BRANCH DYNAMICS in RADIATA PINE: LITERATURE REVIEW

J.C. GRACE

REPORT NO. 28   **JULY 1992**

EXECUTIVE SUMMARY

The current state of knowledge of radiata pine branching characteristics is reviewed in the light of data requirements for generating a realistic description of the crown for estimating log quality and for growing the crown forward in time.

There are a lot of data in some aspects of branching, namely the height of whorls on the stem and final diameter of the largest four branches per whorl.

There are not sufficient data for developing models of whorl position with respect to age, branch length growth, branch diameter growth, and branch senescence.

BRANCH DYNAMICS IN RADIATA PINE

Literature Review

J. C. Grace

INTRODUCTION

The structure of a tree crown is important for two main reasons. Firstly the distribution of foliage within the crown affects the interception of solar radiation, photosynthesis and indirectly tree growth. (Tree growth results from net tree photosynthesis being greater than tree respiration.) Secondly the position and size of the branches which support the foliage affect the quality of timber obtained at the end of the rotation.

Rawley and Hayward (1991) suggest that improved estimation of stand log outturn could be achieved by developing:

> a methodology for projecting through time, a list of trees complete with quality attributes, to any future age, producing a compatible tree list with biologically consistent quality attributes.

Within this "statement" there are three major objectives related to the tree crown which need research:

> to develop a realistic description of the tree crown at any point in time.

> to develop sub-routines to predict crown development over time, i.e given a realistic description of a tree crown at a point in time, equations are needed to "grow" the tree crown for a given number of years and then to develop a realistic description of the crown at the new age.

> a reassessment of inventory methodology to either improve measurement of crown variables and / or development of equations to convert subjective inventory assessments into an input file for the "crown growth model". This project will thus consider what level of detail is needed in an inventory to be able to develop a realistic description of the tree crown at that point in time.

The objective this study is to review the literature on distribution, size and growth of radiata pine branches, specifically in relation to prediction of quality. (Unless stated results quoted are for *radiata pine*).

This review will pinpoint areas for future research and is the first step towards developing a realistic description of the crown at any point in time and growing the crown forward in time.

REALISTIC DESCRIPTION OF A RADIATA PINE CROWN FOR ESTIMATING LOG QUALITY

The crown variables, considered necessary for developing a realistic description of a radiata pine crown for the purpose of estimating log quality are:

> height of each whorl of branches

> depth of each whorl of branches

> number of branches in each whorl

> diameter of each branch in each whorl

> angle each branch makes with the stem

> length of each branch originating from the stem

> whether the branches are alive or dead

These data will enable internode lengths to be estimated and should be sufficient for estimating log quality.

These data would not be sufficient to position all the secondary and higher order branches on the tree. Neither would they be sufficient for precisely placing the foliage on the tree.

Both:

> height to each pruning

> diameter over stubs at each pruning

will be an integral part of the description of the stand and will affect the shape of the crown.

Other variables which will influence log quality are:

sweep of stem

resin pockets

rot

broken tops

height of forks

position of epicormic shoots

Prediction of these variables will not be addressed as part of this report.

CROWN DEVELOPMENT

Some basic questions on crown development which need to be answered are:

How many whorls are formed each year?

What variables control the number of whorls formed each year?

What variables control whorl depth?

Does whorl depth change as the tree ages?

What variables control the length of internodes?

Does the length of a particular internode change as the tree ages?

What controls the number of branches per whorl?

What angle do branches make with the stem and how does this angle change with time?

What is the rate of branch length development?

What variables control the rate of branch length development?

What is the rate of branch diameter growth?

What variables control the rate of branch diameter growth?

When do branches stop growing ?

When do branches die?

How do branches respond to increased space/light following a thinning ?

If a branch has stopped growing will it respond to a thinning?

DEVELOPMENT OF BRANCH GROWTH MODEL

In order to be able to grow a tree crown thought time, equations will need to be developed to:

predict the position of whorls (and internodes) not currently formed

predict the number of branches in whorls not currently formed

predict the angle new branches will make with the stem

predict how branch angle will change with time

predict the diameter and length growth of branches currently on the tree and those not yet formed

predict when branches stop growing and when they die

predict how branches will respond to stand management

Ideally the equations developed should be of a form that can be included in any growth modelling system. This would necessitate growth equations being a function of only individual tree size, stand average parameters, genetics and environmental variables.

