

SEASONAL CHANGES IN THE BIOMASS OF A YOUNG PINUS RADIATA STAND

H. A. I. MADGWICK

Forest Research Institute, New Zealand Forest Service,
Private Bag, Rotorua, New Zealand

(Received for publication 10 November 1982; revision 18 January 1983)

ABSTRACT

The dry matter content of above-ground components of a clonal plantation of *Pinus radiata* D. Don was estimated at eight intervals throughout its fifth growing season after planting. Total above-ground dry matter increment over the 11-month period was 20 t/ha. Stem increment varied from less than 1 t/ha/month in winter to 3 t/ha/month in summer. Branch growth was approximately 3 t/ha/annum and occurred mostly in spring and summer. Production of 5 t new foliage/ha followed a sigmoid growth curve similar to other pine species and was predominantly restricted to a 4-month period late spring and early summer.

INTRODUCTION

The growth of young *P. radiata* trees around Rotorua is characterised by a seasonal maximum of height extension in spring and of basal area increase in late summer with increases in both diameter and height occurring in all months (Jackson *et al.* 1976). Studies of a variety of pine species have indicated marked seasonal fluctuations in needle mass with seasonal maxima 1.2 to 2.0 times the minima (Hatiya *et al.* 1966; Rutter 1966; Madgwick 1968; Satoo 1971). Seasonal changes have also been found in branch biomass (Hatiya *et al.* 1966; Madgwick 1968).

Published studies on the biomass of *P. radiata* have neglected seasonal effects. This paper presents information on seasonal changes in the biomass of a young *P. radiata* stand approaching canopy closure. In order to facilitate comparisons with Northern Hemisphere results, dates are expressed as season and the New Zealand winter of June, July, August, is assumed to coincide with the Northern Hemisphere winter of December, January, February.

MATERIAL AND METHODS

The sample stand was located near the Forest Research Institute, Rotorua, and comprised a randomised block layout of nine clones (FRI No. 448, 450, 451, 454, 455, 456, 457, 459, and 460) grown from juvenile cuttings and planted at a square spacing of 1.2 m giving 6730 stems/ha. The stand was first sampled at age 4 years when canopy closure was nearing completion. At that time branch death at the base of the crown was negligible, but ground vegetation was absent. The site is a well-

drained, uniform, sandy-loam pumice soil with unrestricted rooting depth. Foliage samples from the same nine clones on an adjacent site have been studied by Knight (1978). Nitrogen and phosphorus levels were close to those accepted as the threshold of deficiency. Two clones (450 and 459) displayed needle tip chlorosis and these clones had the lowest magnesium levels of the nine clones examined.

Six replicates of the nine clones were measured for total height and diameter at breast height at approximately 6-week intervals from late autumn (April) 1971 to autumn (March) 1972. At the beginning of the period of observation all branch clusters were labelled and their position along the stem was measured. All branches were numbered and those bearing needles ("live branches") were measured for diameter 25 mm from the stem. At each subsequent measurement 36 sample branches were removed for detailed study. Four branches were taken from each of the nine clones, one from each of four of the six replicates. Two individuals per clone were left unsampled so that, at the completion of the study, final tree size could be examined for any effect of sampling on growth. The four sample branches of each clone at each sampling date were selected in a stratified random way taking one branch from each of four approximately equal layers within the crown (i.e., upper, upper middle, lower middle, and lower crown positions) based on the numbers of branch clusters present at each sampling date.

Sample branches were taken to the laboratory where they were measured for length and diameter and the number of growth flushes was recorded. They were then divided into their components by year of initiation. For each component the total numbers of fascicles and fascicle scars were counted. Bark and wood were separated and composited for each branch, and the needles, bark, and wood were dried at 65°C and weighed.

The canopy weight for each component and the total numbers of fascicles and fascicle scars by age class (X) were determined using the formula:

$$X = \frac{\sum x_i}{\sum d_i^2} \cdot \sum D^2$$

where x_i is the value of the variable in question for the i^{th} sample branch having a branch diameter of d_i at the first measurement date, and $\sum D^2$ is the sum of all branch diameters squared for the first measurement date. Branches emerging during the growing season were recorded as having a zero value of d .

Twenty-three trees in another part of the stand were sampled at the beginning of the observation period, and 30 trees at the end, to develop regressions for estimating stem weight from diameter at breast height (1.4 m) and height. These regressions were used to estimate stem weights from stem diameter and height measured at each sampling date. Stand values per unit land area were obtained by multiplying estimated average tree weight by stocking.

