Master Thesis

The relationship between growth efficiency and individual tree leaf area index in an even-aged coast redwood (*Sequoia sempervirens* [Lamb. ex D.Don] Endl.) stand.

Handed in by

Martin Gspaltl

At the

Institute of Forest Growth and Yield Research
University of Natural Resources and Applied Life Sciences, Vienna

Supervisors:

Ord. Univ. Prof. DI Dr. Hubert Sterba
Prof. Kevin O'Hara Ph.D.

Table of Contents

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1 Abstract

Leaf area and area potentially available were used to predict leaf area efficiency and area available efficiency for a 28 year old redwood (*Sequoia sempervirens* [Lamb. ex D.Don] Endl.) stand in Scotia, California, United States of America. 13 plots with 5 different treatments and a control were measured two times (2003-2007) for diameter, height, sapwood and bark thickness, which led to the basal area increment and the volume increment. The projected leaf area was predicted from the sapwood area from each tree. Coordinates of every individual tree could be calculated based on the very precise planting process and special guidelines for the handling of multiple trees per grid point. The area potentially available was calculated following the approach of RÖMISCH (1995).

The leaf area was found to be a very powerful variable to predict basal area increment and volume increment. The leaf area efficiency was increasing with increasing leaf area for the general model, but decreasing when the relative height was held constant. For a leaf area of more than 300 m^2 the leaf area efficiency maintained moderate values. The efficiency of the area potentially available is declining in a negative exponential fashion with increasing area potentially available. Higher relative height led to higher efficiencies in both models.

The theory of an optimum tree leaf area index could be confirmed in this study. This is an optimum curve of the available area efficiency over the leaf area index, where the leaf area index is defined as a ratio between the leaf area and the area potentially available.

Zusammenfassung

Blattfläche und Standfläche wurden verwendet um die Blattflächeneffizienz und die Standflächeneffizienz für einen 28 Jahre alten Küstenmammutbaumbestand (*Sequoia sempervirens* [Lamb. ex D.Don] Endl.) in Scotia, Kalifornien, Vereinigte Staaten von Amerika, zu schätzen. 13 Probeflächen mit 5 verschiedenen Behandlungsformen und einer Kontrollfläche wurden zweimal gemessen (2003-2007) auf Durchmesser, Höhe, Splintholz und Borkendicke was den Grundflächen- und Volumszuwachs ergab. Die projizierte Blattfläche wurde über die Splintholzfläche für jeden Baum bestimmt. Es war möglich die Koordinaten zu berechnen, da der Pflanzprozess sehr präzise erfolgte und für Fälle wo mehrere Stämme auf einen Rasterpunkt fielen wurden spezielle Richtlinien erarbeitet. Die Standflächen wurden nach dem Verfahren von RÖMISCH (1995) berechnet.

Die Blattfläche erwies sich als starke Variable um Grundflächen- und Volumszuwachs vorherzusagen. Im generellen Modell nahm die Blattflächeneffizienz mit zunehmender Blattfläche zu, jedoch wenn die relative Höhe konstant gehalten wurde nahm sie mit zunehmender Blattfläche ab. Ab einer Blattfläche von 300 m^2 bewahrte die Blattflächeneffizienz moderate Werte bei. Die Standflächeneffizienz nahm mit zunehmender Standfläche in negativ exponentieller Form ab. Für beide Effizienzen gilt das eine höhere relative Höhe zu höheren Effizienzen führt.

Die Theorie eines optimalen individuellen Blattflächenindex wurde in dieser Studie bestätigt. Sie beschreibt eine Optimumkurve der Standflächeneffizienz über dem Blattflächenindex, welcher als Verhältnis zwischen Blattfläche und Standfläche definiert ist.

2 Introduction

2.1 Coast redwood (Sequoia sempervirens [Lamb. ex D.Don] Endl.)

The genus *Sequoia* is now subordinated by the family of the Cupressaceae while it was former classified in Taxodiaceae. The only species in this genus is the coast redwood (*Sequoia sempervirens* [Lamb. ex D.Don] Endl.). Close related to it are the genus *Sequoiadendron* with the only species giant sequoia (*Sequoiadendron giganteum* [Lindl.] J.Buchholz) and the genus *Metasequoia* with the only species dawn redwood (*Metasequoia glyptostroboides* Hu & Cheng) (USDA 2008).

Coast redwood stands are considered to be the largest biomass accumulations of the world. For example, in Humboldt Redwoods State Park redwood stands were found to have basal areas of up to 329 m^2/ha and a stem biomass of 3,000 to 5,200 ton/ha (BUSING & FUJIMORI 2004). In comparison to that Norway Spruce (*Picea abies* [L.] H.Karst.) showed up to 54.8 m^2/ha with a stem biomass of 305 to 610 ton/ha (RÖHLE 1995).

The coast redwoods are occupying an area of about 800,000 hectare along the Pacific coast, reaching from the tip of southern Oregon to Monterey County in California. They are found from sea level up to 1,000 m elevation and grow up to distances of 71.6 km from the coast depending on the coastal fog. The natural range is strongly determined by the availability of water. Coast redwoods grow on sites with an annual precipitation from 64 to 310 cm, with most of it coming from winter rain. The fog is known to moderate the effects of the rainless summers. In the northern regions of its natural range, these trees are reaching heights of more than 110 m and ages up to 2,000 years (DAGLEY & O'HARA 2003).

These trees are growing on various types of soils, from rocky loams, over some of the steepest slopes to deep sandy loams on flats and benches (alluvial flats) where they are most productive (ROY 1966).

Redwoods are known to be flexible trees considering their ability to adopt their crown to changing light conditions. As very shade-tolerant species, they can survive in the understory for many decades and as soon as they receive some light, they can accelerate their growth rates very fast. These trees are also known for their great ability to produce stump sprouts. The probability of producing sprouts is generally higher for younger and smaller trees (DAGLEY & O'HARA 2003).

Primary disturbances in redwood regimes are fire, wind, flooding (alluvial flats), peeling or browsing by black-tailed deer (*Odocoileus hemionus*), black bear (*Ursus americanus*), wood rats (*Neotoma fuscipes*) and damages by *Botrytis* fungi (on seedlings) (DAGLEY & O'HARA 2003).

2.2 Leaf area definition

The canopy is the interaction point of a tree to the atmosphere. Several processes like radiation extinction, water interception, water and carbon gas exchange are taking place in the canopy. Many of these processes are part of photosynthesis, which happens in all green parts of a tree and allows it to gain energy in the form of carbohydrates. This energy is used for the tree to grow taller, expand its canopy and its root system.

The leaves, as represented by the leaf area, are a very important factor, in affecting the vigor and the productivity of a tree. Any change in the leaf area, due to frost, storm, defoliation, drought or management practice is accompanied by a modification of the productivity (BRÈDA 2003).

There are several ways how to define this leaf area. The first and most accurate way is to take the total leaf area. This is very simple for flat leaves, where the measure of one side gives the one-sided leaf area and, multiplied by two, leads to the total leaf area. The border of the leaf can be neglected because the area would be very small. However for foliage with wavy, cylindrical or bended surface the total leaf area would be hard to determine. Thus a projected leaf area was defined as the vertical projection of leafs or needles to the ground surface (JONCKHEERE ET AL. 2004). Several conversion factors from the projected to the total leaf area have been published, but they are species specific (HAGER & STERBA 1985).

2.3 Leaf area – Sapwood area relationship

The first published relationship was the pipe model theory by SHINOZAKI ET AL. (1964). The idea was that the size of the canopy depends on the amount of water and nutrients provided by the roots. Since root mass and canopy mass are hard to determine, it was hypothesized that the stem should have a significant influence. A larger cross sectional area can transport more water and nutrients to the canopy, which will yield a larger canopy biomass. ECKMÜLLNER (1988) found a close linear relationship between the sapwood area at breast height and the needle mass, and an even closer relationship using the sapwood area at crown base for Norway spruce. This relationship was nearly independent of site quality. ECKMÜLLNER & STERBA (2000) could enhance this relationship by reducing the sapwood area by its latewood proportion.

STANCIOIU & O'HARA (2005) found a sapwood area – leaf area relationship for coast redwood with a dataset ranging from 7.7 - 45.2 m in height and 9.4 - 92.7 cm in diameter at breast height (DBH). A close linear relationship through the origin was found using the sapwood area at breast height (SA_{BH}) and the sapwood area at base of the live crown (SA_{BLC}). To estimate the leaf area (LA) the SA_{BH} has to be multiplied with a factor of 0.4005 m^2/cm^2 (R^2=0.9605) and the SA_{BLC} with 0.5672 m^2/cm^2 (R^2=0.9833).

The authors developed a taper model to estimate SA_{BLC} (equation 2.1) since a leaf area estimation from SA_{BLC} is more accurate.

$$A_{SBLC}[cm^2] = 0.7460 \cdot A_{SBH}[cm^2] - 3.8293 \cdot (H_{BLC}[m] - 1.37) \qquad 2.1$$

where H_{BLC} is the height to base of the live crown and the other variables are as defined above. This model estimates SA_{BLC} with an R^2=0.9939.

2.4 Individual tree growth efficiency

To describe the efficiency of an individual tree, a relationship between a growing component of the tree and the tree's occupied resource space can be built. The common growing factors are either the volume increment or the basal area increment. The occupied resource space describes the available area for the tree to use limiting resources like light, water and nutrients. Two factors that define this area are the canopy and the roots. As the area of the root system itself is hard to estimate, the assumption is made that the area of the root system and the canopy area are in balance. Hence the crown projection area as a vertical projection of the canopy to a horizontal ground would be a good estimate.

Another way would be to use the leaf area to define the occupied resource space, since it is highly correlated to the volume increment (O'HARA 1988). The main advantage is that it explains a three-dimensional space occupancy, as the leaf area has its layers in different heights.

Since both of the so defined growth efficiencies are not area consistent, a new definition was made by ASSMANN (1961, cit. STERBA & AMATEIS 1998). The area potentially available also considers gaps or overlapping crowns and distributes these conflict areas to the most vigorous adjacent trees.

Since the term of growth efficiency was being used for all of these three kinds in past publications, an attempt of distinct differentiation was made in this study. Thus the terms crown efficiency (CE), leaf area efficiency (LAE) and available area efficiency (AAE) are used.

2.4.1 Crown efficiency

The crown efficiency (CE) is calculated as a ratio between the volume increment (VI) and the crown projection area (CPA) or as a ratio between the basal area increment (BAI) and CPA (equation2.2).

$$CE = \frac{VI}{CPA} \text{ or } CE = \frac{BAI}{CPA} \qquad 2.2$$

The CPA is usually estimated by projecting the crown on the horizontal ground surface, for example with a clinometer held at 90°. Two or more radii are measured to calculate a circular, or oval CPA (STERBA & AMATEIS 1998). If more than one radius is measured the mean of the radii gives a good estimate (O'HARA 1988).

O'HARA (1988) found that for thinned stands, tall trees with medium sized crowns were most efficient, but for unthinned stands tall trees with relatively large crowns were superior. The author suggested that thinning to a particular stand structure is more appropriate than thinning to a particular level of stand density.

Investigations of STERBA AND AMATEIS (1998) showed that crown efficiency decreased within crown classes for trees below the dominant height. The crown efficiency also decreased with increasing stand density. The basal area increment per hectare increased until the total crown closure was approached, and then stayed constant, which led the authors to question the usefulness of the crown efficiency as an indicator for unit area growth.

2.4.2 Leaf area efficiency

Leaf area efficiency (LAE) can be calculated as the ratio between increment (whether volume increment or basal area increment) and the leaf area (LA) (equation 2.3).

$$LAE = \frac{VI}{LA} \text{ or } LAE = \frac{VI}{SA} \qquad 2.3$$

Sapwood area (SA) (O'HARA 1988) and leaf biomass (BURKES ET AL. 2003) can be used as surrogates for leaf area, due to their close relationship (BRÈDA 2003).
Past studies described a lot of different variables influencing the LAE in many different ways. COYEA & MARGOLIS (1994) studied the influence of the LAE to natural mortality and to the vulnerability to insects (spruce budworm - *Choristoneura fumiferana*) in balsam fir (*Abies balsamea* [L.] Mill. var. *balsamea)* ecosystems. They found that surviving trees had a greater LAE than trees that died later on. LAE showed to be more significant for the vulnerability to spruce budworm, than DBH and basal area growth. Thus the authors suggested LAE as a sensitive, physiologically based index for forest health.
Greater tree size (height and diameter) was found to enhance, and greater past suppression to diminish the LAE for red spruce (*Picea rubens* Sarg.) (MAGUIRE ET AL. 1998). Age showed a negative influence on LAE which was independent from the effect of increasing leaf area (SEYMOUR & KENEFIC 2002). An influence of planting density could be shown by BURKES ET AL. (2003) where the LAE of the plot with the lowest number of trees per hectare was significantly lower than all the others.
Concerning crown classes, REID ET AL. (2004) ascertained suppressed trees to be more efficient than dominant and codominant trees. Additional measurements of nitrogen and phosphorus content in leaves showed highest amounts for suppressed trees. Thus it seems that this advantage led to their higher efficiency.
Contrary to these investigations, BERRILL & O'HARA (2007) showed the highest LAE for emergent overstory redwood trees, followed by dominant and codominant trees.
GERSONDE & O'HARA (2005) were studying the LAE of five conifer species with a range of shade-tolerant to shade-intolerant species. For shaded understory conditions the LAE showed a slow increase over the leaf area, followed by a peak for intermediate sized trees in mid-canopy positions. For larger trees LAE was decreasing again. Tree species with lower shade-tolerance showed higher LAE than species with higher shade-tolerance.

This peak in the development of the LAE over leaf area could also be found by SEYMOUR & KENEFIC (2002) which led them to postulate three general forms of patterns (Figure 2.1). Pattern A describes a monotonic nonlinear decreasing form which leads to a mechanistic explanation. When the crown size is getting higher, a higher percentage of the leaf area is growing on large, long and old branches in the lower canopy. These branches are sustained on the expense of the stem volume increment. That would mean that trees with a smaller leaf area are more efficient, which may be the case for shade-intolerant species. For shade-tolerant species there is a trade-off, which leads to a lower LAE with smaller leaf areas (pattern B). The more efficient, smaller crown does not get enough light because of higher strata. So the effect of lower light suppresses the effect of the more efficient crown architecture. For greater leaf areas LAE is decreasing (same reason as for pattern A) leading to a peak in the curve. If the data range is just limited to lower strata or young cohorts, it is very possible that this peak will not appear, which would lead to pattern C. And also pattern A could be a truncated pattern B because shade-intolerant species will not survive long, once they lapse into a lower crown class.

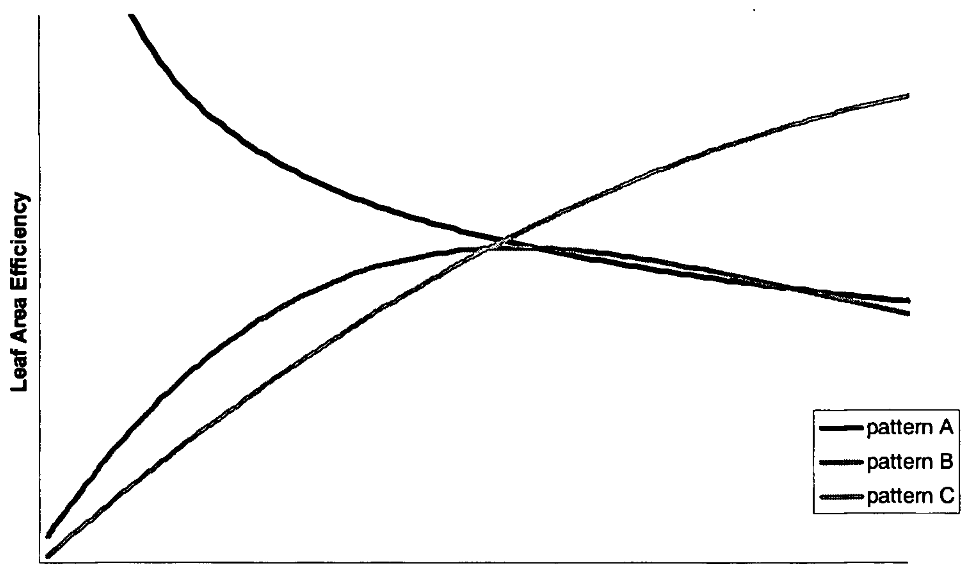


Figure 2.1: *Three possible patterns of leaf area efficiency (SEYMOUR & KENEFIC 2002). Pattern A typically for shade-intolerant tree species, Pattern B typically for shade-tolerant species, Pattern C for lower strata or young stands missing a peak in LAE.*

2.4.3 Available area efficiency

The calculation of the available area efficiency (AAE) is similar to the former definitions, with the difference that it is using the area potentially available (APA) instead of the leaf area (equation2.4).

$$AAE = \frac{VI}{APA} \text{ or } AAE = \frac{BAI}{APA} \tag{2.4}$$

The area potentially available was first defined by ASSMANN (1961, cit. STERBA & AMATEIS 1998) as the crown projection area plus a portion of the not covered stand. The idea is that assuming no crown closure, the tree has the potential to use more than the crown projection area to seize water, nutrients and sunlight. If crown closure already passed and the crowns are interlocked, a portion of this interlocking zone has to be subtracted from the crown projection area.

If the crown projection area is not given, the APA can be defined using a dirichlet tessellation. When the coordinates of the trees are known, the dirichlet tessellation just calculates the distance between two trees, bisects it and puts a perpendicular line to it (BROWN 1968, cit. NANCE ET AL. 1988). To be more specific, the lines between the trees can be weighted by a certain dimension of a tree (STÖHR 1968, cit. KINDERMANN 2000). For example a tree with a larger DBH gets a greater portion of the line than a smaller one. With this procedure the stand area is not going to be apportioned completely, therefore its not area congruent.

