GROWTH EFFICIENCY OF *PINUS RADIATA* STAND ELEMENTS: IMPLICATIONS FOR STAND GROWTH MODELLING STRATEGIES

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ABSTRACT

Individual tree growth rates and growth efficiencies were assessed for different stand elements from *Pinus radiata* D. Don pruning trials in New Zealand. Growth rates were higher for non-crop elements, but crop elements had significantly higher rates of efficiency (basal area increment per unit of crown length or per unit of sapwood cross-sectional area at crown base (as a representation of leaf area)). Sapwood basal area was more strongly related to tree basal area increment than to measured crown length, indicating it may be a better measure of crown size in growth models and in measures of crown growth efficiency. Weak correlations between plot basal area increment and average crown length per tree indicated that the primary effect of crown length per hectare on basal area increment was through its relationship to stocking density rather than crown length. Inclusion of a growth efficiency variable in the EARLY growth model resulted in some minor improvements to the model for productive farm sites, but not for less-productive pumice forest sites. Future modifications which may enhance the EARLY model might include adding calliper cross-sectional area at crown base as a production variable to represent leaf area.

Keywords: growth efficiency; growth modelling; pruning; plantation management; *Pinus radiata*.

INTRODUCTION

Measures of crown size are frequently used in stand growth and yield models to enhance the prediction of stand growth and increment. They are particularly useful for capturing the effects of silvicultural treatments such as pruning. Ideally, crown size should be relatively easy to measure in the field. The utility of any crown measure is therefore its ability to simultaneously enhance growth prediction and provide ease of measurement. Crown length is probably the easiest crown parameter to measure in the field. For young *Pinus radiata*

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plantations, cumulative crown length per hectare is used to predict stand volume increment in the EARLY growth model (West *et al.* 1982, 1987; Knowles & West 1986). Use of crown length per hectare is based on the assumption that the crown productivity of plantation-grown *P. radiata* trees is sufficiently uniform both within and between trees to mean that stand growth is not greatly affected by different combinations of tree stocking and average crown length for a given total crown length per hectare. However, this assumption has been tested only with stand-level comparisons where the growth differences between individual crowns of various lengths may be concealed (Knowles & West 1986).

In a typical New Zealand *P. radiata* plantation management regime, repeated selective pruning may result in a single stand having trees with three or more different crown lengths, or stand elements (Knowles 1995). The use of crown length per hectare as a driving variable in growth models assumes that increment in basal area varies at a constant rate per unit of crown (West *et al.* 1982; Knowles & West 1986). However, there may be variation in increment per crown length between different trees, leading to significant variation in basal area increment per hectare between stands with different crown structures. A typical stand may have an average cumulative crown length that corresponds to the average rate of increment. Alternatively, some plantation structures may diverge from the "typical" structure and have larger or smaller average crown lengths and rates of increment. Given data sets with mostly "typical" plantation structures, or plantations with compensating numbers of long or short average crown lengths, it is possible that a plantation-level modelling approach may not recognise these differences in structure. An individual tree-level analysis may reveal patterns in tree increment per crown length that could identify potential biases in plantation-level growth prediction. It is also possible that tree increment is not sufficiently related to crown length and some other measure of crown size would produce more accurate predictions of growth.

There is evidence which suggests tree increment per crown length (crown length efficiency) may not be constant for trees pruned to different heights. O'Hara (1991) summarised a series of studies that reported no, or a slight positive, effect of light pruning on increment, suggesting lower branches on some trees were not making important contributions to stand increment. Among these studies was Sutton & Crowe's (1975) *P. radiata* study which reported a 10% increase in basal area increment with a single 20% crown length removal treatment. Additionally, studies of photosynthate production and transport from individual branches have found lower branches produce low amounts of photosynthate and may export none to the stem (Woodman 1971; *see also* Sprugel *et al.* 1991). Measures of growth or crown efficiency (ratios of increment per unit crown size) may therefore be useful indices of differential growth between stand elements.

An alternative variable used in stand and tree increment studies is leaf area. Leaf area is a more difficult crown parameter to measure than crown length, but is an accepted standard for representation of crown size and photosynthetic potential (Vose *et al.* 1994; Waring & Running 1998). Leaf area can be indirectly estimated for individual trees through allometric relationships with sapwood cross-sectional area at the base of the crown (Waring *et al.* 1982; Margolis *et al.* 1995) although these relationships have been found to vary with geographic region, stand density, crown position, and sapwood permeability in some studies (*see* Margolis *et al.* 1995). Correlations between leaf area and tree increment are generally high, particularly for trees in even-aged, single-species stands (Waring *et al.* 1980; Gilmore &

Seymour 1996) but also in mixed-species (O'Hara *et al.* in press) and multi-aged stands (O'Hara 1996). A strong relationship between crown length and leaf area would provide additional support for the use of crown length as a driving variable in the EARLY growth model.

This study used existing data collected from New Zealand *P. radiata* permanent sample plots to examine individual tree increment in relation to crown size, and stand increment in relation to crown structure parameters. Study objectives were to compare tree increment per crown length and per sapwood cross-sectional area at crown base (to represent leaf area) as measures of growth (crown) efficiency and to assess the efficacy of these measures for stand-level growth prediction.

DATA SETS AND METHODS

Individual-tree Data

Permanent sample plot (PSP) data from a *P. radiata* "followers" trial (Dipton FR195) and three "second-log" pruning trials (Ngaumu FR201, Waiotahi FR243, and Otago Coast FR-247) were used. Location, date planted, site, measurement intervals, and mean tree sizes for these trials are given in Table 1. The followers trial was designed to assess the effect of non-crop "followers" on the growth of the crop tree element on farm sites. Followers are the stand elements which may be unpruned or partially pruned, but are carried along with the fully-pruned element until a later thinning.

