New Zealand Journal of Forestry Science Vol. 10 No. 3 (1980): 461-75

EFFECT OF THINNING ON THE DISTRIBUTION AND BIOMASS OF FOLIAGE IN THE CROWN OF RADIATA PINE

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Replicated plots in a 15-year-old plantation of radiata pine (**Pinus radiata** D. Don) of basal area approximately 40 m^2/ha were thinned from below to approximately 11, 18, 23, and 28 m^2/ha respectively. The plots were re-thinned periodically thereafter to these same basal areas; one replicate of plots was retained relatively unthinned. Regression equations relating needle dry weight to branch cross-sectional area were developed and used to examine the distribution of foliage of various ages within the crowns.

In the upper crown (70–80% height decile and above), the percentage of 1-year foliage increased acropetally from 52 to 75% whereas that of 2-year and 3-year and older foliage decreased slightly (28 to 22%) and markedly (20 to 3%) respectively. In the middle and lower crown, i.e., all deciles below the 70–80% decile, the distribution of foliage across age classes was approximately constant at 37% (1-year), 28% (2-year), and 36% (3-year and older). The combined biomass of 1- and 2-year leaves within the whole crown averaged 73% of total leaf biomass under all thinning regimes.

Though stand density had little effect on proportionate distribution of foliage by position in the crown or leaf age, the total amounts of foliage varied greatly. Total foliage biomass ranged from 4.9 to 11.3 tonnes/ha and annual foliage production from 2.4 to 4.3 tonnes/ha in stands of mean stand density ranging from 15 m^2/ha (biomass) or 21 m^2/ha (annual production) to 46 m^2/ha.

INTRODUCTION

Tree growth depends largely on the amount, distribution, and relative efficiency of living foliage and is affected by silvicultural treatment, particularly thinning. Thinning within stands of most tree species results in an increase in both the length of the green crown and the number and size of branches on the trees remaining, but this does not necessarily imply a change in foliage biomass per unit area.

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Received 31 January 1978; revision 24 November 1980

In recent years there has been an explosion in both the quantity and diversity of biomass research (Hitchcock & McDonnell 1979) but, as yet, no estimates have been made of foliage biomass or of the effect of thinning on foliage distribution and biomass in Australian plantations of radiata pine (*Pinus radiata* D. Don) older than 12 years. The aim of this study was to gather some raw data from a more mature stand of radiata pine and undertake some preliminary analyses.

MATERIALS AND METHODS

The study was located in Green Hills State Forest, Tumut, N.S.W., and was based on material collected from a thinning experiment of 6 treatments with 4 replications arranged in a randomised block layout. Five of these treatments were chosen for examination. Two plots from the control treatment were not sampled owing to wind damage, so a total of 18 plots was involved. The experiment and selection of sample trees for this and other studies have been described elsewhere by Shepherd & Forrest (1973) and Siemon *et al.* (1976) respectively. At the time of sampling in July 1970, the stand was 23 years old. The history of thinning and stand data are summarised in Table 1.

Using published data (Loomis *et al.* 1966; Hutnik & Hickok 1967; Forrest & Ovington 1971), a minimum sample of 60 branches per treatment was judged necessary to predict the size and weight characteristics of tree crown components with a probability of less than 0.05 of errors exceeding ± 5%. Foliage was present on the upper stems of most trees but was sparse in comparison to branch foliage and so was ignored in sampling.

Approximately 10% of all trees in treatment plots were sampled, although 8 trees (19%) were sampled from the intensively thinned Treatment 1. Numbers of trees sampled in Treatments 3, 4, 5, and 6 were 8, 12, 16, and 12 respectively. The number of branches sampled per tree ranged from 4 to 10 depending on the number of trees sampled per treatment. Before sampling, the green crown of each tree was divided into height strata containing equal numbers of whorls. One branch was then selected at random from each stratum and its diameter over bark, 5 cm from its junction with the stem, was measured by caliper. A 2-dimensional matrix of branch diameter (1-cm classes) against height in tree (3-m classes) was compiled for each treatment to ensure the selected branches adequately represented the range of branch sizes and positions within the canopy. A second or third random choice was used if a matrix cell was already occupied. Selected branches, 330 in all, were cut flush with the stem, placed in heavy duty paper bags and stored at 2°C for 6 weeks (a practical necessity). Foliage on each branch was then separated into 3 leaf age classes (current or 1-year, 2-year, and 3-year and over) after Jacobs (1936) and dried to constant weight at 85°C. Some 4- and 5-year-old leaves were found in the lower crowns, particularly of trees in the more heavily thinned treatments, but their numbers were few and their weights too variable to justify additional classes so they were grouped with the 3-year-old leaves.