LITERATURE REVIEW

HEIGHT OF EACH WHORL

The height to the base of each whorl is related to several other factors:

annual height growth

number of whorls formed per year

position of whorls within annual growth zone

Bannister (1962) measured the position of whorls within the annual shoot for 430 annual shoots (sequences of 5 annual shoots on 86 trees) from Pigeon Valley. (Fig 1 taken from Bannister, 1962) shows the position of the whorls along the annual shoot assuming that the last whorl from the previous year marked the base of the annual shoot. Though there are heights at which the whorls are more likely to occur, there is a wide variation.

This analysis does not address the question:

where does a whorl occur if we know the position of previous whorls within the annual shoot?

There are likely to be regional differences in the position of whorls within the annual shoot. From data collected in Australia, Fielding (1960), found that the length of internodes (ie the distance between successive whorls) varied from a maximum at the base of the shoot to a minimum at the top. However data from Pigeon Valley was not consistent with this conclusion (Bannister, 1962)

NUMBER OF WHORLS PER YEAR

Generally radiata pine produces between one and six whorls per year (Bannister, 1962). The number of whorls produced is strongly influenced by genetics. The number of whorls produced is also influenced by environment. Fewer whorls are produced the further south one goes in New Zealand (Lavery, 1986). The reason is not known but it may well be a temperature effect since Bollmann and Sweet (1979) observed higher annual branching frequency at the warmest of four seed orchard sites all of which had been fertilised in order to produce common foliar nutrient levels.

DEPTH OF EACH WHORL

Knowles and Kimberley (1992) present data on mean whorl depth for whorls between 5.7 m and 11.2 m for 8 sites (four farm and four forest sites). Mean whorl depth varied between 0.15 m and 0.30 m. On some sites there was a trend for mean whorl depth to decrease with increasing number of stems/ha.

INTERNODE LENGTH

Annual height growth, the position of whorls within the annual shoot, and whorl depth determine the length of internodes.

Internode length is under strong genetic control (Carson and Inglis, 1988) and is negatively correlated with number of whorls per year (Lavery, 1986). Internode length is also influenced by crown class. Trees in the higher crown classes tend to have slightly shorter internodes (Lavery, 1986).

Within a tree, internode lengths are initially short, and rise to a maximum around 4 to 6 m and then gradually decrease with increasing height within the tree.

When data on internode length have been collected, age and position within the annual shoot have generally not been collected.

A model predicting stand mean internode length as a function of height to the base of the internode has been developed (Grace and Carson, 1992). The maximum stand mean internode length was found to increase the further south one goes within New Zealand and with increasing annual rainfall. The height in the tree where the maximum internode length occurred was found to increase with increasing altitude.

There are limited data available for the improved breeds of radiata pine. An analysis of the data currently available indicated that the percentage increase or decrease in the maximum stand mean internode length due to genetic improvement may vary with site. There were not sufficient data to determine whether the height within the tree where the maximum internode length occurs changes with level of improvement (Grace and Carson, 1992)

NUMBER OF BRANCHES PER WHORL

The number of first-order branches per whorl bears little or no relation to the number of whorls on the annual shoot (Lavery, 1986) .

Site differences within the Australian Capital Territory have little or no effect on the number of branches per whorl (Fielding, 1960).

The number of branches per whorl is however influenced by the intensity of solar radiation. Young trees grown under 30% or less of incoming solar radiation produced fewer branches per whorl (Fielding, 1960).

An analysis of a thinning experiment (Siemon et al, 1976) indicated that stand density had a negligible effect on the number of branches per whorl within the green crown. However, data presented by Knowles and Kimberley (1992) show a slight tendency for the number of branches per whorl to decrease slightly with increasing stocking on a given site.

A preliminary analysis (M. Kimberley, unpublished results) of data collected by C. Inglis and others indicates that the number of branches per whorls tends to decrease slightly with increasing whorl height. It also indicated that the number of branches per whorl tended to be higher in the New Zealand Forest Service Southland Conservancy compared to other regions within the country.