TABLE 1–Location, site, and average tree characteristics of data sets used for analysis. Dbh and height are mean sizes at end of measurement interval.

Data set	Name	Lat., long.	Site Index (m @ 20 yr)	Date planted	Measurement interval	dbh (cm)	Height (m)
FR195	Dipton	45°48'S, 168°24'E	27.5	1987	8/95 – 5/97	22.4	12.0
FR201A	Ngaumu A	40°50'S, 176°10'E	30	1985	2/95 – 11/96	29.3	15.5
FR201B	Ngaumu B	40°50'S, 176°10'E	30	1985	10/95 – 11/96	29.5	16.1
FR243	Waiotahi	38°1'S, 177°13'E	36	1988	5/95 – 5/96	26.0	14.9
FR247	Otago	45°58'S, 170°11'E	27	1986	5/95 – 10/96	25.1	13.4

Treatments in the followers trial compared the number of followers per hectare and the timing of thinnings. Treatments consisted of different stockings per hectare with equal numbers of pruned trees per plot. Pruning would eventually reach a total height of 6.5 m in three or four lifts, depending on site. Individual tree data for the most recent measurement interval included unpruned followers and trees pruned to different heights.

The "second-log" pruning trials, all on ex-farm sites, were designed to monitor the effect of pruning above 6.0 m on tree growth and log quality. Three measurements at Ngaumu provided two different measurement intervals from two sets of plots; these two sets were analysed separately, giving five data sets. Treatments on the second-log pruning trials varied the final plot stocking, the residual (post-pruning treatment) crown length, and the final pruning height. The effect of these variables was to create alternative pathways for total crown length per hectare towards a series of different final crown lengths per hectare (M. Dean unpubl. data).

The three second-log pruning trials were established in 1993 and 1995 and were still receiving treatments to meet their final pruned height objective when this analysis was conducted. Because measurements were taken in conjunction with pruning treatments, the measurement intervals correspond to the periods between prunings. Plots not pruned at a scheduled entry were not measured at that entry. As a result, data for plots receiving less-severe pruning treatments were less common in the analysed data sets than they were in the design of the trials. Additionally, because pruning schedules were not all completed, actual pruning heights were considerably less than the target pruned heights.

Measurements included diameter at breast height (dbh), total height, internode diameter measured 0.3 m below base of crown—below branch swelling), and pruning height. Only trees with at least one internode (calliper) measurement at the beginning of the measurement interval period were used for this analysis. Few calliper measurements were taken on the unpruned (follower) element. All unpruned followers were assumed to have crown heights of 1 m which was the crown height of unpruned followers that were measured.

Stem volume was estimated by dividing individual trees into three segments: the top, which included the stem above the calliper measurement; the middle, from breast height to the calliper measurement; and the bottom, below breast height. The top and bottom sections were assumed to be represented by geometric solids; the top was assumed to be a cone, and the bottom a cylinder. The volume of the middle section was estimated with a generalised log volume equation (using pruning height less 1.4 m, dbh, and calliper diameter) developed for *P. radiata* and other species in New Zealand (Ellis 1982).

Basal area increment and volume increment were the differences in basal area and volume at each measurement. Basal area was the preferred measure of increment for all analyses. However, volume increment was also estimated to include the effects of second-log pruning on stem form. Volume increment could be estimated only on trees which received multiple calliper measurements.

Sapwood cross-sectional area (SBA) at base of the crown was used to represent leaf area in all analyses because of the linear allometric relationships commonly observed between SBA and leaf area in many conifer species (Waring *et al.* 1982; Margolis *et al.* 1995) including *P. radiata* (Whitehead *et al.* 1990). SBA was calculated from calliper measurements with basal area at crown base reduced by the estimated bark thickness (Gordon 1983). All trees in the present study were assumed to have no heartwood at the crown base. Heartwood formation has been reported to begin at about age 12–14 in New Zealand *P. radiata* from the base of the tree upward (Cown *et al.* 1991). Since the trees used in this study were 11 years old or less at their final measurement, it is unlikely any heartwood had formed at crown base by the beginning of the measurement period.

Measures of individual tree crown size were assumed to be continuous variables within treatments. Analysis of variance and Newman-Keuls multiple comparison tests were used to compare mean basal area increment and tree efficiency values with increment as the total for the measurement period (Table 1). Regression analysis was used to assess individual tree relationships between different treatments within and between study areas. Adjusted coefficients of determination (r^2), standard errors, and analysis of residuals were the primary criteria for model comparisons. Data from the Dipton followers trial were used to test the hypothesis that elements would have equal tree growth efficiencies. Individual tree growth efficiencies were ratios of tree basal area increment to crown size as represented by crown length or SBA.

Stand-level Data

The original plot data used in development of growth functions for the EARLY model were used in this analysis to examine the potential for including a variable to represent growth efficiency. The data used in EARLY have been described previously by West *et al.* (1982, 1987) and Knowles & West (1986), and were subdivided by site quality in the same manner as in previous analyses (West *et al.* 1982, 1987)—high-productivity farm sites, medium-productivity pumice soil forest sites, and low-productivity forest sites. Only the data from high-productivity farm sites and pumice soil forest sites were used in these analyses.