DATA ANALYSIS

All dry weight data were increased by 8% to allow for respiration losses during storage. This adjustment was based on losses in dry weight of 7.6% recorded for radiata pine under similar conditions by Forrest (1968) and 10% suggested as an average dry

TABLE 1—Stand data at ages 15, 17, 20, and 23 years. Values are averages for 4 plots per thinning treatment*

Thinning treatment	1	3	4	5	6
Nominal basal area limits (m^2/ha)	11.5/18.4	18.4/25.3	23.0/29.9	27.6/34.5	Control
Age (years)					
Basal area before and after thinning (m^2/ha)					
15	40.0/11.5	38.1/18.4	42.0/23.0	42.3/27.6	39.7
17	16.5/11.5	24.6/18.4	29.6/23.0	33.8/27.6	45.7
20	17.7/12.4	26.9/18.6	32.1/23.2	36.3/27.8	53.5/41.4
23†	17.6/14.4	25.7/23.4	31.7/27.3	35.6/31.5	45.2/39.4
Average diameter (dbhob) before and after thinning (cm)					
15	19.0/23.9	18.7/21.9	19.6/22.2	19.5/21.5	19.4
17	28.6/30.0	25.3/26.4	25.1/26.4	23.8/25.1	21.0
20	37.2/38.6	31.9/33.3	31.2/33.3	28.8/30.4	22.8/27.5
23†	46.0/46.1	39.2/39.3	38.5/38.3	34.4/34.3	28.7/28.9
Stocking (stems/ha)					
15	1404/257	1286/489	1394/596	1421/759	1347
17	257/163	489/336	596/420	759/556	1320
20	163/106	336/213	420/267	556/383	1312/699
23†	106/86	213/193	267/237	383/341	699/600
Stand mean height (m)					
15	21.3	21.0	21.6	21.9	21.3
23	28.2	28.0	28.5	28.6	28.0

* All data converted from Imperial units to SI metric units.
Conversion factors: ft^2/ac × 0.229568 = m^2/ha
in. × 2.54 = cm
ft × 0.3048 = m
stems/ac ÷ 0.404686 = stems/ha

† Only the sample trees for this study were thinned at age 23 years.

weight loss for several conifers by Bray & Gorham (1964). Young foliage in the crown of radiata pine tends to have a higher moisture content and respire less than older foliage (Wood 1969) which suggests that the correction factor might vary with leaf age class, but data on this are unavailable. Errors resulting from the use of a single correction factor will probably be small.

The 330 sampled branches were stratified into decile height classes (class interval 10% of total height) (Table 2). One-year foliage was present on all branches; however, some branches, particularly in the upper height deciles, did not carry 2-year or 3-year and older foliage. No foliage occurred below the 20–30% height decile. Regression equations were calculated to relate the weight of leaves to branch cross-sectional area. This was done for each age class and for all ages combined. Data were transformed logarithmically as the allometric model ln(leaf weight) *v.* ln(branch sectional area) was found to give the best relationship. Data were pooled across all 5 treatments as relationships for individual treatments did not differ significantly. Where regressions for adjacent deciles were not significantly different, a pooled regression was obtained. Linear regressions on logarithmically transformed data have been used extensively in

TABLE 2—Distribution of sampled branches across height deciles

Decile	No. of branches with foliage of age 1-year	2-year	3-year and older
20–30	8] *	8] *	8] *
30–40	30	30	30
40–50	32	32	32
50–60	48	48	48
60–70	43	43	41
70–80	57	57	52
80–90	62	62	47] †
90–100	50	41	7
Total	330	321	265

* Data from these deciles were combined as 8 points were insufficient for satisfactory regressions and graphical inspection suggested relationships between foliage biomass and branch sectional area for the 2 deciles were similar.

† Data for the 3-year and older foliage in these deciles were combined for the same reasons as above.

forest biomass studies both for comparing treatment effects and summing component weights. Problems associated with this procedure have been discussed by Baskerville (1972) and Madgwick & Jackson (1974).

Total foliage biomass by height decile and age class for each of the 56 sample trees was obtained by applying the calculated allometric relationships to measured diameters of all branches on these trees. All estimates were corrected for bias arising from use of ln–ln relationships by the method described in Baskerville (1972) and Beauchamp & Olson (1973). Many recent researchers have incorporated this correction into their models (e.g., Clark & Schroeder 1977; Brenneman *et al.* 1978).

