SPECIFIC LEAF AREA OF PINUS RADIATA AS INFLUENCED BY STAND AGE, LEAF AGE, AND THINNING

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ABSTRACT

Specific leaf area (SLA) was determined annually for three **Pinus radiata** D. Don stands at Puruki from ages 2 to 12 years old and undergoing periodic thinning .The canopy SLA averaged 160 cm^2/g but decreased with stand age from 190 to 150 cm^2/g, while the SLA of individual leaf age-classes ranged between 100 and 220 cm^2/g.

The most important cause of variation in canopy SLA, based on a theoretical analysis, was fascicle density. Density increased from 0.25 to 0.34 g/cm^3 with stand age and by 7% as leaf age increased from 1 to 2 years old. Additional smaller sources of SLA variation were due to random fluctuations in fascicle average dimensions and a reduction in the number of needles per fascicle with increase in stand age. Most of the variation in canopy SLA was accounted for by stand age (74%) and leaf age (10%).

Keywords: specific leaf area; canopy architecture model; management effects; volume; fascicle density; diameter; fascicle morphology; age series; **Pinus radiata**.

INTRODUCTION

Leaf area is used in light interception, photosynthesis, respiration, and transpiration models (Rook *et al.* 1985). Application of these models to stands of *Pinus radiata* requires information on how specific leaf area (SLA) varies with leaf age, depth in canopy, stand age, silvicultural treatment, and site so that indirect estimates of leaf area can be calculated from leaf weight and SLA. More recently, SLA has been used for characterising growing conditions within the canopy of *P. radiata* (Grace *et al.* 1987).

Specific leaf area of pine fascicles usually decreases with leaf age and increases with depth in the crown (Benecke 1979; Kellomaki & Oker-blom 1981; Halldin 1985; Borghetti *et al.* 1986). It decreases with stand age (Johnson *et al.* 1985) even though older stands have deeper tree crowns. Thinning and tree size effects were confounded in the study by Hager & Sterba (1984), precluding firm conclusions on the effects of silviculture. Site effects were not considered important in a study of loblolly pine (*Pinus taeda* L.) SLA (Shelton & Switzer 1984), but removal of competing vegetation decreased SLA in another study (Zutter *et al.* 1986).

Study Objectives

Specific leaf area was examined from a theoretical point of view, followed by an examination of how SLA and the variables determining SLA vary with leaf age, stand age, and thinning at Puruki.

Theory

An equation for estimating the area of all lateral surfaces of pine fascicles given by Beets (1977) identified the morphological factors determining leaf area. For three-needled fascicles average surface area, $\bar{s}$, is given by:

$$\bar{s} = k_{fas}(\beta)^{-1/2}(\bar{w}\bar{l})^{1/2} \tag{1}$$

where k_{fas} is the shape constant for three-needled pine fascicles, β is the density (g/cm^3), and $\bar{w}$ and $\bar{l}$ are the average weight (g) and length (cm) of the fascicles. The value of the constant, k_{fas}, is insensitive to variations in fascicle shape (Beets 1977) and can therefore be applied to a wide range of species with solid leaves. Beets' (1977) Model 1 makes unnecessary the previous need to calculate leaf area – leaf dry weight regressions (SLA) for estimating leaf area.

Equation 1 can be generalised to be independent of the number of needles per fascicle, which is desirable because both within- and between-species differences occur in this regard. Equation 1 then becomes:

$$\bar{s} = \left[\sum_{i=2}^{n} f_i \left(\frac{i+\pi}{3+\pi}\right)\right] k_{fas} (\beta)^{-1/2}(\bar{w}\bar{l})^{1/2} \tag{2}$$

where f_i is the proportion of fascicles possessing $i = 2,3 \ldots n$ (for monophyll fascicles $i = 0$) needles per fascicle and $(i + \pi)/(3 + \pi)$ converts the area of a three-needled fascicle to one with i needles per fascicle, as is apparent from Beets (1977). An additional assumption in Equation 2 is that the number of needles per fascicle is unrelated to fascicle size; earlier tests verified this, simplifying the measurement procedure and the formulation of Equation 2 (a more general formula could be developed to eliminate this assumption if required).

Specific leaf area is given by:

$$\text{SLA} = \bar{s}/\bar{w} = N\bar{s}/N\bar{w} = S/W \tag{3}$$

where N is the total number of fascicles in the population, and S and W are the population total area and weight, respectively.