Two types of analyses were performed on these stand-level data: (1) evaluation of the relative importance of stocking density and average crown length in affecting stand increment; and (2) evaluation of the improvement of the EARLY growth function by inclusion of a measure of average crown-length efficiency using stand growth data. Stocking density and average crown length were the two components of crown length per hectare used as a basal area increment prediction variable in EARLY (West *et al.* 1982, 1987). Linear correlation analysis was used to assess the relative contributions of different variables in affecting basal area increment of the stand-level data, multiple regression was used to include a measure of growth efficiency in a modified EARLY growth function, and the adjusted coefficient of determination and standard error were used to evaluate the modified function.

RESULTS

Individual Trees

Mean basal area increment at the Dipton followers trial was significantly higher for unpruned and partially pruned non-crop trees than for the pruned crop trees (Table 2). This

TABLE 2–Mean crown length and basal area increment by plot and stand element (sample sizes in parentheses) from the Dipton followers trial. Element 3 is the pruned crop tree element, element 2 the pruned non-crop element, and element 1 is unpruned. Crown lengths are from the beginning of the measurement interval. Common letters within treatments denote non-significantly different basal area increment means from analysis of variance and Newman-Keuls multiple comparison test for unequal sample sizes (a = 0.05). Treatments are indicated by number of followers/initial stocking (stems/ha).

Plot	Treatment	Crown length (m)			Mean basal area increment (cm^2)		
		Ele. 3	Ele. 2	Ele. 1	Ele. 3	Ele. 2	Ele. 1
5	160/410	4.5 (31)	6.2 (3)	7.7 (5)	173.8(31)	220.6(3)a	258.7(5)a
9	340/590	4.5 (30)	6.5 (4)	7.3 (21)	154.8(30)	186.6(4)b	214.7(21)b
10	340/600	4.4 (30)	6.6 (5)	7.7 (24)	150.5(30)	181.1(5)	243.9(24)
12	250/510	4.2 (30)	6.6 (3)	8.2 (14)	167.2(30)	182.8(3)	240.8(14)
13	direct/350	4.6 (29)	6.4 (5)	None	195.3(29)c	239.4(5)c	None
14	250/510	4.4 (30)	6.8 (5)	8.2 (14)	160.8(30)	172.1(5)	260.8(14)
15	250/510	4.4 (30)	5.7 (3)	7.5 (15)	157.1(30)	233.0(3)d	219.5(15)d
16	377/640	4.5 (30)	7.7 (1)	7.4 (24)	140.4(30)	258.5(1)e	191.4(24)e
All	all	4.5 (240)	6.5 (29)	7.7 (117)	162.4(240)	202.7(29)	227.0(117)

pattern was consistent across all plots combined and for all individual plots except plot 13 which was a "direct" plot with no unpruned followers. Differences between mean basal area increments of unpruned and partially pruned non-crop trees were not significant for some plots, but only when sample sizes were small. Volume increment could be estimated only on the pruned crop trees because they were the only trees with multiple calliper measurements recorded.

Mean tree crown efficiency, expressed as basal area increment per metre of crown length, was highest for the pruned crop trees in every plot at Dipton and lower for the unpruned and partially pruned non-crop trees when present (Table 3). These differences were significant for every plot and for all plots combined. Similar results were found for mean tree leaf area efficiency (basal area increment per square centimetre of SBA; Table 3). Averages of all plots combined indicated that the pruned crop trees may be 25% more efficient in use of crown length than unpruned non-crop trees, and over 50% more efficient in use of SBA.

TABLE 3–Mean tree growth efficiencies by element, using basal area increment per crown length and sapwood basal area (SBA) from the Dipton followers trial. Sample sizes are in parentheses. All differences between elements were significant ($p<0.001$). Element 3 is the pruned crop tree element, element 2 the pruned non-crop element, and element 1 is unpruned. Element 2 was not included in leaf area efficiencies because no calliper measurements were collected on this element. Treatments are indicated by number of followers/initial stocking (stems/ha).

Plot	Treatment	Mean crown length Efficiency (cm^2/m)			Mean SBA Efficiency (cm^2/cm^2)	
		Ele. 3	Ele. 2	Ele. 1	Ele. 3	Ele. 1
5	160/410	38.4(31)	36.3(3)	33.4(5)	1.9(25)	1.3(5)
9	340/590	34.6(30)	28.9(4)	29.4(21)	2.1(28)	1.3(21)
10	340/600	33.9(30)	27.3(5)	31.4(24)	1.8(27)	1.2(24)
12	250/510	40.0(30)	28.4(3)	29.5(14)	1.9(28)	1.2(15)
13	direct/350	42.8(29)	37.5(5)	none	2.0(24)	none
14	250/510	36.7(30)	25.9(5)	32.0(14)	1.7(21)	1.0(15)
15	250/510	35.5(30)	41.4(3)	29.2(15)	1.9(29)	1.4(15)
16	377/640	35.0(31)	33.6(1)	26.1(24)	1.9(30)	1.3(25)
all	–	37.1(241)	31.8(29)	29.6(117)	1.9(212)	1.2(120)

The relationship between the crown length and SBA of individual trees varied. In the Otago and Ngaumu A trials, which both had a limited range of crown lengths, there was no apparent relationship between crown length and SBA. For the other three trials, SBA explained from 66% to 77% of variation in crown length (Fig. 1).