DIAMETER OF BRANCHES

The spacing of trees is an important factor affecting branch diameter. Jacobs (1938) showed that the sectional area of branches on trees increased with increased plant spacing from 6 ft to 12ft. Pederick and Abbott (1985) found that final mean branch diameter increased linearly with increased tree spacing in a spacing trial in Warenbayne plantation, Victoria, Australia. Results from a spacing trial at Mt Burr (South Australia) indicated that branch diameter increased with decreasing stocking. However branch diameter was only affected by initial spacing to the extent that stem diameter is controlled by spacing (Cromer and Pawsey, 1957).

In spacing trials in New Zealand, it has been found that the mean diameter of the 16 largest branches between 20 ft and 40 ft (largest branch per 5ft quartile) tends to increase with increasing plant spacing between 6ft and 16 ft square spacing. (Sutton, 1970). The slope of the relationship appears to vary with site. For sites with only 3 data points it is difficult to determine whether the relationship is linear. For the two sites with 5 data points the relationship appears linear.

Tombleson et al (1989) measured branch diameter on whorls between 5.7 m and 11.2 m for a range of site qualities and final crop stockings. They found that branch index (mean diameter of largest four branches per log - one from each quadrant) decreased with both increasing stocking and increasing site quality.

Mean branch size has been found to be larger on the north side compared to the south side for dominant trees in 7- and 9-year-old plantations in Australia (Fielding, 1967), and for trees in shelterbelts (Tombleson and Inglis, 1988). However shelterbelt orientation did not have a significant effect on branch index (Tombleson and Inglis, 1988).

Measurements in rectangular spacings (10x6ft, 10x8ft, 12x9ft, 12x6ft and 24x6ft) on three sites failed to show any measureable difference in "between" row and "within" row branches (Sutton, 1970). This appears to have been based on the measurement of the largest branch in each 5ft "quarter". The orientation of the spacings was not stated.

Inglis and Cleland (1982) developed a model to predict branch index for 5.5 m log lengths from thinned radiata pine stands. Branch index was estimated as a function of site index, diameter at age 20 (DBH20), stand predominant mean height at time of final thinning, and height from ground to top of log length.

This model was valid only for certain types of stands (Inglis and Cleland, 1982 p8). More data were collected to extend the use of the model and the model revised (Inglis, in prep). In the revision separate equations were derived for the first three 5.5 m log lengths (0.2-5.7 m, 5.7-11.2 m, 11.2-16.7 m). Branch index for the first log was predicted as a linear function of 1/ initial stocking, diameter at age 20 years (DBH20), and 1/height at time of thinning. Branch index for the second log was predicted as a linear function of DBH20/site index, 1/height at time of thinning, and site index. Branch index for the third log was predicted as a linear function of DBH20/site index, site index, rotation age/final stocking and 1/height at time of thinning.

Grace (1989) developed a model to predict branch index for variable log lengths in unimproved radiata pine stands on forest sites. Underlying the model was the hypothesis that:

> branches would grow laterally until they touched the crown of another tree

> branches would stop growing and not be able to grow in response to thinning once they were overtopped by other branches.

An analysis (Grace, 1989) indicated that this hypothesis suggests that final branch diameter is proportional to $1/\sqrt{stems/ha}$ (or spacing). This is supported by a number of studies including Pederick and Abbott (1985). Ballard and Long (1988) showed that for lodgepole pine, the mean branch diameter for the five largest branches per tree was proportional to (stand density) $^{-0.5}$. Kilpatrick et al (1981) showed that for Sitka Spruce, the diameter of the two largest branches at 2m up the tree was linearly related to spacing. The data from

Woodhill and Eyrewell (Sutton, 1970) also suggest that branch diameter is linearly related to spacing.

The height to base of green crown was used to decide where final branch size would change due to a thinning. This assumption is reasonable given the results of James and Tustin (1970) (see below for more details).

Grace (1989) found that $1/\sqrt{\text{stems}/\text{ha}}$ did explain some of the variation in final branch size on a whorl basis. Once stocking had been accounted for there were still variations due to site which could be explained by the term D20/site index (a measure of tree taper) and latitude.