By substituting Equation 2 into 3, the variables upon which SLA depend are shown explicitly:

$$\text{SLA} = \left[\sum_{i=2}^{n} f_i \left(\frac{i+\pi}{3+\pi}\right)\right] k_{fas} (\beta)^{-1/2}(\bar{w}\bar{l})^{1/2} (\bar{w})^{-1} \tag{4}$$

Equation 4 is still not very useful because $\bar{w}$ combines fascicle density and average volume ($\bar{v}$) information. However, since $\bar{w}$ equals $\beta\bar{v}$, density effects can be partitioned from dimension effects:

$$\text{SLA} = \left[\sum_{i=2}^{n} f_i \left(\frac{i+\pi}{3+\pi}\right)\right] k_{fas} (\beta)^{-1}(\bar{l}/\bar{v})^{1/2} \tag{5}$$

An alternative form of Equation 5 expresses dimension effects in terms of fascicle average diameter ($\bar{d}$), using the approximation:

$$\bar{d} = k_s\ (\bar{v}/\bar{l})^{1/2}$$

where k_s varies with shape. *Pinus radiata* fascicles conform closely to segmented cylinders in shape, because k_{fas} nearly equals 6.93 (Beets 1977) in which case k_s equals $(4/\pi)^{1/2}$.

Making these substitutions:

$$SLA = \left[\sum_{i=2}^{n} f_i \left(\frac{i+\pi}{3+\pi}\right)\right] k_{fas}\ k_s\ (\beta)^{-1}(\bar{d})^{-1} \qquad (6)$$

Equation 6 indicates that specific leaf area depends on the following three variables:

(1) The proportion f_i of fascicles possessing $i = 2,3 \ldots n$ needles per fascicle;

(2) Fascicle density, β;

(3) Fascicle average diameter, $\bar{d}$.

An additional constant can be incorporated in Equations 1, 2, and 6 to convert area from an all-surfaces basis to a projected-area basis. In cross-section an unsegmented cylinder has a lateral area of πd and a projected area of d, therefore the constant is π. Empirical estimates of this conversion factor (Johnson 1984) give a mean of 3.2 (presumably an estimate of π), irrespective of the number of needles per fascicle.

MATERIALS AND METHODS

Site Description and Stand Management

The forest was established on volcanic ash soils previously under pasture, and converted to *Pinus radiata* in 1973. Puruki has no known moisture or nutrient limitations to tree growth. A detailed description of Puruki given by Beets & Brownlie (1987) includes information on actual stocking, basal area, and height of the three stands (Tahi, Rua, and Toru). Part of Toru was replanted in 1974 because of poor establishment. The effect of time and thinning on the leaf area (all surfaces) index (LAI) of the stands is given in Table 1; stocking reductions were almost identical, though they

TABLE 1—Leaf area index (all surfaces) of three Puruki stands as related to stand age and periodic thinning. The *Pinus radiata* stands were planted in 1973

Sub-catchment	Age (years)										
	2	3	4	5	6	7	8	9	10	11	12
Tahi	1.8	4.2	14.0	20.1	33.1*	8.1	14.4	17.5	18.2†	6.2	10.6
Rua	0.9	3.7	7.6	18.4	26.3	16.8*	9.0	11.3	15.0	14.8	19.5
Toru	0.6	1.6	6.3	16.6	22.1	18.6	18.7*	8.8	14.5	18.7‡	13.3
Inviolate§	-	-	-	-	-	-	-	-	-	-	20.8

* Thinned from 2200 to 550 stems/ha

† Thinned from 550 to 137stems/ha

‡ Thinned from 550 to 275 stems/ha (nominal stocking)

§ Unthinned control plots in Rua

differ slightly in timing, until 1983 when contrasting stockings were established (Beets & Brownlie 1987).

Sample Tree Selection

Between 15 and 21 sample trees were selected annually in winter (between May and August) from 1975 to 1985, with a total of 174 trees sampled individually for leaf area. Fascicle samples were selected from three leaf age-classes (1, 2, and > 2 years old), as part of a standard crown dry-matter sampling procedure, with tree and fascicle selection based on random sampling (Beets & Pollock 1987).

Sampling for Fascicle Average Length, Weight, and Number of Needles per Fascicle

The fascicle sampling procedure varied depending on stand age. Prior to 1983, when tree height ranged from less than 1 m to 14 m, 50 fascicles/leaf age-class were selected from throughout the crown. From 1983 to 1985, when tree heights ranged between 10 and 22 m, the crown was subdivided into 2-m vertical zones for sampling purposes, and 20 fascicles/leaf age-class/2-m zone were selected.