In all of the trials the relationship between basal area increment and SBA was stronger than that between basal area increment and crown length (Fig. 2–6). At best, crown length explained 38.6% of the variation in basal area increment (Waiotahi, Fig. 5). In the Otago and Ngaumu A trials, which had relatively narrow ranges in crown length, there was no relationship between crown length and basal area increment. The relationship between SBA and individual tree basal area increment varied from 57.6% for the Dipton data (Fig. 2) to 21.3% for Ngaumu A (Fig. 3).

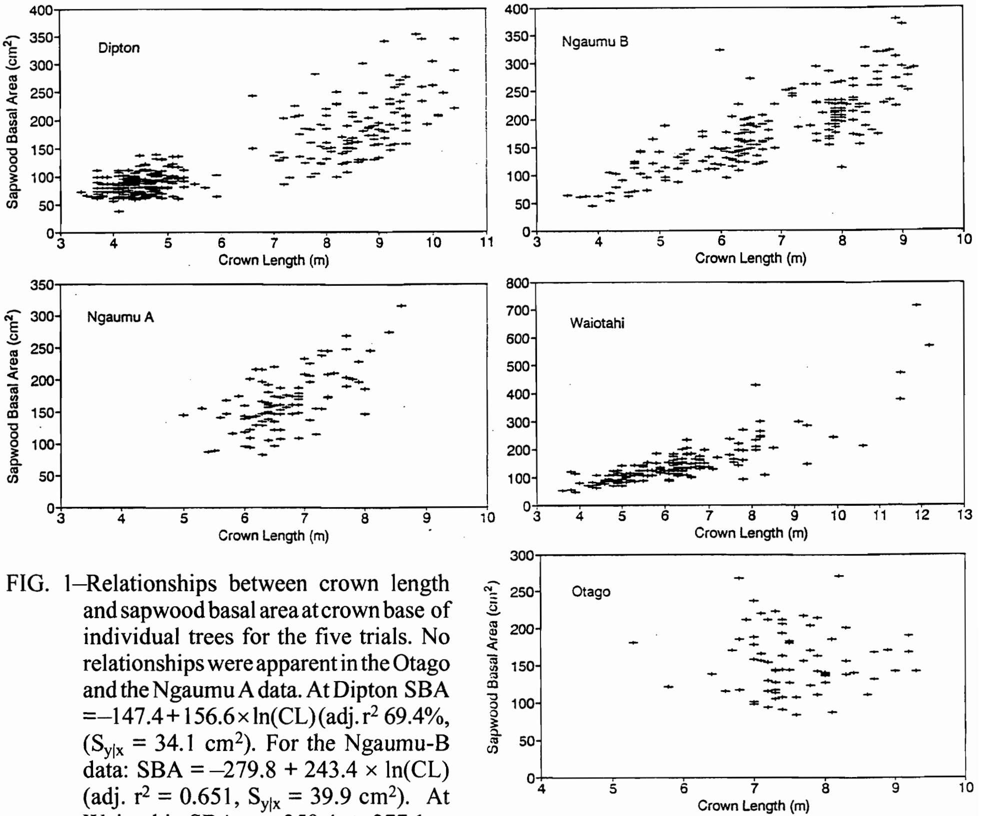

FIG. 1—Relationships between crown length and sapwood basal area at crown base of individual trees for the five trials. No relationships were apparent in the Otago and the Ngaumu A data. At Dipton SBA $= -147.4 + 156.6 \times \ln(CL)$ (adj. r^2 69.4%, ($S_{y|x}$ = 34.1 cm^2). For the Ngaumu-B data: SBA $= -279.8 + 243.4 \times \ln(CL)$ (adj. $r^2 = 0.651$, $S_{y|x} = 39.9$ cm^2). At Waiotahi: SBA $= -350.4 + 277.1 \times \ln(CL)$ (adj. r^2=0.596, $S_{y|x}$ = 53.4 cm^2). CL = crown length (m), SBA = sapwood basal area at crown base (cm^2).

Where volume increment was measured, there was no discernible difference between the trends for basal area increment and volume increment, suggesting no measurable effects of pruning and thinning on stem form using the methods of this study (Fig. 2C and 3C). Ranges of crown length for trees with volume estimates were reduced for most plots because calliper measurements were not taken on non-crop trees (e.g., comparing Fig. 2A and 2C).

Analyses of individual plots revealed patterns similar to those with all plots combined within a trial (Fig. 7 and 8): relationships between basal area increment and crown length were not as strong as those between basal area increment and SBA. Results were consistent whether basal area increment or stem volume increment was used as the dependent variable (not shown).

Stand-level Results

Pearson correlations between basal area increment, cumulative crown length, stocking density, and average crown length were used to assess the importance of cumulative crown length per hectare in affecting basal area increment on the high-productivity farm-site and the medium-productivity forest-site data. Stocking density and average crown length were