RESULTS

The weather as recorded at the Institute during the year of sampling was both wetter and warmer than average (Fig. 1). Mean temperatures exceeded the long-term average in all months except January 1972 and on average were 1.1°C warmer. Total

precipitation for the year was 2036 mm, 40% above the long-term average, though month-to-month variation was very large with exceptionally heavy falls in May 1971 (late autumn) and March 1972 (early autumn).

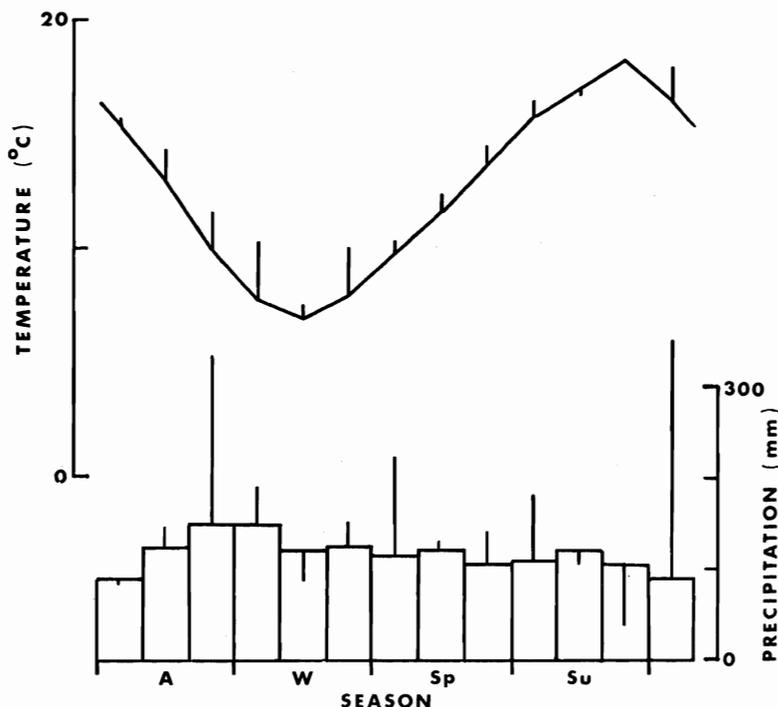


FIG. 1—Long-term monthly mean temperature and precipitation. Vertical lines indicate the departures of actual monthly values from long-term averages.

At the beginning of the observation period the trees had an average height of 3.69 m, and the tree of mean basal area had a diameter of 4.8 cm (Table 1). After 47 weeks of observation mean height was 5.5 m and diameter 6.6 cm. The basal area of the stand increased from 12.1 to 23.0 m²/ha over the same period. Branch sampling appeared to have decreased annual increment by about 10% compared with trees from which no branches had been removed.

There were 2131 live branches on the 54 trees at the beginning of the experiment and 2483 at the conclusion. In addition 288 branches were removed in sampling and 369 branches died during the year of observation.

The average height of the lowest branch cluster carrying a live branch was 0.37 m at the beginning of the experiment. Death alone raised this by 0.04 m, and death and sampling combined raised the lowest live branch 0.15 m during the year. The branches had a very erratic flushing behaviour; thus, sample branches which were attached to the stem three growth-flushes from the top of the tree had produced one to five flushes with a mean of two flushes (Fig. 2). The number of flushes per year decreased down the crown.

TABLE 1—Average size of sample trees at the beginning of observation and average seasonal development (effects of branch sampling and genotype on seasonal development are given as differences between actual and expected increment)

Variable	Initial size	Seasonal increment	Sampling effect		Genotypic effects	
			Size	t-value	Clone No.	Effect
Height (cm)	369	181	-19	2.1	448	-53
d.b.h. (mm)	48	18	-2	2.1	448	+5
					451	+6
No. of branches	51	18	-3	1.3	451	+11
Branch basal area (cm ²)	34	18	-1	1.3	451	+9
					460	-7