RÖMISCH (1995) invented the so called circlebow-model for individual areas potentially available. He divides the whole stand into small squares, and assigns each square to the tree with the smallest distance number T_i (equation2.5).

$$T_i = \frac{(x - x_i)^2 + (y - y_i)^2}{w_i^2} = \frac{E_i^2}{w_i^2} \tag{2.5}$$

where x/y are the coordinates of the center of the square, x_i/y_i the coordinates of the tree number i and w_i the growing factor of the tree number i. The term $(x - x_i)^2 + (y - y_i)^2$ equals the squared distance E_i between the center of the square and the tree number i.

FABER (1981) had the same basic approach when he defined the distance factor U (equation2.6).

$$U = \frac{V^k}{E^2} \quad 2.6$$

with V the stem volume (other growing factors can be used), k the weight of competition and E the distance between the center of the square and the tree.
The advantage of the grid circlebow-model by RÖMISCH (1995) is that it can be easily solved by computer programs. KINDERMANN (1999) wrote the program ACRE to calculate the APA for individual trees. The version ACRE 0.2b was used in this study.

There have just been a few publications calculating and explaining AAE. WEBSTER & LORIMER (2002) measured APA by taking 8 radii from the tree bole to the crown edge of the nearest competing tree. A maximum search distance was defined because a tree can only seize a certain amount of a gap. This distance was set to be two thirds the height of a typical canopy tree (16.67 m). However, the measured APA is not area congruent. A declining AAE with increasing APA was found, where intermediate trees were most efficient followed by codominant and dominant trees. AAE was significantly influenced by the relative height (h_{rel} = total height relative to the mean height of codominant and dominant trees per plot) and the APA with R^2 ranging from 0.59 to 0.83 depending on the species. For a given level of APA, AAE was found to increase with increasing h_{rel}. Shade-tolerant trees were more efficient than shade-intolerant trees.
MAINWARING & MAGUIRE (2004) used APA as a surrogate for the degree of root spread, the available belowground resource pool or a degree of crown crowding. APA was computed as constrained and weighted polygon according to NANCE ET AL. (1988) where the constraints are a function of the mean crown ratio and the expected crown radius of an open-grown tree, and DBH as the weight. MAINWARING & MAGUIRE (2004) found declining AAE with increasing APA.
Contrary to these approaches, PRETZSCH (2006) defined APA as a ratio between the crown projection area and the degree of crown closure, where the degree of crown closure is defined as the sum of crown projection areas divided by the stand area. The author explains AAE as a function of APA and the quadratic mean diameter (dg) (R^2=0.52). AAE showed an optimum curve which is increasing with decreasing dg.

3 Objectives

The first objective of this study was to analyze different relationships concerning the increment, leaf area and area potentially available. The increment prediction power of LA and APA, the behavior of the leaf area efficiency and the available area efficiency are of interest. It was hypothesized that relative height has a significant influence on each of these dependent variables (LA, APA, LAE, AAE).

The second objective is based on the idea of an optimum individual tree leaf area. STERBA (2005) first had the idea to find an optimum individual tree crown coverage. The problem in that study was that the crown coverage did not seem to be an appropriate variable because the optimum of AAE over the crown coverage was either far beyond the data material or widely independent from the crown coverage.
The idea of an optimum individual tree leaf area is based on the following equations (personal communication STERBA 2008):

$$\frac{Inc}{LA} = a + b \cdot LAI^2 \quad (3.1)$$

$$LAI = \frac{LA}{APA} \quad (3.2)$$

$$\frac{Inc}{APA} = \frac{Inc}{APA} \cdot \frac{LA}{LA} = \frac{Inc}{LA} \cdot \frac{LA}{APA} \quad (3.3)$$

$$\frac{Inc}{APA} = \left(a + b \cdot LAI^2\right) \cdot LAI = a \cdot LAI + b \cdot LAI^3 \quad (3.4)$$

$$\frac{\delta \frac{Inc}{APA}}{\delta LAI} = a + 3 \cdot b \cdot LAI^2 = 0 \quad (3.5)$$

$$LAI_{opt} = \sqrt{-\frac{a}{3 \cdot b}} \quad (3.6)$$

In equation 3.1 the LAE is estimated using a linear regression with LAI^2 as independent variable. The LAI is here defined as the ratio between the leaf area and the area potentially available (equation 3.2). To build the connection between LAE and AAE, AAE is simply multiplied by the term LA/LA. The variables in the denominator can be changed as seen in

equation 3.3. In the next step equations 3.1 and 3.2 are inserted in equation 3.3 leading to equation 3.4. In order to calculate the maximum of this equation, the first derivative has to be set zero (equation 3.5) and solved for LAI (equation 3.6).
With increasing APA and the LA held constant it is assumed that the available area efficiency is first increasing over the LAI up to a certain level where it shows an optimum. With a further increasing APA, the tree cannot use this additional space any more and the available area efficiency is decreasing. For a better understanding of these relationships it is important to know the value of this optimum leaf area index.
This idea will be followed in this study by two ways: (1) Direct, in estimating AAE as a function of LAI and LAI^3, and (2) indirect in calculating LAE as function of LAI^2 and the following multiplication with LAI to get AAE.
The last approach is going to estimate AAE under the assumption that there is no optimum curve. The influence of relative height, SDI and treatment shall be investigated.

4 Methods

4.1 Study Area

The young even-aged coast redwood plantation is located south of Scotia, Humboldt County, California (40.461°N, 124.083°W) and is owned by the Pacific Lumber Company. It is bordered by the Eel River on one side, and a four-lane highway on the other side. Originally this area was covered by old redwood forests, and in the 1880s it was all cut down for pasture and later parts of the area were used as a tree nursery.

The precipitation averages about 1230 mm/year (gauging station in Fortuna, California; about 40 linear km distance to study area), where about 80 percent occurs from November through March. The mean monthly temperature extremes range from 11-4°C in December and 21-11°C in August (THE WEATHER CHANNEL INTERACTIVE INC 2008).

The alluvial flat has an average elevation of about 50 m. It comprises deep soils (Ferndale silt loams and fine sandy loams) with plentiful moisture (MC LAUGHLIN & HARRADINE, 1965). Overall those are optimal conditions for redwood forests.

One to two year-old container seedlings, gathered from a local seed source east of the study area, were planted precisely on a 3.05 by 3.05 m (10 by 10 ft) grid. The planting process started in fall/winter 1981/82 and was completed in fall/winter 1982/83. In the following years grasses and other herbaceous plants were treated with herbicides and harrowing. Some seedlings were heavily browsed by deer in the early years, but no monitoring was performed. Occasionally the seedlings developed multiple stems, which is common for coast redwoods.

In 1997 the area was divided into 19 different treatment units with a size ranging from 1.1 to 3.1 ha. The treatments were assigned randomly and no special records were taken. The six different treatments included four geometrical thinnings, one free thinning method (where the most vigorous and well formed trees were abetted) and one control treatment without any thinning:

- removing alternate rows in one direction ("alternate row")
- removing diagonal rows ("diagonal row")
- removing every third row in one direction ("third row")
- removing alternate rows in both directions ("double alternate")
- free thinning
- no thinning ("control")

The thinning started in the growing season 1997 and was completed in the growing season 1998. In 1998 a windthrow in the free thinning and the double alternate treatment areas occurred and obscured the differences between those two. The thinning and windthrow combined for an estimated total removal of about 75 percent of the trees in these treatment methods.

4.2 Plot design

Fifteen rectangular plots were established in 2003 to cover the present treatment units. As the designated term was to have 25 overstory trees at minimum, the plot areas range in size from 0.023 to 0.093 ha, depending on the different treatments. The alternate row included 5 x 10 individual grid points, the diagonal row 6 x 9 and 5 x 8, the third row 5 x 9, the double alternate row 9 x 9, the free thinning 10 x 10 and the control 5 x 5.
Individual tree measurements including diameter at breast height (4.5 ft or 1.37 m), total height, height to crown base (lowest live branch) were taken. Every tree was cored on the west side or as close to the west side as possible on multiple stems. The cores were analyzed by measuring sapwood width using color and translucence to differentiate the sapwood/heartwood boundary. The bark thickness was measured twice adjacent to the core extraction points.

In 2007 the Pacific Lumber Company initiated a thinning program in the study area. Before most of the trees got cut down, new measurements were taken of every tree, similar to the 2003 measurements. Due to the prior cutting (2005) plots 2 and 3 had to be taken out of the studies that led to a total number of 13 plots.
All the data were provided by the Department of Environmental Science, Policy and Management, University of California, Berkeley.

4.3 Analysis

4.3.1 Dataset

Leaf areas and areas potentially available were calculated for the beginning of the observation period 2003, and volume increment and basal area increment for the four year period. Several trees dying in this period were neglected since it has been assumed that their impact was very small. Their APA was therefore assigned to their nearest neighbors with the lowest distance/growing ratio. However as these trees were already dying, they would not have a big APA. Figure 4.1 summarizes the number of dying trees during the period over the DBH classes for all plots. Most of the trees were smaller then 5 cm, one tree in the DBH-class 40 cm was killed by a bear.

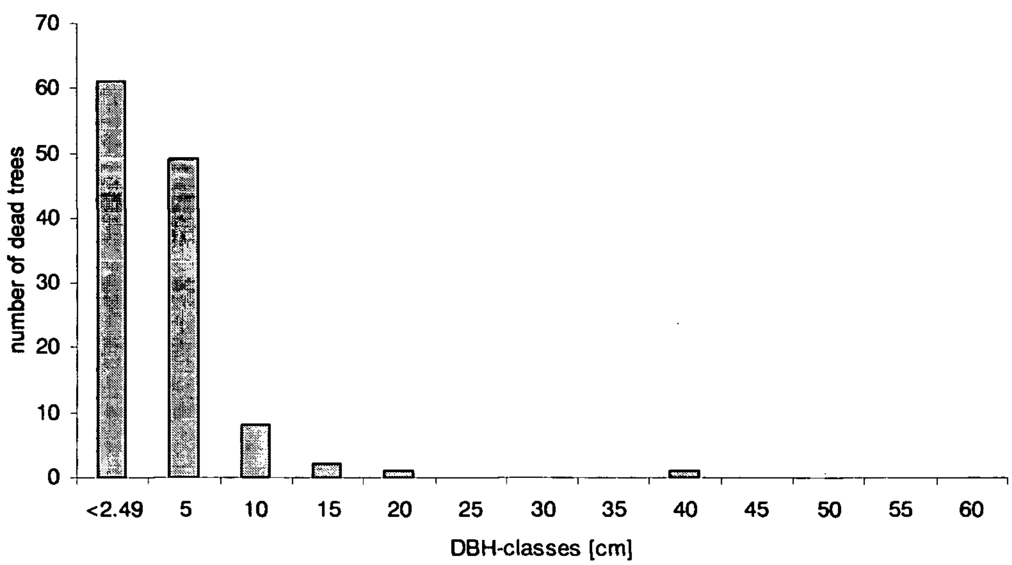


Figure 4.1: *Number of trees dying in the observation period 2003 – 2007 over the DBH-classes.*

The measurements of diameter and height were afflicted with a random error. This error became apparent when increments were calculated. The DBH showed negative increments down to -1.14 cm and the height down to -3.84 m. Considering the law of error propagation, these values are within the normal range of DBH and height measurement errors.

However, for tree individual calculations, these negative increments were set to zero which will cause a slight overestimation of the outcomes, because the negative errors are corrected, but not the positive ones.

A total of 78 trees exhibited several stem defects just as leaning, fork, sweep or crook and a dead top (Figure 4.2). Except the dead tops, all of these defects were neglected. Trees with dead tops were given no height increment.

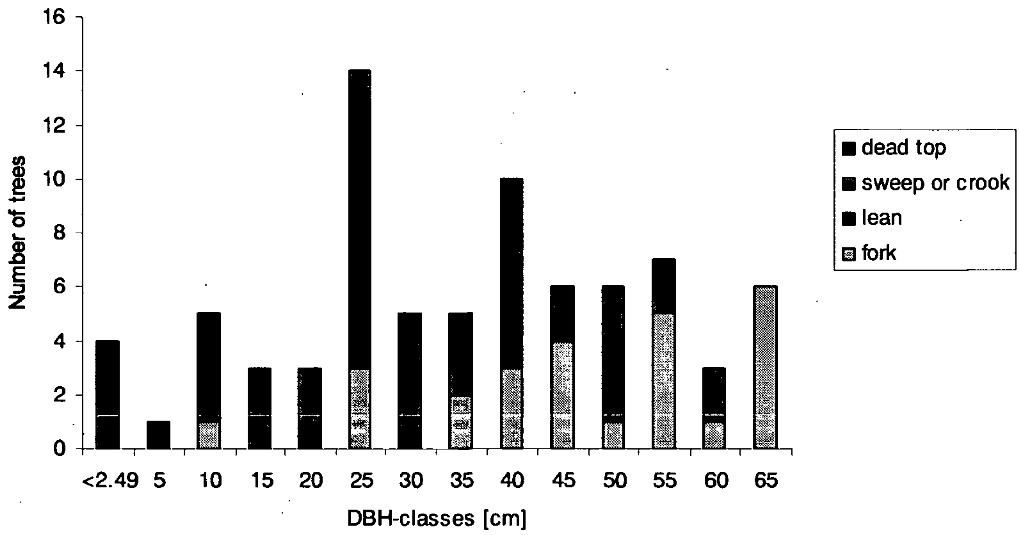


Figure 4.2: Number of trees with stem defects like dead tops, leans, forks, sweeps or crooks over the DBH-classes.

4.3.2 Volume estimation

WENSEL & KRUMLAND (1983) developed an equation to calculate volume for coast redwood. Equation 4.1 gives the volume from a 91.4 cm (3 ft) high stump up to a 12.7 cm (5 in) top. The data of WENSEL & KRUMLAND (1983) started with a DBH of 25.4 cm (10 in). Since about 40 percent of the trees in this study are smaller than 25.4 cm, the volume equation had to be extrapolated to the lower end.

$$V[m^3] = 0.0007903 \cdot DBH[in]^{1.792} \cdot h[ft]^{1.282} \cdot 0.02832 \quad 4.1$$

4.3.3 Sapwood area

As trees with a smaller DBH than 5 cm could not be cored, the sapwood width of these trees was estimated. First attempts were made to build a relationship between the basal area and the sapwood area. This gave a very good model for larger trees, but it overestimated the sapwood area for small basal areas (under 30 cm^2).

The next assumption was that the whole basal area of these small trees could be used as sapwood area. So the radius minus the bark thickness is the sapwood width. However bark thickness was not measured on these small trees. So a relationship between the bark thickness (BT) and the basal area (BA) was modeled, which fitted much better in the small basal areas (equation 4.2).

$$BT[mm] = 0.1820 \cdot BA[cm^2]^{0.6920} \quad 4.2$$

Figure 4.3 shows the measured bark thickness for the given basal area, and the estimated bark thickness using equation 4.2. The analysis of variance and the parameter estimates including the standard error are given in Table 4.1.

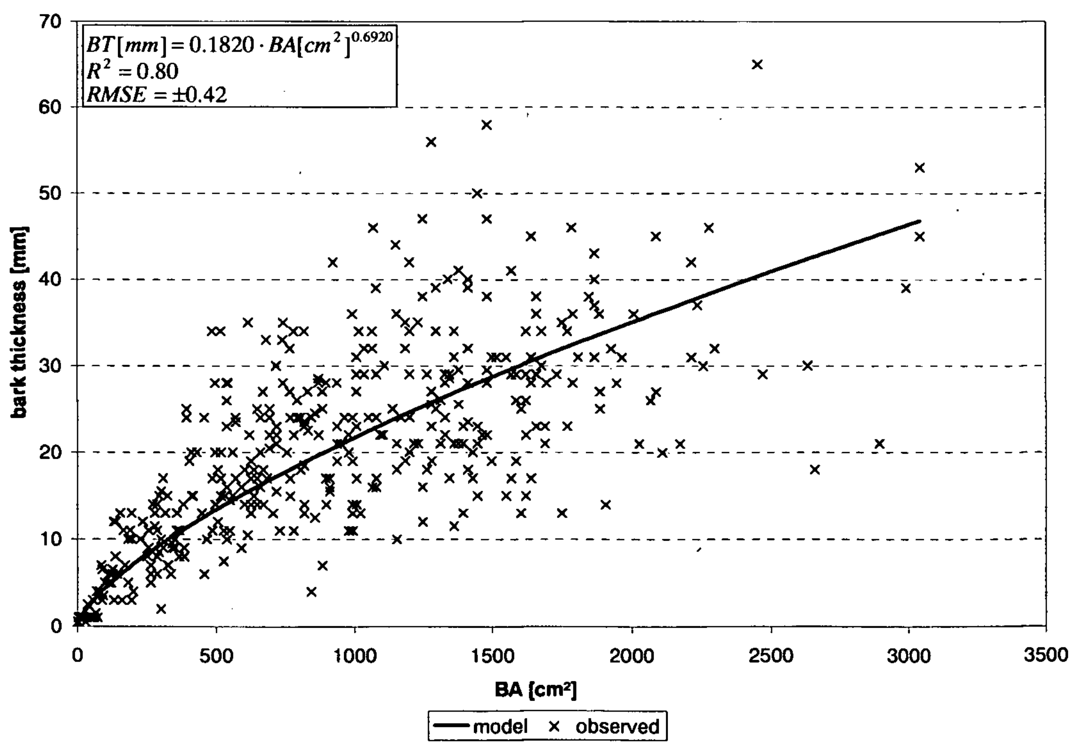


Figure 4.3: Bark thickness (BT) [mm] over basal area (BA) [cm^2] and BT-BA model.