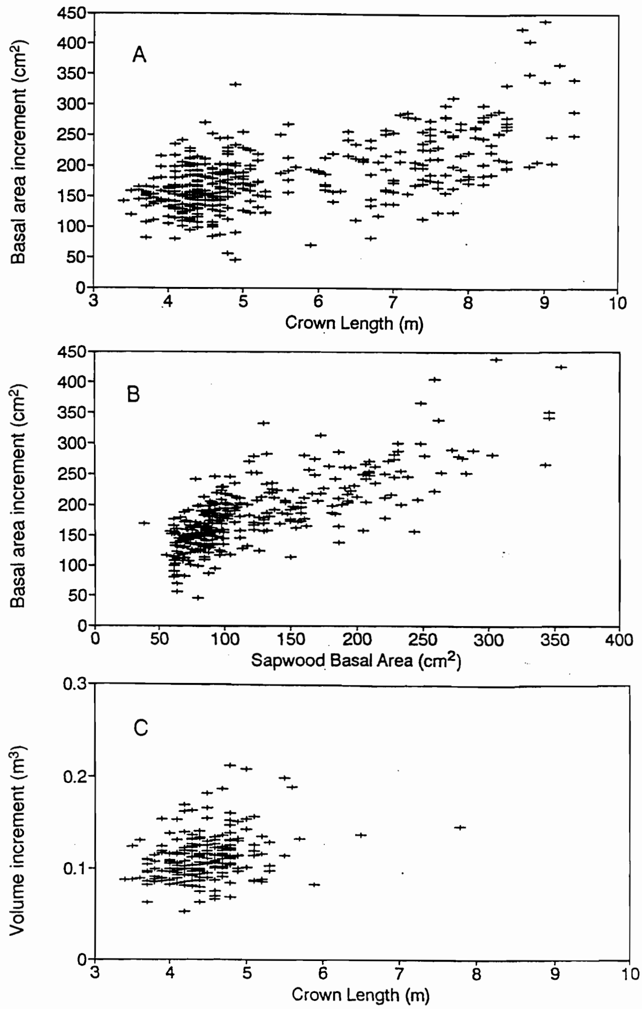

FIG. 2–Basal area increment in relation to crown length (A) and sapwood basal area at crown base (SBA) (B), and between volume increment and crown length (C), for the Dipton followers trial. Crown length (m) explained 36.3% (increment = 67.0 + 21.2 × crown length; $S_{y|x}$ = 44.7 cm^2), and sapwood basal area (cm^2) explained 57.6% (increment = 98.4 + 0.7 × SBA; $S_{y|x}$ =37.2 cm^2) of variation in basal area increment (cm^2). No relationship was found between volume increment and crown length.

assumed to represent the components of cumulative crown length. Cumulative crown length was highly correlated with increment in both data sets (Table 4). Stocking density was moderately correlated and average crown length weakly correlated with basal area increment.

Plot efficiency (basal area increment/cumulative crown length, m^2/m) was strongly negatively correlated with average crown length in both data sets, indicating the importance of the effect of average crown length on efficiency (Table 4). This demonstrates that efficiency of the residual crown on a pruned tree is greater than that of the longer crowns on

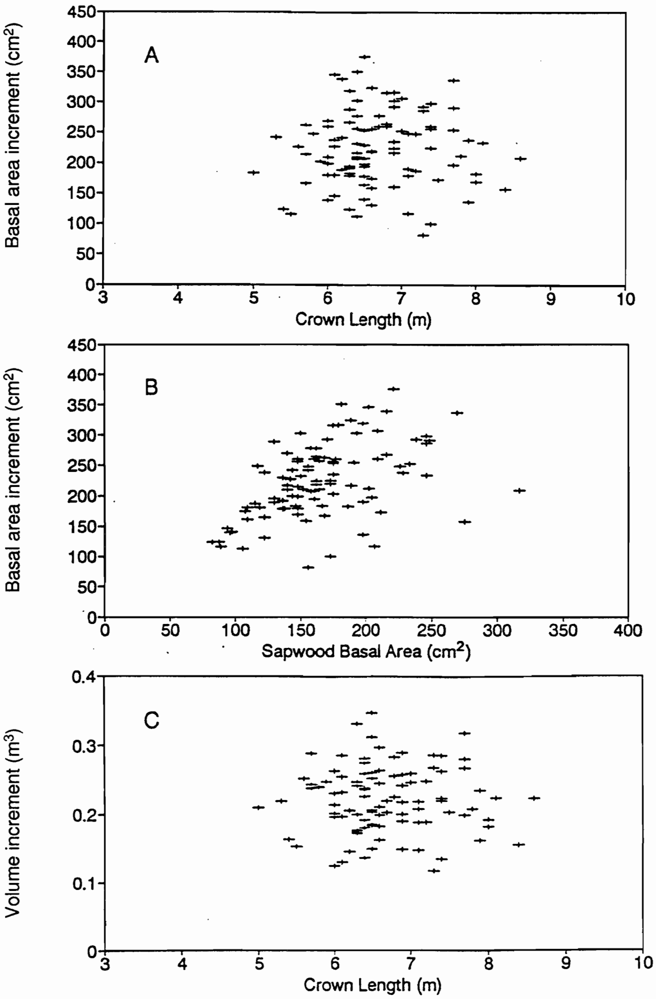

FIG. 3—Basal area increment in relation to crown length (A) and sapwood basal area at crown base (SBA) (B), and between volume increment and crown length (C), for the Ngaumu A second-log pruning trial. No relationship was found between basal area increment and crown length, or between volume increment and crown length. SBA (cm^2) explained 21.3% (increment = 114.4 + 0.7 x SBA; $S_{y|x}$ =54.5 cm^2) of variation in basal area increment (cm^2).

unpruned and partially pruned non-crop trees. However, correlations between plot efficiency and the stand variables basal area increment and crown length per hectare varied from weakly positive to weakly negative between the two data sets. These weak correlations indicate these stand-level variables fail to adequately represent tree-level variations in crown efficiency.