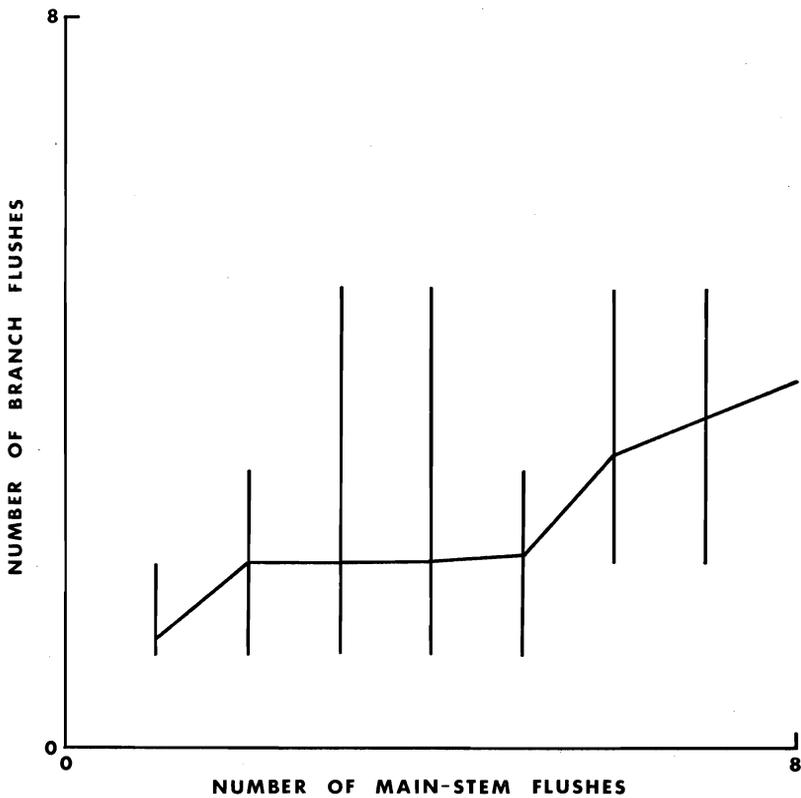


FIG. 2—Mean and range of numbers of growth flushes on sample branches compared with the number of growth flushes on the main stem above the sample branch (based on 72 branches).

TABLE 2—Estimated total numbers of fascicle scars in each age class at eight sampling dates (millions per hectare)

Needle age	Autumn	Winter		Spring		Summer		Autumn	Mean	S.E.
	29/4	2/7	6/8	Sampling date (day/month)		12/12	15/1	20/3		
				17/9	1/11					
Current	0.0	0.0	N.D.	51.5	144.0	185.1	168.1	138.3	—	—
1-year	120.1	155.2	146.7	164.7	127.3	100.9	120.2	159.4	136.8	8.1
2-year	22.8	28.6	36.2	62.3	54.6	37.2	42.0	42.1	40.7	4.6
3-year	3.2	8.2	6.7	9.8	19.9	16.3	13.3	5.8	10.4	2.0
4-year	0.5	0.3	0.0	0.7	4.7	0.0	1.8	0.5	1.1	9.6
Total 1-4	146.6	192.4	189.6	237.4	206.6	154.4	177.3	207.8	189.0	10.5

N.D. = not determined

The estimated total numbers of fascicle scars in each age class are given in Table 2. For fascicle scars at least 1 year old, the eight sampling dates represent eight separate estimates of the numbers present. Since there were 619 small dead branches at the base of the crowns at the beginning of the period of observation, the tabulated numbers of scars will tend to under-estimate the numbers of fascicles produced. From the fifth sampling (late spring) onward the number of current fascicle scars averaged 25% higher than the number of 1-year-old scars.

At the first sampling the observed percentages of 1-, 2-, and 3-year-old needles remaining on the tree were 97, 39, and 0, respectively (Table 3). Needles of all ages were shed throughout the period of observation. Relative losses of needles, particularly of current needles, were greatest in the lower crown where shoots or complete branches died (Fig. 3).

TABLE 3—Average percentage of needle numbers retained

Needle age	Autumn		Winter		Spring		Summer		Autumn
	Sampling date (day/month)								
	29/4	2/7	6/8	17/9	1/11	12/12	15/1	20/3	
Current	—	—	100	100	97	99	99	95	
1-year	97	94	91	94	68	93	69	69	
2-year	39	25	20	16	10	24	22	11	
3-year	0	0	0	trace	1	0	0	0	

Needle retention and the numbers of fascicle scars in each needle age-class were both reflected in the estimated weights of foliage on the stand. From late autumn to late spring the total weight of foliage remained fairly constant; it then increased rapidly over the next 6-week period as the main flush of needle growth took place (Table 4). In part, the stability of foliage weight during spring reflected a technical problem — very small, immature, needles could not be separated easily from the shoots and were weighed with the branch bark, so providing a positive bias to bark weight during the middle of the observation period, when branch elongation was rapid.