***Table 4.1**: Parameter table for the relationship between bark thickness (BT) [mm] to basal area (BA) [cm^2].*

Dependend Variable	Independent Variable	n	R^2	RMSE	F	P > F	Parameter	Estimate	SE	t	P > |t|
ln (BT)	Intercept	408	0.80	0.42	1630	<.0001 ***	a0	-1.7035	0.1119	-15.22	<.0001 ***
	ln (BA)						a1	0.6920	0.0171	40.37	<.0001 ***

The sapwood area (SA) was then calculated with equation 4.3:

$$SA[cm^2] = \frac{DIB[cm]^2 \cdot \pi}{4} - \left(\frac{DIB[cm]}{2} - SW[cm] \right)^2 \cdot \pi \qquad 4.3$$

where DIB is the diameter inside bark and SW the sapwood width and the other variables are as defined above.

4.3.4 Leaf Area

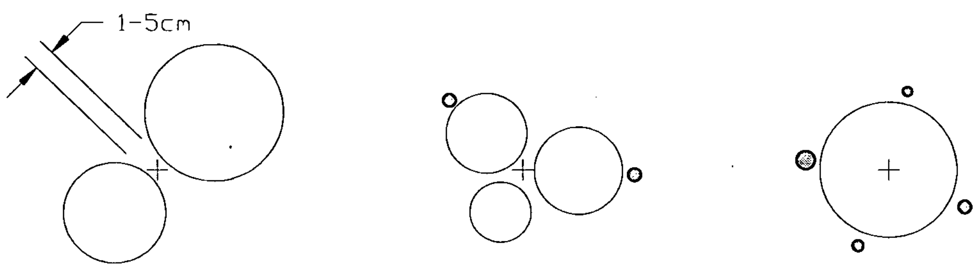
For trees with a height to crown base greater than 1.37 m, a total height of more than 7.7 m and a DBH larger than 9.4 cm, the SA_{BLC} was calculated using the taper model of STANCIOIU & O'HARA (2005) (equation2.1). The SA_{BLC} of these trees was multiplied by the factor of 0.5672 m^2/cm^2 and for smaller trees the SA_{BH} was multiplied by 0.4005 m^2/cm^2.

4.3.5 x/y coordinates

To calculate the area potentially available for individual trees, the coordinates of the trees were needed. Since the planting was done precisely on a 3.05 x 3.05 m grid, the coordinates were easily determined. However this just applies for single trees. As there were multiple stems on some grid points, the individual coordinates of these multiple-stem points were unknown. To assess these coordinates special guidelines were developed to arrange the multiple stems around or on the grid point. Because the real positions of the multiple stems were unknown, these guidelines try to reproduce the locations of the stems in a realistic range.

Given are all diameters at breast height per grid point and belonging to the first or the second cohort. Cohort 1 are the trees which were planted in the year 1982/83, and cohort 2 are stump sprouts which appeared after the thinning in 1997.

The assumption is that multiple trees of the cohort 1 are located around the grid point, displaced by the half of the DBH of each tree plus more space, to create a gap between the trees of 1 to 5 cm (Figure 4.4a). As cohort 2 trees appeared later, the cohort 1 trees already used most of the light resources hence it is assumed that cohort 2 trees started on the outer edge of cohort 1 treestems (Figure 4.4b). The location was chosen randomly, and when there were more than two trees of cohort 2, they were evenly distributed around the cohort 1 trees (Figure 4.4c).



a) *b)* *c)*

Figure 4.4: *Guidelines for arrangement of multiple stems. Trees from the second cohort are colored grey. a) 1-5 cm gap between two trees, b) arrangement of cohort 2 trees on the outer side of cohort 1 trees, c) cohort 2 trees evenly distributed around one cohort 1 tree.*

4.3.6 Area potentially available

The areas potentially available were computed with the program ACRE 0.2b (KINDERMANN 1999) using the circlebow-model of RÖMISCH (1995). Instead of using the crown projection area like ASSMANN (1961) the leaf area was used to partition the areas into APAs. When the area is partitioned by the leaf area, the distances should be proportional to the square root of the leaf areas.

A typical value for the distance of influence would be the crown width of an open-grown tree with the same DBH. The problem is that there are no existing publications describing this relationship. So the distance of influence was set same as the growing factor: the square root of the leaf area. Several percentages of this value were tested, but one times the growing factor was preferred because there were no gaps in each plot.

The APA of border trees can not be used for further calculations, as APA is not defined to the outer side of the plots. To identify the border trees the program was used twice. First to calculate APA with fixed borders of the plot (FB), and second without these borders (WOB). Trees where APA_{WOB} is higher than APA_{FB} are supposed to be border trees. This algorithm could be easily supervised using the optic outputs of the program.

Trees with an APA smaller than 0.5 dm^2 were dropped for further calculations. The number of these trees, the border trees and the cohort1 and cohort2 trees are given in Figure 4.5. The resolution was set to 1000, and the APAs calculated with fixed borders were used.

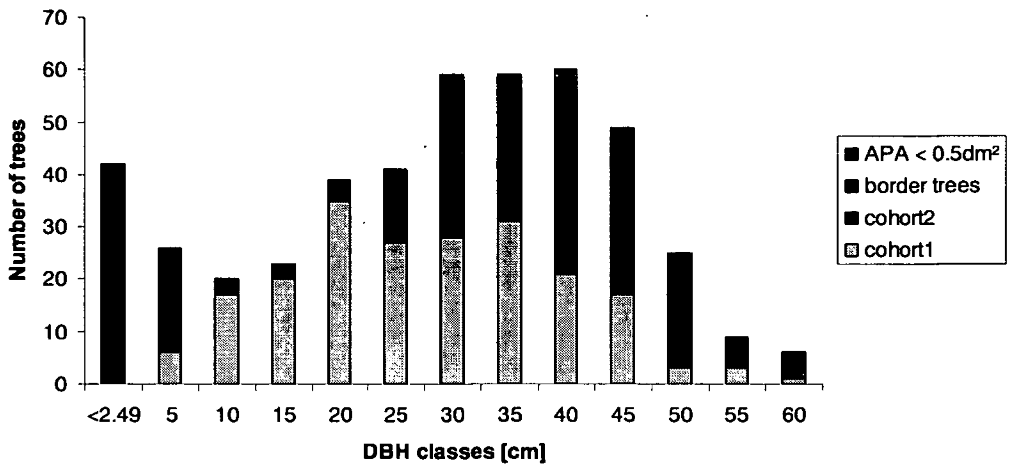


Figure 4.5: Number of trees belonging to cohort1 or 2, border trees and trees with a APA smaller than 0.5 dm^2 displayed in their DBH class.

4.3.7 Competition Index – A_{Johann}

JOHANN (1993, cit. STERBA & MONSERUD 1997) designed an equation to define what competitors shall be removed in a thinning. By converting this equation to the A-value it can be used to describe distance dependent competition (equation 4.4).

$$A_{Johann} = \frac{H}{E} \cdot \frac{dbh}{DBH} \tag{4.4}$$

where H and DBH are the height and the diameter at breast height of the analyzed tree, dbh the diameter at breast height of the competitor tree, and E the distance between the two trees. Every tree of the plot will get N-1 A-values (with N the number of trees on the plot). In this study it was assumed that the strongest competitor had the most impact on the tree. Hence the highest A-value of every tree is used for further calculations.

4.3.8 Stand description

In Table 4.2 the plots are assigned to treatments. For each plot the number of trees (n) and the area of the plots (area) are given. Basal area (BA), basal area increment (BAI), volume (V) and volume increment (VI) were summed up per plot, and blown up for hectare-values.
The diameter of the stem with mean basal area (dg) was calculated following equation4.5:

$$dg = \sqrt{\frac{BA}{N} \cdot \frac{4}{\pi}} \qquad 4.5$$

The mean height according to LOREY (1878) (h_L) was computed as the sum of the products of the basal area times the height of each tree, divided by the sum of the basal area. The dominant height according to WEISE 1880 (h_O) is defined as the mean h_L of the 20 percent strongest trees.
As a measure of stand density the stand density index (SDI) was implemented using equation 4.6:

$$SDI = N \cdot \left(\frac{25}{dg}\right)^{-1.605} \qquad 4.6$$

The stand leaf area index (LAI) was calculated as the sum of the leaf areas per plot, divided by the plot area.

Table 4.3 gives a similar itemization. Mean, minimum and maximum values and standard deviation are given for the diameter at breast height, height and leaf area for every plot.

As there was a lack of trees in some of the crown classes (especially crown class 1), the relative height was used to express the vertical position of the crown in the stand. It was calculated as the ratio between the individual tree height and the dominant height on the plot.

The site index for every plot was calculated using the model of KRUMLAND & ENG (2005) for a 28 year old redwood stand. It was assumed that the breast high age was 28 - 4 = 24 year. Total height was calculated as mean of the tallest 3 trees per plot. The plot site indices were calculated by interpolating from the tables and converted to meters. The overall mean is 43.5 m indicating that a 50 year old stand would have that height (Table 4.2).

Table 4.2: *Stand description with number of trees (n), plot area (area), basal area per year (BA), basal area increment per year (BAI), volume per year (V), volume increment per year (VI), diameter of stem with mean basal area (dg), mean height (hL), dominant height (h_O), stand density index (SDI), stand leaf area index (LAI), site index (SI).*

Plot#	n	area	BA	BAI	V	VI	N	BA	BAI	V	VI	dg	hL	h_o	SDI	LAI	SI
				per plot					per hectare								
		m²	m²	m²	m³	m³		m²	m²	m³	m³	cm	m	m		m²/m²	m
alternative row																	
1	63	465	0.71	0.31	4.25	2.59	1354	15.31	6.66	91.47	13.93	12.00	21.20	22.68	417	9.96	41.6
4	27	465	0.75	0.33	4.72	3.12	580	16.15	7.18	101.39	16.75	18.82	23.22	24.75	368	9.03	45.0
13	49	465	0.73	0.30	4.40	2.66	1053	15.59	6.37	94.59	14.30	13.73	21.67	23.77	403	10.44	43.0
mean			0.73	0.31	4.46	2.79	996	15.68	6.74	95.82	14.99	14.85	22.03	23.73	396	9.81	43.2
std			0.02	0.02	0.24	0.28	390	0.43	0.41	5.07	1.53	3.55	1.06	1.04	25.07	0.72	1.7
diagonal row																	
11	37	502	0.86	0.33	5.67	3.22	737	17.02	6.58	112.85	16.02	17.15	23.64	24.78	402	9.99	44.8
15	38	372	0.65	0.25	4.22	2.41	1021	17.46	6.74	113.33	16.17	14.75	23.34	24.81	438	12.07	45.3
mean			0.75	0.29	4.94	2.81	879	17.24	6.66	113.09	16.10	15.95	23.49	24.80	420	11.03	45.1
std			0.15	0.06	1.03	0.57	201	0.31	0.11	0.34	0.10	1.70	0.22	0.02	25.20	1.47	0.4
3rd row																	
9	35	419	0.81	0.24	5.43	2.85	836	19.35	5.77	129.82	17.02	17.16	23.79	25.45	457	12.08	46.4
10	35	419	0.71	0.25	4.24	2.62	836	16.85	6.00	101.40	15.62	16.02	21.49	21.98	409	10.36	42.6
14	34	419	0.68	0.28	4.29	2.75	812	16.24	6.81	102.54	16.44	15.96	22.62	23.51	395	10.06	43.6
mean			0.73	0.26	4.66	2.74	828	17.48	6.19	111.25	16.36	16.38	22.63	23.65	421	10.83	44.2
std			0.07	0.02	0.67	0.12	14	1.65	0.54	16.09	0.70	0.68	1.15	1.74	32.59	1.09	2.0
70%																	
6	28	754	0.54	0.38	2.77	2.63	372	7.11	5.05	36.83	8.71	15.61	19.62	20.24	175	4.23	37.3
free																	
7	25	930	0.77	0.45	4.22	3.37	269	8.23	4.80	45.42	9.06	19.75	21.30	21.05	184	4.57	41.0
12	28	930	1.11	0.54	7.17	5.26	301	11.98	5.85	77.09	14.15	22.51	23.75	24.34	254	6.42	44.0
mean			0.94	0.50	5.70	4.32	285	10.11	5.32	61.25	11.60	21.13	22.53	22.70	219	5.50	42.5
std			0.25	0.07	2.08	1.34	23	2.65	0.75	22.39	3.60	1.96	1.74	2.33	49.75	1.31	2.1
control																	
5	29	233	0.61	0.16	4.36	1.83	1247	26.16	6.79	187.51	19.70	16.34	24.88	26.01	630	13.82	47.0
8	30	233	0.55	0.14	3.71	1.65	1290	23.85	6.15	159.56	17.77	15.34	23.42	24.52	589	14.53	44.5
mean			0.58	0.15	4.04	1.74	1268	25.00	6.47	173.54	18.73	15.84	24.15	25.26	610	14.17	45.8
std			0.04	0.01	0.46	0.13	30	1.64	0.45	19.76	1.36	0.71	1.03	1.05	29.14	0.50	1.8

Table 4.3: Mean, minimum, maximum and standard deviation (std) for diameter at breast height (DBH), height (h) and leaf area (LA).

Plot#		Dbh [cm]				h [m]				LA [m²]			
	n	mean	min	max	std	mean	min	max	std	mean	min	max	std
alternative row													
1	63	19.55	0.51	52.58	14.01	15.04	1.90	25.00	7.67	73.53	0.08	321.84	73.90
4	27	33.96	2.29	62.23	16.54	20.03	3.40	26.20	5.82	155.53	1.51	382.94	106.21
13	49	22.85	0.51	48.01	15.37	15.35	1.75	25.20	8.83	99.13	0.08	285.46	85.97
diagonal row													
11	37	31.99	6.60	50.04	12.57	21.45	10.30	26.20	4.40	135.57	9.83	334.83	80.48
15	38	22.89	0.46	49.78	18.87	14.30	0.58	26.60	10.80	118.18	0.06	320.67	115.40
3rd row													
9	35	32.53	8.13	53.59	11.12	22.12	9.20	27.40	4.00	144.45	14.87	448.83	89.82
10	35	30.83	6.60	45.97	8.85	20.42	8.00	25.40	3.26	123.94	12.01	298.96	62.55
14	34	29.09	0.89	56.11	13.32	19.89	2.14	25.50	5.67	123.84	0.23	355.72	95.00
70%													
6	28	25.75	2.54	50.55	17.98	14.02	3.70	21.80	7.13	113.72	1.85	301.78	100.21
free													
7	25	32.62	0.74	57.91	22.73	15.41	1.60	24.00	8.30	170.05	0.16	469.10	140.46
12	28	44.49	27.69	62.23	7.10	23.55	19.20	25.50	1.52	213.30	61.32	375.27	73.10
control													
5	29	30.98	13.97	51.82	10.61	23.52	15.30	27.40	3.04	110.82	14.54	373.17	90.10
8	30	28.55	8.64	49.28	11.43	21.95	14.60	26.30	3.11	112.63	2.57	417.07	94.24
Total	458	29.70	0.46	62.23	13.89	19.00	0.58	27.40	5.66	130.36	0.06	469.10	92.88

4.3.9 Statistical methods

All statistical analyses were made using the program JMP IN vs. 5.1.2 of the SAS INSTITUTE INC (2004). Multiple linear regression were used to describe the data although sometimes logarithmic transformation was necessary. The multiple linear regression was analyzed using analyses of variances including the coefficient of determination R^2, the root mean square error RMSE and the standard error of the individual parameters.

4.3.9.1 Dummy Variables

The handling of dummy variables in JMP IN differs from usual techniques. For n levels there are n-1 dummy columns. Each dummy variable is a zero-or-one indicator for a particular level, except for the last level, which is coded -1 for all dummy variables. This coding causes the parameter estimates to be interpreted as how much the response for each level differs from the averages across all levels. Therefore the coefficient of the last level is the negative sum of all other coefficients.

5 Results

For calculations where just leaf areas and increments are used, the whole dataset could be employed. It comprises 458 observations (trees), but because of the logarithmic function data with an increment of zero could not be used since the logarithm of zero is infinite.

For all calculations including the area potentially available, a smaller dataset of just 217 trees could be used because the border trees of every plot had to be removed, since their APA to the outer side was undefined.

Table 5.1 lists the data check of the used variables including mean, minimum and maximum values and the standard error.

***Table 5.1**: Data check of the variables used in the following calculations. Number of trees (n), mean, minimum and maximum values, standard error (se) and outlier for the total observations (first six lines) and for trees with an estimated area potentially available (last 12 lines).*

Variable	Unit	n	mean	min	max	se	outlier
BAI	dm^2/y	458	86.73	0.00	500.97	4.32	
VI	dm^3/y	458	81.37	0.00	435.62	3.71	
LA	m^2	458	124.02	0.06	469.10	4.54	
hrel	m/m	458	0.78	0.06	1.16	0.30	
BAI/LA	dm^2/m^2	458	0.58	0.00	2.70	0.44	
VI/LA	dm^3/m^2	458	0.52	0.00	2.29	0.39	
BAI	dm^2/y	217	67.86	0.00	500.97	5.31	
VI	dm^3/y	217	65.93	0.00	435.62	4.78	
LA	m^2	217	102.30	1.51	448.83	5.41	
APA	m^2	217	10.29	0.01	79.47	0.92	
LAI	m^2/m^2	217	140.25	2.70	1016.07	15.68	1307
hrel	m/m	217	0.81	0.14	1.16	0.01	
BAI/LA	dm^2/m^2	217	0.54	0.00	2.37	0.03	
VI/LA	dm^3/m^2	217	0.52	0.00	2.29	0.03	
BAI/APA	dm^2/m^2	217	47.16	0.00	290.85	8.61	1352;712;618;615
VI/APA	dm^3/m^2	217	66.93	0.00	341.06	4.54	541
SDI		13	1257.84	531.00	1917.00	21.99	
A_{Johann}		217	67.29	2.55	310.45	3.99	

5.1 Increment in relation to Leaf area

Basal area increment could be explained by a power model with a R^2 of 0.82. The relative height showed to have highly significant influence which enhanced the R^2 to 0.83 (Table 5.2). The BAI was increasing over the leaf area as expected (Figure 5.1) and increasing with increasing relative height (Figure 5.2).