A simulation study comparing both models of branch index is given in Grace (1990).

These models of branch index will not be suitable for projecting branch size forward in time.

ANGLE OF BRANCHES

Branches initially grow at an acute angle with respect to the stem but then bend outwards under their own weight. Their position tends to become fixed by subsequent diameter growth. (Jacobs, 1938).

At Puruki, an experimental forest about 40 km south-west of Rotorua, branch diameter 2.5 cm from the stem, branch length and branch angle (taking account of direction of about the proximal 30 cm of branch) were measured on a random branch per whorl on trees felled for biomass (21 trees in 1984 and 20 trees in 1985 - tree age 11 and 12 years respectively). The data on branch angle from plots which had been thinned were analysed by Lane and Grace (1986). They found no obvious relationship between branch angle and either branch length or branch diameter. However when mean branch angle per whorl was plotted against whorl number they found that at the top of the tree mean branch angle varied between 25° and 35°. Below the top six whorls mean angle was around 60°.

Branches on trees with long internodes tend to be more steeply inclined with respect to the horizontal than multinodal trees (Fielding, 1960).

Rawley (unpublished data) found a small but significant difference in the inclination angles of the branch tip with respect to the horizontal at Ngatira, 42° for multinodal "850" breed and 47.9° for long internode breed.

RELATIONSHIP BETWEEN BRANCH LENGTH AND BRANCH DIAMETER

The branch diameter must be large enough to support the branchwood and foliage. Ford (1985) suggested that the ideal branching pattern might be one that supports and displays foliage with the minimum amount of branch wood. King and Loucks (1978) have shown that the theoretical relationship between branch length and diameter at the base of the branch to achieve minimal branch wood varies according to the forces acting on the branches. If branch dimensions are limited by the need to keep from breaking under their own weight, then diameter is proportional to length squared. If branch dimensions are limited by the necessity to resist wind forces then diameter is proportional to length. If the principle of elastic similarity is assumed then diameter is proportional to length to the power 3/2. In deriving these relationships they assumed that wood density and chemical composition was constant throughout the tree and that form is based on a cylindrical shape.

Morgan and Cannell (1988) considered branch design using the theory for cantilever beams. Their research indicated that when laterals were "moved" from 6.7 cm to 33.3 cm from the base of the branch there was a 16% increase in the basal diameter of the branch.

Branch length and branch diameter were measured on two three-year-old tissue culture plantlets and one 5 year old-seedling in the Long Mile as part of a study on light penetration. Graphs indicated that the relation between branch length and diameter was linear. (Grace et al. 1990b)

Branch length and diameter were also measured on live and dead branches at Matea (site index 24, age 22 years) and Northern Boundary, (site index 33, age 21 years), both at a nominal stocking of 150stems/ha (Grace et al, 1990b). Again graphs indicated that the relation between branch length and branch diameter was linear. The relationship appeared to be unaffected by site and unaffected by whether the branch had green foliage of not.

A preliminary analysis of data collected in a radiata pine progeny trial (B. Rawley, pers. comm) indicated that branch diameter was linearly related to branch length and there were no significant differences between families. However the slope of the relationship did appear to vary with location within New Zealand.

Will and Hodgkiss (1977) found that for clones of radiata pine growing under different levels of fertility, low levels of nitrogen and/or phosphorus retarded branch length growth more than stem growth. This resulted in trees with narrow crowns compared to trees growing in more fertile sites. Branch diameter growth also appears to be reduced (Will and Hodgkiss, 1977, Fig 6), however, whether the relationship between branch length and diameter varies with fertility is not discussed.

Fielding (1967) measured trees growing on two sites in Australia which contrasted both in soil and climate. He assumed that the major differences in growth were due to fertility. Trees growing on infertile sand dunes had short thin branches compared to trees growing on fertile loam. The branch length- diameter relationship was, however, similar for both sites.