During the period studied there was an apparent marked seasonal shift in the allocation of dry matter increment among the various components. From late autumn to late winter almost all growth occurred in the stem, which increased in estimated weight by about 20%. No increment in crown dry matter was detected in this period and the sample branches examined in late winter had increased in diameter by only 1%. Detectable crown weight increment had almost stopped by mid summer but active bole increment continued at least into the final period of measurement. Branches and foliage appear to grow over a longer period but this is because there is a relatively small number of shoots flushing near the tops of the trees.

At the beginning of the period of observation the trees carried the equivalent of 0.05 t dead branches/ha and 57% of stem and branch growth had occurred as stem wood. During the 11 months of detailed study 73% of stem and branch increment was stem wood.

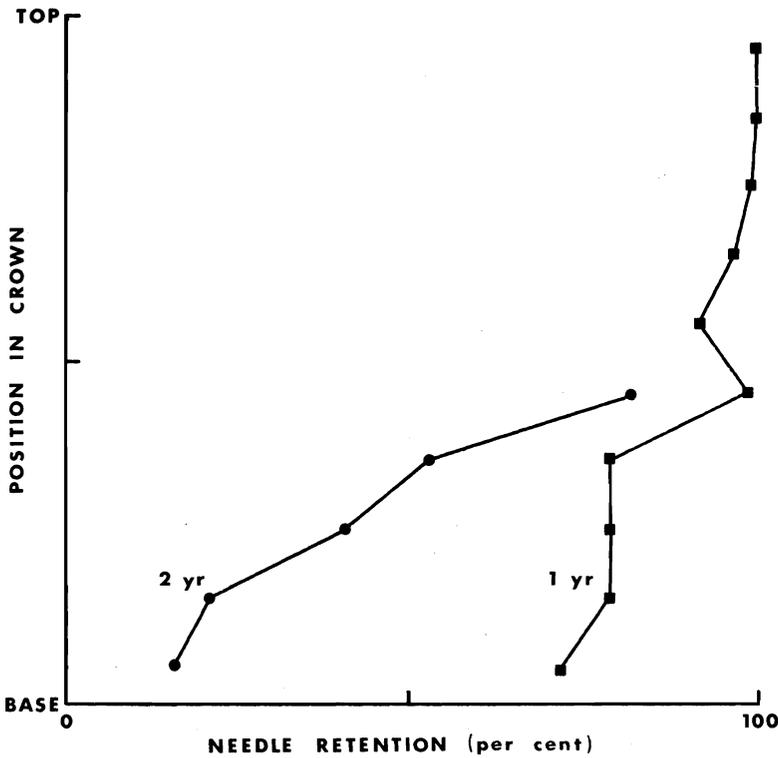


FIG. 3—Effect of position in crown on the numbers of 1- and 2-year-old needles retained, averaged over all sampling dates.

DISCUSSION

The total growth of the above-ground part of the stand amounted to about 20 t dry matter/ha over 11 months. This compared with an estimated average current increment of 28 t/ha/annum for a nearby stand of similar stocking between ages 5 and 13 years (Madgwick 1981). Differences between the two values reflect the lower foliage mass, height growth, and basal area of the stand reported here. The heights of the two stands at age 5 years were 5.5 and 7.7 m respectively, and their basal areas 23 and 30 m²/ha. These differences are too large to be accounted for by variations in soil, given that the two sites are adjacent, or by differences in the type of planting stock, namely seedlings and juvenile cuttings *per se*. Comparable growth rates of seedlings and juvenile cuttings have been reported for *P. radiata* by Sherry (1947) and Brown (1974), and Sherry also noted that the form of plants derived from 2-year ortets and that of seedlings were comparable. However, at the time when the stand described in this paper was established, techniques for handling cuttings in New Zealand, or differences in planting stock size, could have affected stand growth (Sweet 1973).