In upper deciles, where 2- or 3-year and older foliage did not occur on some branches, overestimates of biomass in the age classes were obtained in the initial application of the regressions. This arose as the regressions were developed for data only from branches where foliage was present. From the sampled branch data (Table 2), the proportion (p) of branches in each decile not carrying 2- or 3-year and older foliage was estimated. Chi-squared tests showed that there was no difference between treatments in any of these proportions. Thus, for the sectional area of each measured branch, a random number between 0 and 1 was generated. If this number was between 0 and p, a foliage weight of zero was taken; if the number was between p and 1, the regression estimate of weight was taken.

In order to extend the foliage biomass estimates for the 56 sample trees to the whole stand, relationships between estimated foliage biomass per tree and tree variables* d, d_b, d × h, and g × h were investigated. For reasons discussed later, estimates of total foliage biomass were obtained for the whole stand for each treatment from the allometric model relating total foliage biomass per tree to d, again correcting for bias in ln–ln regression.

* d, d_b, h, and g are diameter of stem overbark at 1.3 m, diameter at the base of the green crown, total height, and tree basal area respectively.

RESULTS

Relationships between branch cross-sectional area and foliage weight for each age class and height decile are summarised in Table 3. For 1-year foliage and all ages combined relationships are good ($r^2 > 0.7$); however, those for some deciles in 2-year and 3-year and older foliage are weaker but still highly significant.

Application of these relationships to all branches on the 56 sample trees yielded foliage biomass estimates for each tree. As a consequence of using the same regressions for all treatments to estimate foliage biomass, and the similar wide range in branch size (< 1 cm to 6 cm) in all treatments (Siemon *et al.* 1976), thinning had no effect on the percentage distribution of foliage by age class within height deciles. Thus percentage distributions of total weights over all 56 trees, hence treatments, are presented in Table 4. These percentages give some indication of average distribution of foliage biomass by leaf age in this stand of radiata pine. One- and 2-year-old leaves in the crown comprised 73% of total leaf weight. For all deciles below the 70–80% decile, the distribution of foliage across age classes was approximately constant; however, in the upper 3 deciles the percentage of 1-year foliage increased acropetally from 52 to 75% whereas that of 2-year and 3-year and older foliage decreased slightly (28 to 22%) and markedly (20 to 3%) respectively.

Within each treatment, total biomass within deciles was calculated over all trees sampled. These values indicate the average distribution of leaf biomass across height deciles for a stand of that treatment. Thus the effect of thinning on the distribution of biomass across deciles is determined by comparing these distributions (Table 5). Trees in heavily thinned stands generally carry a greater proportion of their foliage lower down the stem than trees in lightly thinned stands. Since the regression relationships were the same for all treatments, these differences in proportions reflect the greater average branch size and greater numbers of branches in lower deciles of trees in thinned stands. Live foliage did not occur below the 40–50% height decile in the very lightly thinned control (Treatment 6) but ranged from 8% in Treatment 5 to 15% in the most heavily thinned stand (Treatment 1). Differences between treatments for percentage distribution of foliage biomass are consistent over all age classes, with 1-year foliage having slightly higher percentages in upper height deciles and slightly lower percentages in lower deciles, 3-year and older foliage exhibiting the opposite trend and 2-year foliage approximating the overall distribution.

To obtain estimates of stand leaf biomass from the biomass estimates for the 56 sample trees, relationships between various stem variables and leaf biomass per tree were investigated. Table 6 sets out the results of linear and allometric regression relationships for each of 4 stem variables and foliage age class. Linear relationships generally differed between treatments whereas the allometric relationships did not. Since there was only a relatively small number of trees per treatment (between 8 and 16), using individual treatment regressions to estimate biomass would have proved unsatisfactory. Consequently allometric relationships based on all 56 trees were preferable. There was little to choose between d and d_b as predictors of biomass among the stem variables tested. However, d is much simpler and much less costly to assess. Thus d was measured on the remaining trees in the stands as a basis for predicting stand leaf biomass. Regression coefficients used for this are presented in Table 7 and stand estimates averaged over plots within

TABLE 3—Linear regression constants relating ln (foliage biomass) (g) within a height decile to ln (branch cross-sectional area) (cm^2). All thinning treatments combined