In a thinning x pruning x fertiliser experiment at Aupouri forest, branch diameter for a given branch length was found to increase with thinning and pruning (Grace et al, 1990a). This increase appeared to be related to needle loss which occurred following thinning and pruning (I. Hunter, pers comm.). That foliage loss caused the branches to become larger in diameter is plausible since Morgan and Cannell (1988) theoretically showed that "laterals" further away from the stem caused the diameter to increase.

BRANCH AND DIAMETER GROWTH

The extension growth of branches in the first year has been found to be less than but correlated with leader extension for a number of conifer species. The extension growth of the primary axis of branches in any one year is usually greatest at the top of the tree and decreases as one progresses downward through the crown (see Madgwick et al (1986) for further details).

For radiata pine, branches of the first whorl formed per growing season tend to be longer and larger in diameter than the other whorls (Jacobs, 1937).

WHEN DO BRANCHES STOP GROWING AND DIE?

The senescence and death of a branch results from a series of events (Larson, 1969). A healthy branch has an ample amount of foliage and produces a complete growth ring along its entire length. This assures the branch of a steady supply of water and nutrients. Senescence is generally triggered by a decrease in light, due to shading, that limits photosynthesis. This is followed by a smaller bud that further decreases the potential for photosynthesis. These events lead to decreased wood production on the branch and the formation of an incomplete growth ring (i.e. one that does not reach the stem). Since no growth ring is produced at the base of the branch, the branch is no longer able to compete favourably for water and nutrients in times of stress. These growth-suppressing events operate as a "negative-feedback system" until the branch dies.

Data on radial growth and longevity of Douglas Fir branches support the above description of branch senescence (Kershaw et al, 1990). For 2153 branches immediately below the current live crown of Douglas fir growing in southwestern Oregon, branch longevity averaged

24 years with a range of 4 to 72 years. The number of years the branches remained alive without perceptible annual ring production ranged from 0 to 49 years with a mean of 8 years. The branches were not, however, sectioned lengthwise which would have shown whether incomplete whorls were being formed during the years without perceptible annual ring production.

For radiata pine, Brown, (1962) concluded that branches initially put on rapid diameter growth. This is then followed by a period where there is negligible branch diameter increment, the second period being about twice as long as the first.

HOW DO BRANCHES RESPOND TO INCREASED LIGHT FOLLOWING THINNING?

A few studies have examined the response of branch diameter following a thinning.

For Pinus resinosa, Forward and Nolan (1961) examined branch growth in a tree planted at 6 x 6 ft spacing and thinned to 24 x 24 ft spacing after serious suppression was evident.

At the time of thinning the 6th and 8th whorls from the top were showing signs of suppression but had not stopped growing (deceasing ring width with time), however after thinning there was an increase in ring width for one or two years before whorl widths again decreased with age.

Another way of looking at the data is to compare the ring widths formed at a given "branch age".

From Fig. 11 (Forward and Nolan, 1961) it can be concluded that ring width laid down at branch ages between 4 and 11 years were larger after the thinning than before.

James and Tustin (1970) examined branch diameter growth for 13 trees in a stand of radiata pine planted at 2150 stems/ha and thinned to 371 stems/ha at age 10 years (mean height (51.5 ft (15.7 m)). Branch diameter growth was examined for the largest branch per quartile for each whorl between 20 ft (6.1 m) and 35 ft (10.7m) (101 branches). Branches were classified into two groups, those where branch diameter growth was slowing down prior to thinning, and where there was increased diameter growth after thinning; and those where there was no check to branch diameter growth. It was found that there was an increase in branch diameter growth after a check prior to thinning between 24.9 ft (7.6 m) and 35 ft (10.7m).

In lightly thinned stands such a response in branch diameter growth was rarely observed (Brown, 1962).

RESEARCH OPTIONS AND MODEL DEVELOPMENT

There are five variables which influence the position of branches on the stem:

annual height growth

number of whorls formed

position of whorls formed each

depth of whorls

internode length

Internode lengths are determined form the first four variables. I suggest that internode lengths should be determined from modelling the first four variables.

At some stage it may be advantageous to develop height growth models which are driven by environmental variables.

Currently there are little data available which allow the position of whorls within the annual shoot to be modelled. One data set is that of Bannister (1962). These data (if still available) should be re-analysed to predict the position of whorls within the annual shoot given the position of previous whorls within the annual shoot.