Leaf Density

A further sample of 20 (to 1982, inclusive) or 30 fascicles per leaf age-class was selected from throughout the crown. The displacement volume and oven-dry weight of these fascicles were determined as described by Beets (1977) for computing fascicle density. Initially, fascicles were measured individually but from 1982 they were grouped in bundles of 10, to speed up processing. No density samples were available in 1975 and 1980 so these years were excluded from any statistical analyses. Density values in 1975 and 1980 were interpolated from density *v.* stand age graphs to complete data in Table 1.

Calculations

Leaf area by leaf age-class was estimated for each tree using the equation:

$$\sum_{i=2}^{n} \left[(f_i \, x N) \left(\frac{i+\pi}{3+\pi}\right)\right] (0.200 + 6.955 \, (\beta)^{-1/2}(\bar{w}\,\bar{l})^{1/2}) \qquad (7)$$

and SLA using Equation 3 of this paper. Equation 7 is equivalent to Equation 2 of this paper but k_{fas} has been replaced by the linear regression estimator (Beets 1977) and S instead of $\bar{s}$ is estimated. Zonal samples were first weighted by the leaf dry-weight data of each zone (Beets & Pollock 1987) to obtain crown means of SLA, fascicle weight, length, and the proportion of fascicles possessing different numbers of needles. N was estimated from the total weight of fascicles divided by the average weight of the sample by leaf age-class and zone, as appropriate.

Canopy estimates of fascicle SLA, density, and diameter were derived by averaging the individual tree data by subcatchment and year and the effects of stand age, leaf age, and subcatchment were analysed using analysis of variance. This analysis was restricted to 1- and 2-year-old leaves because leaf retention beyond 2 years was very variable.

Data on number of needles per fascicle were averaged across subcatchments because of the high variability, and only the 1-year-old leaf age-class data were included.

No data on within- or between-tree variation in SLA are included here, but SLA increased with depth in crown in line with other studies.

RESULTS AND DISCUSSION

Number of Needles per Fascicle

The number of needles per fascicle decreased with increasing stand age as the proportion of fascicles with four or more needles declined and two-needled fascicles increased (Fig. 1). Between stand ages 6 and 11 years more than 90% of the 1-year-old fascicles were three-needled.

The effect on SLA was quite small. For example, with four needles per fascicle $(i + \pi)/(3 + \pi)$ in Equation 6 takes the value 1.16, indicating that four-needled fascicles have 16% more surface area than three-needled fascicles. Hence, prior to stand age 6, when between 10% and 23% of the fascicles were four-needled, the effect was to increase SLA by around 3%. After stand age 10 the effect of a reduced number of needles per fascicle was to decrease SLA by around 2%.

Because the number of needles per fascicle changes with stand age, leaf age effects could be expected.

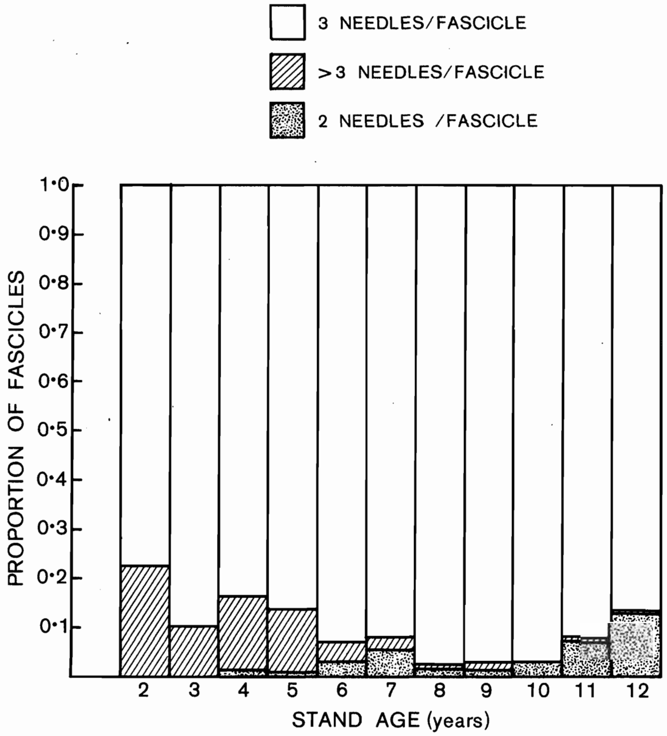

FIG. 1—Time trends in the proportion of 1-year-old fascicles with two, three, or more than three needles per fascicle averaged over the three **Pinus radiata** stands at Puruki.