Volume increment was better explained by leaf area using a power model with an R^2 of 0.90. The relative height was highly significant and could improve the model to a R^2 of 0.91 (Table 5.2). Volume increment was increasing with increasing leaf area and increasing relative height (Figure 5.3 and Figure 5.4).

***Table 5.2**: Parameter table for the relationship between the natural logarithm of basal area increment (BAI) [$dm^2/year$] and the natural logarithm of volume increment (VI) [$dm^3/year$] to the natural logarithm of the leaf area (LA) [m^2] and the relative height (h_{rel}) [m/m].*

Dependend Variable	Independent Variable	n	R^2	RMSE	F	P > F	Parameter	Estimate	SE	t	P > |t|
ln(BAI)	Intercept	428	0.82	1.06	1935	<.0001 ***	a0	-1.9065	0.1301	-14.65	<.0001 ***
	ln(LA)						a1	1.2551	0.0285	43.99	<.0001 ***
ln(BAI)	Intercept	428	0.83	1.01	1080	<.0001 ***	a0	-2.5986	0.1645	-15.80	<.0001 ***
	ln(LA)						a1	0.8451	0.0694	12.18	<.0001 ***
	hrel						a2	2.9462	0.4585	6.43	<.0001 ***
ln(VI)	Intercept	438	0.90	1.01	3820	<.0001 ***	a0	-3.6933	0.1182	-31.25	<.0001 ***
	ln(LA)						a1	1.6155	0.0261	61.80	<.0001 ***
ln(VI)	Intercept	438	0.91	0.95	2185	<.0001 ***	a0	-4.3809	0.1436	-30.52	<.0001 ***
	ln(LA)						a1	1.1855	0.0619	19.16	<.0001 ***
	hrel						a2	3.0563	0.4035	7.57	<.0001 ***

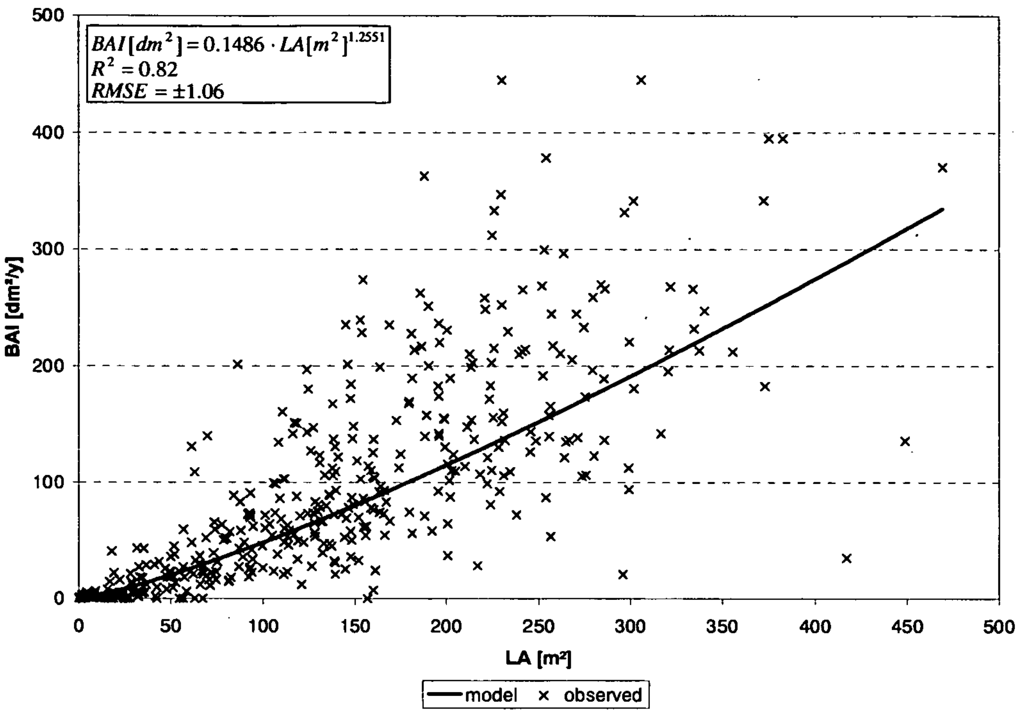


***Figure 5.1:** Observed annual basal area increment (BAI) [dm^2/year] over leaf area (LA) [m^2] and BAI-LA model.*

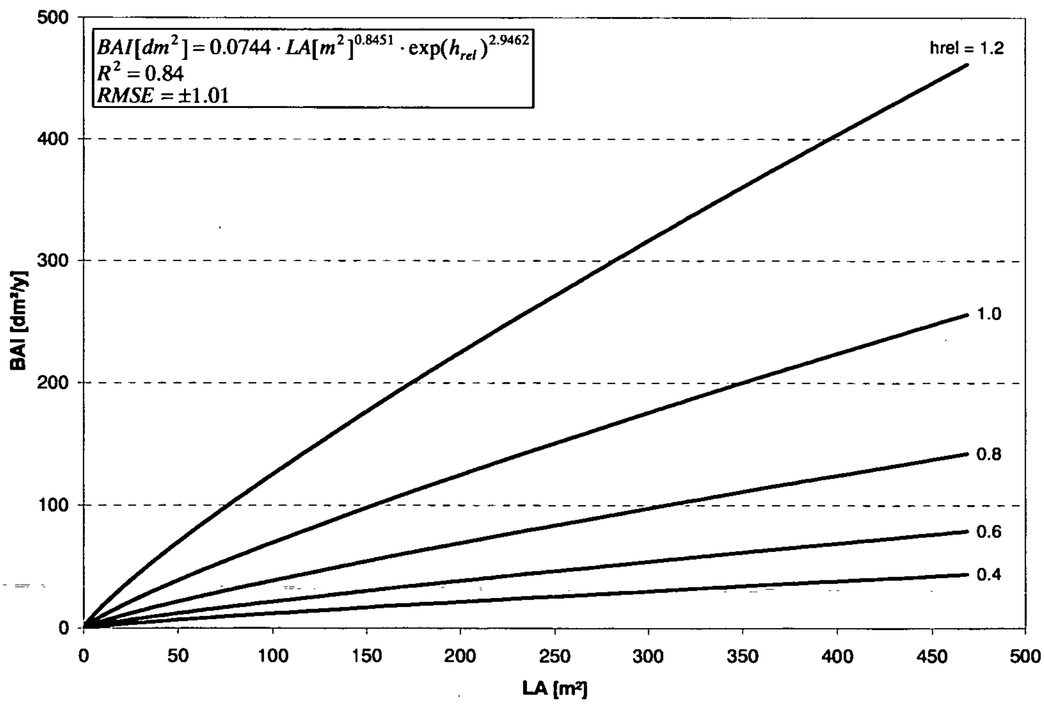


***Figure 5.2:** Annual basal area increment (BAI) [dm^2/year] to leaf area (LA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

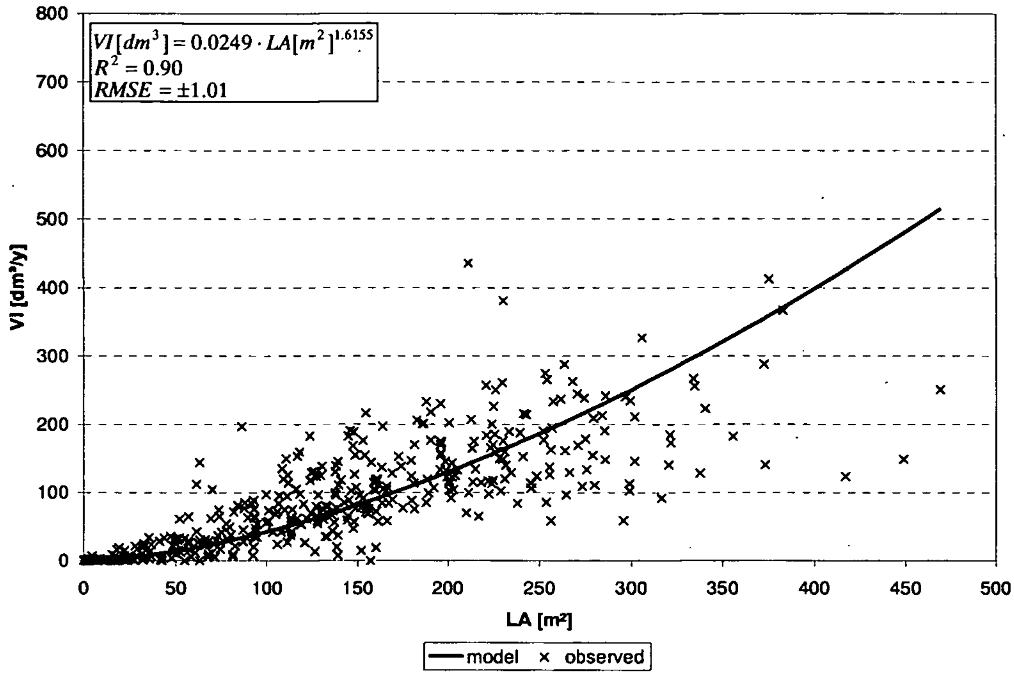


Figure 5.3: *Observed annual volume increment (VI) [dm³/year] over leaf area (LA) [m²] and VI-LA model.*

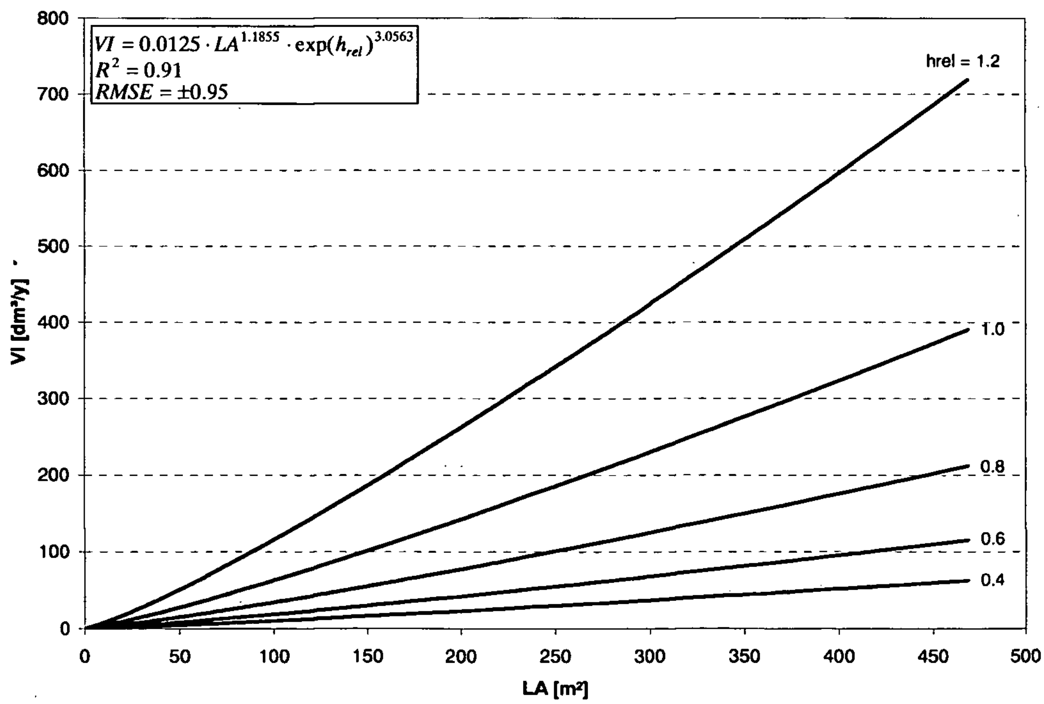


Figure 5.4: *Annual volume increment (VI) [dm³/year] to leaf area (LA) [m²] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

5.2 Leaf area efficiency in relation to leaf area

The leaf area efficiency could be described by a power model. The model for LAE_{BAI} could described 16 percent of the variation. The addition of the independent variable h_{rel} enhanced the model to a R^2 of 0.23 percent (Table 5.3). For the general model LAE_{BAI} was increasing with increasing leaf area (Figure 5.5), however subdivided into constant values for h_{rel}, LAE_{BAI} was decreasing with increasing leaf area (Figure 5.6). Although increasing relative height led to increasing efficiencies.

The prediction model of LAE_{VI} could explain 56 percent of the variation. Including the relative height in the model led to an enhancement and a R^2 of 0.61 (Table 5.3). Both in the general model and in the model subdivided into constant h_{rel} values, LAE_{VI} was increasing with increasing leaf area (Figure 5.7). LAE_{VI} was also increasing with increasing relative height (Figure 5.8).

Table 5.3: *Parameter table for the relationship between the natural logarithm of basal area increment per leaf area (BAI/LA) [dm^2/m^2/year] and the natural logarithm of volume increment per leaf area (VI/LA) [dm^3/m^2/year] to the natural logarithm of the leaf area (LA) [m^2] and the relative height (h_{rel}) [m/m].*

Dependend Variable	Independent Variable	n	R²	RMSE	F	P > F		Parameter	Estimate	SE	t	P > |t|	
ln(BAI/LA)	Intercept	428	0.16	1.06	79.9	<.0001	***	a0	-1.9065	0.1301	-14.65	<.0001	***
	ln(LA)							a1	0.2551	0.0285	8.94	<.0001	***
ln(BAI/LA)	Intercept	428	0.23	1.01	64.4	<.0001	***	a0	-2.5986	0.1645	-15.80	<.0001	***
	ln(LA)							a1	-0.1549	0.0694	-2.23	0.0261	*
	hrel							a2	2.9462	0.4585	6.43	<.0001	***
ln(VI/LA)	Intercept	438	0.56	1.01	554	<.0001	***	a0	-3.6933	0.1182	-31.25	<.0001	***
	ln(LA)							a1	0.6155	0.0261	23.55	<.0001	***
ln(VI/LA)	Intercept	438	0.61	0.95	342	<.0001	***	a0	-4.3809	0.1436	-30.52	<.0001	***
	ln(LA)							a1	0.1855	0.0619	3.00	0.0029	**
	hrel							a2	3.0563	0.4035	7.57	<.0001	***

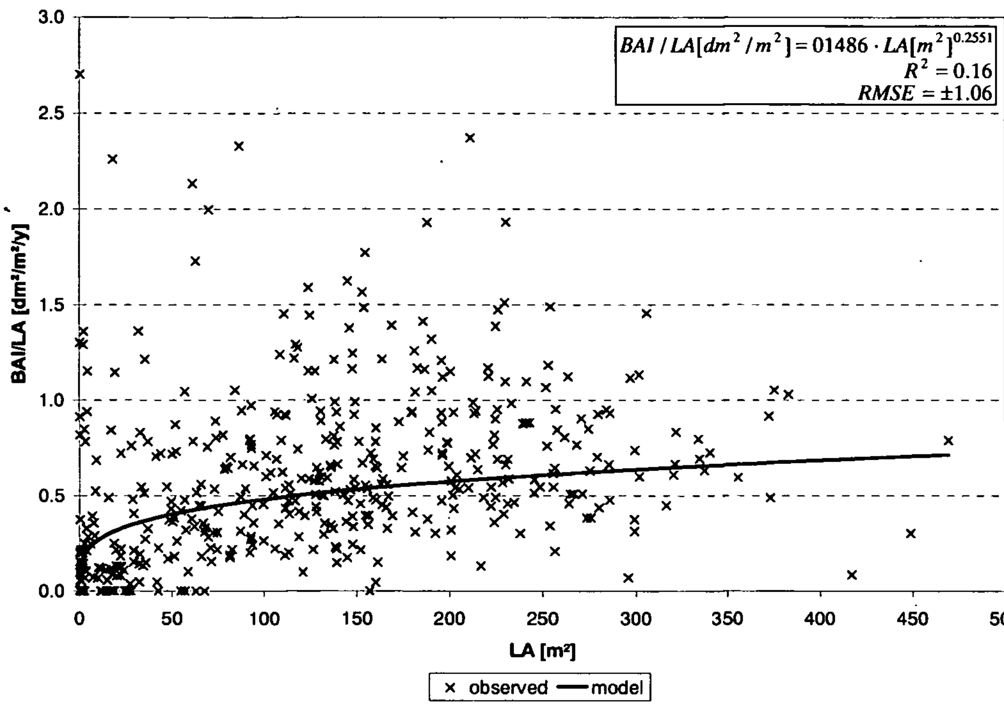


***Figure 5.5:** Observed annual basal area increment per leaf area (BAI/LA) [$dm^2/m^2/year$] over leaf area (LA) [m^2] and BAI/LA-LA model.*

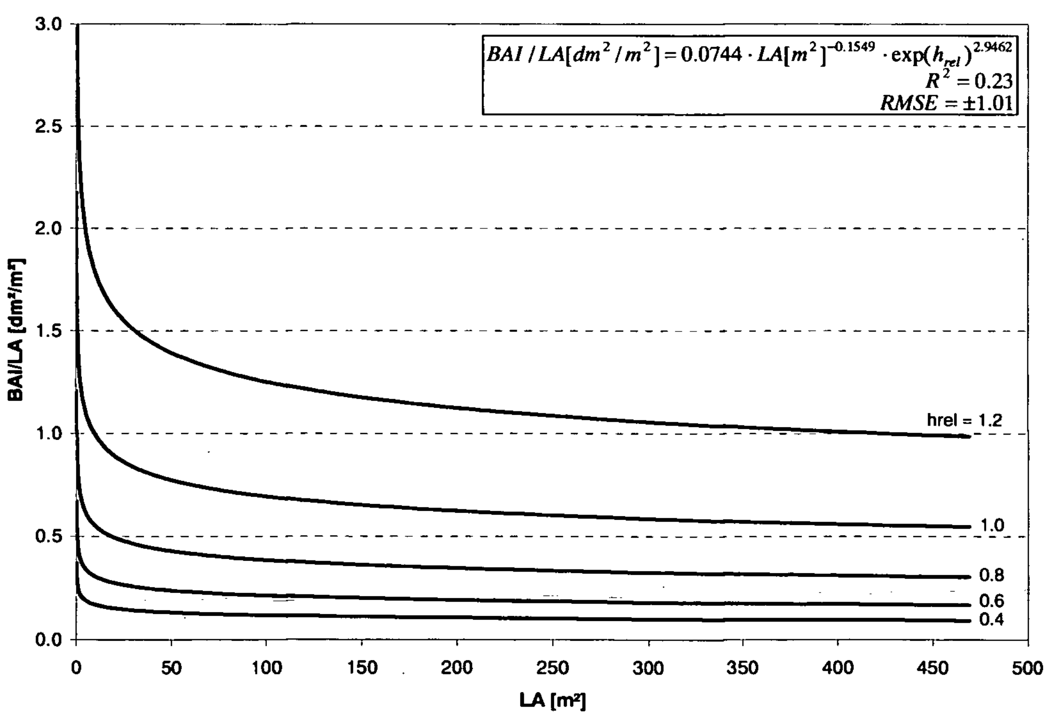


***Figure 5.6:** Annual basal area increment per leaf area (BAI/LA) [$dm^2/m^2/year$] to leaf area (LA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

