens et al. in prep.). The greater value is primarily due to the greater volume of clear wood formed over the knotty core in butt logs. Because of their larger crowns, lower stem growth was much greater in thinned trees at the Olney site compared to unthinned trees (Hibbs et al. 1994). Thus, the volume of knot-free wood will be much greater in the butt logs of thinned trees, making them much more valuable than unthinned trees. Because of this, thinning should be a viable economic and silvicultural strategy.

Increased taper following thinning will reduce the amount of recoverable lumber per unit volume of wood for a tree of given *DBH* (Lowell and Dwyer 1988). Thus, an increase in stem-volume growth after thinning will be greater than the growth in recoverable volume. Among the two thinning treatments at the Olney site, no significant differences in stem taper developed after stand treatment (equation 11). However, smaller, more widely-spaced

knots, and greater clear bole lengths impart superior wood quality attributes to the more narrowly-respaced red alder. By age 26 years, trees respaced to an average distance of 4.2 m were clearly superior to trees thinned to 5.8 m.

From an economic perspective, the choice between these two spacings is evident. At a respacing distance of 5.8 m, there are about 295 stems ha^{-1} in the residual stand after thinning, compared to about 560 stems ha^{-1} in a stand thinned to 4.2 × 4.2 m. Thus, in a comparison of these two treatments, by age 26 years stands thinned to 4.2 m will yield the greatest volume ha^{-1} of clear, knot-free wood.

It is important to realize that the act of thinning can result in increased average stem taper, irrespective of changes in form caused by changes in growth patterns. If large-crowned, dominant trees are favored in the residual stand, then average relative diameters will decrease immediately as a direct result of the thinning itself (Larson 1963). This clearly was not the cause of changes in stem form observed at Olney. Precise measurements were taken of individual-tree growth through time. Both height growth and stem taper diverged significantly from a single mean value after thinning.

SUMMARY AND CONCLUSIONS

An understanding of the relationship between crown size, length, and vigor, and growth patterns of tree stems is crucial to the development of approaches to management of wood yield and quality. Planting density strongly affected crown development of red alder; for example, 73 percent of the variation in live crown ratios was explained by spacing alone. Trees planted at high densities developed short, narrow crowns, and small branches, while trees planted at progressively wider spacings had progressively wider and longer crowns, and larger branches. Stem growth patterns were subsequently affected.

Rates of annual stem diameter growth increased faster and culminated earlier at intermediate (3 to 4 m) spacings than at wider spacings. Total diameter growth of trees planted at spacings closer than 3 × 3 m and wider than 6 × 6 m was markedly reduced throughout the first twelve years of growth. The greatest height growth was attained by trees planted at 2, 3, and 4 m spacings; significant long-term height growth reductions occurred in trees planted at the high and low ends of the density spectrum. Trees planted at high densities developed cylindrical form, and widely-spaced trees developed stems with significant taper. These differences in growth patterns among spacing treatments will undoubtedly affect wood yield and quality to the end of a rotation.

Spacing accounted for a relatively small proportion of the explained variation (from 0.9 to 16.4 percent) in the diameter-age and height-age relationships of plantation-grown alder. Results presented in this thesis, however, were consistent with results of previous studies, and show that a balance between the negative and positive effects of stand density on growth should guide silvicultural strategies.

During at least the first decade after plantation establishment, optimal diameter and height growth occur at spacings of about 3 to 4 m (see, for example, Figures 16 and 17). When size and spacing of knots, clear bole lengths, and stem taper are important management considerations, it becomes clear that red alder exhibits its best growth characteristics at moderate levels of competition (i.e., at spacings near 3×3 m).

Results from the thinning study showed that in response to thinning, crown recession slowed, crown areas expanded, more branch wood was produced, and height growth was reduced. These effects were more pronounced in trees thinned to the widest spacing. Although stem diameter growth increased after thinning (Hibbs et al. 1994), relative diameters decreased (i.e., stem taper increased). Because it appears that post-thinning allocation of growth to crown expansion occurs at the expense of stem height growth, production of large crowns with increased growing space has important implications for red alder silviculture.

More rigorous economic analyses are needed to determine the degree to which increased post-thinning taper affects lumber recoverability. However, properly timed and spaced thinnings will undoubtedly increase the value of a stand. Because of the small sample size taken from the Olney site, one cannot make statistically valid inferences to other sites; however, future studies should be committed to the investigation of post-thinning changes in growth allocation patterns.

Finally, models developed in this study for plantation-grown alder should not be extrapolated beyond age 12 years, nor should they be used to predict growth patterns of red alder planted on unproductive or xeric sites. More information will become available from recently established long-term spacing trials. These data will facilitate the development of

more robust growth models, and should elucidate the dynamics of red alder growth patterns across a wider range of site conditions and ages.

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APPENDIX

The following figures were used to select initial models for height-age and diameter-age relationships, and live crown ratios. The partial annual growth that had occurred during spring, 1993 was ignored for all analyses in this thesis.

Figures 18 through 20 are graphs of average *DBH* by spacing treatment plotted over age, for all trees from the Cascade Head, Centralia, and Apiary spacing studies. Figures 21 through 23 show average total tree height by spacing treatment plotted over age, for all trees from the Cascade Head, Centralia, and Apiary spacing studies.

Figures 24 through 29 show scatterplots of diameters and heights over spacing, for all trees from the Cascade Head, Centralia, and Apiary spacing studies. These relationships are compared graphically with predicted lines from equations 1 and 2 (*DBH*) and equation 4 (height).

Figures 30 through 41 are scatterplots of reconstructed live crown ratios, for all sample trees from the Centralia and Apiary spacing studies. Measured live crown ratios from the Cascade Head spacing study were also used as data points to develop the live crown ratio model.