	Foliage age															
	1-year				2-year				3-year & older				All ages combined			
Ht. decile	a	b	S_b(%)	r^2	a	b	S_b(%)	r^2	a	b	S_b(%)	r^2	a	b	S_b(%)	r^2
90–100	3.097	1.007	7.0	0.81	1.960	0.748	22.7	0.33 †								
									1.307	0.690	18.2	0.37	3.314	1.013	3.7	0.87
80–90					1.775	1.070	7.1	0.77								
	2.824	1.054	4.0	0.84												
70–80									2.277	0.684	25.5	0.23	3.697	0.942	7.9	0.75
60–70					2.081	1.083	4.4	0.78								
50–60																
	2.151	1.123	4.9	0.72												
40–50					1.415	1.309	11.5	0.72	1.864	1.146	7.2	0.55	3.128	1.137	4.7	0.74
20–40 *					2.333	0.894	14.7	0.56								

* Deciles 20–30 and 30–40 were combined because of insufficient branches in decile 20–30.

† Deciles 80–90 and 90–100 were combined for 3-year and older foliage because of insufficient branches in decile 90–100.

All regressions significant at $P < 0.001$.

TABLE 4—Percentage distribution of leaf biomass by age class within height deciles in the crown of 23-year-old radiata pine. All thinning treatments combined

Height decile (% of total ht.)	Foliage age 1-year	2-year	3-year and older
90-100	75	22	3
80-90	65	26	8
70-80	52	28	20
60-70	36	29	35
50-60	36	29	35
40-50	37	27	36
30-40	37	27	36
20-30	37	27	36
All deciles	45	28	27

TABLE 5—Percentage distribution of leaf biomass by treatments across height deciles in the crown of 23-year-old radiata pine

Height decile (% of total ht.)	Treatment 1	3	4	5	6
90-100	2	3	4	5	7
80-90	10	14	13	14	17
70-80	21	22	21	22	28
60-70	26	18	23	20	23
50-60	17	17	19	19	20
40-50	9	12	11	12	5
30-40	11	10	8	7	NIL
20-30	4	4	2	1	NIL

treatments are given in Table 8. Estimated weights of all ages of foliage increase with increase in stand density. Weights of 2- and 3-year and older foliage are similar at each density and approximate from 65% (at 15 m^2/ha) down to 55% (at 46 m^2/ha) of the biomass of 1-year foliage.

DISCUSSION

Few data have been published on the relative contribution of leaves of different ages to the total weight of foliage in the crown of radiata pine. In the present study of 23-year-old trees, 1- and 2-year-old leaves together comprised 73% of the total foliage biomass irrespective of the past thinning history of the stand. This percentage is less than figures recorded by other workers after the complete harvesting of younger trees, e.g., 82% for a 6-year-old tree in the Australian Capital Territory (Wood 1974) and 75–77% for 5- to 7-year-old trees in Kaingaroa Forest, New Zealand (Rook & Whyte 1976). The reason for the lower figure in 23-year-old trees is not known but we feel that an increased longevity of needles as trees age might be involved. A high proportion of 1- and 2-year leaves would seem essential for good growth of radiata pine because this foliage has been shown to be photosynthetically more efficient (Wood 1969; Rook & Brown, quoted by Rook & Whyte 1976).

TABLE 6—Statistics for regressions relating total foliage biomass per tree to various stem variables

Foliage age class	Variable	Linear relationships: Signif. of diffs. between regressions for each treatment		Linear relationships: Regression for all treatments combined[3]		Allometric relationships[4]: Regression for all treatments combined	
		Slopes[1]	Intercepts[2]	r^2	RMS	r^2	RMS
1-year	d	**	—	—	—	0.91	0.0203
	d_b	**	—	—	—	0.90	0.0224
	d × h	**	—	—	—	0.87	0.0279
	g × h	NS	NS	0.91	3.4039	0.90	0.0227
2-year	d	*	—	—	—	0.90	0.0266
	d_b	*	—	—	—	0.91	0.0257
	d × h	*	—	—	—	0.87	0.0360
	g × h	NS	NS	0.90	1.5964	0.89	0.0296
3-year and older	d	NS	NS	0.84	2.9002	0.87	0.0432
	d_b	NS	NS	0.82	3.1147	0.90	0.0336
	d × h	*	—	—	—	0.83	0.0561
	g × h	NS	NS	0.85	2.6092	0.85	0.0479
All ages	d	*	—	—	—	0.90	0.0252
	d_b	**	—	—	—	0.90	0.0243
	d × h	**	—	—	—	0.87	0.0343
	g × h	NS	NS	0.89	20.0860	0.89	0.0282

(1) **, $P < 0.01$; *, $P < 0.05$; NS, not significant.