In future, when data is collect on position of whorls on stems, the age at which the whorl was formed should be recorded if possible.

It is anticipated that equations to predict the position of whorls within the annual shoot given number of whorls per year should be equally applicable for both unimproved and improved radiata pine as tree improvement has altered the mix of trees within.

Previous research indicates that the number of whorls per year may depend on environmental variables. However, further data will need to be collected before the number of whorls per year can be modelled as a function of environmental variables.

Currently available data indicate that whorl depth may be a function of stocking.

The data previously collected by C. Inglis should be suitable for developing a model of how whorl depth varies.

These data may also be sufficient for generating a model of how the number of branches per whorl varies.

For both whorl depth, and number of branches per whorl, there may be a need to collect more data for improved breeds, and for farm sites.

There are a number of studies which have examined branch diameter. These studies indicate that stocking has a major influence on branch diameter. Tree diameter also appears to influence branch diameter (e.g. Cromer and Pawsey, 1957; Inglis and Cleland, 1982).

There is a need for further understanding of the relationship between branch diameter, tree diameter, and site variables. This will best be achieved by analysing data from well-designed experiments.

There is however little data to model branch growth through time. The ability to model this is particularly important if one is to be able to project quality variables through time. A major effort is needed to collect data on branch growth, and in particular how branches grow in response to different silviculture treatments. The mechanisms of branch senescence and death are also poorly understood.

It has been hypothesized that branch length plays an important role in determining when branches stop growing in diameter (Grace 1989). There is the opportunity for well-designed experiments to determine the validity of these assumptions by monitoring branch growth through canopy closure. The silviculture/breeds trials established by the stand growth modelling co-operative would be suitable.

It is proposed to examine stem analysis techniques for obtaining data on branch growth. A workplan for a pilot study is being written and if successful the technique will be used to collect branch growth data over a representative range of genetic material, environmental conditions and silvicultural treatments.

While it appears that the mechanism of branch development is similar for many species the exact mechanisms are not fully understood. Any model developed is likely to be empirical in nature even if there is a theory underlying its development. Hence the applicability of models developed will depend on wide coverage of data.

REFERENCES

BANNISTER, M.H. 1962. Some variation in the growth pattern of Pinus radiata in New Zealand. New Zealand Journal of Science 5:342-70.

BOLLMANN, M.P.; SWEET, G.B. 1979. Bud morphogenesis of *Pinus radiata* in New Zealand. II. The seasonal shoot growth pattern of seven clones at four sites. New Zealand Journal of Forestry Science 9: 153-65.

BROWN, G.S. 1962 Stages in branch development and their relation to pruning. New Zealand Journal of Forestry 8:608-22

CARSON M.J. and INGLIS, C.S. 1988. Genotype and location effects on internode length of Pinus radiata in New Zealand. Management of Improved Radiata Breeds Cooperative report No. 8.

CROMER, D.A.N. and PAWSEY, C.K. 1957. Initial spacing and growth of Pinus radiata. Forestry and Timber Bureau, Canberra, Bulletin, No. 36, 42pp

FIELDING, J.M. 1960. Branching and flowering characteristics of Monterey pine. Forestry and Timber Bureau, Canberra, Bulletin No. 37, 59pp.

FIELDING, J.M. 1967. Some characteristics of the crown and stem of Pinus radiata. Forestry and Timber Bureau, Canberra, Bulletin No. 43, 32pp.

FORD, E.D. 1985. Branching, crown structure, and control of timber production. In Trees as crop plants. Eds M.G.R. Cannell and J.E. Jackson. Institute of Terrestrial Ecology, Monks Wood, Huntington. pp228-252.

FORWARD, D.F. and NOLAN, N.J. 1961 Growth and morphogenesis in the canadian forest species IV. radial growth in branches and main axis of Pinus resinosa Ait. under conditions of open growth suppression and release. Canadian Journal of Botany 39:385-409.

GRACE, J.C. 1989. Branch size prediction for radiata pine. Management of Improved Radiata Breeds Cooperative report No 18.

