FOLIAGE AND GROWTH DISTRIBUTION WITHIN CROWNS OF *PINUS RADIATA*: CHANGES WITH AGE IN A CLOSE-SPACED STAND

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ABSTRACT

Needle and branch weight were estimated for each 2-m height zone of the crown in *Pinus radiata* D. Don trees of five size-classes for each year from ages 5 to 13 years. The fraction of needles aged 1 year decreased down the crown and with increasing tree age. The ratio of branch to needle production did not differ significantly with position in crown, tree size-class, or tree age, and averaged 0.75.

Keywords: weight; needles; branches; growth; *Pinus radiata.*

INTRODUCTION

In an earlier paper the overall dry weight content and growth of a close-spaced *Pinus radiata* stand were described (Madgwick & Oliver 1985). Between ages 5 and 13 years, growth distribution to crown components declined while allocation to stem increased. The purpose of this paper is to present details of the distribution of growth within crowns.

MATERIALS AND METHODS

Seventy-two trees were sampled in a stand nominally spaced at 1 × 1.5 m. The stand had been established by planting successive rows at intervals so that there were five annual age-classes in a total area of about 0.5 ha. Sampling over a 4-year period resulted in an age range from 5 to 13 years (for further details, *see* Madgwick & Oliver 1985). For the purpose of this paper it is important to note that samples of each of each age-class of trees included the largest- and smallest-diameter individuals and two each of trees of mean diameter and of diameters approximately mid-way between the mean and both the largest and the smallest diameters. Tree size-class was designated on an integer scale from 1 (smallest) to 5 (largest). After felling, each stem was marked at 2-m intervals from the base and the dry weight of needles by age-class and of branches in each section were determined. Where component weights within a crown section weighed less than 1 kg, the whole sample was dried. Larger samples were weighed fresh and subsamples taken to estimate the fraction of oven-dry material. Drying temperature was 70°C.

To investigate growth of needles and branches in terms of weight, data for each pair of mid-small-, mean-, and mid-large-diameter trees were averaged by tree age and crown section. If T_{ijk} is the total weight of needles on the tree of age i, size-class j, and crown section k, and F_{ijk} and B_{ijk} the corresponding weights of 1-year-old needles and live and dead branches respectively, then for size-class j and crown section k at tree age t

foliage growth was assumed to be $F_{t,j,k}$

branch growth was assumed to be $B_{tjk} - B_{(t-1)jk}$

and mean total foliage weight (kg) of the growing period was assumed to be $0.5(T_{(t-1)jk} + T_{tjk})$.

Within the live crown, dead branches were normally restricted to the lowest 2-m section containing live branches. Shedding of dead branch material was negligible and ignored in the analysis.

There were 196 observations for 1-year-old needles and 174 for branch growth and mean total foliage weight. In the above calculations crown zone was counted from ground level. For statistical analysis crown section (N_k) was counted from the tree apex. Using tree apex as the basis for measuring location proved more useful than stand top height which was tested and discarded. Using tree apex also overcame the problem of a variable number of stem sections without needle-bearing branches at the base of the crown. Data were analysed using regression analysis. Residuals were plotted against regressor variables as a check on possible polynomial effects.

RESULTS

The average proportion of foliage in each needle age-class and crown zone is shown in Fig. 1. With increasing age there was a smaller fraction of needles on the main stem and a relative shift from a preponderance of 1-year-old needles to an increasing proportion of 3-year-old needles. The fraction of 1-year-old needles decreased and that of 3-year-old needles increased down the crown. There was an increase in crown length for larger size-classes with tree age (Table 1).

Regression analysis indicated that the fraction of total needles on the main stem (L_{stem}) was related to tree age in years (A) and tree size-class (C) as follows:

$$L_{stem} = 0.46 - 0.032\ A - 0.090\ C + 0.0065\ A.C$$

with r^2 of 0.74 and each regressor variable statistically significant ($p < 0.001$).

One-year-old needles per tree as a fraction of total needle mass ($L_{1\text{-year}}$) was negatively correlated with the square of tree age ($r = -0.68$, $p < 0.001$) but was also affected by tree size-class. The regression

$$L_{1\text{-year}} = 0.72 - 0.0045\ A^2 - 0.015\ C^2 + 0.011\ A.C$$

accounted for 53% of the variation in $L_{1\text{-year}}$ (Fig. 2). (Note that C and C^2 are highly correlated ($r = 0.98$); which one appears in the regression is largely fortuitous.) The fraction of 3-year-old needles was positively correlated with the square of tree age ($r = 0.75$, $p < 0.001$)