Figure 42 is a graph of the average total tree height at a given calendar year, by thinning treatment, for all nine sample trees from the Olney thinning study. Trees ranged in age from 14 to 16 years at the time of treatment; therefore, average heights in Figure 36 were calculated based on the calendar year to show more clearly the height growth reduction after thinning.
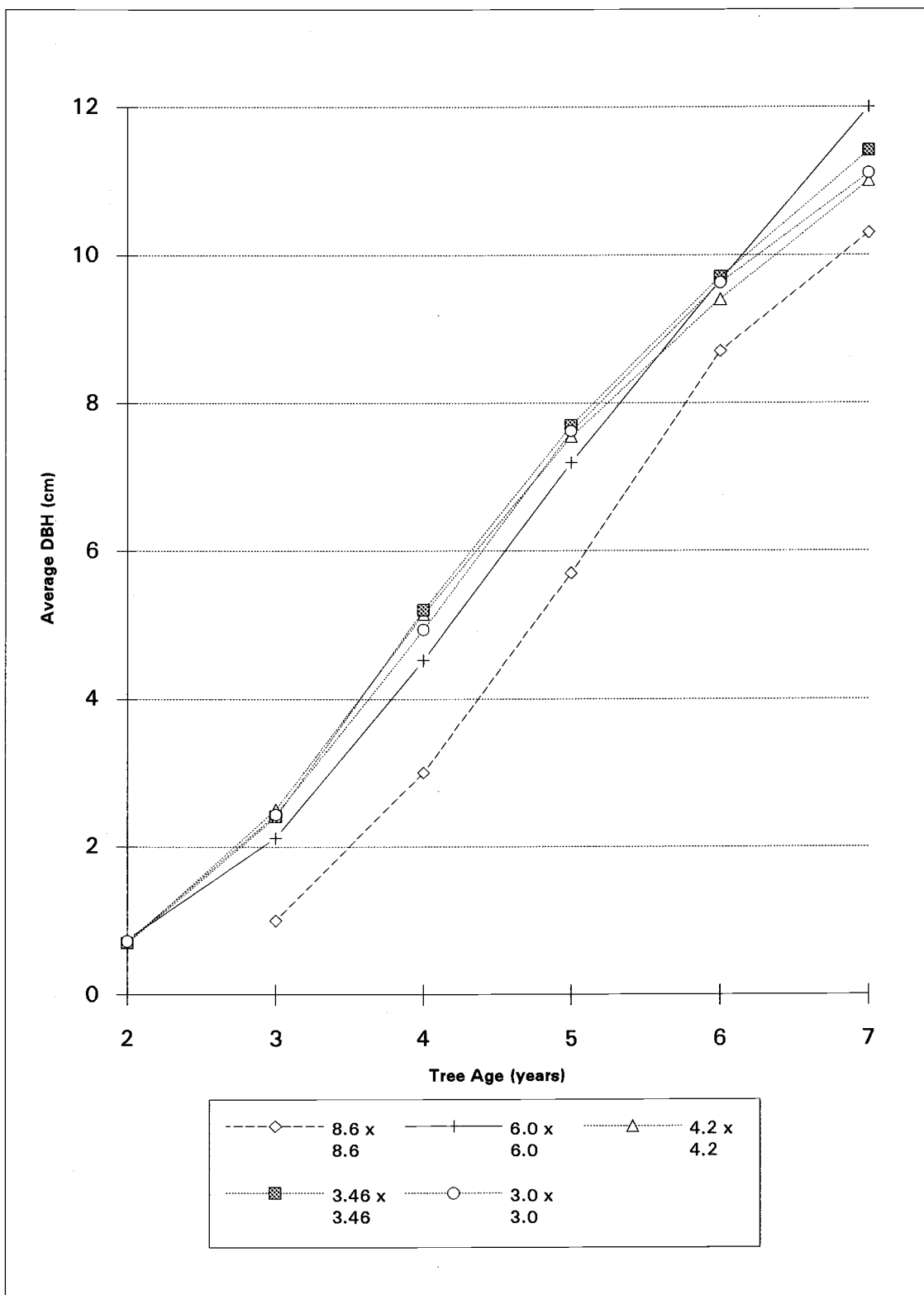
Figure 18. Average DBH (cm) by spacing treatment (m), plotted over tree age (years), for all trees from the Cascade Head spacing study.
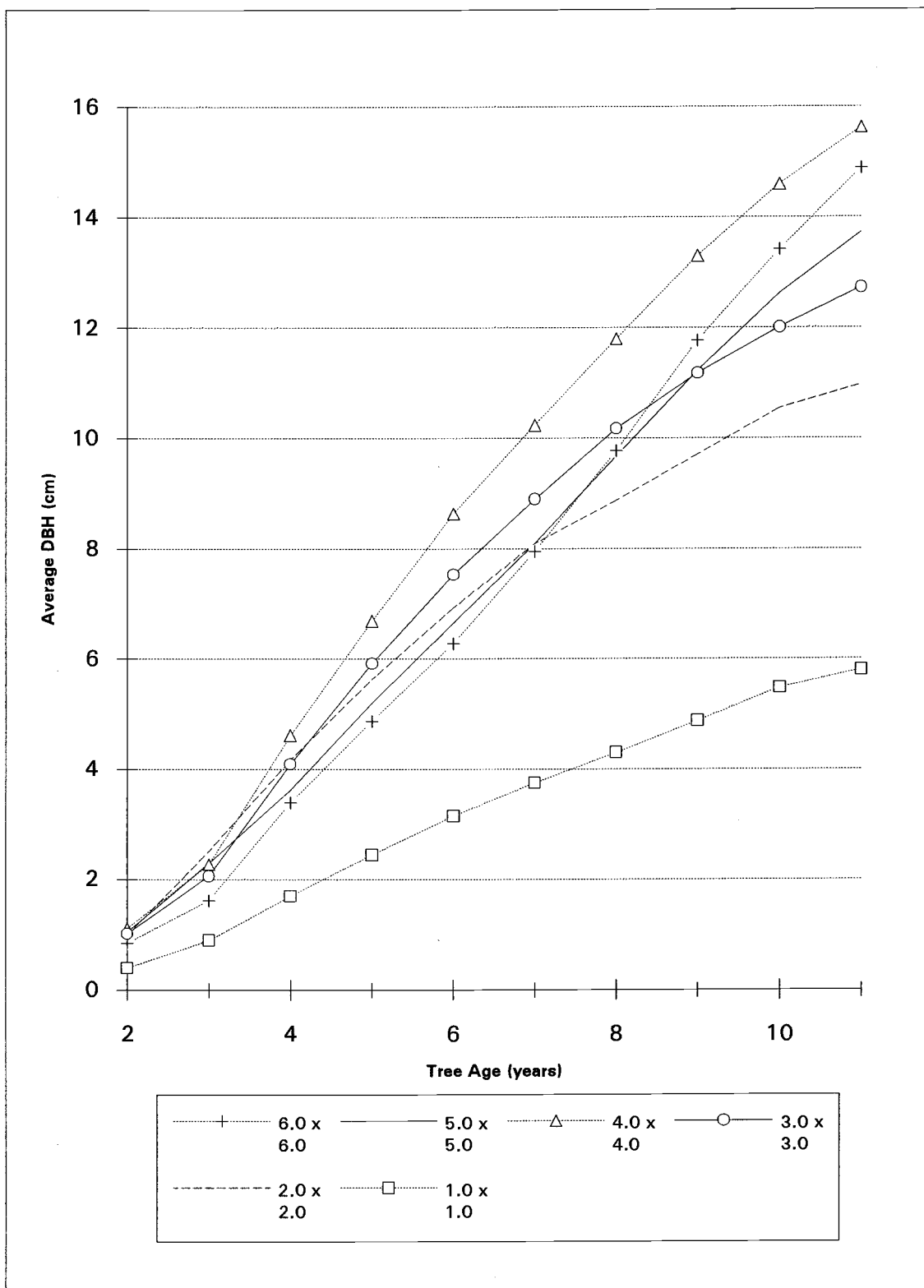
Figure 19. Average DBH (cm) by spacing treatment (m), plotted over tree age (years), for all trees from the Centralia spacing study.
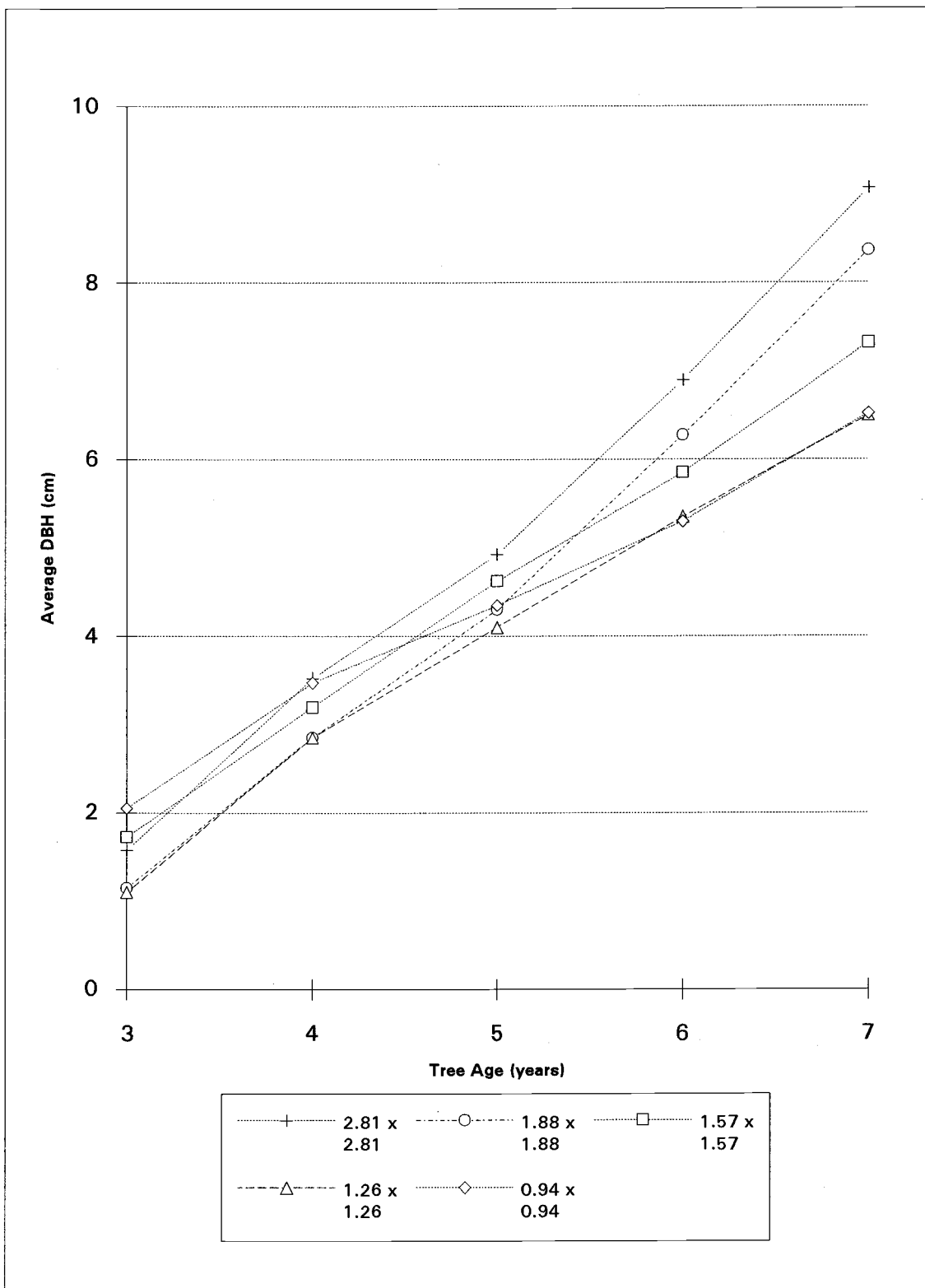
Figure 20. Average DBH (cm) by spacing treatment (m), plotted over tree age (years), for all trees from the Apiary spacing study.
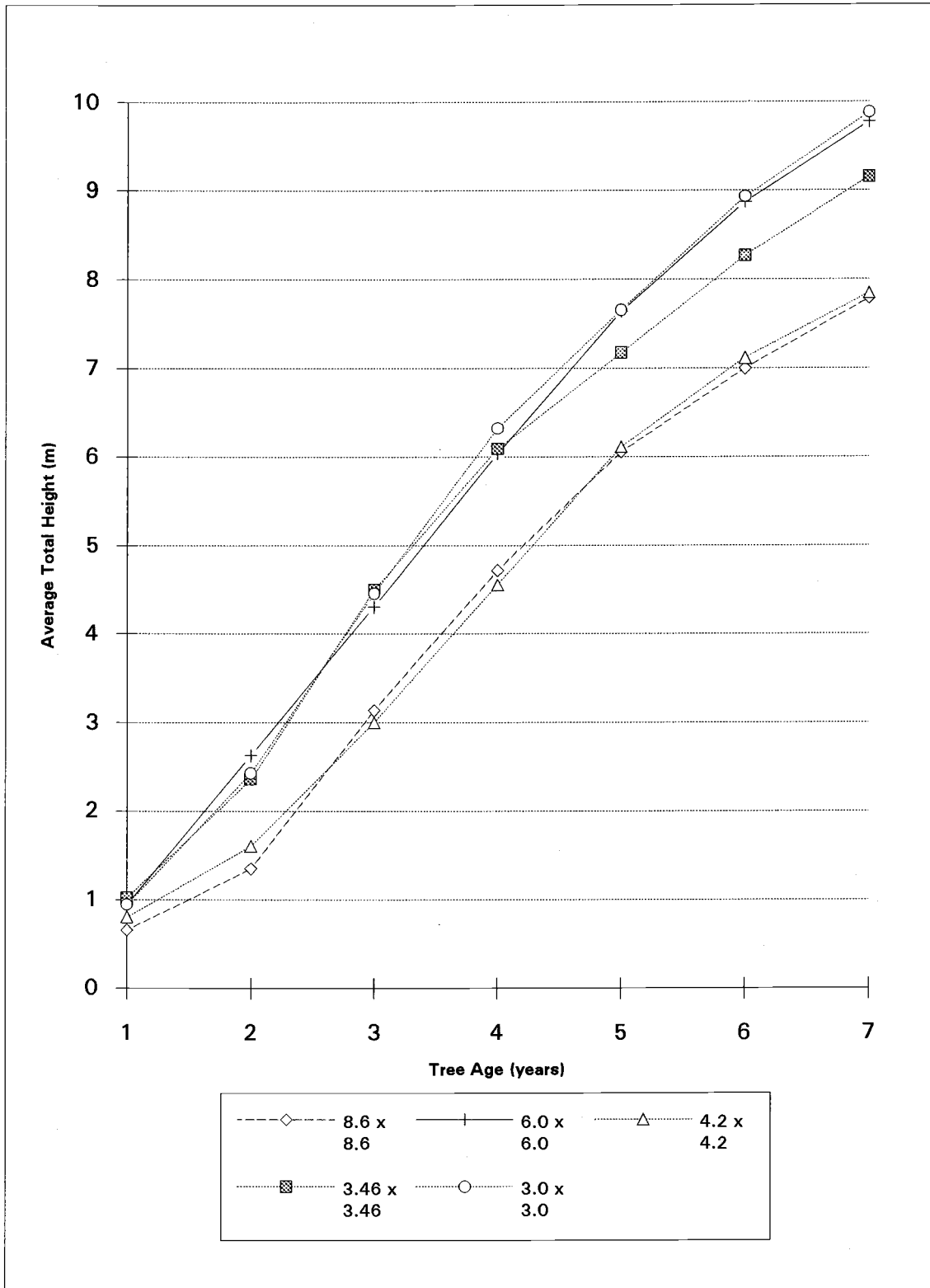
Figure 21. Average total tree height (m) by spacing treatment (m), plotted over age (years), for all trees from the Cascade Head spacing study.
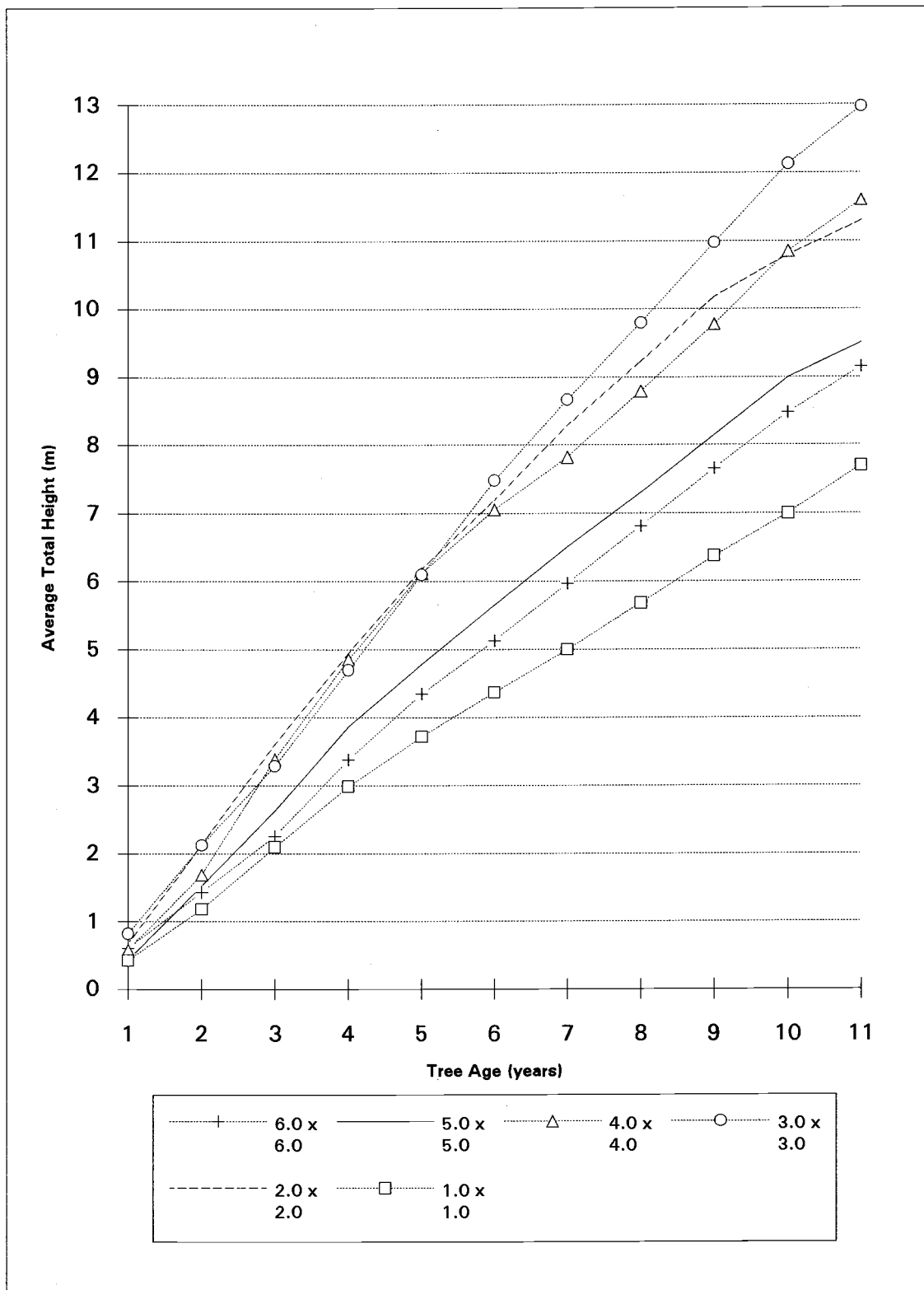
Figure 22. Average total tree height (m) by spacing treatment (m), plotted over age (years), for all trees from the Centralia spacing study.
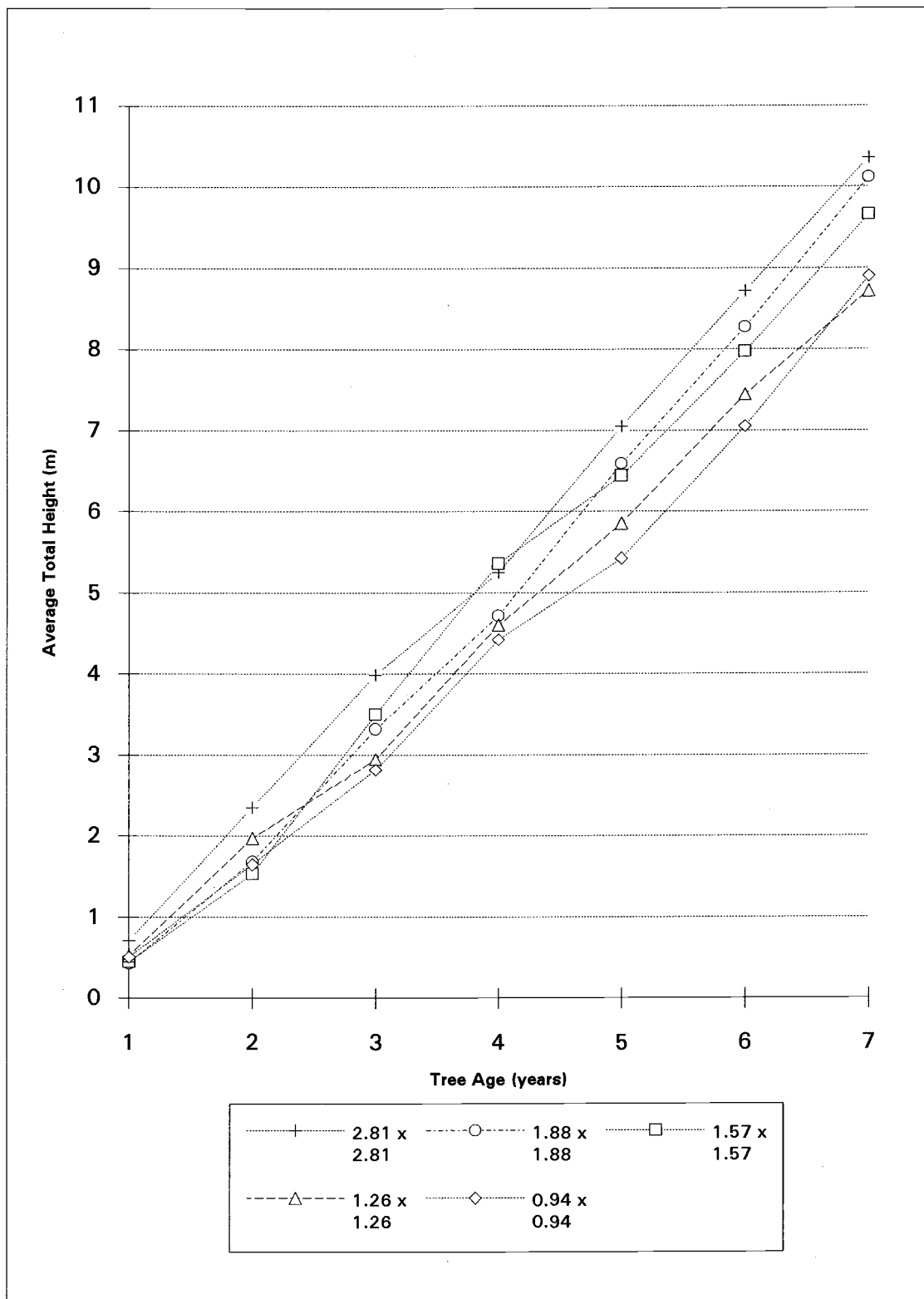
Figure 23. Average total tree height (m) by spacing treatment (m), plotted over age (years), for all trees from the Apiary spacing study.
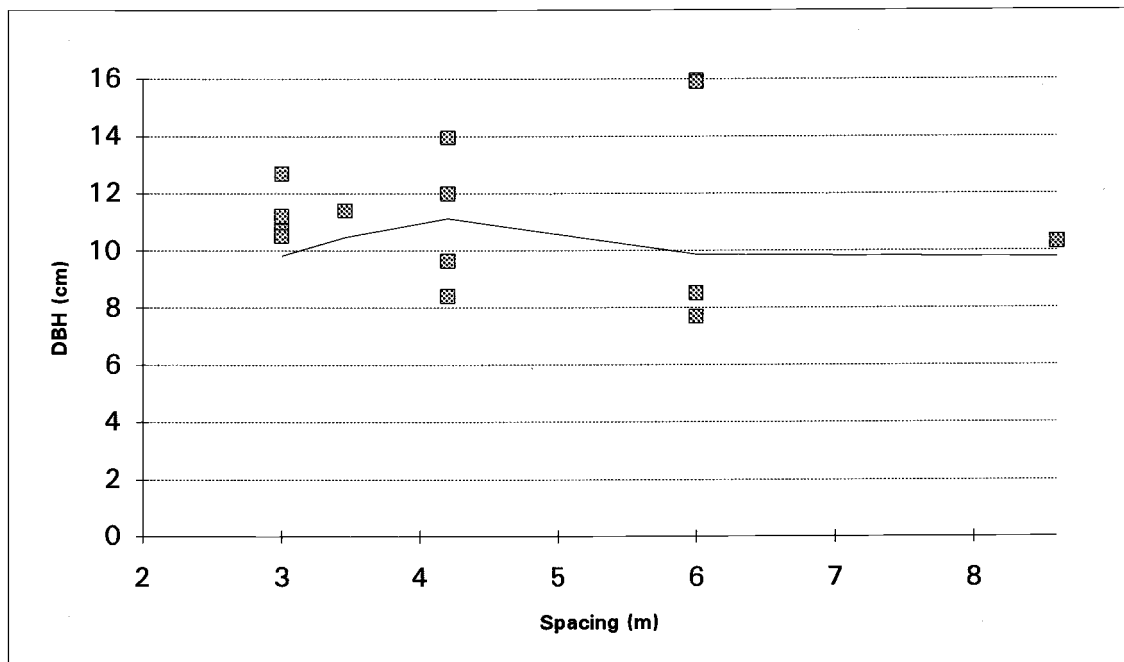
Figure 24. Relationship between DBH (cm) at age 7 years and spacing (m), for all trees from the Cascade Head spacing study, with the predicted line from equations 1 and 2.
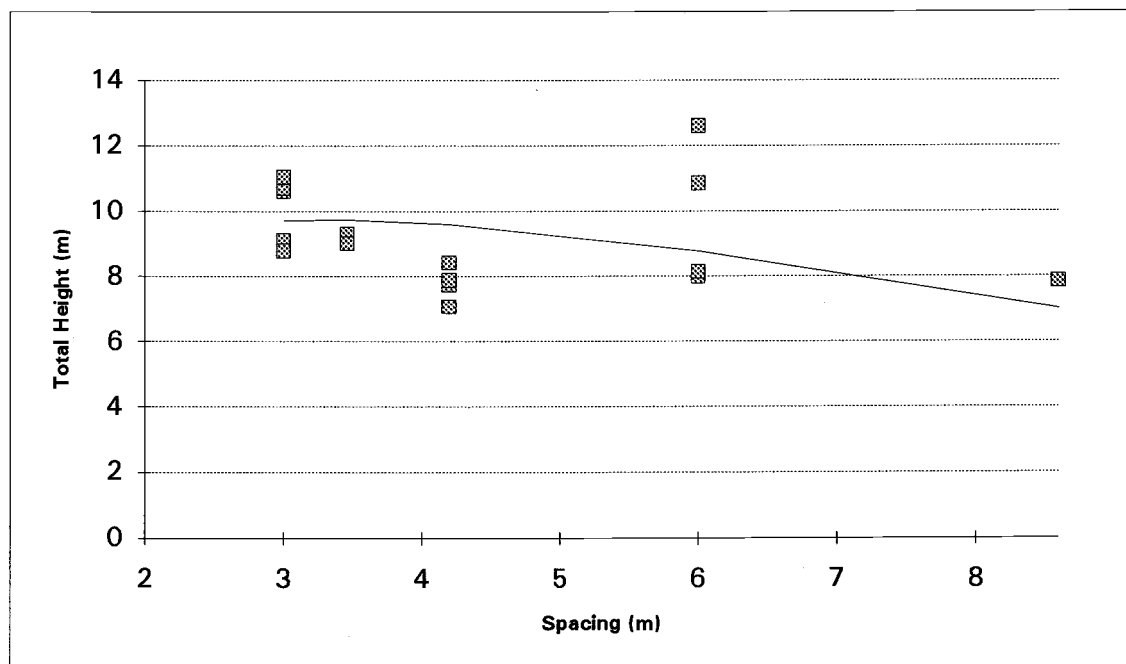