(2) Testing between intercepts is not meaningful when slopes are significantly different.

(3) Pooled regression not obtained when difference between treatment regressions was significant.

(4) All differences in slope and intercept between regressions for each treatment were not significant.

TABLE 7—Linear regression constants for estimating ln (foliage biomass : kg) from ln (d : cm)

Foliage age (years)	Regression constants: Intercept	Slope	s_b	r^2	RMS
1	—5.829	2.314	0.100	0.91	0.0203
2	—7.299	2.583	0.115	0.90	0.0266
3 and over	—7.954	2.753	0.147	0.87	0.0432
All ages combined	—5.672	2.481	0.112	0.90	0.0252

TABLE 8—Estimates of foliage biomass (tonnes/ha) for 23-year-old radiata pine at various stand densities

Thinning treatment	Stand density	Foliage age (years) 1		2		3 & over		All ages combined	
	(m^2/ha)	$\bar{x}$	s*	$\bar{x}$	s*	$\bar{x}$	s*	$\bar{x}$	s*
1	~ 15	2.20	0.08	1.42	0.05	1.43	0.06	4.89	0.18
3	~ 21	3.10	0.08	1.93	0.05	1.89	0.06	6.74	0.18
4	~ 26	3.75	0.08	2.33	0.05	2.28	0.06	8.14	0.18
5	~ 31	4.11	0.08	2.47	0.05	2.37	0.06	8.74	0.18
6	~ 46	5.40	0.11	3.16	0.08	2.98	0.08	11.29	0.25

* Standard deviations are based on the error terms from analyses of variance comparing treatments.

In forest biomass studies, the weight of various tree components is commonly related to an easily measured stem variable for the purpose of predicting biomass. The regression of foliage weight against a parameter of stem size found most suitable in this study was that with d (cf. Weetman & Harland 1964; Baskerville 1965; Gary 1976). As stated earlier, regressions based on d were comparable with those based on d_b (Table 6), and d is so much simpler to measure on standing trees. The variables g × h and d × h have been used successfully by Young *et al.* (1964) and Forrest & Ovington (1970) respectively. Loomis *et al.* (1966) found d_b to be the best predictor of branch and foliage biomass in *P. echinata,* and Madgwick (1979) reports it to be a slightly better predictor for both *P. radiata* and *P. virginiana.*

The field trial had a wide range of thinning treatments, ranging from plots with trees in a freely growing condition without aerial competition to closed stands including severely suppressed trees on the point of death. Nevertheless, there is no significant difference between treatments for regression equations relating leaf weight per branch (by leaf age class and total) to branch sectional area or for those relating total leaf weight per tree (again by leaf age class and total) to d, i.e., stem diameter at breast height. The slopes of regressions used to predict total foliage biomass of trees ranged from 2.31 for 1-year leaves to 2.75 for 3-year and older leaves and was 2.48 for all leaves combined (Table 7). These are consistent with coefficients of 1.70 and 3.32 recorded by Forrest (1969) for 5- and 12-year-old stands of radiata pine respectively.

Though the regression equations are independent of thinning, branches and trees differ between treatments in both size and frequency. Consequently there are marked differences between treatments in the weights of leaves for trees of a given size and in the total weight of foliage per unit area. Total foliage weight ranged from 4.9 tonnes/ha in the least dense to 11.3 tonnes/ha in the most dense stands (Table 8) but these are likely to be slight underestimates due to bias resulting from factors, apart from size, affecting the relationship between leaf weight and branch size (Madgwick & Jackson 1974).

The proportions of leaves within each age class were independent of thinning. Consequently it seems either leaf efficiency varies markedly between treatments or, more probably, within the heavily thinned stands the tree crop is not fully utilising the site. This is supported by observation made at the time of sampling that undergrowth was present in all but the control plots. An independent study, conducted within the experimental area 12 months after sampling for this present study, indicated the total amounts of vegetation subordinate to the main crop were 1.25, 0.91, 0.25, and 0.08 tonnes/ha for thinning treatments 1, 3, 5, and 6 with stand basal areas of 18.5, 27.6, 39.1, and 50.6 m^2/ha respectively (Forrest, unpubl. data). Comparison of stand volume increments reported by Shepherd & Forrest (1973) also supports the conclusion that heavily thinned plots are less than fully productive.