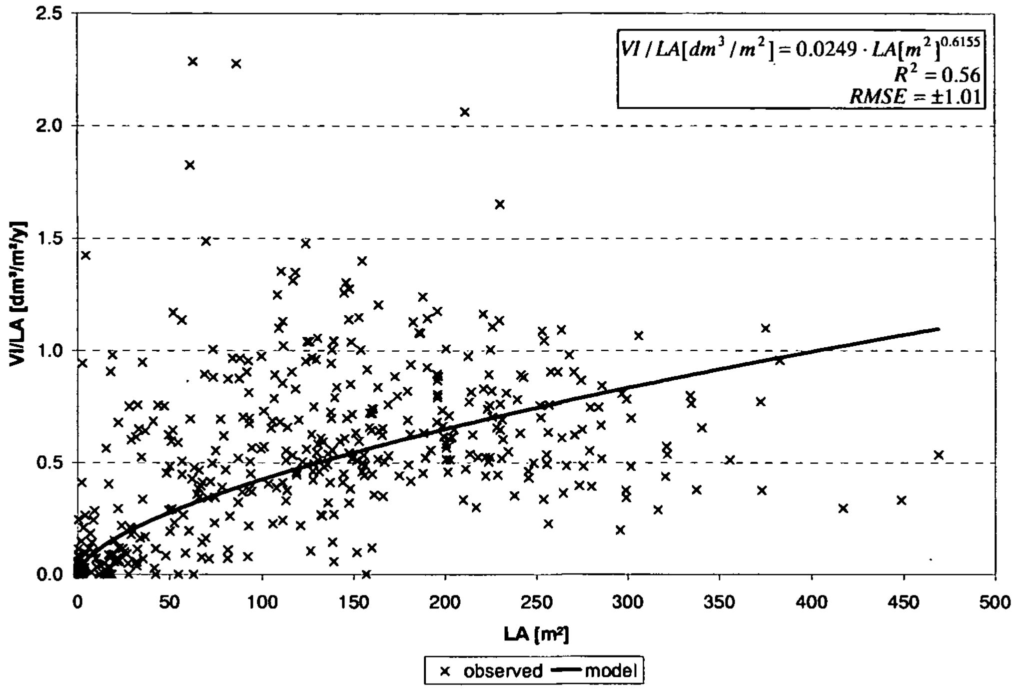


Figure 5.7: *Observed annual volume increment per leaf area (VI/LA) [$dm^3/m^2/year$] over leaf area (LA) [m^2] and VI/LA-LA model.*

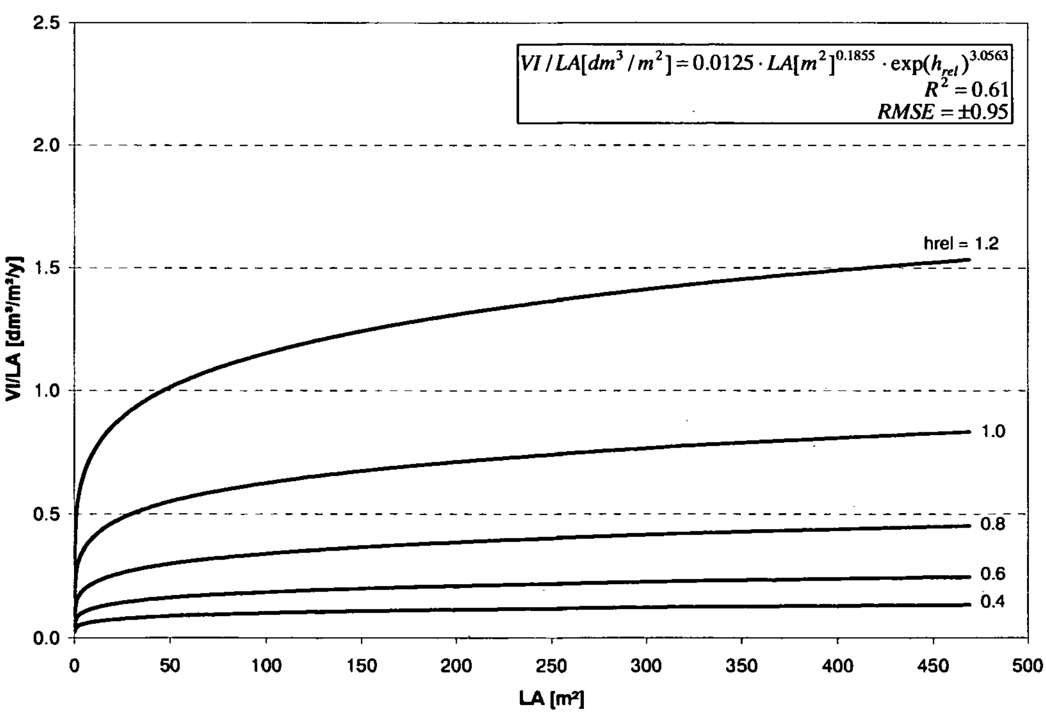


Figure 5.8: *Annual volume increment per leaf area (VI/LA) [$dm^3/m^2/year$] to leaf area (LA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

5.3 Increment in relation to the area potentially available

A power model was used to estimate the increment. For BAI estimation a R^2 of 0.55 could be reached. By adding h_{rel} to the model, the intercept lost its significance so it was removed from the model. The model with ln(APA) and h_{rel} as independent variables could explain 62 percent of the variation (Table 5.4). BAI was increasing with increasing APA (Figure 5.9) and decreasing relative height (Figure 5.10).

The VI prediction model showed a R^2 of 0.63. When adding the relative height, the intercept had to be zeroed, but the model was enhanced to explain 71 percent of the (Table 5.4). VI showed the same behavior as BAI and was increasing with increasing APA (Figure 5.11) and decreasing relative height (Figure 5.12).

Table 5.4: *Parameter table for the relationship between the natural logarithm of basal area increment (BAI) [dm^2/year] and the natural logarithm of volume increment (VI) [dm^3/year] to the natural logarithm of the area potentially available (APA) [m^2] and the relative height (h_{rel}) [m/m].*

Dependend Variable	Independent Variable	n	R²	RMSE	F	P > F	Parameter	Estimate	SE	t	P > |t|
ln(BAI)	Intercept	205	0.55	1.25	255	<.0001 ***	a0	2.8920	0.0920	31.45	<.0001 ***
	ln(APA)						a1	0.5652	0.0354	15.95	<.0001 ***
ln(BAI)	Intercept	205	0.61	1.17	162	<.0001 ***	a0	0.0847	0.5059	0.17	0.8672
	ln(APA)						a1	0.3598	0.0492	7.31	<.0001 ***
	hrel						a2	3.5573	0.6317	5.63	<.0001 ***
ln(BAI)	Intercept	205	0.62	1.16	1009	<.0001 ***	a0	zeroed	-	-	-
	ln(APA)						a1	0.3541	0.0353	10.04	<.0001 ***
	hrel						a2	3.6616	0.1068	34.29	<.0001 ***
ln(VI)	Intercept	208	0.63	1.20	356	<.0001 ***	a0	2.7418	0.0872	31.45	<.0001 ***
	ln(APA)						a1	0.6366	0.0337	18.87	<.0001 ***
ln(VI)	Intercept	208	0.71	1.06	258	<.0001 ***	a0	-0.3310	0.4069	-0.81	0.4168
	ln(APA)						a1	0.4055	0.0423	9.58	<.0001 ***
	hrel						a2	3.9349	0.5116	7.69	<.0001 ***
ln(VI)	Intercept	208	0.71	1.06	1237	<.0001 ***	a0	zeroed	-	-	-
	ln(APA)						a1	0.4281	0.0319	13.43	<.0001 ***
	hrel						a2	3.5262	0.0967	36.46	<.0001 ***

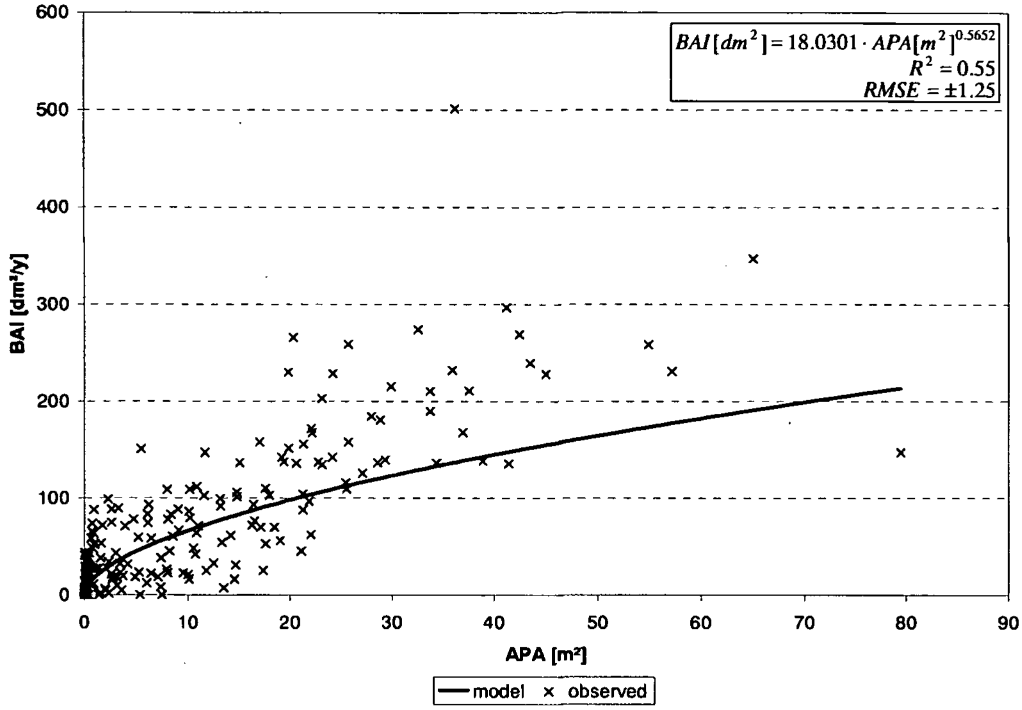


Figure 5.9: *Observed annual basal area increment (BAI) [dm^2/year] over area potentially available (APA) [m^2] and BAI-APA model.*

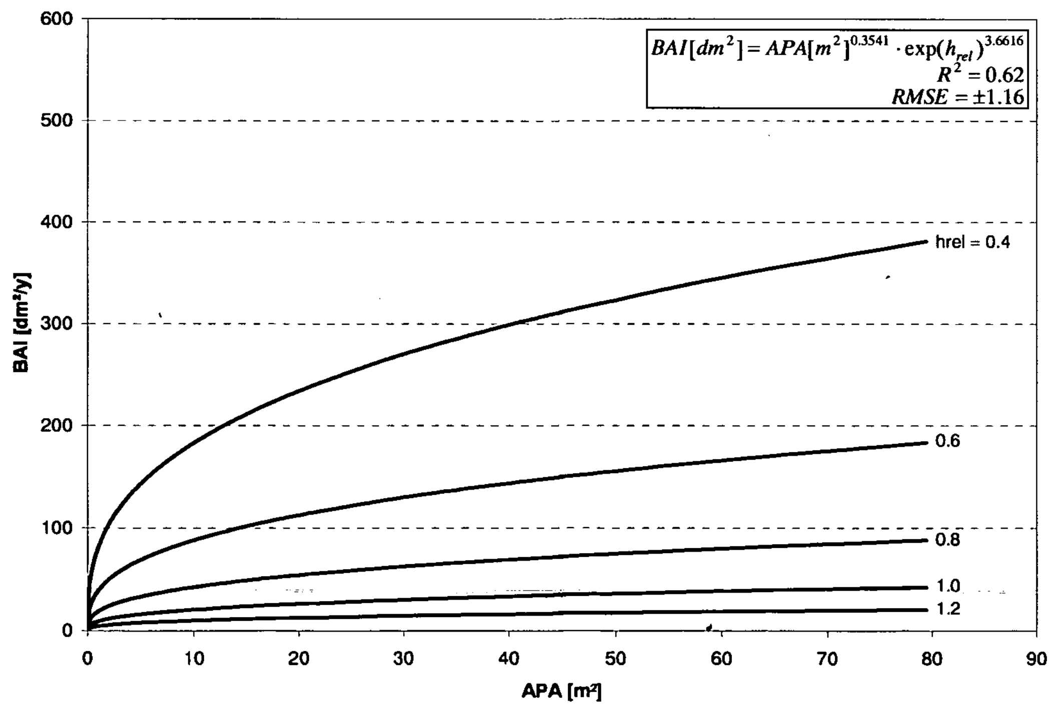


Figure 5.10: *Annual basal area increment (BAI) [dm^2/year] to area potentially available (APA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

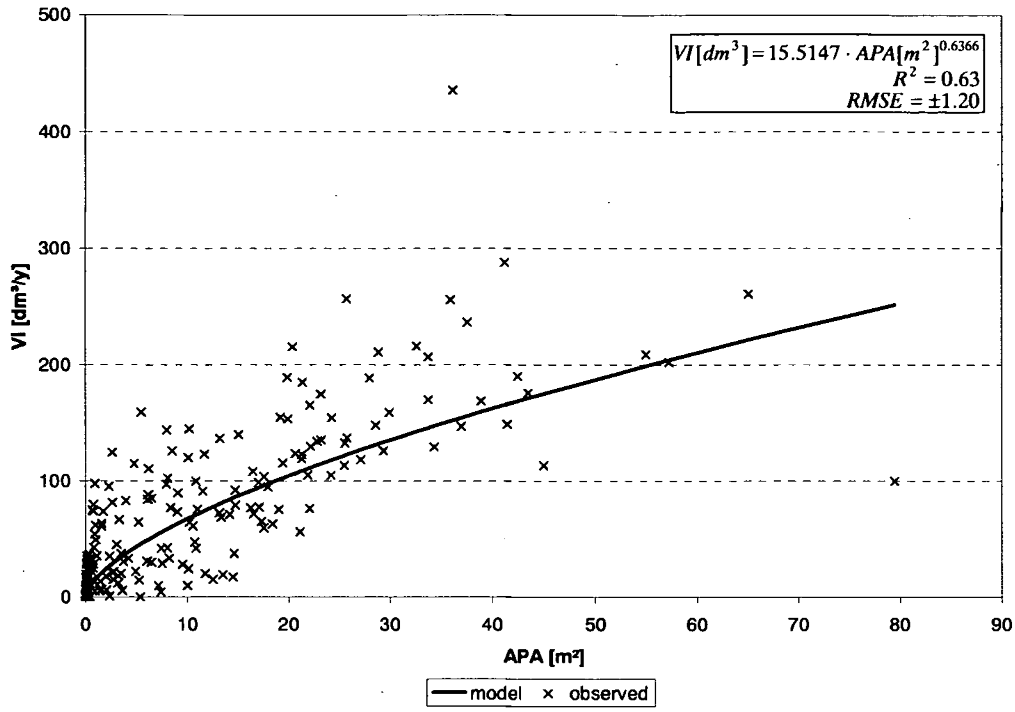


***Figure 5.11:** Observed annual volume increment (VI) [dm^3/year] over area potentially available (APA) [m^2] and VI-APA model.*

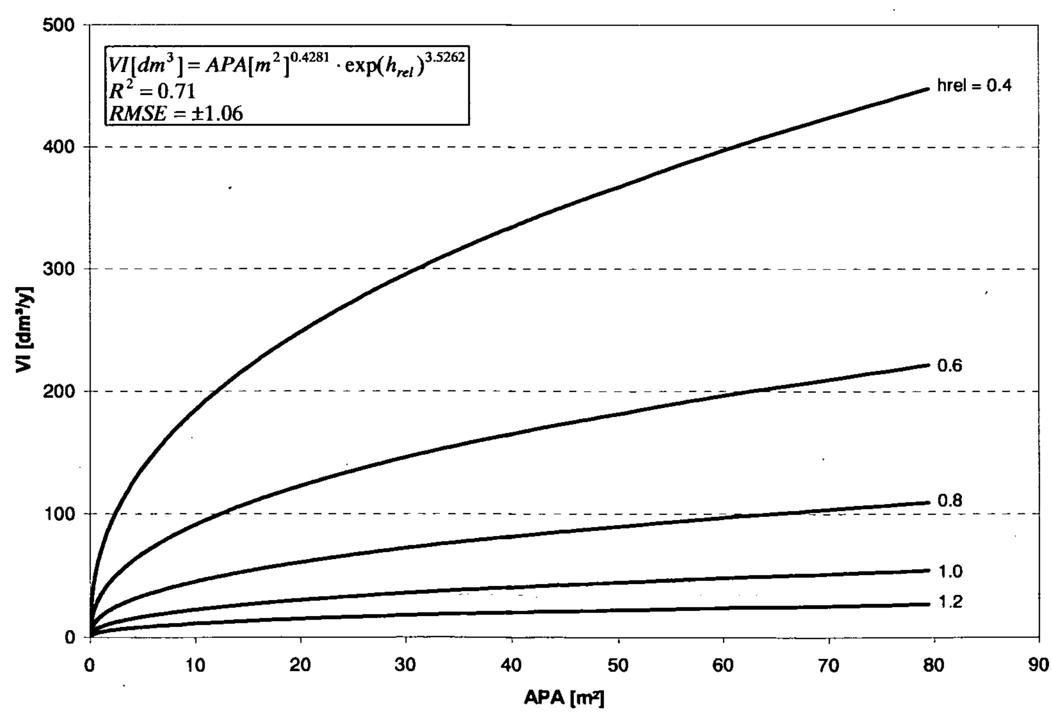


***Figure 5.12:** Annual volume increment (VI) [dm^3/year] to area potentially available (APA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

5.4 Available area efficiency in relation to the area potentially available

A power model was used to predict the available area efficiency. For AAE_{BAI} the model showed a R^2 of 0.42. By adding the relative height as an independent variable the intercept lost its significance and was removed. The enhanced model explained 50 percent of the variation (Table 5.5). AAE_{BAI} was decreasing with increasing APA (Figure 5.13), but increasing with increasing relative height (Figure 5.14).