Fascicle Density

Fascicle density increased with both year of sampling and leaf age, and Toru had a significantly lower density than Rua and Tahi (Table 2). Subcatchment effects on density were not significant when stand age (counted from replanting data for Toru) was used. Similar tree age effects on fascicle density have been reported in loblolly pine (Shelton & Switzer 1984; Johnson *et al.* 1985). Fascicle density of 1- and 2-year-old leaves increased by 26% with stand age (Table 3), averaged over subcatchments.

Because fascicle density depends on stand age the effect of leaf age on density was determined for each cohort of leaves (Table 4). On average, fascicle density increased by approximately 7% as leaf age increased from 1 to 2 years old, and by a further 4% beyond age 2, excluding cohorts with missing data (Table 4).

The inverse relationship between SLA and density (Equation 6) means that the 26% increase in leaf density with stand age caused a comparable decrease in SLA.

TABLE 2—Puruki average fascicle diameter, density, and specific leaf area (SLA) and association with sampling date, leaf age, and subcatchment

Variable	Mean†	Sampling date	Leaf age	Subcatchment
Diameter (cm)	0.162	***	NS	NS
Density (g/cm^3)	0.30	***	***	**‡
SLA (cm^2/g)	166	***	***	**‡

NS Not significant
** Significant at p = 0.01
*** Significant at p = 0.001
† 1- and 2-year-old leaves only
‡ Subcatchment not significant when analysis based on age from successful establishment

TABLE 3—Association of stand age with fascicle average diameter, density, and specific leaf area (SLA) for *Pinus radiata* canopies* at Puruki. Analysis based on 1- and 2-year-old fascicles only. Stand age counted from 1973 for all stands

Stand age (yr)	Diameter (cm)	Density (g/cm^3)	SLA (cm^2/g)
3	0.161 b	0.30 c	173 b
4	0.172a	0.25a	190a
5	0.162 bc	0.28 b	184a
6	0.168ab	0.26ab	183a
8	0.167ab	0.30 c	159 c
9	0.167ab	0.32 d	148 d
10	0.150 d	0.33 d	162 c
11	0.156 cd	0.34 d	147 d
12	0.153 cd	0.34 d	150 d

* Inviolate data excluded from analysis: Diameter = 0.139 cm, density = 0.34 g/cm^3, and SLA = 168 cm^2/g. Measurements followed by the same letter are not significantly different at p = 0.05.

TABLE 4—Effect of leaf age on density (g/cm³) of cohorts of fascicles by year of initiation, averaged over all subcatchments at Puruki

Year initiated	Leaf age (years)		
	1	2	3
1975	0.29	0.26	0.32
1976	0.25	0.28	0.29
1977	0.27	0.28	–
1978	0.25	–	0.30
1979	–	0.31	0.32
1980	0.29	0.33	0.34
1981	0.32	0.33	0.34
1982	0.32	0.35	0.34
1983	0.33	0.35	–
1984	0.34	–	–
Mean (SE)	0.30 (0.011)	0.31 (0.012)	0.32 (0.008)

– Signifies density not measured

Likewise, SLA decreased by 7% as 1-year-old leaves aged a further year. The inverse relationship between SLA and density reported previously (Shelton & Switzer 1984; Johnson *et al.* 1985) was not examined from a theoretical point of view.

Leaf density was not related to canopy closure, suggesting that light level has a negligible effect on fascicle density. Generally, no or only small decreases in fascicle density with depth in crown have been reported (Beets 1977; Shelton & Switzer 1984).

Unpublished leaf density data collected from Woodhill Forest, established on stabilised nitrogen-deficient sand dunes, were comparable to Puruki at the same stand age (0.33 g/cm³ at age 10). At Woodhill 1-year-old leaf density averaged 0.35 and 0.38 g/cm³ at stand ages 17 and 42 years old, respectively, suggesting further increases are possible at Puruki. Clearly, stand and leaf age have a greater influence on fascicle density than vertical position of leaf within the crown.

Fascicle Diameter

Fascicle diameter fluctuated significantly with stand age but not with leaf age or subcatchment. Surprisingly, these variations in fascicle diameter were unrelated to leaf area index, suggesting that self-shading is important in large open-grown trees. Differences in within-crown variation due to thinning found by Benecke (1979) were small. Compared with the variation in $\bar{d}$ with vertical position in crown (0.09 to 0.21 cm) computed from data presented by Beets (1977), the effect of stand age was quite small with $\bar{d}$ ranging from 0.15 to 0.17 cm (Table 3). Given the above, the inverse relationship between SLA and diameter (Equation 6) is more important in space than time.