Möller (1947) proposed the classic theory that within a wide range of stand densities the amount of foliage in stands of a given species remains constant with age and differs little with site. This proposal has been confirmed by many researchers working in diverse forest types, including Senda & Satoo (1956), Ovington (1957), and Hutnik & Hickok (1967).

Möller (1947) showed constant foliage biomass in stands of both *Picea abies* (L.) Karst. and *Fagus sylvatica* L., the latter including 50-year-old stands at basal areas ranging from 18 to 35 m^2/ha. This range corresponds with that of Treatments 3 to 5 of the present study, but here foliage biomass decreases with decreasing stand density (Table 8). Possibly the regular thinning of the stands every 2–3 years is a contributing factor. Average leaf life of radiata pine is 3–4 years so stands might not regain full canopy structure in the interval between thinnings. Whatever the explanation, it appears that thinning has a much more lasting effect on foliage production in radiata pine than in spruce and beech. A similar conclusion was drawn by Madgwick & Olson (1974) for yellow poplar (*Liriodendron tulipifera* L.). Thus, the evidence suggests that Möller's theory does not apply to managed radiata pine plantations in southern New South Wales. This is not surprising because a relatively intolerant conifer such as *Pinus radiata* might be expected to react differently under a heavy thinning regime from the shade tolerant conifer *Picea abies* and the extremely shade tolerant deciduous species, *Fagus sylvatica,* thinned under the light European regimes. Möller himself was careful to point out that his theory cannot with assurance be extended to all other species and conditions (Möller 1954).

The maximum estimate of foliage biomass in this study was 11.3 tonnes/ha in a stand of density 46 m^2/ha. This biomass is about 25% higher than estimates of 9 tonnes/ha (G* 47 m^2/ha: Will 1964) and 9.2 tonnes/ha (G 33 m^2/ha: Forrest &

* G = stand basal area

Ovington 1970) for unthinned 12-year-old radiata pine stands in New Zealand and Australia respectively. This finding does not support Forrest & Ovington's (1970) suggestion that after the 10th year, foliage biomass in unthinned stands stabilises at just less than 10 tonnes/ha with possibly a very gradual decrease with time.

Tadaki (1966) reviewed published work on leaf biomass in forest trees and stands and concluded that a reasonable total leaf biomass for *Pinus* forest is 5–6 tonnes dry weight/ha. This estimate is conservative for stands of *Pinus contorta, P. radiata, P. resinosa,* and *P. sylvestris,* particularly stands with basal area exceeding 30 m^2/ha (Fig. 1).