The model to predict AAE_{VI} explained 30 percent of the variation. The intercept had to be zeroed because it lost its significance after adding the variable h_{rel}. This improved the model and led to a R^2 of 0.45 (Table 5.5). AAE_{VI} showed the same behavior as AAE_{BAI}. It was decreasing with increasing APA (Figure 5.15) but increasing with increasing relative height (Figure 5.16).

Table 5.5: *Parameter table for the relationship between the natural logarithm of basal area increment per area potentially available (BAI/APA) [$dm^2/m^2/year$] and the natural logarithm of volume increment per potentially available (VI/APA) [$dm^3/m^2/year$] to the natural logarithm of the area potentially available (APA) [m^2] and the relative height (h_{rel}) [m/m].*

Dependend Variable	Independent Variable	n	R^2	RMSE	F	P > F	Parameter	Estimate	SE	t	P > |t|
ln(BAI/APA)	Intercept	205	0.42	1.26	147	<.0001 ***	a0	2.8853	0.0924	31.22	<.0001 ***
	ln(APA)						a1	-0.4315	0.0356	12.12	<.0001 ***
ln(BAI/APA)	Intercept	205	0.49	1.17	101	<.0001 ***	a0	0.0580	0.5081	0.11	0.9092
	ln(APA)						a1	-0.6384	0.0494	12.92	<.0001 ***
	hrel						a2	3.5826	0.6345	5.65	<.0001 ***
ln(BAI/APA)	Intercept	205	0.50	1.17	584	<.0001 ***	a0	zeroed	-	-	-
	ln(APA)						a1	-0.6423	0.0354	18.13	<.0001 ***
	hrel						a2	3.6540	0.1073	34.07	<.0001 ***
ln(VI/APA)	Intercept	209	0.30	1.27	90.3	<.0001 ***	a0	2.6897	0.0922	29.17	<.0001 ***
	ln(APA)						a1	-0.3382	0.0356	9.50	<.0001 ***
ln(VI/APA)	Intercept	209	0.45	1.13	86.8	<.0001 ***	a0	-0.5454	0.4316	-1.26	0.2078
	ln(APA)						a1	-0.5843	0.0451	12.96	<.0001 ***
	hrel						a2	4.1493	0.5436	7.63	<.0001 ***
ln(VI/APA)	Intercept	209	0.45	1.13	571	<.0001 ***	a0	zeroed	-	-	-
	ln(APA)						a1	-0.5465	0.0338	16.19	<.0001 ***
	hrel						a2	3.4748	0.1029	33.76	<.0001 ***

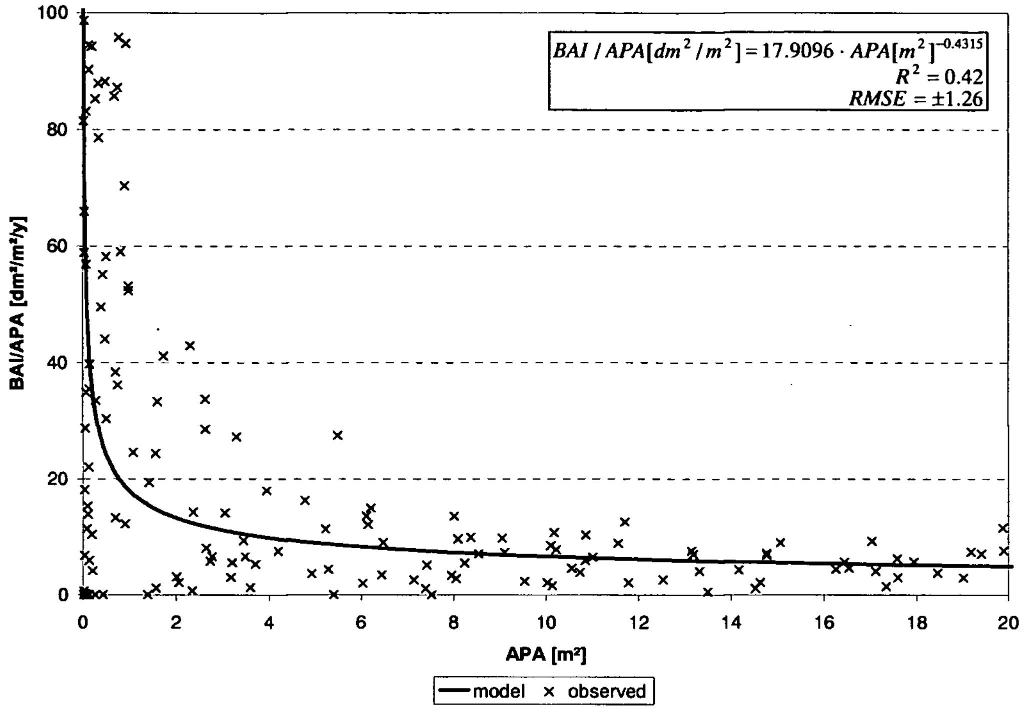


***Figure 5.13:** Observed annual basal area increment per area potentially available (BAI/APA) [dm^2/m^2/year] over area potentially available (APA) [m^2] and BAI/APA-APA model.*

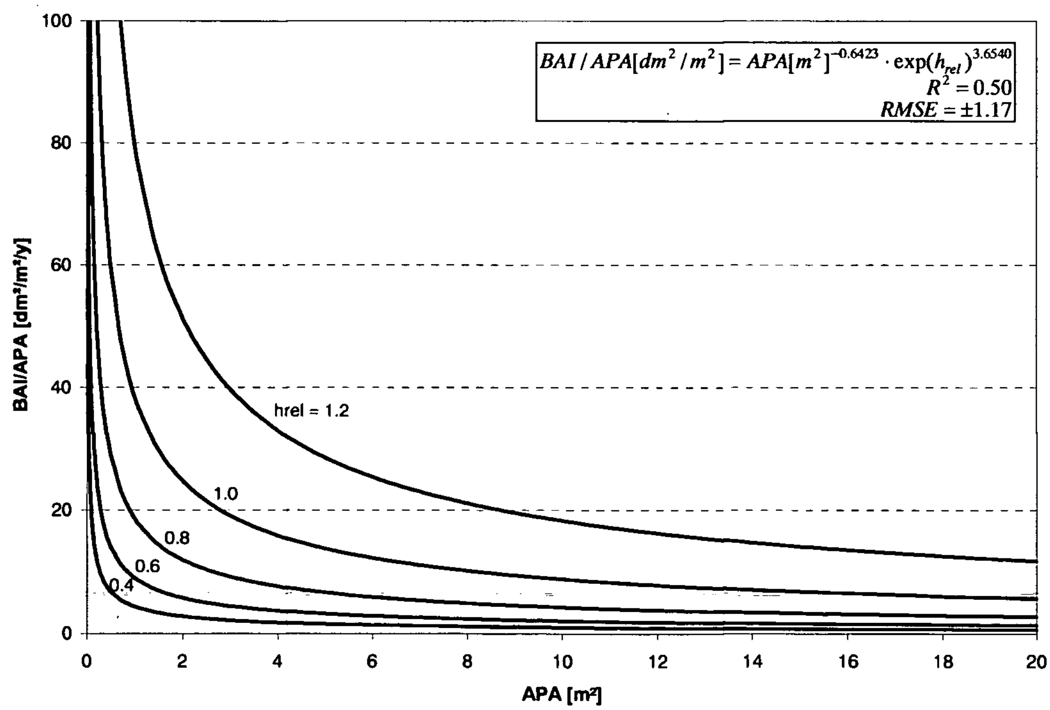


***Figure 5.14:** Annual basal area increment per area potentially available (BAI/APA) [dm^2/m^2/year] to area potentially available (APA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

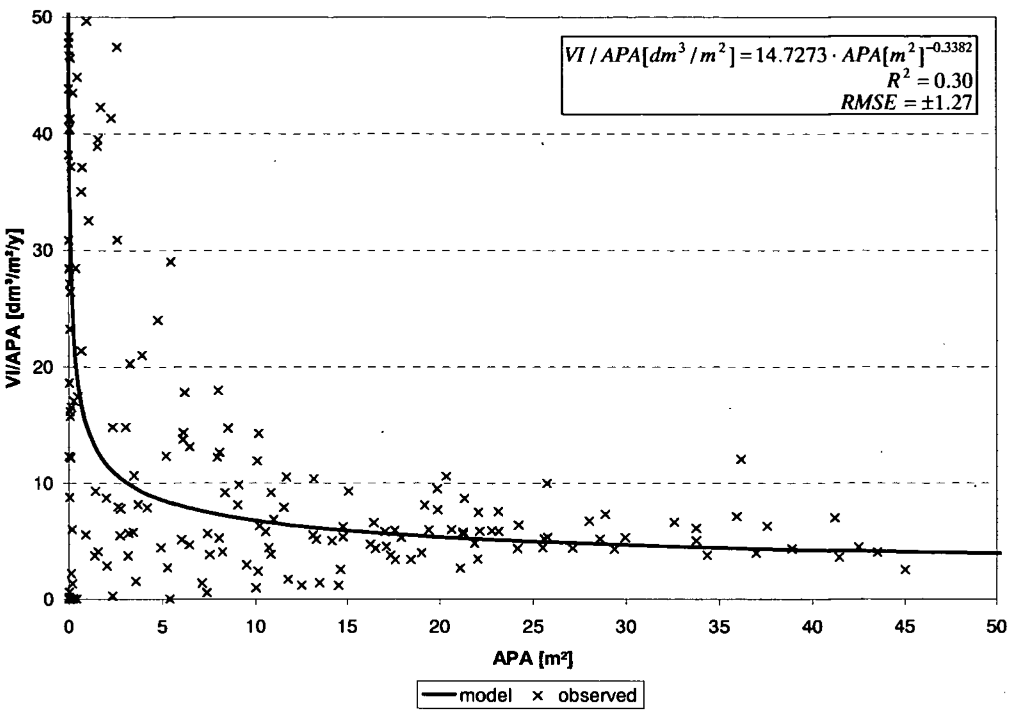


***Figure 5.15:** Observed annual volume increment per area potentially available (VI/APA) [dm^3/m^2/year] over area potentially available (APA) [m^2] and VI/APA-APA model.*

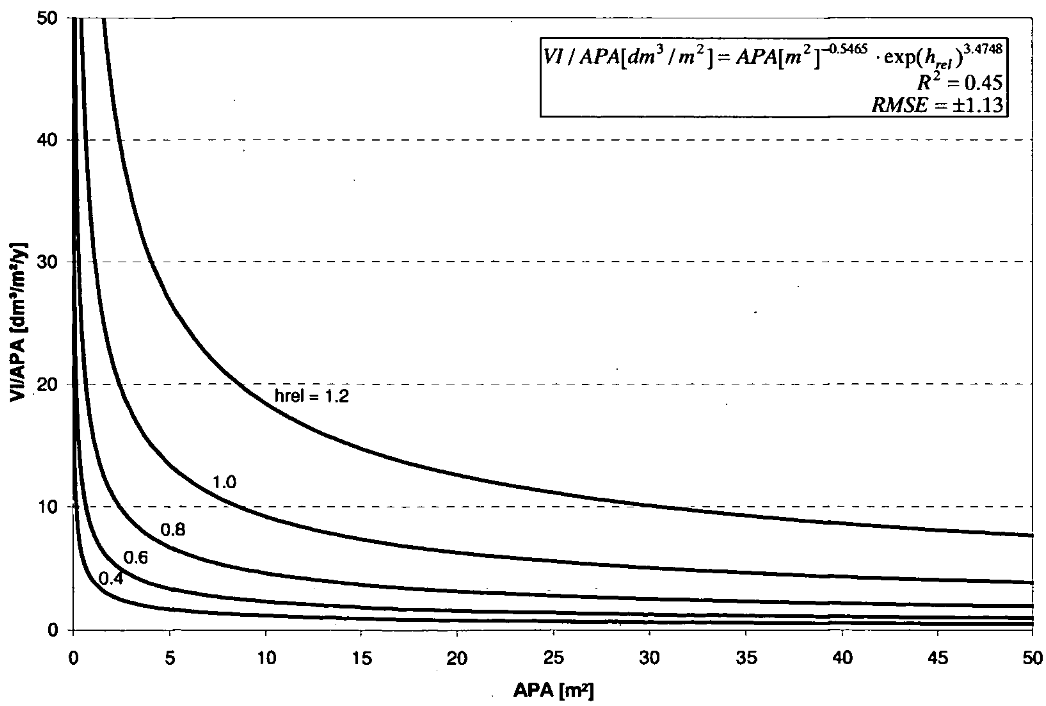


***Figure 5.16:** Annual volume increment per area potentially available (VI/APA) [dm^3/m^2/year] to area potentially available (APA) [m^2] model for relative heights (h_{rel}) from 0.4-1.2m/m.*

5.5 Available area efficiency in relation to leaf area index with optimum

The available area efficiency was here tried to be described as a function of leaf area index (and other variables) which shows an optimum. This was done in two ways, direct and indirect, which were compared in the last point.

5.5.1 Direct estimation of available area efficiency

The models of AAE_{BAI} and AAE_{VI} were able to describe 28 percent and 28 percent of the variation with corresponding RMSEs of ± 229 and 172 percent (Table 5.6). The optimum leaf area index of that function was calculated by setting the first derivative to zero. AAE_{BAI} showed an optimum at a LAI of 743 m^2/m^2 and AAE_{VI} at 673 m^2/m^2.

Table 5.6: *Parameter table for the relationship between basal area increment per potentially available (BAI/APA) [$dm^2/m^2/year$] and volume increment per potentially available (VI/APA) [$dm^3/m^2/year$] to the leaf area index (LAI) [m^2/m^2].*

Dependend Variable	Independent Variable	n	R^2	RMSE	RMSE%	F	P > F	Parameter	Estimate	SE	t	P > |t|
BAI/APA	Intercept	217	0.28	107.92	229	62.51	<.0001 ***	a0	zeroed	-	-	-
	LAI							a1	0.4397	0.0443	9.93	<.0001 ***
	LAI^3							a2	-2.65E-07	5.64E-08	-4.7	<.0001 ***
VI/APA	Intercept	217	0.28	56.79	172	79.13	<.0001 ***	a0	zeroed	-	-	-
	LAI							a1	0.2768	0.0233	11.89	<.0001 ***
	LAI^3							a2	-2.04E-07	2.97E-08	-6.86	<.0001 ***

5.5.2 Indirect estimation of available area efficiency

Leaf area efficiency was estimated and then multiplied with the leaf area index in order to compute the available area efficiency.

To estimate the leaf area efficiency different independent variables were used. Nevertheless LAI^2 always had to be part of the equation to follow the basic idea.

The model with LAI^2 as the only independent variable could explain 6 and 12 percent of the variation and showed a standard error of ± 74 and 69 percent (for AAE_{BAI} and AAE_{VI} respectively). Adding treatment as a dummy variable enhanced the model to a R^2 of 0.31 and 0.23 with corresponding RMSEs of ± 65 and 66 percent (Table 5.9).

It should be mentioned that treatment D, with only 9 trees, did not fulfill all restrictions of a variance analysis since the variances were significantly different.

Furthermore it was tried to arrange the treatments from 6 to 3 groups. Treatments A, B, C, D, E and F were summarized into the groups ABC, DE and F (Table 5.7). Table 5.8 lists the analysis of variance calculated for 6 and 3 groups and the improvement of having 6 instead of 3 groups. This improvement was not significant, which led to the conclusion that the model to predict LAE out of LAI^2 and 6 groups of treatments had no significant improvement than using LAI^2 and 3 groups of treatments. In other words, it does make sense to arrange the treatments into groups. This was assumed because of the similar mean values for the basal area and SDI in between the new groups (Table 5.7).

Table 5.7: *Number of trees in every treatment (n), arrangement of groups, definition, mean basal area (BA) [m^2/ha] and mean stand density index (SDI).*

Treatment	n	Group n	Definition	BA [m^2/ha]	SDI
A	71		alternate row	62.7	1204
B	31	158	diagonal row	69.0	1278
C	56		third row	69.9	1279
D	9	28	double alternate	28.5	531
E	19		free thinning	40.4	667
F	31	31	control	100.0	1855

Table 5.8: The improvement of 6 instead of 3 groups shows to be not significant (p>0.05).

Analysis of Variance. 6 groups

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	6	11.2813	1.8802	15.45	<.0001 ***
Error	210	25.5553	0.1217		
C. Total	216	36.8366			

Analysis of Variance. 3 groups

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	3	10.7150	3.5717	29.12	<.0001 ***
Error	213	26.1216	0.1226		
C. Total	216	36.8366			

Analysis of Variance. Improvement

Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Improvement	3	0.5663	0.1888	1.57	0.1968
Res 6 groups	213	25.5553	0.1200		
Res 3 groups	216	26.1216			

The LAE estimation using LAI^2 and the grouped treatments could explain 25 and 21 percent of the variation and showed RMSEs of ± 67 and 66 percent (Table 5.9).