Canopy Specific Leaf Area

Stand age, leaf area, and subcatchment affect SLA and density in parallel (Tables 2 and 3) which is hardly surprising in view of the strong dependence of SLA on density. Eighty-four percent of the variation in SLA was accounted for by stand age (74%)

and leaf age (10%). Regressions of SLA on density accounted for 81%, 73%, and 35% of the variation in 1-, 2- and > 2-year-old leaves, respectively. Regressions of SLA on diameter were not significant for 1- and 2-year leaves but accounted for 48% of the variation in > 2-year-old leaves, suggesting that the reduced variation in density of older leaves (Table 4) increased with importance of leaf size effects.

During the 10-year period of study SLA decreased by 23%, owing mostly to the variation in fascicle density. The range in SLA from 100 to 220 cm^2/g is comparable to the range associated with vertical position in crowns of this and other species (Benecke 1979; Schulze *et al.* 1977). Equation 2 depends on $(\beta)^{-1/2}$ and so is less sensitive to variations in density than Equation 6 which depends on $(\beta)^{-1}$. Direct estimates of S using Equation 2 may be more useful than indirect estimates of S involving SLA when developing a general leaf area model.

CONCLUSIONS

In stands without any major moisture or nutrient limitations:

(1) Variation in canopy SLA is due mostly to fascicle density and, to a lesser extent, fascicle size and the number of needles per fascicle;

(2) Most of the variation in canopy SLA can be accounted for by stand age and leaf age;

(3) Density increases associated with leaf aging average 7% and 4% from 1 to 2 and 2 to > 2 years, respectively.

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REFERENCES

BEETS, P. 1977: Determination of the fascicle surface area for **Pinus radiata. New Zealand Journal of Forestry Science 7:** 397–407.

BEETS, P. N.; BROWNLIE, R. K. 1987: Puruki experimental catchment: Site, climate, forest management, and research. **New Zealand Journal of Forestry Science 17:** 137–60.

BEETS, P. N.; POLLOCK, D. S. 1987: Accumulation and partitioning of dry matter in **Pinus radiata** as related to stand age and thinning. **New Zealand Journal of Forestry Science 17:** 246–71.

BENECKE, U. 1979: Surface area of needles in **Pinus radiata** – Variation with respect to age and crown position. **New Zealand Journal of Forestry Science 9:** 267–71.

BORGHETTI, M.; VENDRAMIN, G. G.; GIANNINI, R. 1986: Specific leaf area and leaf area index distribution in a young Douglas-fir plantation. **Canadian Journal of Forest Research 16:** 1283–8.

GRACE, J. C.; ROOK, D. A.; LANE, P. M. 1987: Estimation of canopy photosynthesis for **Pinus radiata** stands. **New Zealand Journal of Forestry Science 17:** 210–28.

HAGER, H.; STERBA, H. 1985: Specific leaf area and needle weight of Norway spruce (**Picea abies**) in stands of different densities. **Canadian Journal of Forest Research 15:** 389–92.

HALLDIN, S. 1985: Leaf and bark area distribution in a pine forest. Pp. 39–58 **in** Hutchison, B. A.; Hicks, B. B. (Ed.) "The Forest-Atmosphere Interaction". D. Reidel Publishing Company, Dordrecht.

JOHNSON, J. D. 1984: A rapid technique for estimating total surface area of pine needles. **Forest Science 30:** 913–21.

JOHNSON, J. D.; ZEDAKER, S. M.; HAIRSTON, A. B. 1985: Foliage, stem, and root interrelations in young loblolly pine. **Forest Science 31:** 891–8.

KELLOMAKI, S.; OKER-BLOM, P. 1981: Specific needle area of Scots pine and its dependence on light conditions inside the canopy. **Silva Fennica 15:** 190–8.

ROOK, D. A.; GRACE, J. C.; BEETS, P. N.; WHITEHEAD, D.; SANTANTONIO, D.; MADGWICK, H. A. I. 1985: Forest canopy design: Biological models and management implications. Pp. 507–24 **in** Cannell, M. G. R.; Jackson, J. E. (Ed.) "Attributes of Trees as Crop Plants". Institute of Terrestrial Ecology.

SCHULZE, E.-D.; FUCHS, M. I.; FUCHS, M. 1977: Spacial distribution of photosynthesis capacity and performance in a mountain spruce forest of Northern Germany. **Oecologia (Berl.) 29:** 43–61.

SHELTON, M. G.; SWITZER, G. L. 1984: Variation in the surface area relationships of loblolly pine fascicles. **Forest Science 30:** 355–63.

ZUTTER, B. R.; GJERSTAD, D. H.; GLOVER, G. R. 1986: Effects of interfering vegetation on biomass, fascicle morphology and leaf area of loblolly pine seedlings. **Forest Science 32:** 1016–31.