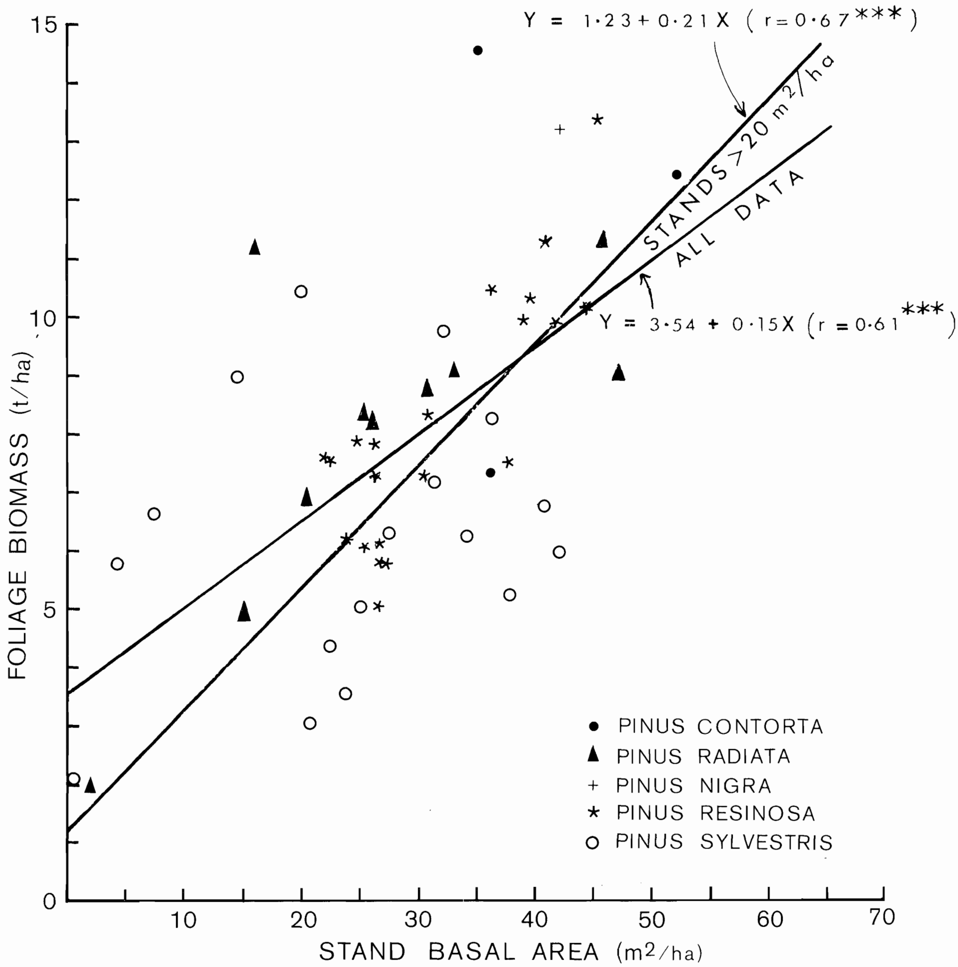

FIG. 1—Relationship between total foliage biomass and stand basal area in **Pinus** stands. Sources of data: **P. contorta** (Johnstone 1972).
P. radiata (Will 1964; Forrest & Ovington 1970; present study).
P. nigra (Ovington 1957).
P. resinosa (H. A. I. Madgwick, unpubl. data).
P. sylvestris (Ovington 1957; Ovington & Madgwick 1959; H. A. I. Madgwick, unpubl. data).

Foliage biomass and stand basal area are related and it is surprising that basal area often either is not recorded or is excluded from results in forest biomass studies. Reference to the literature indicates that the foliage biomass for a number of *Pinus* species averages 0.25 ± 0.06 tonnes/m^2 of basal area in stands exceeding 20 m^2/ha. In less dense stands the mass per unit of stand basal area is greater (Fig. 2). This probably reflects ontogenetic differences or reduced competitive effects in younger and/or more open stands.

Annual foliage production was assessed as the mean biomass of 1- and 2-year foliage to overcome problems involved in sampling foliage produced in a single year (Madgwick 1970). This estimate may differ from actual annual production because it does not allow fully for factors such as any decline in the weight of leaves at the

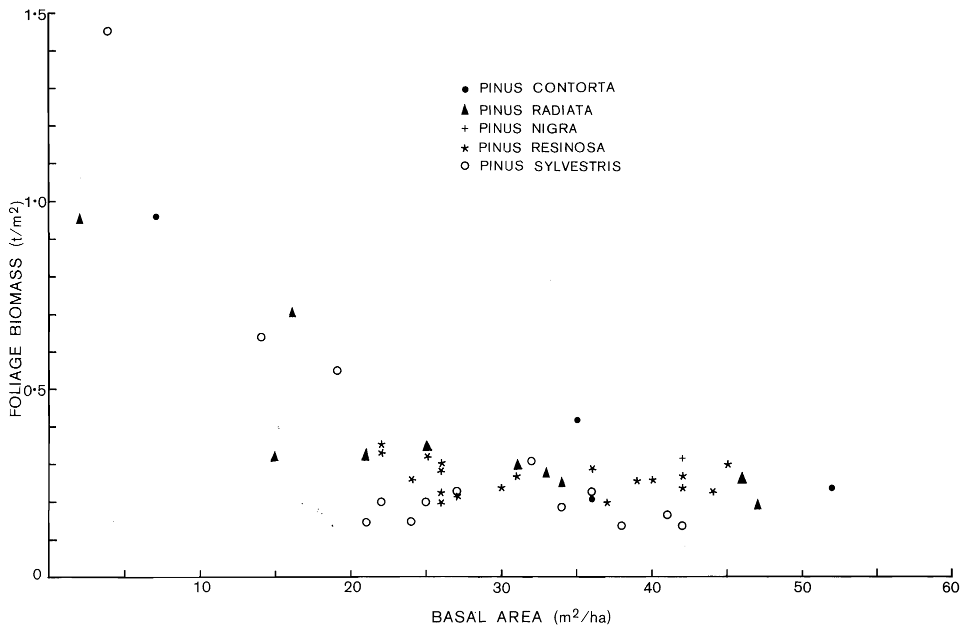

FIG. 2—Total foliage biomass per unit of stand density. Sources of data: see Fig. 1.