Pinus radiata crown development is characterised by a number of growth flushes per year, with the number varying among genotypes (Burdon 1971) and decreasing from the apex to the base of the crown. The sum of the growth of the various flushes

TABLE 4—Estimated dry weights (t/ha) of above-ground components at eight sampling dates

Component	Autumn	Winter		Spring		Summer		Autumn
	29/4	2/7	6/8	Sampling date (day/month)		12/12	15/1	20/3
				17/9	1/11			
Needles								
Current	0.0	0.0	trace	0.3	1.1	4.8	5.2	4.7
1-year	6.6	6.3	6.9	5.9	5.5	5.4	4.2	4.3
2-year	0.6	0.5	0.4	0.5	0.2	0.4	0.5	0.3
3-year	0.0	0.0	0.0	trace	trace	0.0	trace	0.0
Total	7.2	6.8	7.3	6.7	6.8	10.6	9.9	9.3
Branches								
Bark	1.7	1.7	2.0	2.5	2.5	3.1	2.5	2.4
Wood	3.9	3.2	3.7	4.4	4.6	5.4	6.1	6.5
Total	5.7	4.9	5.7	6.9	7.1	8.5	8.6	8.9
Stems								
Bark	1.7	1.8	1.9	2.1	2.3	2.5	2.8	3.0
Wood	9.7	11.0	11.9	13.0	15.3	17.2	19.9	22.1
Total	11.4	12.8	13.8	15.1	17.6	19.7	22.7	25.1
TOTAL	24.3	24.5	26.8	29.0	31.5	38.8	41.2	43.3

in spring resulted in a typical sigmoid growth curve for current foliage (Fig. 4) which occurred earlier in the season than, but otherwise closely paralleled, the development pattern of growth reported for *Pinus densiflora* Siebold (Hatiya *et al.* 1966; Satoo 1971) and *P. virginiana* Mill. (Madgwick 1968). A similar growth pattern has been observed for *P. taeda* L. which also produces multiple growth flushes (Smith *et al.* 1971).

Loss of older foliage varies considerably within a species, as can be seen by comparing data for *P. densiflora* (Hatiya *et al.* 1966; Satoo 1971) as illustrated in Fig. 5. The similarity in the results for *P. radiata*, *P. virginiana* (Madgwick 1968), and *P. densiflora* (Satoo 1971) may be fortuitous. Loss of older foliage is affected by nutrition (Madgwick *et al.* 1970) and, in some cases, tree age (Madgwick *et al.* 1977). Comparison of the estimated percentage needle retention at the beginning and end of the period of observation (Table 3) suggests that retention in the year of observation may have exceeded that in the previous year. The decrease in needle retention towards the base of the crown appears to contradict the findings of Burdon (1976) for *P. radiata* and Maillette (1982) on *Pinus nigra* var. *maritima* (Ait.) Melville for which needle retention was greatest low in the crown.

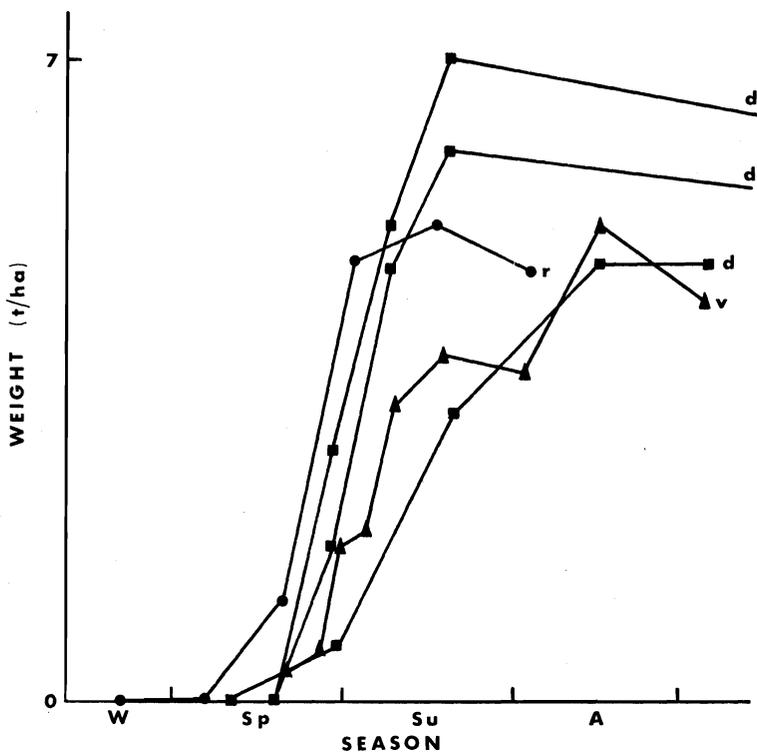


FIG. 4—Seasonal development of new needles on three species of pine (d, *P. densiflora*; r, *P. radiata*; v, *P. virginiana*). (*Pinus densiflora* data from Hatiya *et al.* 1966 and Satoo 1971; *P. radiata* this paper; *P. virginiana*, Madgwick 1968.)