Figure 25. Relationship between total heights (m) at age 7 years and spacing (m), for all trees from the Cascade Head spacing study, with the predicted line from equation 4.
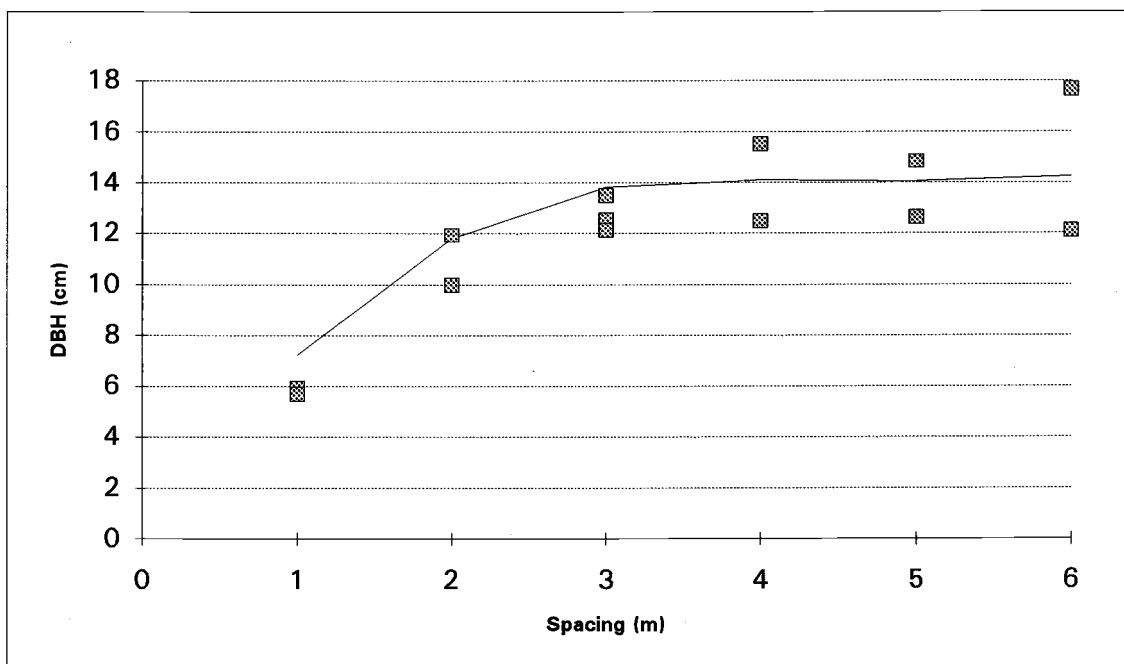
Figure 26. Relationship between DBH (cm) at age 11 years and spacing (m), for all trees from the Centralia spacing study, with the predicted line from equations 1 and 2.
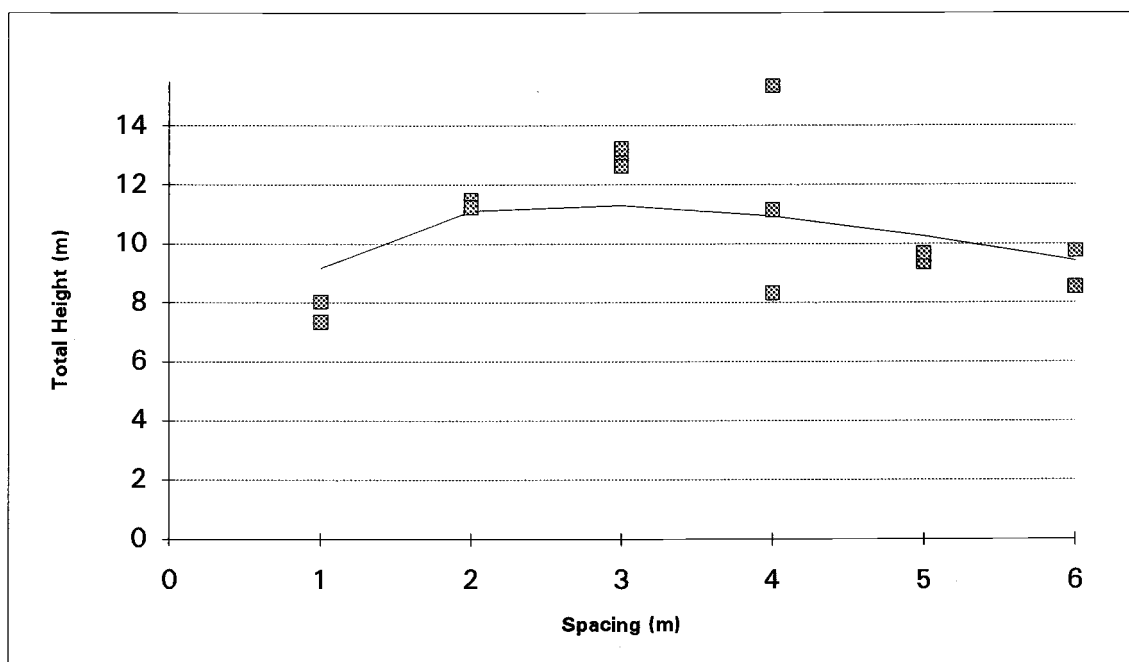
Figure 27. Relationship between total heights (m) at age 11 years and spacing (m), for all trees from the Centralia spacing study, with the predicted line from equation 4.
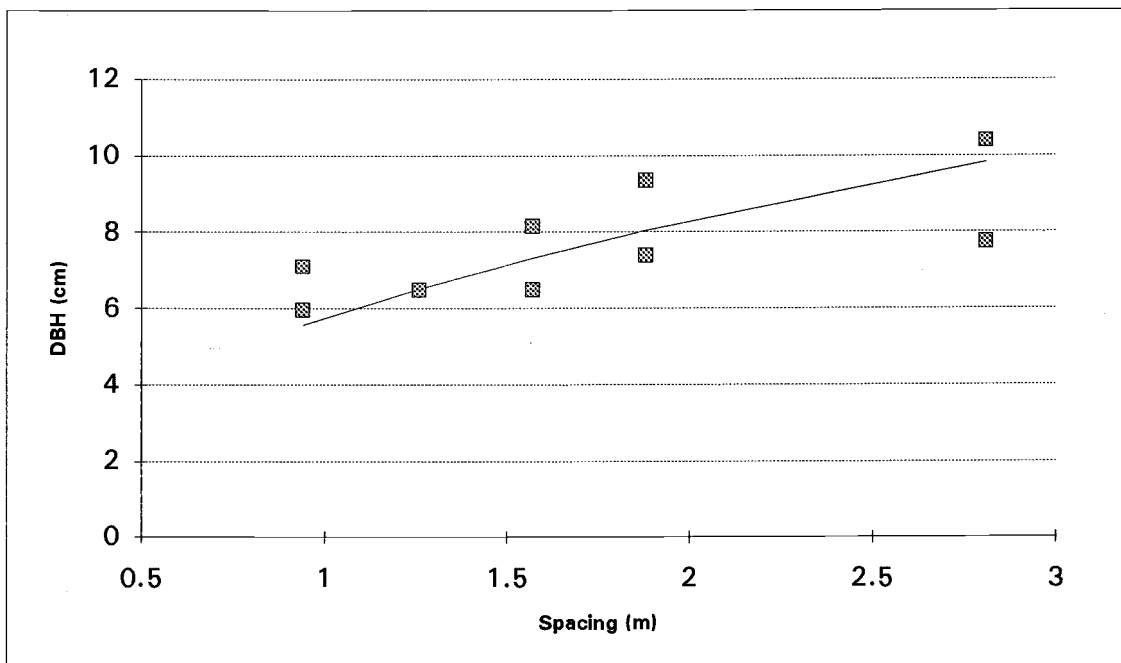
Figure 28. Relationship between DBH (cm) at age 7 years and spacing (m), for all trees from the Apiary spacing study, with the predicted line from equation 1.