Since treatment is a very general dummy variable including a lot of stand characteristics it was tried to substitute by the logarithm of the SDI. The model showed R^2 of 0.28 and 0.19 and standard error of ± 65 and 67 percent (Table 5.9).

For the next model LAI^2, ln(SDI), relative height and the competition factor of JOHANN (A_{Johann}) were used as independent variables. The model seemed to be better than former models with R^2 of 0.42 and 0.39 percent and RMSEs of ± 59 and 58 percent. The problem was that as soon the relative height was added to the model, LAI^2 lost its significance (Table 5.9), which means that LAI^2 and h_{rel} are highly intercorrelated.

Because of the fact that LAI^2 is needed for the following calculations, the model with LAI^2 and ln(SDI) as independent variables was chosen to estimate the leaf area efficiency.

Table 5.9: *Parameter table for the relationship between basal area increment per leaf area (BAI/LA) [dm^2/m^2/year] and volume increment per leaf area (VI/LA) [dm^3/m^2/year] to leaf area index (LAI) [m^2/m^2], treatment method (TREAT), natural logarithm of stand density index (SDI), relative height (h_{rel}) [m/m], competition index (A_{Johann}).*

Dependend Variable	Independent Variable	n	R^2	RMSE	RMSE%	F	P > F	Parameter	Estimate	SE	t	P > |t|
BAI/LA	Intercept	217	0.05	0.40	74.5	12.70	0.0005 ***	a0	0.5755	0.0291	19.80	<.0001 ***
	LAI²							a1	-4.88E-07	1.37E-07	-3.56	0.0005 ***
BAI/LA	Intercept	217	0.29	0.35	64.6	15.45	<.0001 ***	a0	0.7018	0.0309	22.71	<.0001 ***
	LAI²							a1	-5.90E-07	1.22E-07	-4.83	<.0001 ***
	TREAT							TREAT A	-0.1503	0.0455	-3.30	0.0011 **
								TREAT B	-0.2626	0.0595	-4.42	<.0001 ***
								TREAT C	-0.1617	0.0484	-3.34	0.001 ***
								TREAT D	0.5390	0.0996	5.41	<.0001 ***
								TREAT E	0.3237	0.0718	4.51	<.0001 ***
								TREAT F	-0.2880	0.0594	-4.85	<.0001 ***
BAI/LA	Intercept	217	0.28	0.35	64.9	29.12	<.0001 ***	a0	0.6760	0.0328	20.59	<.0001 ***
	LAI²							a1	-5.599E-07	1.199E-07	-4.67	<.0001 ***
	TREAT							TREAT ABC	-0.1528	0.0357	-4.28	<.0001 ***
								TREAT DE	0.4157	0.0499	8.33	<.0001 ***
								TREAT F	-0.2629	0.0486	-5.41	<.0001 ***
BAI/LA	Intercept	217	0.27	0.35	65.3	41.3	<.0001 ***	a0	5.2933	0.5813	9.11	<.0001 ***
	LAI²							a1	-6.01E-07	1.21E-07	-4.98	<.0001 ***
	ln(SDI)							a2	-0.6635	0.0817	-8.12	<.0001 ***
BAI/LA	Intercept	217	0.41	0.32	58.7	38.7	<.0001 ***	a0	4.1962	0.5440	7.71	<.0001 ***
	LAI²							a1	8.14E-08	1.48E-07	0.55	0.5826
	ln(SDI)							a2	-0.5966	0.0749	-7.97	<.0001 ***
	hrel							a3	0.7899	0.1315	6.01	<.0001 ***
	AJohann							a4	-0.0010	0.0005	-2.14	0.0331 *
VI/LA	Intercept	217	0.12	0.36	69.3	30.48	<.0001 ***	a0	0.5666	0.0259	21.87	<.0001 ***
	LAI²							a1	-6.74E-07	1.22E-07	-5.52	<.0001 ***
VI/LA	Intercept	217	0.21	0.34	65.8	10.40	<.0001 ***	a0	0.6258	0.0301	20.76	<.0001 ***
	LAI²							a1	-7.08E-07	1.19E-07	-5.95	<.0001 ***
	TREAT							TREAT A	-0.1090	0.0444	-2.45	0.0149 *
								TREAT B	-0.1704	0.0580	-2.94	0.0037 **
								TREAT C	-0.0174	0.0472	-0.37	0.713
								TREAT D	0.2087	0.0972	2.15	0.0329 *
								TREAT E	0.2429	0.0701	3.47	0.0006 ***
								TREAT F	-0.1548	0.0580	-2.67	0.0082 **
VI/LA	Intercept	217	0.20	0.34	66.0	19.1	<.0001 ***	a0	0.6224	0.0320	19.44	<.0001 ***
	LAI²							a1	-7.15E-07	1.17E-07	-6.11	<.0001 **
	TREAT							TREAT ABC	-0.0847	0.0348	-2.43	0.0158 *
								TREAT DE	0.2360	0.0487	4.85	<.0001 ***
								TREAT F	-0.1513	0.0474	-3.19	0.0016 **
VI/LA	Intercept	217	0.19	0.35	66.7	25.54	<.0001 ***	a0	2.9900	0.5691	5.25	<.0001 ***
	LAI²							a1	-7.32E-07	1.18E-07	-6.19	<.0001 ***
	ln(SDI)							a2	-0.3408	0.0800	-4.26	<.0001 ***
VI/LA	Intercept	217	0.38	0.30	58.1	34.37	<.0001 ***	a0	1.8164	0.5159	3.52	0.0005 ***
	LAI²							a1	5.14E-08	1.40E-07	0.37	0.7144
	ln(SDI)							a2	-0.2534	0.0710	-3.57	0.0004 ***
	hrel							a3	0.7531	0.1247	6.04	<.0001 ***
	AJohann							a4	-0.0017	0.0005	-3.78	0.0002 ***

AAE was then calculated by multiplying LAE with LAI. AAE then shows an optimum curve over the LAI which is shown in Figure 5.17 using the basal area increment and Figure 5.18 using the volume increment both for constant SDI values. The efficiencies are increasing with decreasing SDI. Also with decreasing SDI the optimum is shifting to the upper right side. So for a given SDI of 1400 the optimum leaf area index is 520 m^2/m^2 and for a SDI of 400 LAI_{opt} is 855 m^2/m^2.

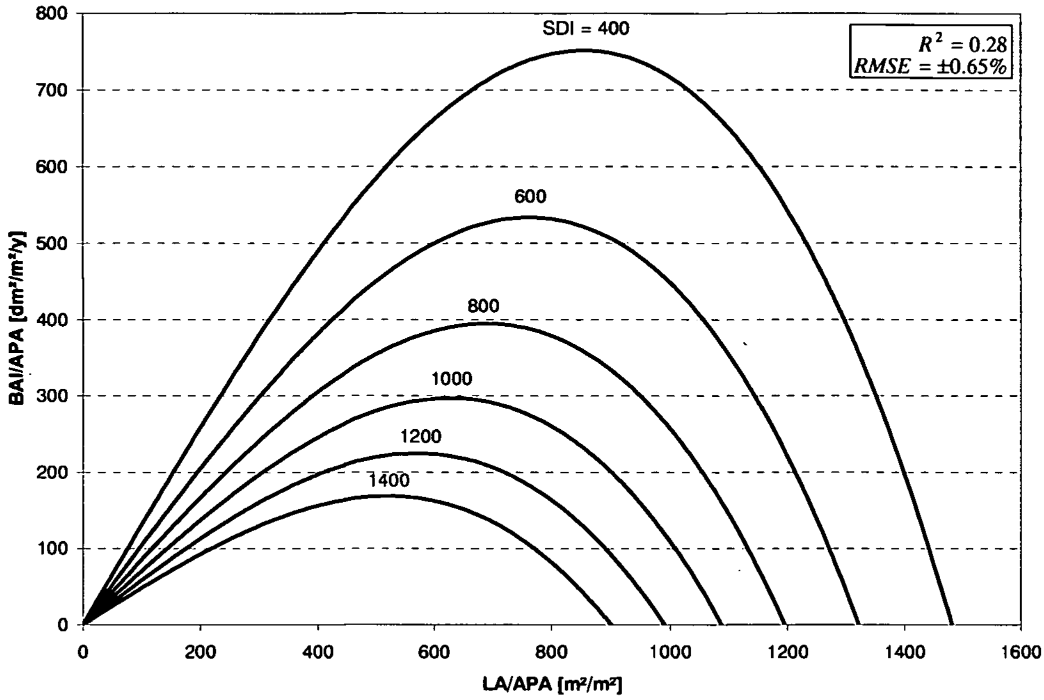


Figure 5.17: *Annual basal area increment per area potentially available (BAI/APA) [$dm^2/m^2/year$] to leaf area per area potentially available (LA/APA) [m^2/m^2] model for stand density index (SDI) from 400-1400.*

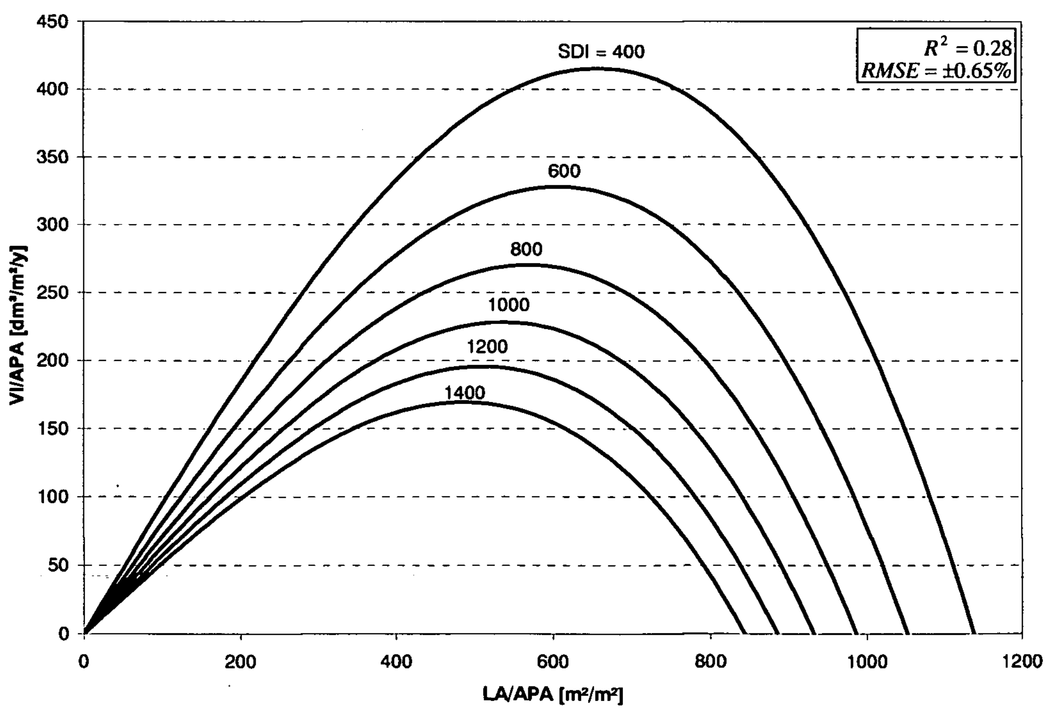


Figure 5.18: *Annual volume increment per area potentially available (VI/APA) [$dm^3/m^2/year$] to leaf area per area potentially available (LA/APA) [m^2/m^2] model for stand density index (SDI) from 400-1400.*

5.5.3 Comparison of the optimum leaf area index - direct vs. indirect method

The optimum leaf area index, defined as the ratio between leaf area and area potentially available, varies pretty strong depending on the method. For the direct method its value scatters between 673 and 744 m^2/m^2 for indirect method between 487 and 855 m^2/m^2. So the general borders for all data (SDI=mean for indirect method) ranges from 504 and 744 m^2/m^2 which is a difference of 240 m^2/m^2 (Table 5.10).
BAI/APA calculated with its LAI_{opt} ranges between 207 and 218 dm^2/m^2/year which is just a difference of 11 dm^2/m^2/year. VI/APA calculated with its optimal leaf area index ranges between 124 and 187 dm^3/m^2/year which is a difference of 63 dm^3/m^2/year (Table 5.10).
The models are shown in Figure 5.19 for the BAI/APA in dark and VI/APA in light colors.

Table 5.10: *Optimum leaf area index (LAI_{opt}) [m^2/m^2], annual basal area increment per area potentially available (BAI/APA) [dm^2/m^2/year] and annual volume increment per area potentially available (VI/APA) [dm^3/m^2/year] for direct and indirect method. Indirect method with stand density index (SDI) set to mean (1258), 400 and 1400.*

		indirect SDI		
	direct	**mean**	**400**	**1400**
LAIopt [m^2/m^2] for BAI/APA	743.67	556.35	855.06	519.70
VI/APA	673.23	503.96	657.15	487.20
BAI/APA [dm^2/m^2/year]	217.97	206.95	751.37	168.70
VI/APA [dm^3/m^2/year]	124.24	187.34	415.34	169.25

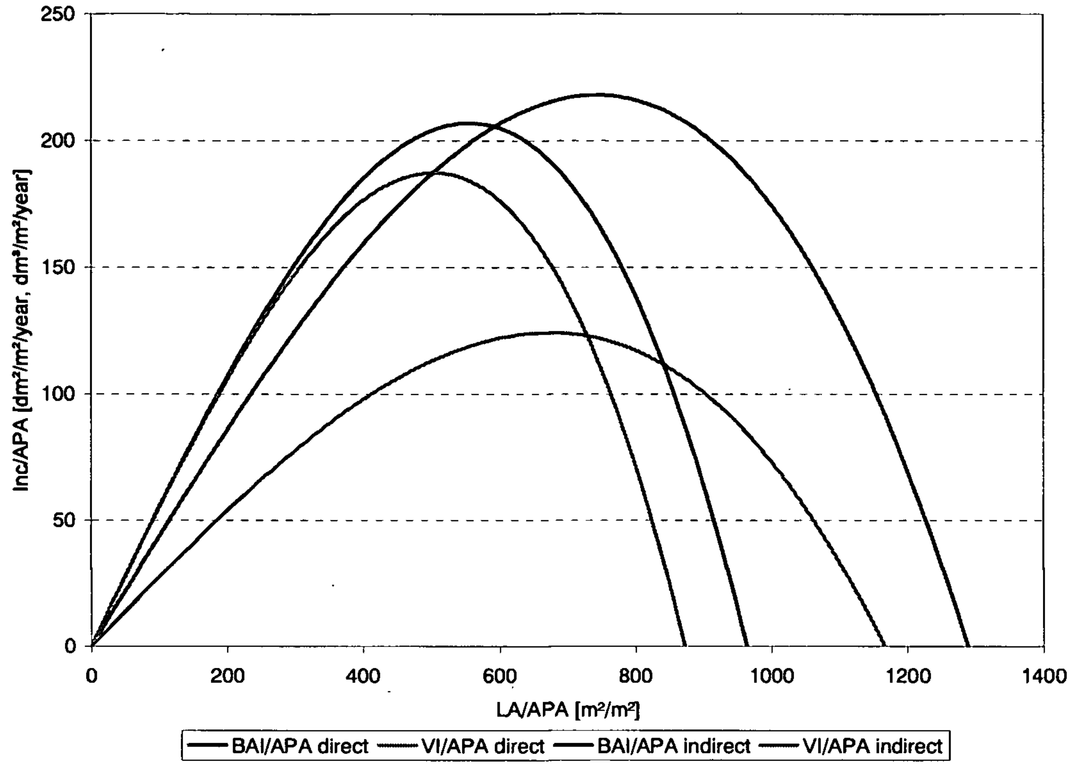


***Figure 5.19:** Annual increment per area potentially available (Inc/APA) [dm^2/m^2/year, dm^3/m^2/year] over leaf area per area potentially available (LA/APA) [m^2/m^2]. Models for BAI/APA direct, VI/APA direct, BAI/APA indirect and VI/APA indirect. Stand density index (SDI) set to mean (1258) for indirect models.*

5.6 Available area efficiency in relation to leaf area index without optimum

The available area efficiency was estimated using a power model. The influence of leaf area index, relative height, stand density index, quadratic mean diameter and competition index A_{Johann} was analyzed. Quadratic mean diameter and A_{Johann}-value had no significant influence to the model, so AAE_{BAI} was estimated with equation 5.1 and AAE_{VI} with equation5.2.

$$\frac{BAI}{APA} = 4577.18 \cdot LAI^{0.8867} \cdot h_{rel}^{1.4073} \cdot SDI^{-1.2229} \quad 5.1$$

$$\frac{VI}{APA} = 332.90 \cdot LAI^{0.8108} \cdot h_{rel}^{1.7820} \cdot SDI^{-0.8155} \quad 5.2$$

The model to predict AAE_{BAI} was able to explain 59 percent of the variation. The AAE_{VI} prediction model had a R^2 of 0.57 (Table 5.11).

For both increments, AAE was found to increase with increasing leaf area index and relative height (Figure 5.20 and Figure 5.22), but decreasing with increasing stand density index (Figure 5.21 and Figure 5.23).