A function to predict basal area increment of individual trees from crown length was derived from the Dipton followers trial data. This equation (basal area increment (cm^2) = 66.97 + 21.17 × crown length (m); $S_{y|x}$ = 44.65 cm^2; r^2= 0.36) was used to estimate average

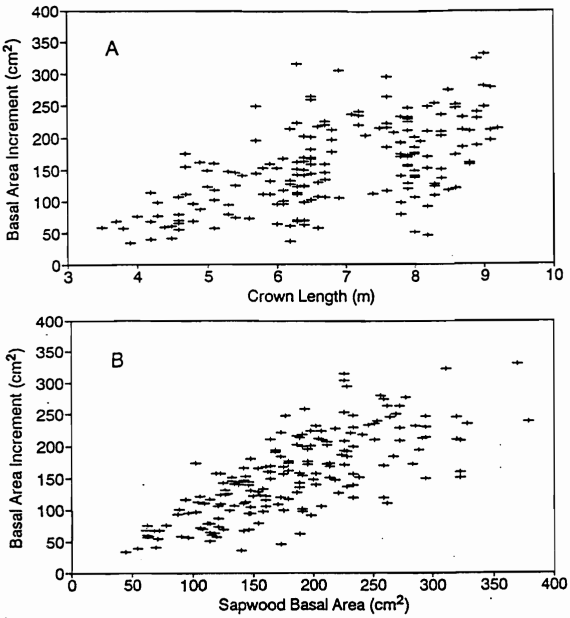

FIG. 4—Basal area increment in relation to crown length (A) and sapwood basal area at crown base (SBA) (B) for the Ngaumu B second-log pruning trial. Crown length (m) explained 33.3% (increment = –27.3 + 26.7 × crown length; $S_{y|x}$ = 53.2 cm^2), and SBA (cm^2) explained 55.7% (increment = 23.4 + 0.7 × SBA; $S_{y|x}$ = 43.4 cm^2) of variation in basal area increment (cm^2).

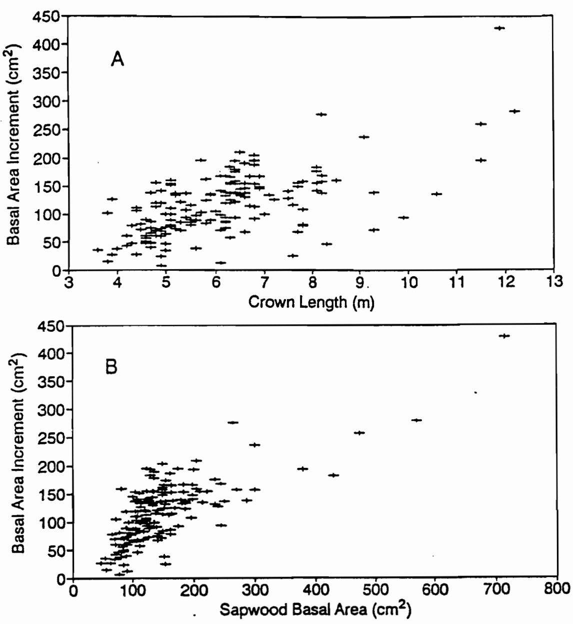

FIG. 5—Basal area increment in relation to crown length (A) and sapwood basal area at crown base (SBA) (B) for the Waiotahi second-log pruning trial. Crown length (m) explained 38.6% (increment = –22.2 + 22.6 × crown length; $S_{y|x}$ = 44.1 cm^2), and SBA (cm^2) explained 54.5% (increment = 44.2 + 0.5 × SBA; $S_{y|x}$ = 37.9 cm^2) of variation in basal area increment (cm^2).

stand basal area increment from average crown length from the farm-site and medium-site data sets. The average stand basal area increment predicted by the equation of the previous sentence was divided by average crown length to provide a measure of average tree crown length efficiency (cm^2/m). This variable was then added to the original data used to develop EARLY (West *et al.* 1982) to evaluate the utility of inclusion of a variable to represent crown

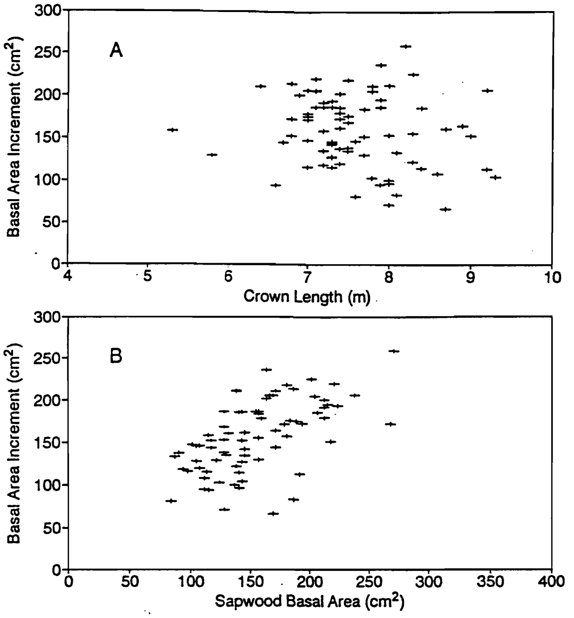

FIG. 6—Basal area increment in relation to crown length (A) and sapwood basal area at crown base (SBA) (B) for the Otago second-log pruning trial. No relationship was found between crown length and basal area increment. SBA (cm^2) explained 32.6% (increment = 66.2 + 0.6 × SBA; $S_{y|x}$ = 34.8 cm^2) of variation in basal area increment (cm^2).