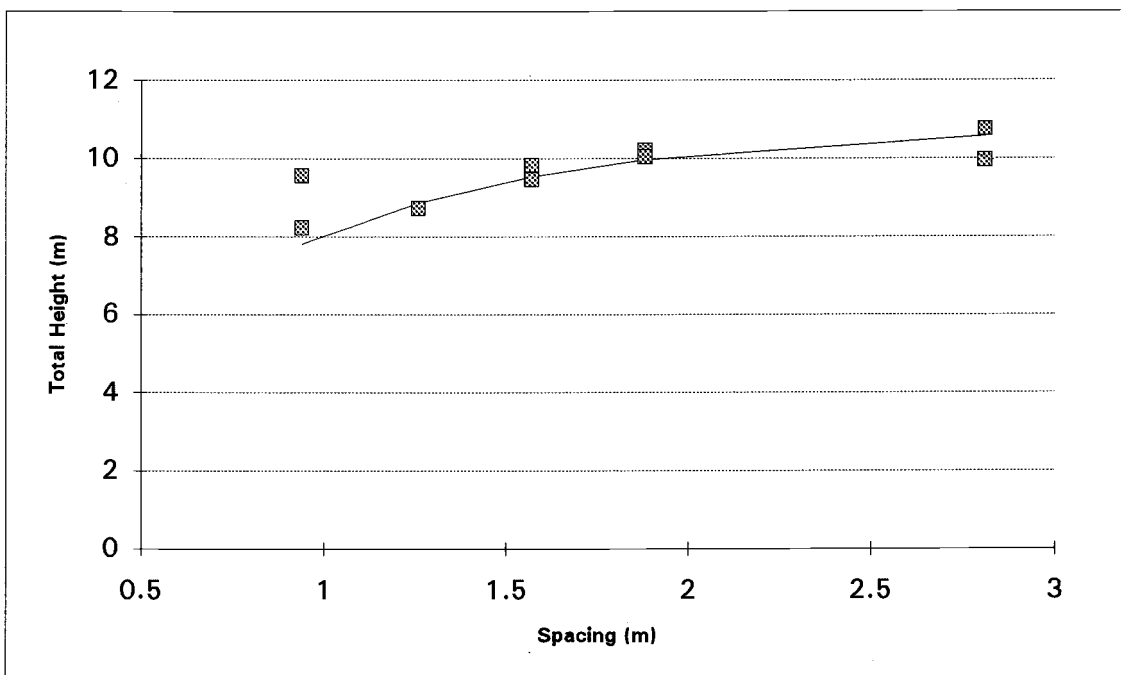
Figure 29. Relationship between total heights (m) at age 7 years and spacing (m), for all trees from the Apiary spacing study, with the predicted line from equation 4.
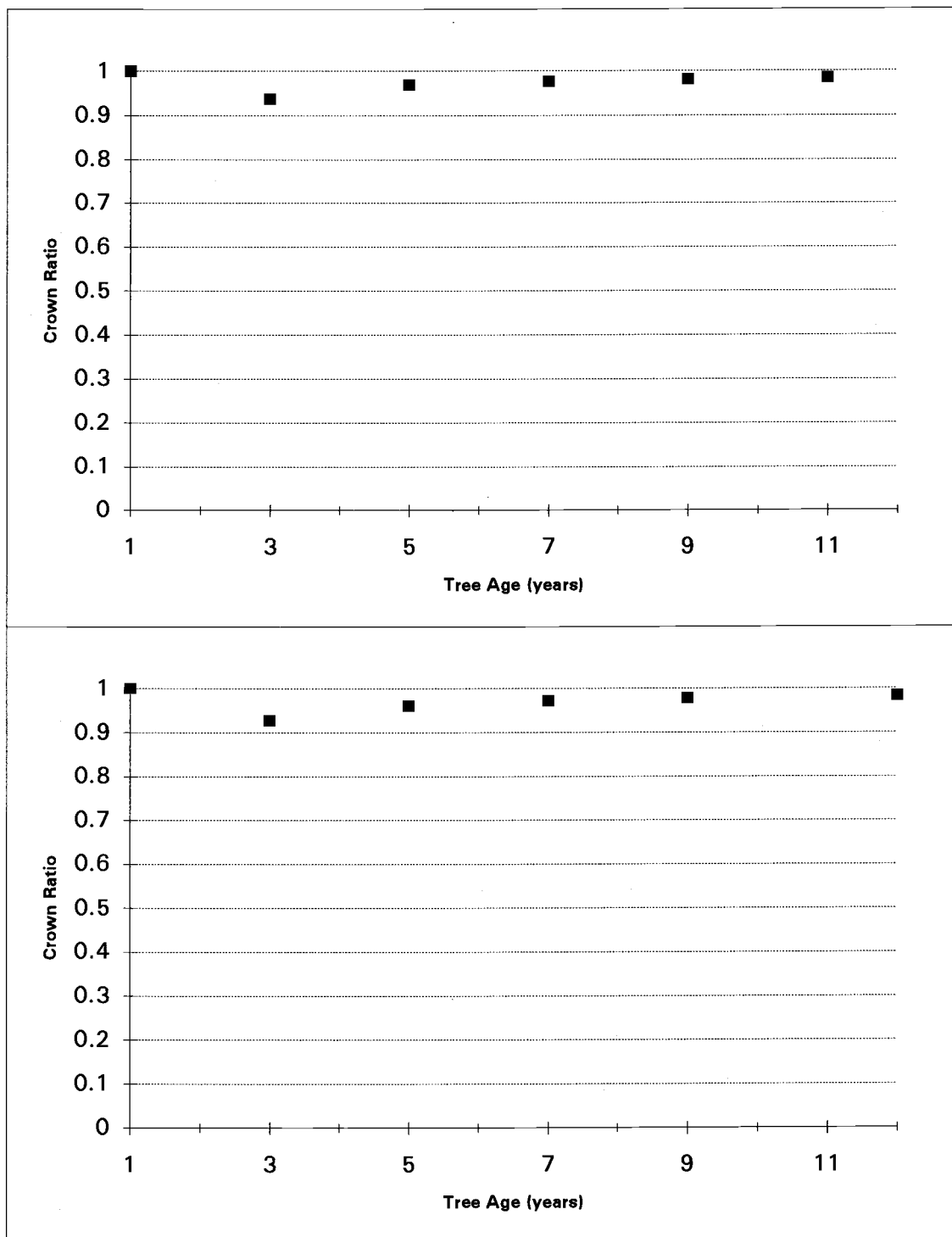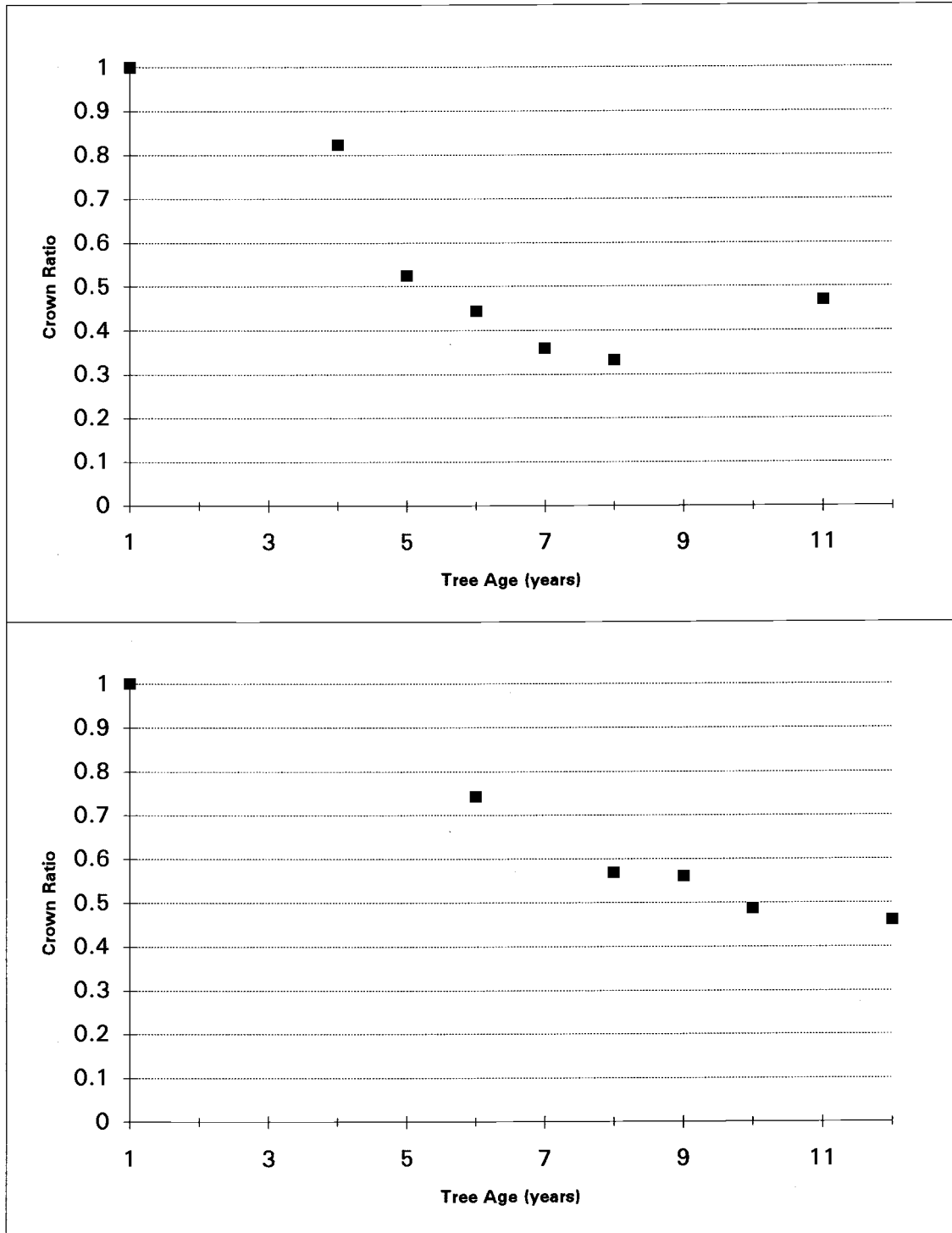
Figure 30. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 6.0 x 6.0 m from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as a data point in the development of the crown ratio model (equation 6).
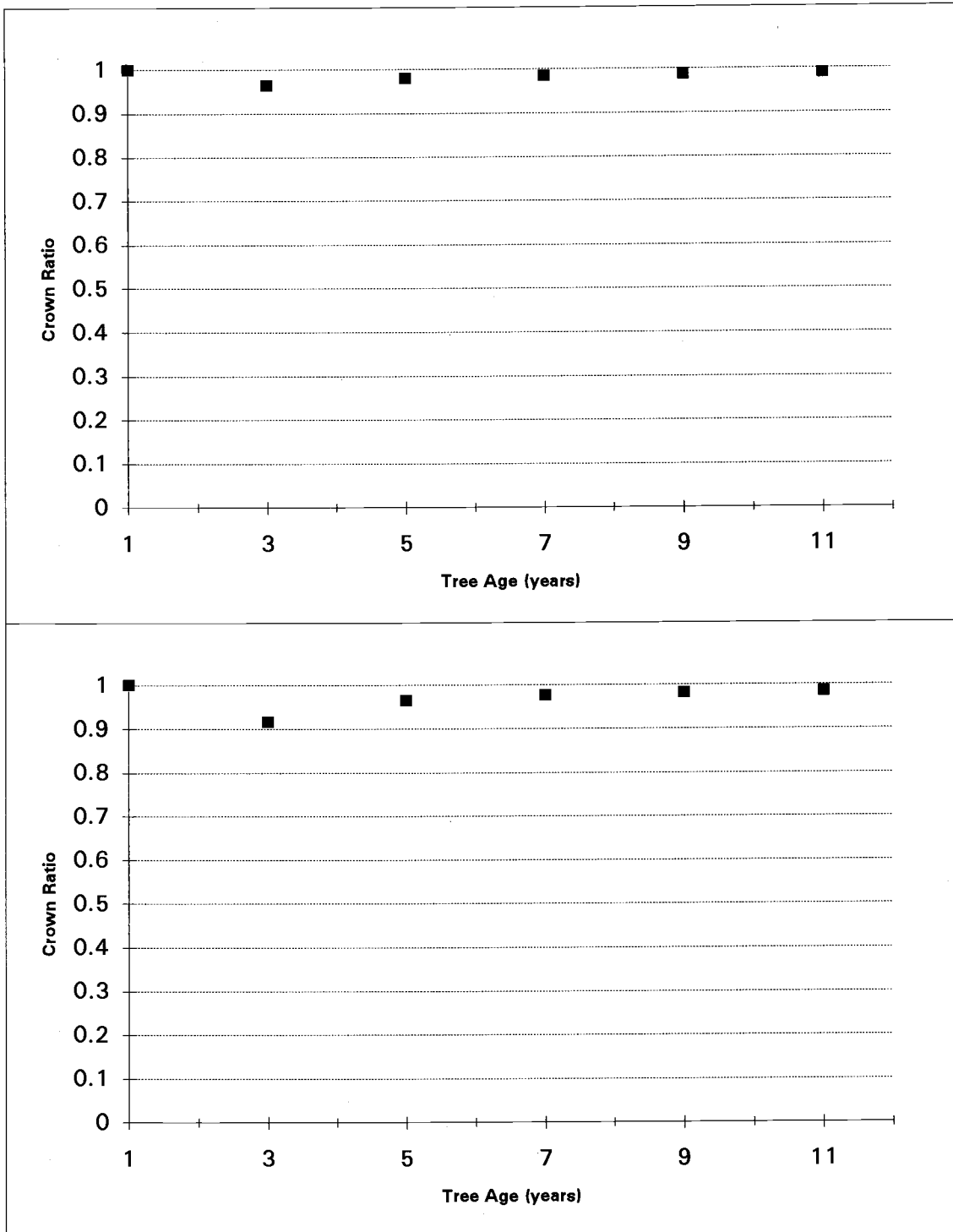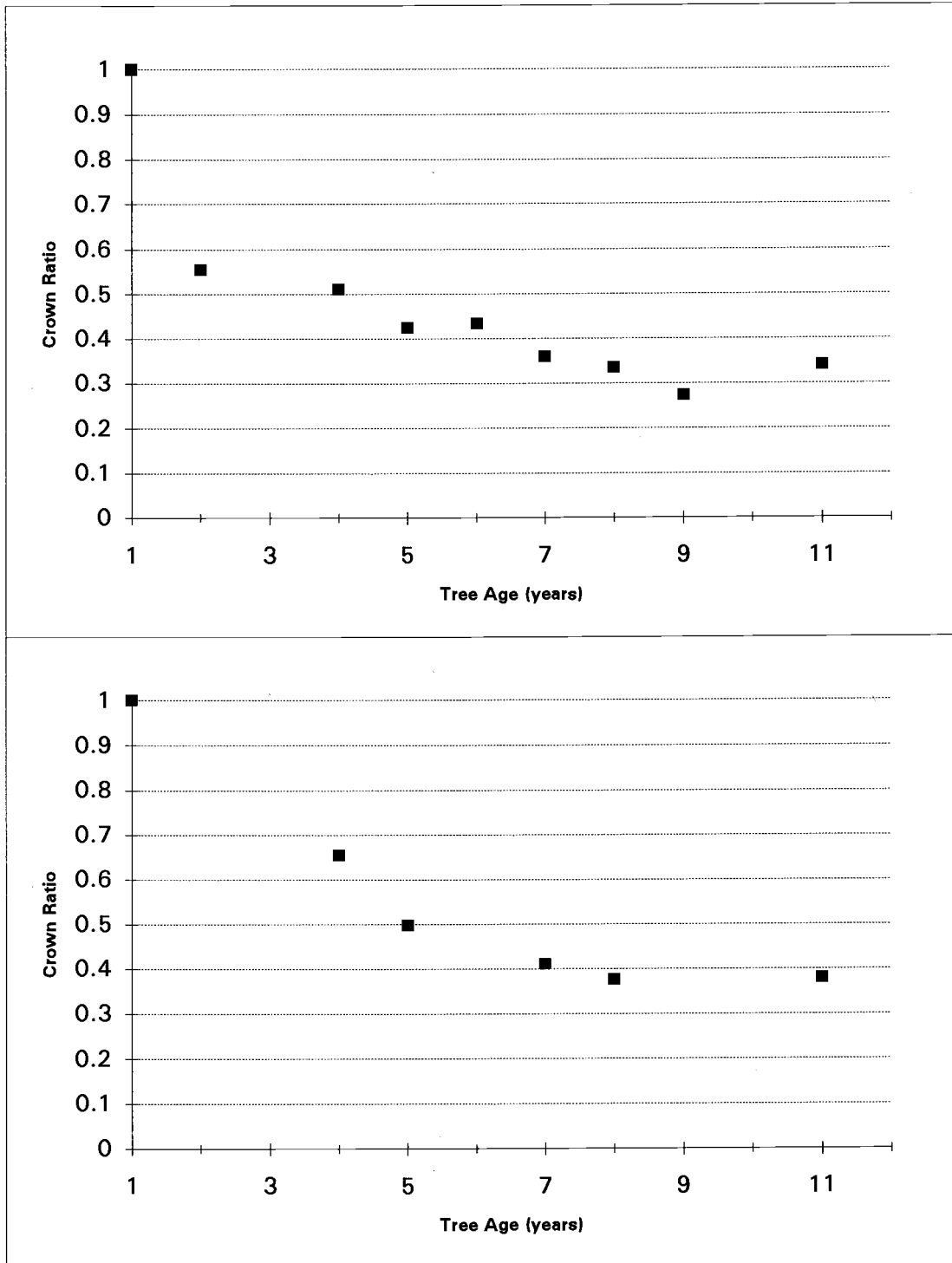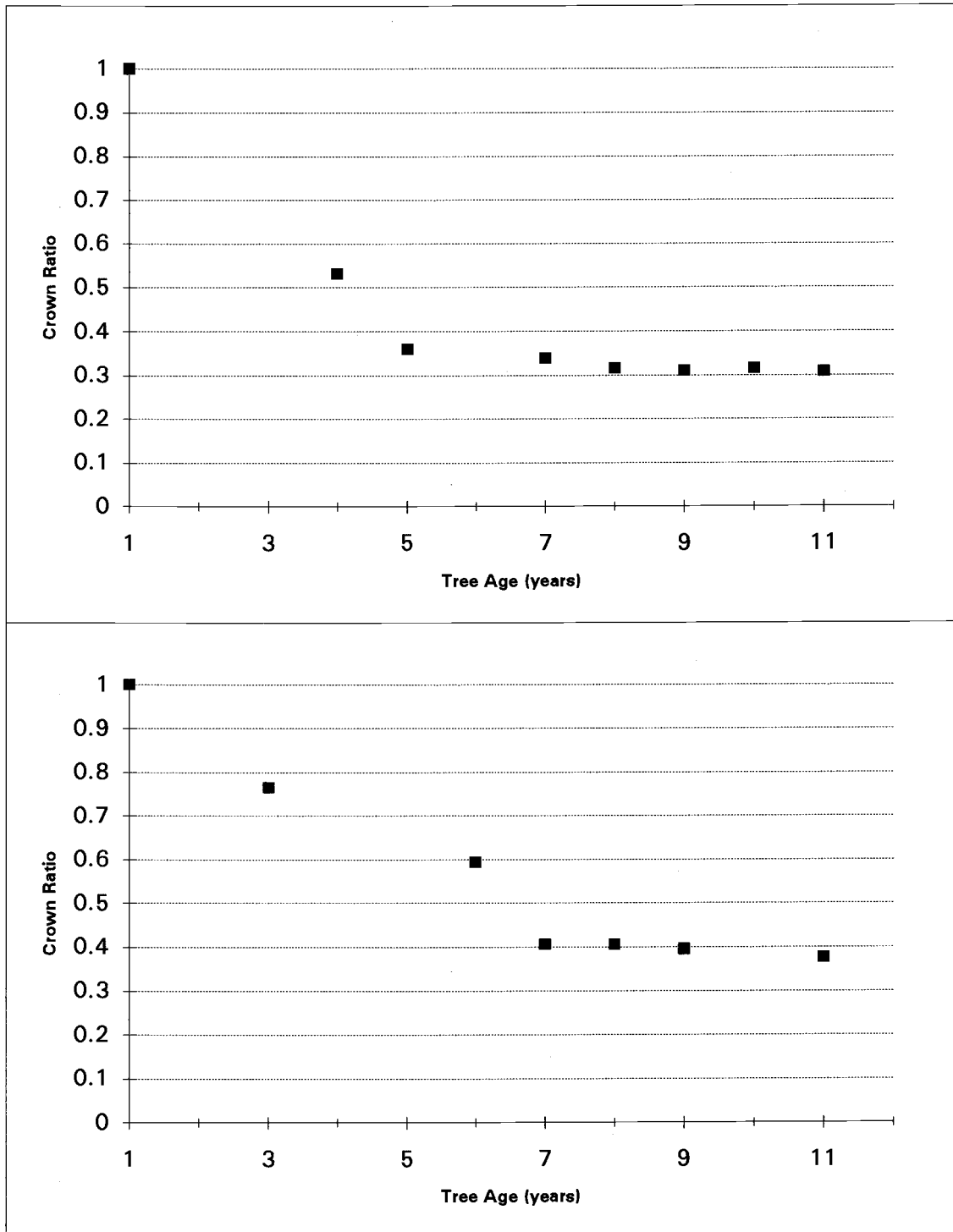
Figure 31. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 5.0 x 5.0 m from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as a data point in the development of the crown ratio model (equation 6).