***Table 5.11:** Parameter table for the relationship between the natural logarithm of basal area increment per area potentially available (BAI/APA) [$dm^2/m^2/year$] and the natural logarithm of volume increment per area potentially available (VI/APA) [$dm^3/m^2/year$] to the natural logarithm of leaf area index (LAI) [m^2/m^2], the natural logarithm of relative height (h_{rel}) [m/m], the natural logarithm of stand density index (SDI).*

Dependend Variable	Independent Variable	n	R²	RMSE	F	P > F		Parameter	Estimate	SE	t	P > |t|	
ln(BAI/APA)	Intercept	205	0.58	1.07	95.0	<.0001	***	a0	8.4288	1.7929	4.70	<.0001	***
	ln(LAI)							a1	0.8867	0.0567	15.64	<.0001	***
	ln(hrel)							a2	1.4073	0.3039	4.63	<.0001	***
	ln(SDI)							a3	-1.2229	0.2553	-4.79	<.0001	***
ln(VI/APA)	Intercept	209	0.57	1.00	91.6	<.0001	***	a0	5.8078	1.6754	3.47	0.0006	***
	ln(LAI)							a1	0.8108	0.0491	16.52	<.0001	***
	ln(hrel)							a2	1.7820	0.2354	7.57	<.0001	***
	ln(SDI)							a3	-0.8155	0.2380	-3.43	0.0007	***

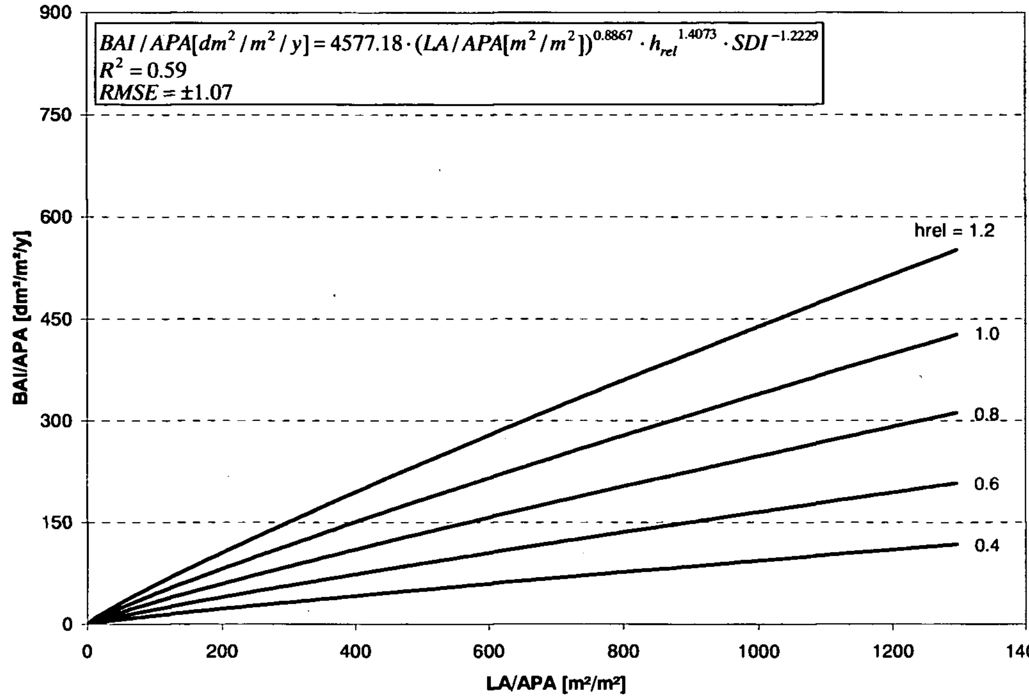


Figure 5.20: *Annual basal area increment per area potentially available (BAI/APA) [$dm^2/m^2/year$] to leaf area per area potentially available (LA/APA) [m^2/m^2] model for relative heights (h_{rel}) from 0.4-1.2 m/m. Stand density index (SDI) set to its mean value.*

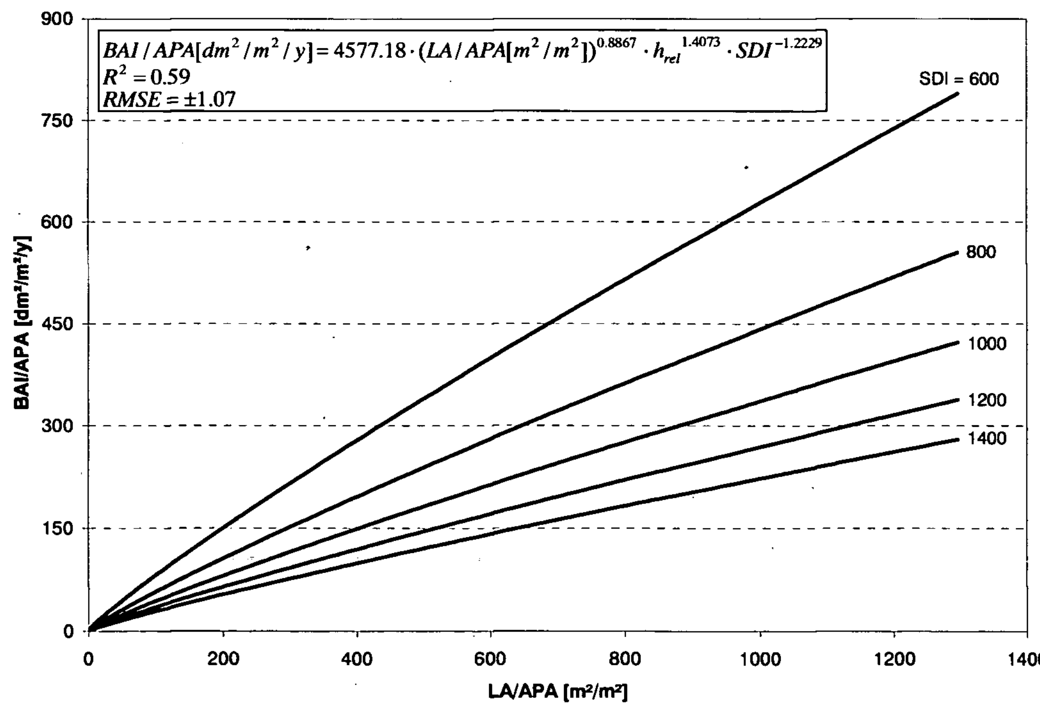


Figure 5.21: *Annual basal area increment per area potentially available (BAI/APA) [$dm^2/m^2/year$] to leaf area per area potentially available (LA/APA) [m^2/m^2] model for stand density index (SDI) from 400-1400. Relative height (h_{rel}) [m/m] set to its mean value.*

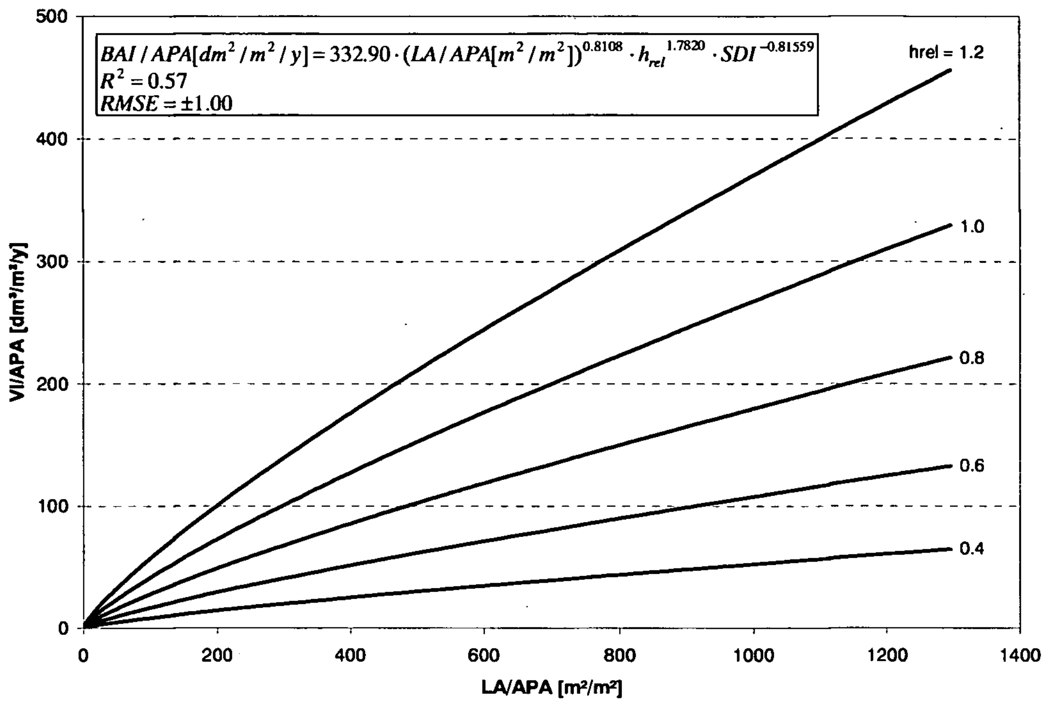


Figure 5.22: *Annual volume increment per area potentially available (VI/APA) [dm^3/m^2/year] to leaf area per area potentially available (LA/APA) [m^2/m^2] model for relative heights (h_{rel}) from 0.4-1.2 m/m. Stand density index (SDI) set to its mean value.*

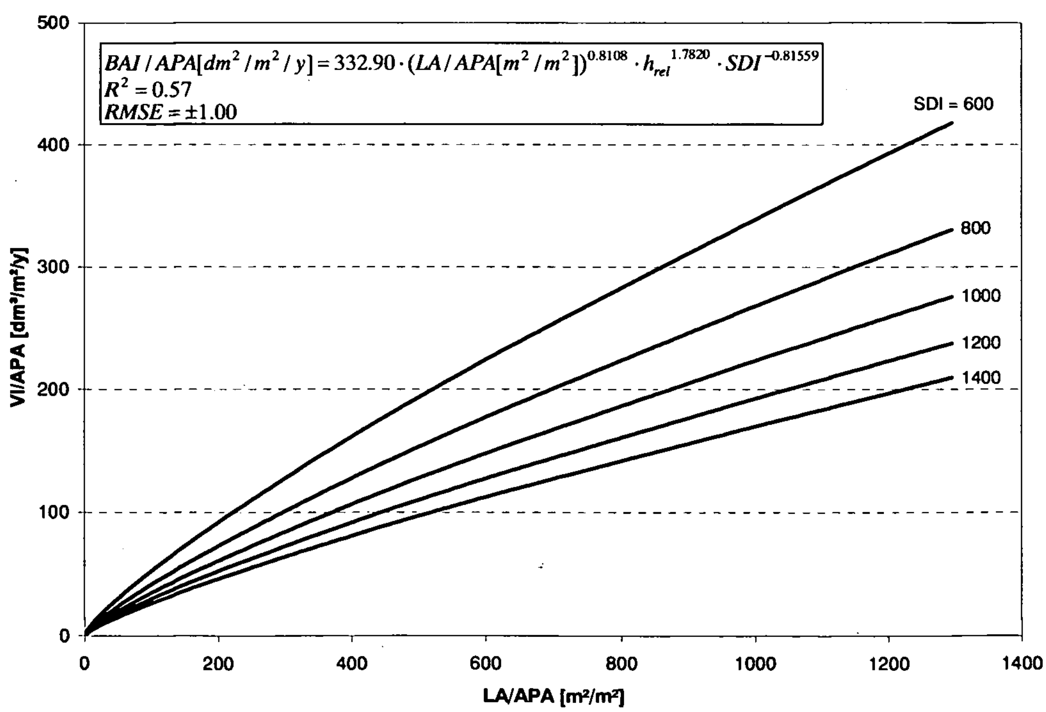


Figure 5.23: *Annual volume increment per area potentially available (VI/APA) [dm^3/m^2/year] to leaf area per area potentially available (LA/APA) [m^2/m^2] model for stand density index (SDI) from 400-1400. Relative height (h_{rel}) [m/m] set to its mean value.*

6 Discussion

First it has to be mentioned that this study is based on some basic assumptions. The exact coordinates of the multiple stems were estimated using realistic guidelines, the volume equation had to be extrapolated to the lower end, and the sapwood area for trees smaller than 5 cm was assumed to equal the basal area (without bark). Despite these assumptions most of the analyzed relationships could be statistically ensured and led to reasonable and interpretable conclusions. However calculations using the basal area are supposed to be more accurate than those using the volume.

6.1 Increment and Leaf area efficiency

The strong relationship between increment and leaf area corresponds to the investigations of BERRILL & O'HARA (2007) for even-aged and multi-aged coast redwood. In their study, the trees were subdivided into 3 strata (A-stratum, emergent trees; B-stratum, main canopy and C+D-strata, understory trees). The B-stratum was further subdivided into crown classes (dominant, codominant, intermediate and suppressed). This led to a prediction of VI using LA with R^2 between 0.50 and 0.85. Using the relative height as additional independent variable led to even greater R^2 of 0.91 for VI prediction in the present study. Increment (whether basal area increment or volume increment) showed to increase with increasing leaf area.
Increasing leaf area efficiency with increasing leaf area corresponds to the pattern C of SEYMOUR & KENEFIC (2002). Pattern C is described as a short version of pattern B which is assumed to describe shade-tolerant species. When the stand is still young, the LAE does not show a peak, which leads to pattern C. The shade-tolerant species coast redwood in a 28 year old stand (analyzed in this study) is exactly following this pattern (Figure 2.1).
Although MAINWARING & MAGUIRE (2004) analyzed LAE for two shade-intolerant species (ponderosa pine and lodgepole pine) which led to generally decreasing LAE over LA, LAE maintained moderate values with increasing LA. The models for LAE_{VI} showed just a slightly increase for leaf area measures higher than 300 m^2 and for LAE_{BAI} just a slightly decrease, which could lead to the same statement.
While the leaf area efficiency in the general model is increasing with increasing leaf area, LAE_{BAI} is decreasing when the relative height is held constant. Greater relative height led to

greater leaf area efficiency. The same pattern seems to be generally accepted for the crown efficiency (STERBA 2005), where CE is decreasing in between crown classes.
The fact that LAE_{BAI} is decreasing with h_{rel} held constant while LAE_{VI} is increasing could be explained with the basic assumptions of this study. The main difference in the models for LAE_{BAI} and LAE_{VI} is found in the leaf areas, where two assumptions are made. The extrapolation of the volume increment and the assumption that the sapwood area consists of the whole basal area minus the bark for small trees. As only one of these assumption is valid for the LAE_{BAI} model, it should be more accurate.

6.2 Increment and Available area efficiency

Increment prediction using the area potentially available seems to be suboptimal in comparison to the leaf area due to lower R^2 of 0.62 and 0.71 (for BAI and VI respectively). However these values seem to be higher than calculated for hemlock, red maple, sugar maple and yellow birch with R^2 between 0.25 and 0.51 (WEBSTER & LORIMER 2002).
AAE is declining in a negative exponential fashion with increasing APA which was also found for ponderosa pine and lodgepole pine (MAINWARING & MAGUIRE 2004) and hemlock, red maple, sugar maple and yellow birch (WEBSTER AND LORIMER 2002).
The fact that AAE is increasing with increasing relative height would mean that trees in a good social position with less APA are most efficient.

6.3 Available area efficiency and leaf area index with optimum

The comparison of the indirect to the direct method shows that the indirect method tends to give lower estimates but also lower differences between the optimum AAE_{BAI} and AAE_{VI}.
The observed mean value for AAE_{BAI} with 47.2 dm^2/m^2/year is way lower than the estimated optimal range between 207 and 218 dm^2/m^2/year. This means that most trees in the plots can not reach their full efficiency because either their area potentially available is too small or their leaf area is too great. However there are some trees present which are most efficient because the maximum of the observed AAE_{BAI} is with 291 dm^2/m^2/year (outliers excepted) in between the estimated optimum of the two methods.
The same is valid for the observed mean for AAE_{VI} with 66.93 dm^3/m^2/year. It is smaller than the estimated range between 124 and 187 dm^3/m^2/year which leads to the same conclusion as

above. However the observed maximum of AAE_{VI} is with 341 dm^3/m^2/year about double as high as the range, which would lead to the conclusion that more trees are most efficient than examined using AAE_{BAI}.

However since volume was calculated by extrapolating the volume function to the lower side, it is the basal area increment which should be more accurate.

The observed mean value for AAE_{BAI} is lower than the estimated optimum range, which would lead to the conclusion that the leaf area index should be higher to get more efficient trees. The only variable in the leaf area index that is manageable is the area potentially available. In order to increase the leaf area index the area potentially available should become smaller. So more trees per hectare or lighter thinnings should lead to more efficient trees.

In general it could be shown that there is an optimum individual tree leaf area index and a corresponding maximum area available efficiency. Although the direct model shows higher coefficients of determination, it is not recommended since the higher accuracy is just pretended because the variable APA appears on both sides of the model function. However the indirect model confirmed the theory of an optimum individual tree leaf area index.

The fact that treatment had a highly significance to the model showed that the thinning in 1997/98 still effects the current efficiencies.

6.4 Available area efficiency and leaf area index without optimum

Available area efficiencies calculated with equations that do not allow an optimum are showing higher coefficient of determinations (0.58 and 0.57 respectively). Their importance though is doubtful, because they do not follow physical rules. It would not make sense that the available area efficiency would increase till infinity because with constant APA and increasing leaf area there will be a point where more leaf area will not lead to a higher efficiency because of biological limitations, and the available area efficiency will then start to decrease.

Only the assumption that the optimum is outside the data range would make this method reasonable.

7 Conclusions

- Basal area increment and volume increment were best explained by the leaf area. The relative height was found to have a highly significant influence and could enhance the model.
- The area potentially available was less powerful in comparison with the leaf area concerning the ability to predict basal area increment and volume increment. However the given models showed higher coefficients of determination than published studies so far.
- The model for leaf area efficiency could confirm the pattern C of the 3-pattern-model of SEYMOUR & KENEFIC (2002) which predicts increasing leaf area efficiency with increasing leaf area and no optimum (for young stands) (Figure 2.1).
- The leaf area efficiency maintained moderate values for trees with a leaf area of more than 300 m^2.
- The leaf area efficiency of the general model is increasing with increasing leaf area, while it is decreasing within a given social position (relative height held constant).
- The efficiency of the area potentially available is declining in a negative exponential fashion with increasing area potentially available.
- Trees in a good social position with a small area potentially available are most efficient.
- The treatment as dummy variable still has a significant influence when estimating the leaf area efficiency.
- The theory of an optimum tree leaf area index could be confirmed. Lower stand density index led to higher available area efficiencies.

8 List of tables

9 List of figures

10 References

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