TABLE 9—Annual foliage production in **Pinus** stands of basal area exceeding 20 m^2/ha

Species	Age range (years)	Basal area range (m^2/ha)	No. of plots	Annual production (tonnes/ha) Range	$\bar{x}$	s
P. radiata D. Don(1)	23 only	21–46	14	2.4–4.3	3.1	0.6
P. resinosa Ait.(2)	29–32	22–45	20	2.1–3.3	2.8	0.4
P. sylvestris L.(3)	23–71	21–42	12	1.5–4.0	2.7	0.7

(1) Data of present study.
(2) Data ex Dr H. A. I. Madgwick (unpubl.).
(3) Data ex Dr H. A. I. Madgwick (unpubl.) and Ovington (1957).

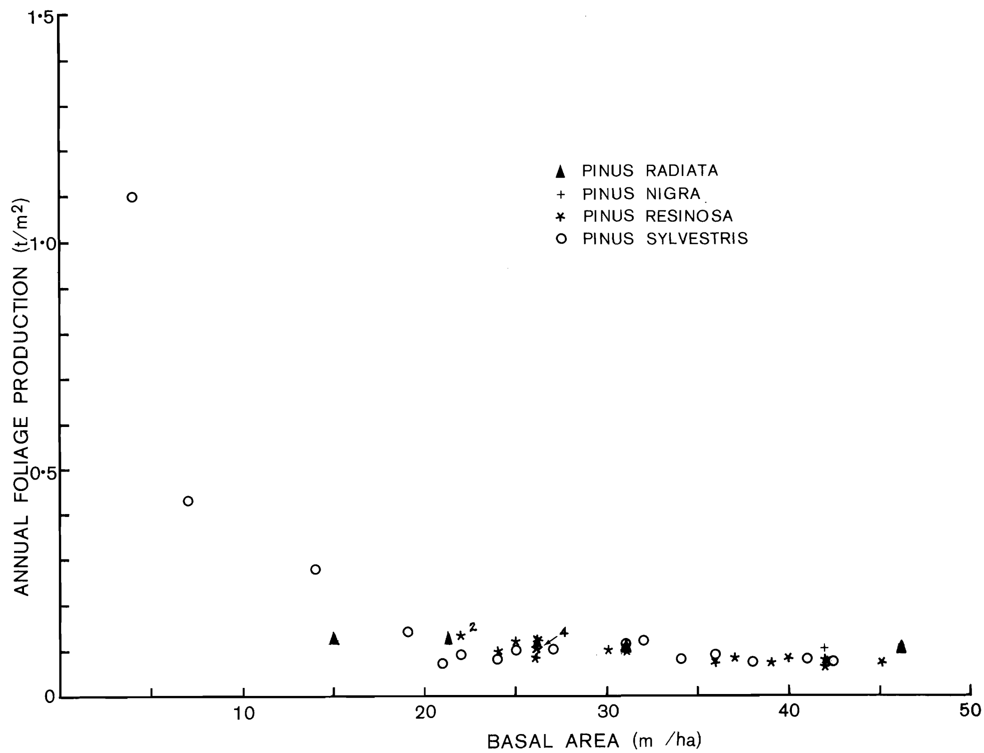

FIG. 3—Annual foliage production per unit of stand density. Sources of data: see Fig. 1.

end of the growing season, losses due to insects, pathogens and other causes, and the year-to-year variation in foliage production referred to by Bray & Gorham (1964). Annual production in stands of radiata pine of density greater than 20 m^2 basal area ranged from 2.4 to 4.3 tonnes/ha and averaged 3.1 tonnes/ha. This is comparable with 3 tonnes/ha estimated by Forrest (1969) for younger radiata pine of similar stand density, but slightly higher than production in red pine and Scots pine stands of similar density (Table 9). Production per unit of stand density is also slightly higher in radiata pine and averaged 0.11 $\pm$ 0.01 tonnes/m^2 compared to 0.09 $\pm$ 0.02 tonnes in both red pine (21 observations) and Scots pine (12 observations). In less dense stands, production appears to increase sharply paralleling the increase in total foliage biomass per unit of stand density noted earlier (Figs 2, 3).

ACKNOWLEDGMENTS

This study was supported by a Commonwealth Postgraduate Scholarship awarded to the Senior Author. The Forestry Commission of N.S.W. is thanked for permission to undertake the study in Green Hills State Forest, Tumut, and for the use of other unpublished data. The authors are grateful also to Dr H. A. I. Madgwick for access to unpublished biomass data on red pine and Scots pine (Table 9).

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