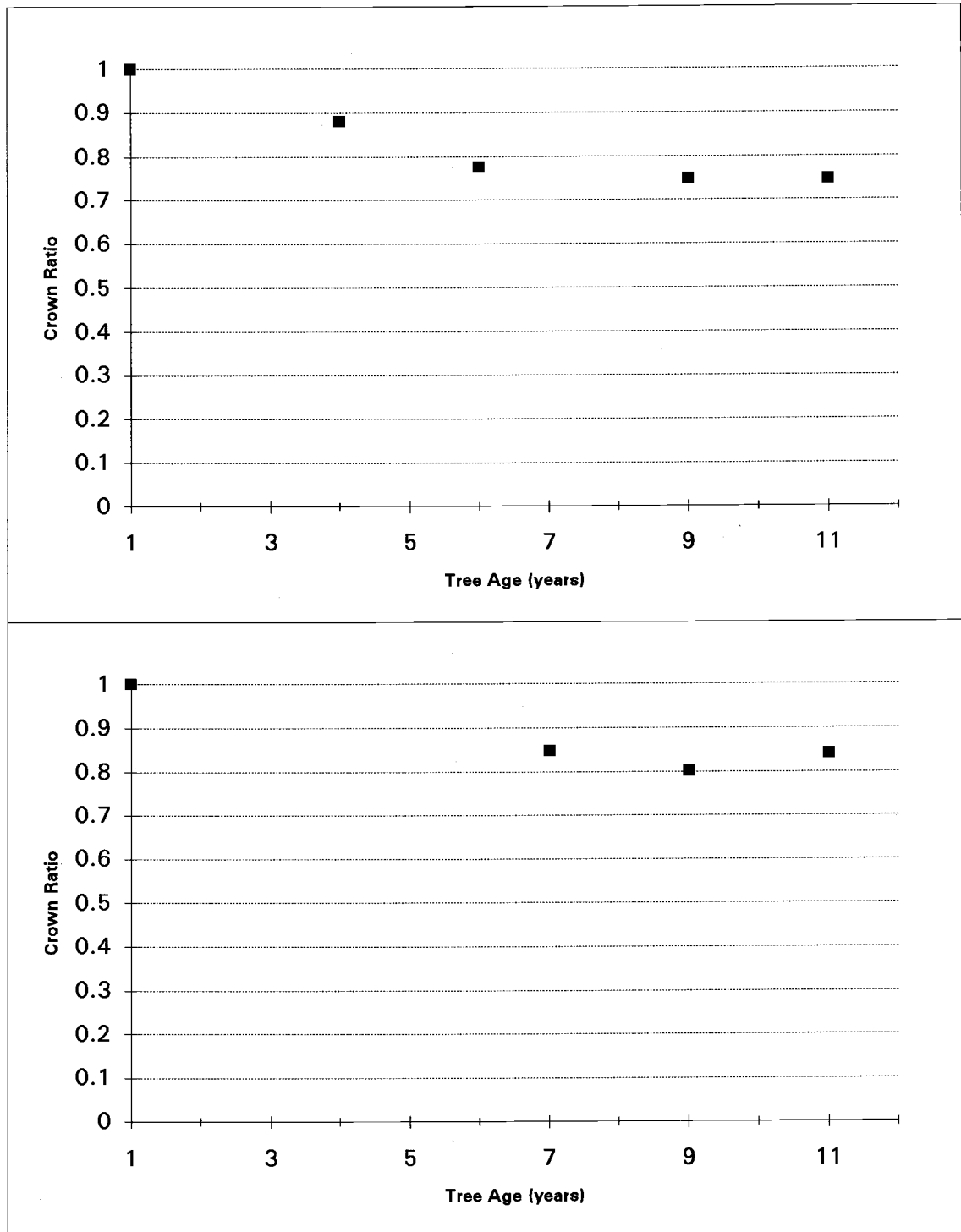
Figure 32. Scatterplots of crown ratios (ratios of live crown length to total tree height) for two sample trees planted at 4.0 x 4.0 m from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as a data point in the development of the crown ratio model (equation 6).
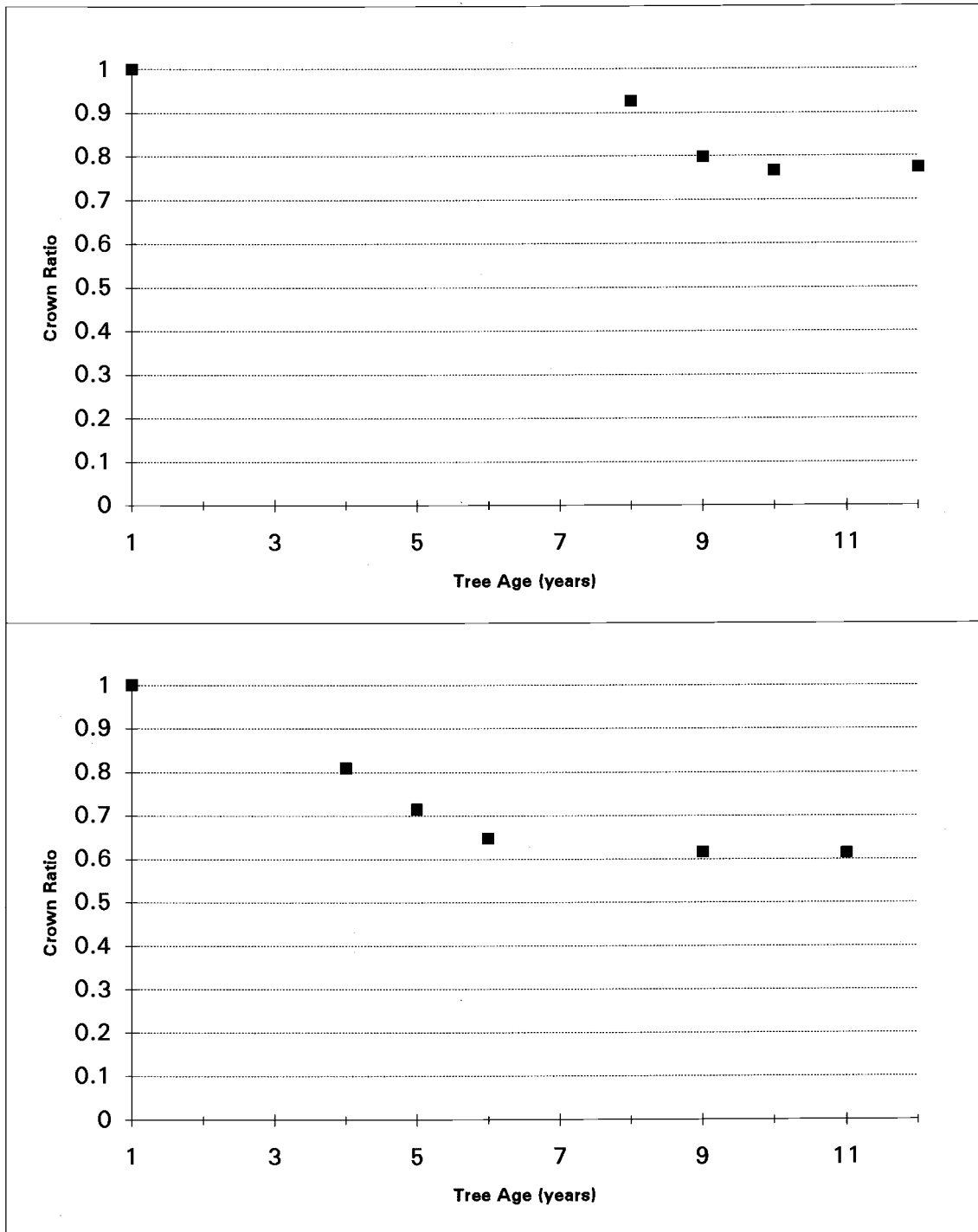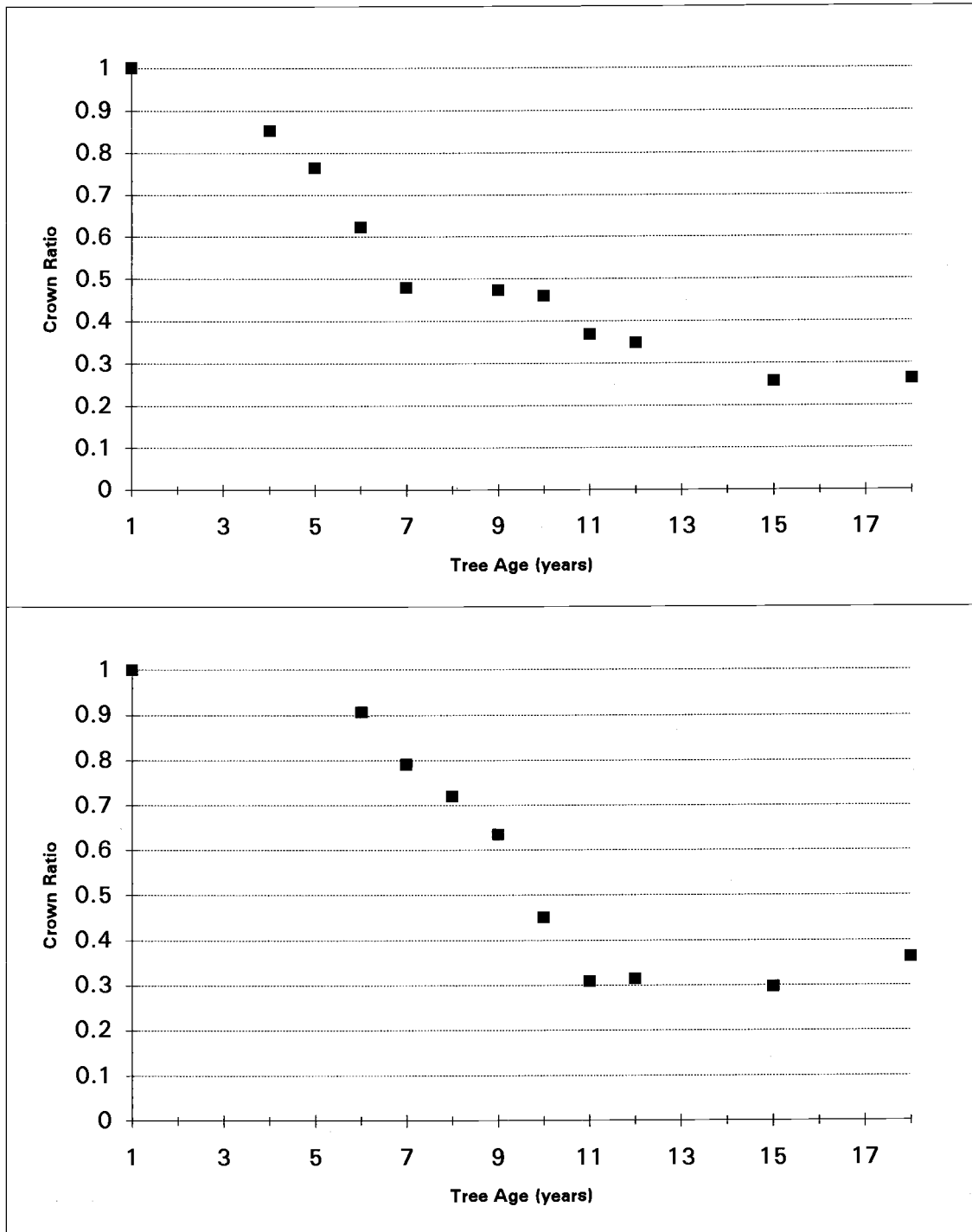
Figure 33. Scatterplots of crown ratios (ratios of live crown length to total tree height) for a sample tree planted at 4.0 x 4.0 m (top graph) and a sample tree planted at 3.0 x 3.0 m (bottom graph) from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as data point in the development of the crown ratio model (equation 6).