$$L_{3\text{-year}} = -0.05 + 0.0021\ A^2$$

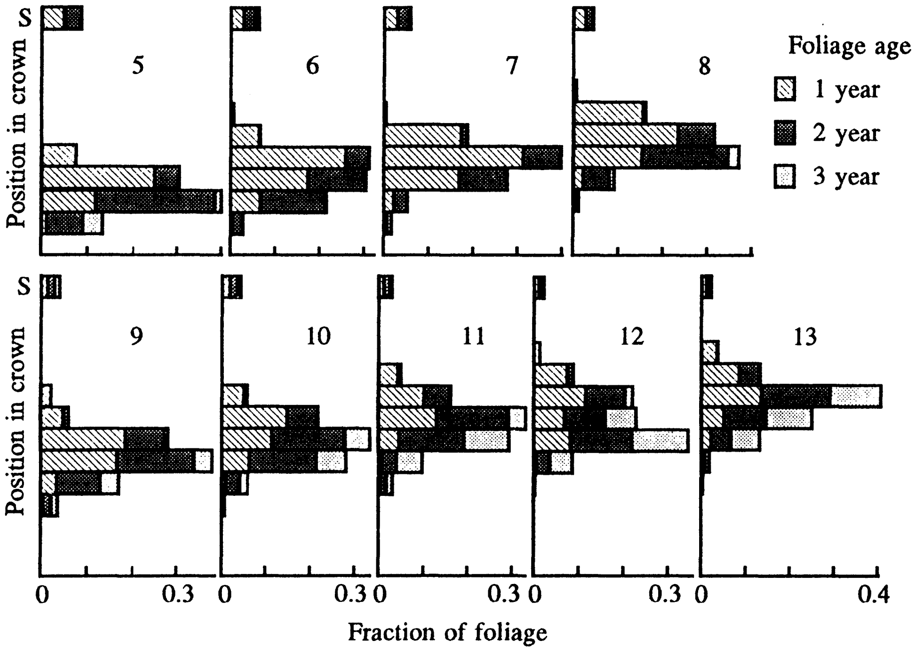

FIG. 1–The fraction of total needle weight by age-class in 2-m zones of crowns of trees ranging from 5 to 13 years old. S = stem needles.

TABLE 1–Crown length and total needle weight as affected by tree age and diameter class

Diameter size-class	Tree age (years)								
	5	6	7	8	9	10	11	12	13
Crown length (m)									
Smallest	3.78	4.64	2.74	3.12	4.40	3.90	3.84	4.13	2.73
Mid-small	4.85	5.67	3.44	5.73	6.54	3.99	7.52	4.76	5.04
Mean	6.69	5.84	6.61	5.75	7.34	6.87	6.27	7.62	7.64
Mid-large	6.55	9.63	6.36	9.16	9.44	8.37	10.33	10.86	9.28
Largest	6.76	9.20	9.76	10.77	12.12	11.98	9.23	11.05	11.49
Total needle weight (kg)									
Smallest	0.25	0.41	0.09	0.11	0.04	0.19	0.10	0.37	0.10
Mid-small	0.65	1.92	0.52	1.17	1.59	0.31	1.57	0.57	0.51
Mean	1.81	1.69	1.97	2.42	3.51	2.08	1.93	2.33	1.57
Mid-large	3.34	4.59	2.57	4.45	5.66	3.79	6.50	6.49	4.33
Largest	3.23	8.77	5.60	10.97	7.25	11.27	9.14	12.45	10.57

Annual needle production (kg) by size-class and crown section (F_{ijk}) was described by the relationship

$$F_{ijk} = -0.147 + 0.23\,T_{ijk} - 0.021\,A_i + 0.110\,C_j + 0.22\,N_k - 0.045\,N_k^2$$

where T_{ijk} was the estimated average weight (kg) of needles over the previous year, and N_k the crown 2-m section numbered from the apex. This regression accounted for 62% of the variation in F and had a standard error of estimate of 0.24 kg.

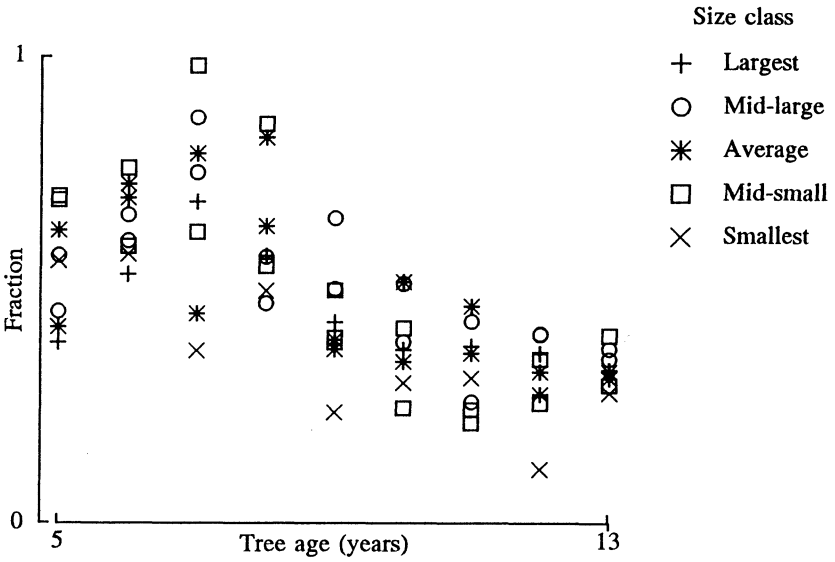

FIG. 2–1-year-old needles as a fraction of total needle weight in five diameter size-classes of trees ranging from 5 to 13 years old.