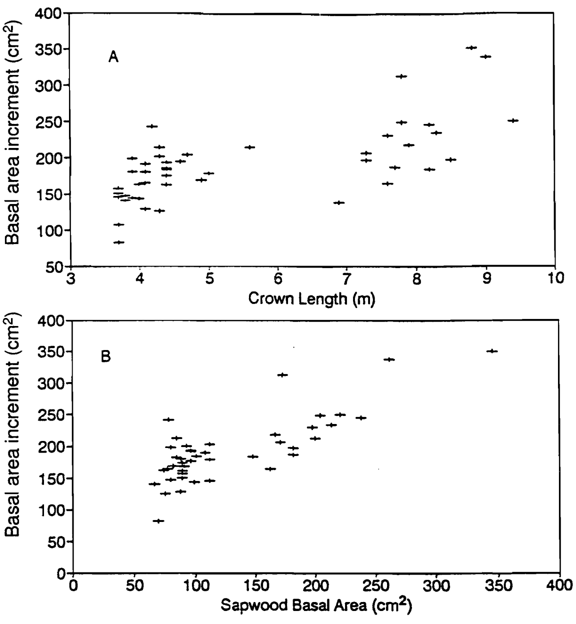

FIG. 7—Basal area increment in relation to crown length (A; increment = 85.4 + 19.0 × crown length; adj. r^2 = 0.449, $S_{y|x}$ = 39.2 cm^2) and sapwood basal area at crown base (SBA) (B; increment = 109.0 + 0.7 × SBA; adj. r^2 = 0.618, $S_{y|x}$ = 32.5 cm^2) for a typical second-log pruning trial plot (plot 12 at the Dipton followers trial).

length efficiency in a stand growth model. A comparison of the modified growth function with the original EARLY growth function indicates the crown length efficiency variable improved the farm-site model (Table 5). The efficiency variable was significant in the modified growth function ($p < 0.0001$) and the significance of the other variables was enhanced. The modified growth function explained 3.2% more variation in basal area

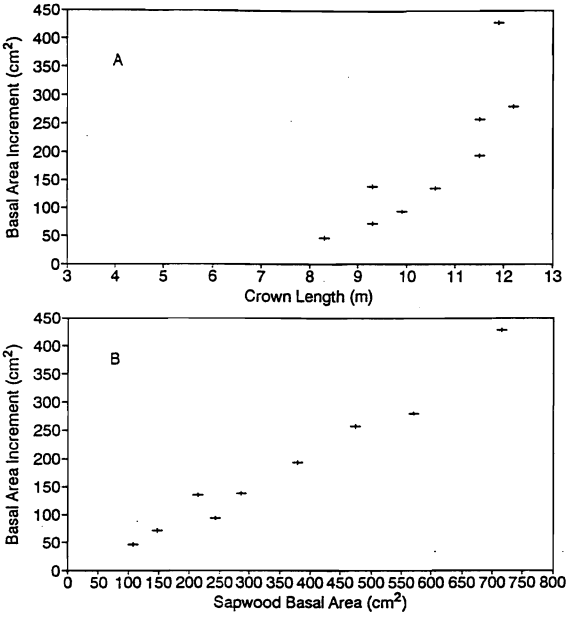

FIG. 8–Basal area increment in relation to crown length (A; increment = 612.6 + 75.7 × crown length; adj. r^2 = 0.680, $S_{y|x}$ = 69.0 cm^2) and sapwood basal area at crown base (SBA) (B; increment = –22.9 + 0.6 × LA; adj. r^2 = 0.962, $S_{y|x}$ = 23.6 cm^2) for plot 15 at the Waiotahi second-log pruning trial. Plot 15 was unique in having a schedule of pruning to a final height of only 4 m. This relatively low pruning provided for a range in both crown length and SBA that was not found in any other plots in the second-log pruning trials.

TABLE 4–Pearson correlation matrix for basal area increment (BAINC), crown length per hectare (CLHA), mean crown length (AVGCL), stocking (stems/ha), and growth efficiency (basal area increment per unit of crown length for the high-productivity farm-site and medium-productivity forest-site data.

	BAINC (m^2/ha)	CLHA (ha)	AVGCL (m)	Stocking (stems/ha)
High-productivity farm sites				
CLHA (ha)	0.84			
AVGCL (m)	0.24	0.34		
Stocking (stems/ha)	0.59	0.63	–09.44	
EFF (cm^2/m)	0.26	0.34	–0.89	0.45
Medium-productivity forest sites				
CLHA (ha)	0.83			
AVGCL (m)	0.16	0.26		
Stocking (stems/ha)	0.60	0.64	–0.48	
EFF (cm^2/m)	–0.16	–0.24	–0.90	0.52

increment, and had a standard error of estimate that was 0.06 m^2/ha/year lower, than the original function. Alternatively, predicted basal area increment was added to the original EARLY model in place of the efficiency variable, resulting in a slightly weaker function (r^2 = 0.82; $S_{y|x}$ = 0.56 m^2/ha/year). This indicates the improvement in the model is through the efficiency variable and not the predicted basal area used to estimate efficiency. The crown length efficiency variable was not significant ($p > 0.26$) and had no effect on the medium productivity forest-site model.

TABLE 5—Original farm site growth function to predict basal area increment (m^2/ha/year) (from West *et al.* 1982), and a modified function including a measure of crown length efficiency.