Figure 34. Scatterplots of crown ratios (ratios of live crown length to total tree height) for two sample trees planted at 3.0 x 3.0 m from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as a data point in the development of the crown ratio model (equation 6).
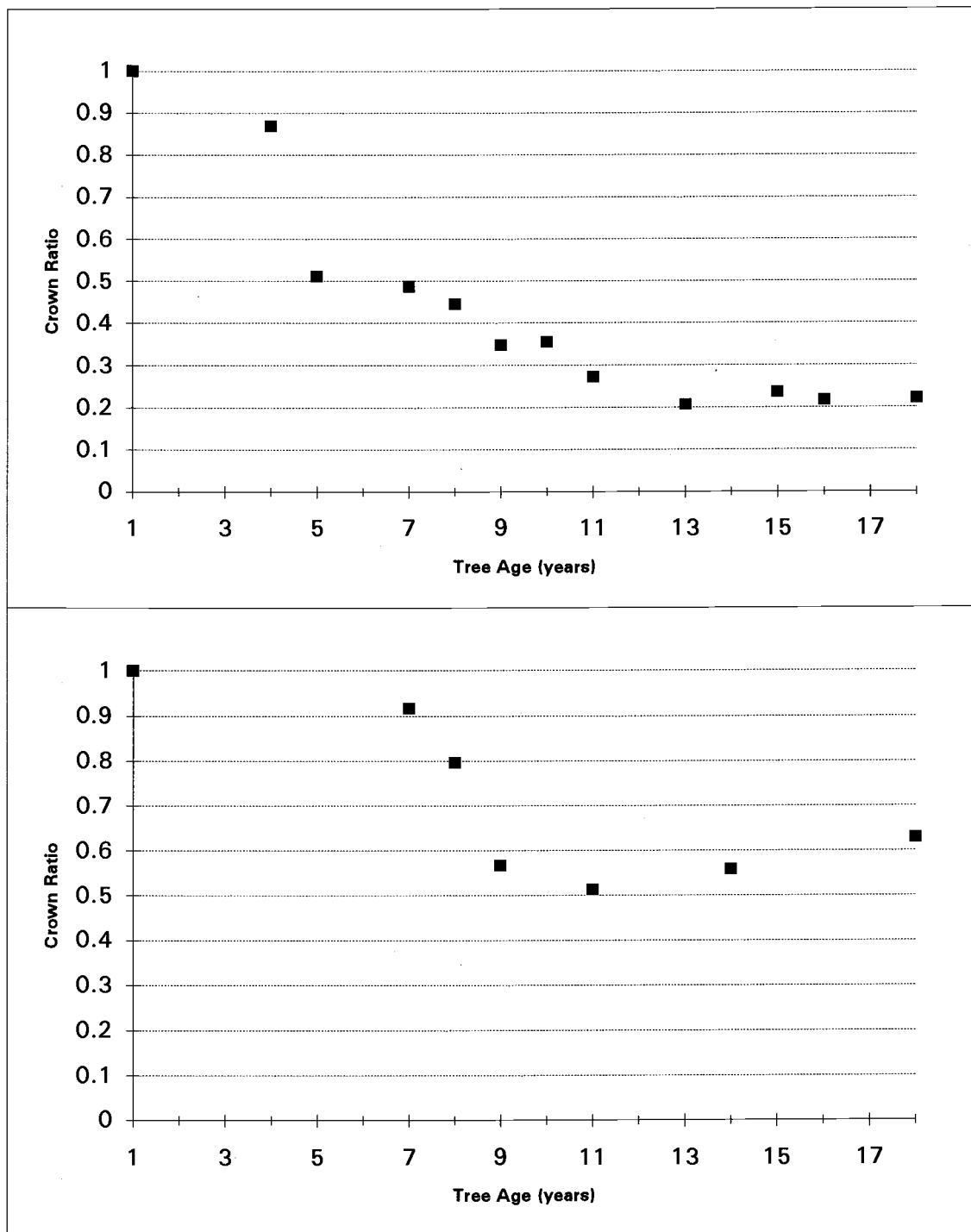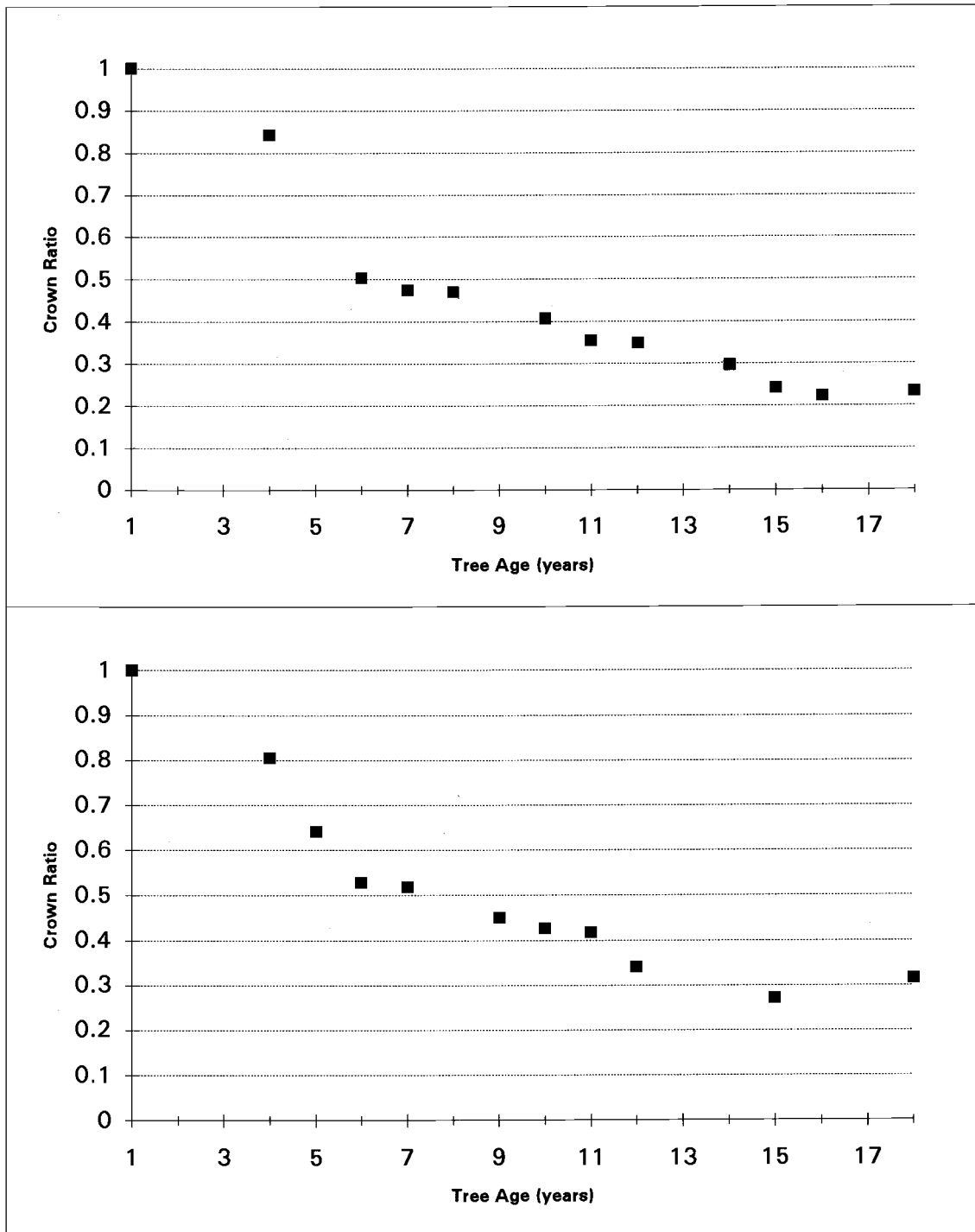
Figure 35. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 2.0 x 2.0 m from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as a data point in the development of the crown ratio model (equation 6).