The best single predictor of annual branch production (kg) by tree age, size-class, and crown section (B_{ijk}) was the corresponding needle production (F_{ijk}) with $r^2 = 0.31$ and an intercept which was not significantly different from zero. The ratio of mean branch production to mean needle production was 0.75. This regression had a higher mean square than any derived using combinations of tree age, size-class, crown section, and average weight of needles over the previous year.

DISCUSSION

As *P. radiata* ages there is normally a shift to a higher proportion of older needle age-classes (Madgwick *et al.* 1977; Mead *et al.* 1984; Madgwick & Oliver 1985; Snowdon & Benson 1992) though no such trend was found by Beets & Madgwick (1988). From data presented by Beets & Pollock (1987) the change in distribution appears to be related to canopy closure. Needle production declines with increasing canopy closure. In young stands, prior to closure, exponential growth would result in a high fraction of young needles. In the close-spaced stand, canopy closure was virtually complete at age 5 years with a zone of dead branches at the base of each crown. The increasing fraction of older needles with tree age found in the results reported in this paper appears to have been a true aging effect. This conclusion is supported by regression analysis of data on needle production. Each regression coefficient is sensible: predicted growth increases with the weight of needles already present and with the relative size of the tree in the stand. Maximum production is estimated to be in the third section from the tree apex. Other things being equal, production decreases with tree age.

It may be argued that using average needle weight over the previous year biases the estimate of foliage production since such production is part of the average needle weight. If the regression analysis is repeated excluding average needle weight, then the result is

$$F_{ijk} = -0.25 + 0.29\ N_k - 0.091\ N_k^2 + 0.067\ C_j.N_k$$

with $r^2 = 0.53$ and all coefficients statistically significant ($p << 0.001$. While tree age was not significant on an individual tree basis, it must be remembered that stocking decreased from 6780 to 5190 stems/ha between ages 5 and 13 years through mortality. Allowing for changes in stocking, needle production per hectare declines. Moreover, because crown length increases with tree age, N_k is correlated with age and acts as a surrogate for age in the regression.

Published data for forest canopies of *P. radiata* suggest that the ratio of branch to foliage production may be affected by a variety of factors. Madgwick (1983a) found a ratio of branch to needle production of 0.68 in a plantation of grafted cuttings between ages 4 and 5 years. Data of Mead *et al.* (1984) gave a mean ratio of 1.03 in a thinning × fertiliser experiment with no significant treatment or year effects between ages 7 and 9. Data from Beets & Pollock (1987) indicate an overall ratio of 0.92 and a significant increase of 0.09 per annum with stand age from 2 to 12 years. Data of Snowdon & Benson (1992) indicate highly significant variation from year to year with a range of 0.48–1.29 (mean 0.98) over all treatments which overshadowed any effect of irrigation and nutrition.

Published data on the relative growth of needles and branches within crowns are sparse. In a study of *Picea abies* (L.) Karst. (Madgwick & Tamm 1987) we found that the ratio of wood to needle growth was at a minimum in the mid-crown zone. No such effect was apparent in *P. radiata* where the ratio remained constant over tree size-class, tree age, and position in crown. Data for whole canopies in young unthinned stands (Madgwick & Oliver 1985; Beets & Pollock 1987) indicate that needle and branch production are correlated but the ratio of production is not significantly affected by stand age. The detection of within-crown trends in *P. abies* may be attributable to the greater precision of that study as each sample branch was measured at the beginning and at the end of the growth period. The two species also differ greatly in needle longevity, with needles being retained for up to 11 years on *P. abies*.

Efforts to determine growth of crown components by sampling different trees at intervals are hampered by sampling problems. Individual crown sizes are variable and not closely related to tree size (Madgwick 1983b; Baker *et al.* 1984). Errors in estimating amounts of different components, such as needles and branches, within crowns tend to be correlated. Consequently, results obtained from measurement of branch size at the beginning and end of a sample period and the determination of final weight are likely to provide more accurate estimates of needle and branch growth. Such a sampling procedure allows many environmental factors to be examined with relative ease, so providing a better understanding of crown development.

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