	Farm site growth function			Modified growth function		
Variable	Coefficient	t value	Standard error	Coefficient	t value	Standard error
Constant	–2.2395	8.2	0.2726	–5.2424	12.5	0.4182
Crown/ha (km)	3.0531	19.4	0.1570	3.4386	23.3	0.1475
$(\text{Crown/ha})^2$ (km^2)	–0.3363	8.8	0.0382	–0.3920	11.2	0.0349
dbh/ht (cm/m)	0.8922	8.6	0.1033	1.2953	12.5	0.1033
HPHS	–0.1350	10.1	0.0133	–0.1398	11.7	0.0120
Efficiency (cm^2/m)	n/a			0.0476	8.9	0.0054
Statistic						
$S_{y\|x}$ (m^2/ha/year)	0.54			0.49		
Adjusted r^2	0.83			0.87		
N	327			327		

DISCUSSION

Reduced tree increment after pruning (Table 2) is an expected consequence of reducing a tree's crown size. Although removals of only the lowermost branches may not affect tree increment (Sutton & Crowe 1975; O'Hara 1991), the branch removals in these *P. radiata* trials were relatively severe. The reductions in increment indicate some productive branches or whorls were removed.

The higher crown efficiencies of crop elements (Table 3) indicate that while these pruning treatments removed some productive branches, the net effect on the tree was to improve total efficiency. Evidently, pruning treatments that leave at least 3 to 5 m of crown length are leaving the most productive parts of the crown in young trees similar to those in this study. Differences in efficiency based on crown length suggest similar differences in stand productivity may exist for stands with widely different structures but equal cumulative crown lengths.

For all five data sets, considerable variation in SBA between trees was apparent for trees with longer crown lengths (Fig. 1). For example, trees at Dipton with a crown length of 9 m had SBA ranging from about 130 to 340 cm^2 (Fig. 1). Although there is potential for error in both measurements, the variation between them suggests substantial differences in the manner in which leaf area (as represented by SBA) is distributed within *P. radiata* crowns of similar or constant crown length. This variation also implies differences in the manner in which these two measures of crown size represent the photosynthetic potential of individual trees.

The primary driving variable in EARLY is cumulative crown length per hectare (West *et al.* 1982, 1987; Knowles & West 1986). The low correlation coefficients between basal area increment and average crown length (Table 4) suggest the strength in the relationships between cumulative crown length and basal area increment in EARLY are primarily the result of a strong relationship with stocking density rather than average crown length. Average crown length does enhance prediction of increment, but probably not to the degree previously believed. This conclusion is supported by the relative weakness of the relationships between increment and crown length for individual trees (Fig. 2–6). Although crown length does provide some representation of photosynthetic potential, there appears to be sufficient variation in *P. radiata* crown form for a given crown length to confound any relationship between crown length and increment. SBA (as a surrogate for leaf area), as indicated by the stronger relationships with increment for every trial (Fig. 2-6), appears to be a superior measure of crown size.

The results of this study indicate differences in crown efficiency do exist between elements and may be quite significant in terms of their effect on prediction of stand increment. Integration of leaf area or SBA, because of its apparent superiority over crown length, into prediction of stand increment may be relatively easy if the stem is measured by calliper at crown base. Since little or no heartwood is present at crown base of young *P. radiata* trees (Cown *et al.* 1991), leaf area could be represented by cross-sectional area derived from stem calliper measurement with only a small adjustment to account for bark thickness. With stem diameter either measured by calliper or predicted (e.g., from dbh accounting for stem taper), adjustments for variable efficiency of trees with different crown lengths could be incorporated into a stand-level growth model. For example, a crown efficiency factor could be used to adjust the relative growth per unit of crown for each stand element in an intensively managed stand. It should be noted, however, that the current absence of accurate functions for *P. radiata* in New Zealand to predict stem taper across a range of sites and silvicultures (e.g., where taper could be modified by changes in crown height), and heartwood formation which could be similarly modified, could reduce the utility of SBA for rotation-length growth modelling.

The superiority of SBA as a measure of the size of the green crown would tend to support the use of a variable-lift pruning approach (e.g., Koehler 1984) where pruning is limited by minimum calliper diameter. This pruning could be considered a "variable-lift/constant leaf area" pruning because although it may leave variable residual crown lengths, leaf area may be relatively constant for a constant calliper measurement. This may permit identification of optimal crown efficiencies and design of pruning regimes to achieve target leaf areas per tree and per stand.

The very crude measure of stand crown length efficiency used in the modified EARLY growth function provided a small improvement to the original function for farm sites (Table 5). A measure of efficiency derived as a stand average from individual-tree measurements of both increment and crown size would likely result in additional model strength. Nevertheless, these results suggest there is potential merit to inclusion of some representation of crown efficiency into a stand-level growth model. Representing crown size with leaf area or a surrogate (e.g., calliper measurement) would probably result in superior predictive abilities over crown length. The lack of improvement in the medium forest site equation may be because the growth efficiency function was developed for the Dipton followers trial on a farm site.

CONCLUSIONS

Stand elements of pruned *P. radiata* plantations had different rates of increment and different crown efficiencies. Crop elements had the slowest rates of increment, but the highest efficiencies. Using SBA (as a surrogate for leaf area) in these growth efficiency measures indicated greater differences in efficiency than using crown length. SBA appears to be a better measure of crown size than crown length. However, relationships between crown length and SBA became weaker with increasing crown length, indicating great differences in SBA for longer crowned trees with constant crown length. Relationships between tree increment and crown length were weak whether assessed at plot or trial level. Stronger relationships were generally observed between tree increment and SBA.

Integration of tree level efficiency information into stand growth models such as "EARLY" may enhance accuracy of growth prediction. Modifications to the data used to develop the EARLY function for farm sites indicate a variable to represent efficiency can enhance increment prediction over the existing function. Use of a measure of efficiency based on either leaf area, or stem diameter measured by calliper at crown base as a surrogate for leaf area, may result in greater improvement of growth prediction.

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