Figure 36. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 1.0 x 1.0 m from the Centralia spacing study. The starting value of 1.0 is hypothetical and was not used as a data point in the development of the crown ratio model (equation 6).

Figure 37. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 2.81 x 2.81 m from the Apiary spacing study. Only the first seven years of data were used in statistical analyses, however, reconstruction of past crown base heights began at the position of the current live crown base.
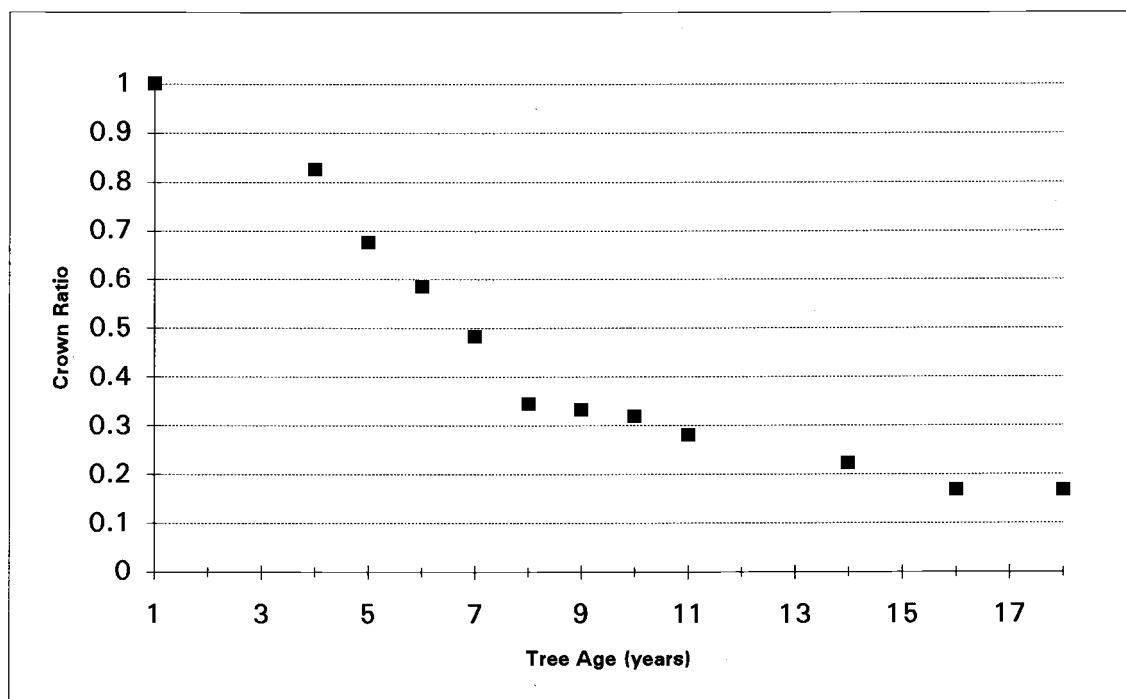
Figure 38. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 1.88 x 1.88 m from the Apiary spacing study. Only the first seven years of data were used in statistical analyses, however, reconstruction of past crown base heights began at the position of the current live crown base.
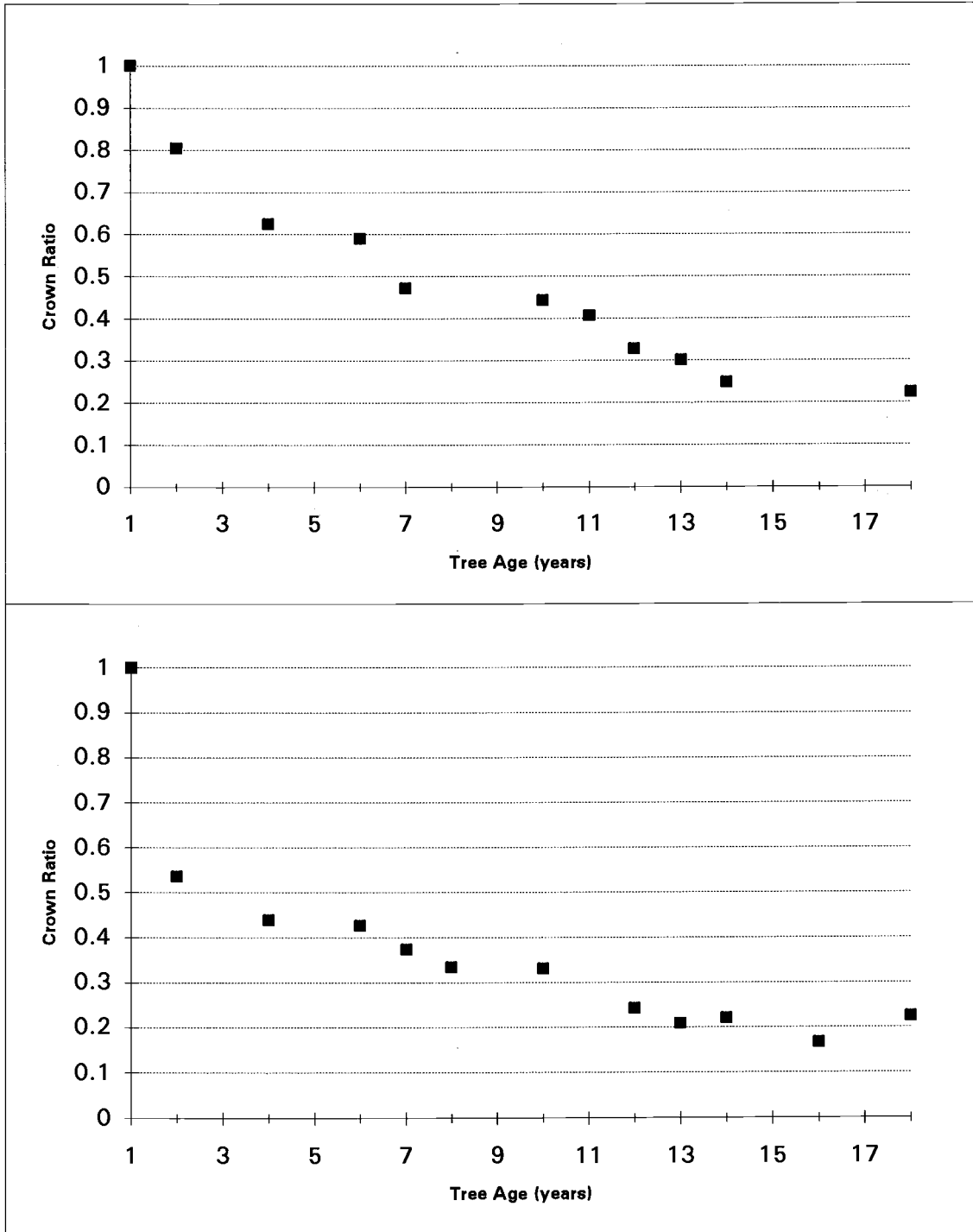
Figure 39. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 1.57 x 1.57 m from the Apiary spacing study. Only the first seven years of data were used in statistical analyses, however, reconstruction of past crown base heights began at the position of the current live crown base.