GRACE J.C. 1990. Prediction of final branch size for radiata pine. FRI Project Record No.2414 (unpublished)

GRACE, J.C. and CARSON, M.J. 1992. Prediction of Internode length in Pinus radiata stands. Stand Management Cooperative Report No. 27.

GRACE, J.C.; HUNTER, I.; and OLIVER, G. 1990a. Relationship between branch length and branch diameter for Pinus radiata at Aupouri. FRI Project Record No. ?? (unpublished)

GRACE, J.C.; BROWNLIE, R.K.; and TOMBLESON, J.D. 1990b. Characteristics of live branches within Pinus radiata crowns. FRI Project Record No. 2356. (unpublished)

INGLIS, C.S. and CLELAND, M.R. 1982. Predicting final branch size in thinned radiata pine stands. FRI Bulletin No. 3, Forest Research Institute, Rotorua 17 pp

JACOBS, M.R. 1937. The detection of annual stages of growth in the crown of Pinus radiata. Commonwealth Forestry Bureau, Canberra, Bulletin No. 19, 16pp.

JACOBS, M.R. 1938. Notes on pruning Pinus radiata Part I. Observations on features which influence pruning. Commonwealth Forestry Bureau, Canberra, Bulletin No. 23, 47pp.

JAMES, R.N. and TUSTIN, J.R. 1970 Diameter response of Branches after thinning in radiata pine. Economics of Silviculture Report No. 27, FRI, Rotorua (unpublished)

KERSHAW, J.A., MAGUIRE, D.A., and HANN, D.W. 1990 Longevity and duration of radial growth in Douglas-fir branches. Canadian Journal of Forest Research 20:1690-1695.

KING, D. and LOUCKS, O.L. 1978. The theory of tree bole and branch form. Rad. and Environm.Biophys. 15:141-165.

LANE, P. and GRACE J.C. 1986 Branch angle of Pinus radiata at Puruki. Forest Research Institute, Project Record No. 1257 (Unpublished)

LARSON, P.R. 1969. Wood formation and the concept of wood quality. Yale University, School of Forestry, Bulletin No. 74. 54pp.

LAVERY, P.B. 1986. Plantation forestry with Pinus radiata - Review Papers. Paper No. 12. School of Forestry, University of Canterbury, Christchurch. 255pp.

MADGWICK, H.A.I.; TAMM, C.O.; and FU MAO-YI 1986. Crown Development in young Picea abies stands. Scandinavian Journal of Forest Research 1:195-204.

MORGAN, J. and CANNELL, M.G.R. 1988. Support costs of different branch designs:effects of position, number, angle and deflection of laterals. Tree Physiology 4: 303-13

PEDERICK, L.A. and ABBOTT, I.D. 1985. Relationship between branch thickness and stand density in radiata pine. Research Branch Report No. 306. State Forests and Lands Service, Department of Conservation, Forests and Lands, Melbourne (unpublished)

RAWLEY, B. and HAYWARD, W. 1990. A new paradigm for growth models - Discussion paper. Stand Growth Modelling Co-operative (unpublished).

SIEMON, G.R., WOOD, G.B. and FORREST, W.G. 1976. Effects of thinning on crown structure in radiata pine. New Zealand Journal of Forestry Science 6:57-66.

SUTTON, W.R.J. 1970. Effect of initial spacing on branch size - Summary of results to date. In Sutton, W.R.J. (ed) Pruning and thinning practice. FRI Symposium No. 12 Volume 2: papers. pp 106-107

TOMBLESON, J.D. and INGLIS, C.S. 1988. Comparison of radiata pine shelterbelts and plantations. In Maclaren,P. (ed) Agroforestry Symposium Proceedings FRI Bulletin, No.139. pp 261-78.

TOMBLESON, J.D., GRACE, J.C., INGLIS, C.S. 1990. Response of radiata pine branch characteristics to site and stocking. In James, R.N. and Tarlton, G.L. (eds). New Approaches to spacing and thinning in plantation forestry. FRI Bulletin No. 151. pp229-231.

WILL, G.M.; and HODGKISS, P.D. 1977: Influence of nitrogen and phosphorus stresses on grown and form of radiata pine. New Zealand Journal of Forestry Science 7: 307-320.