Figure 40. Scatterplot of crown ratios (ratios of live crown length to total tree height) for the one sample tree planted at 1.26 x 1.26 m from the Apiary spacing study. Only the first seven years of data were used in statistical analyses, however, reconstruction of past crown base heights began at the position of the current live crown base.

Figure 41. Scatterplots of crown ratios (ratios of live crown length to total tree height) for the two sample trees planted at 0.94 x 0.94 m from the Apiary spacing study. Only the first seven years of data were used in statistical analyses, however, reconstruction of past crown base heights began at the position of the current live crown base.
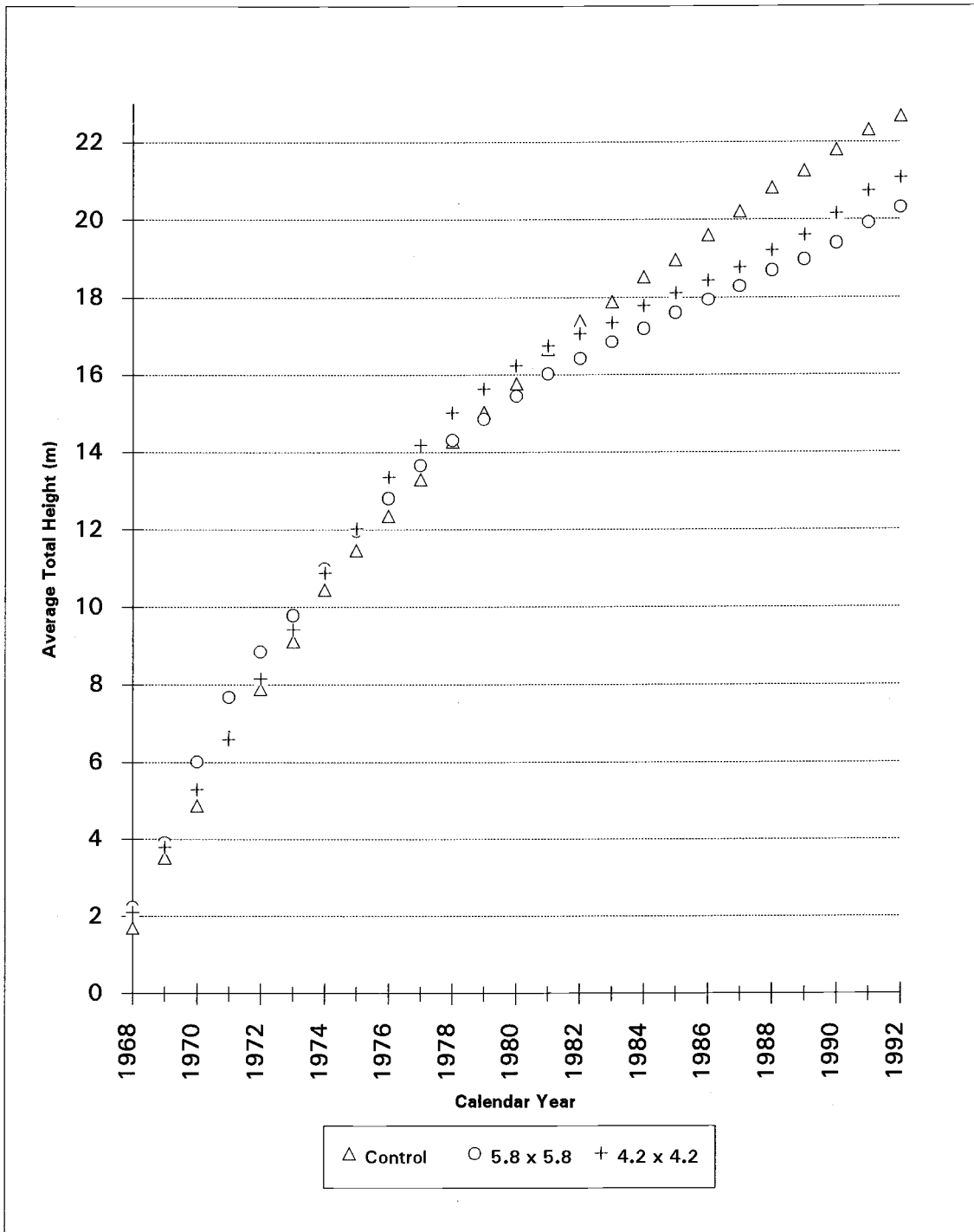
Figure 42. Average total tree height (m) at a given calendar year, by thinning treatment, for all nine trees from the Olney thinning study. Plots were thinned in 1981. Because trees ranged in age from 14 to 16 years at the time of treatment, it was necessary to incorporate a timing variable to model the effects of thinning on height growth (see text).