The total weight of foliage on a stand is the net result of initiation and growth of new needles and the loss of old needles. *Pinus densiflora*, *P. radiata*, and *P. virginiana* stands cited and *P. sylvestris* L. (Rutter 1966) all show a summer maximum (Fig. 6). The relative fluctuations from maximum to minimum and the dates of occurrence of these extremes are dependent on differences in the amounts and dates of initiation, growth, and loss of needles which will be affected by season (Kishchenko 1978; Orlov 1980), site (Madgwick *et al.* 1970), species (Ewers & Schmid 1981), tree age (Madgwick *et al.* 1977), and through its effect on canopy depth, stocking (Beekhuis 1965). In the *P. radiata* stand a comparison of the age distribution of foliage at the beginning and end of the period of observation indicates the effects of increasing stand closure. In the first 4 years of growth the amount of foliage produced annually will have increased approximately logarithmically but with increasing stand closure there will be a transition towards a more uniform distribution of age classes of needles.

Marked shifts in the distribution of growth among the above-ground components appeared to occur throughout the year. Part of this shift was an artifact since emerging needles were not separated from bark on young expanding shoots. The differential loss of foliage within the crown (Fig. 3), coupled with the effects of needle position on needle weight, tends to obscure estimates of needle growth. Both Rutter (1957) and

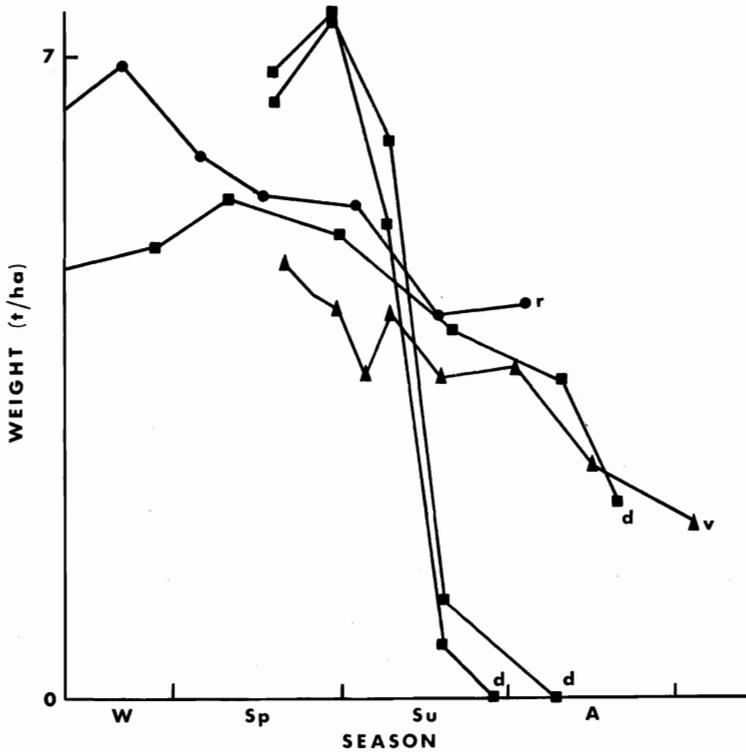


FIG. 5—Seasonal change in total weight of 1-year-old needles on stands of three species of pine (Key as for Fig. 4).

Smith *et al.* (1971), working with *P. sylvestris* and *P. taeda* respectively, have shown that substantial increases in needle weight occur during the winter months. The static values of canopy needle mass during the winter period when needle fall in *P. radiata* occurs (Will 1959) indicate that growth of individual needles must be occurring in this species, too. A comparison of the average weight of individual needles (which may be obtained by combining data from Tables 2, 3, and 4) is hardly justified since the average weight per needle varied almost 10-fold between the top and base of the crown, and the average values obtained at any sampling were subject to large errors. Additional difficulties arise in estimating stem weight growth as a constant proportion of volume increment. Volume increment reflects seasonal changes in rates of cell division and expansion but does not account for changes in the rates of cell wall thickening.

ACKNOWLEDGMENTS

This study was suggested by Dr D. S. Jackson and was made possible by the support of a Senior Research Fellowship. The encouragement and assistance provided by Dr Jackson and other staff of the Forest Research Institute are highly valued.

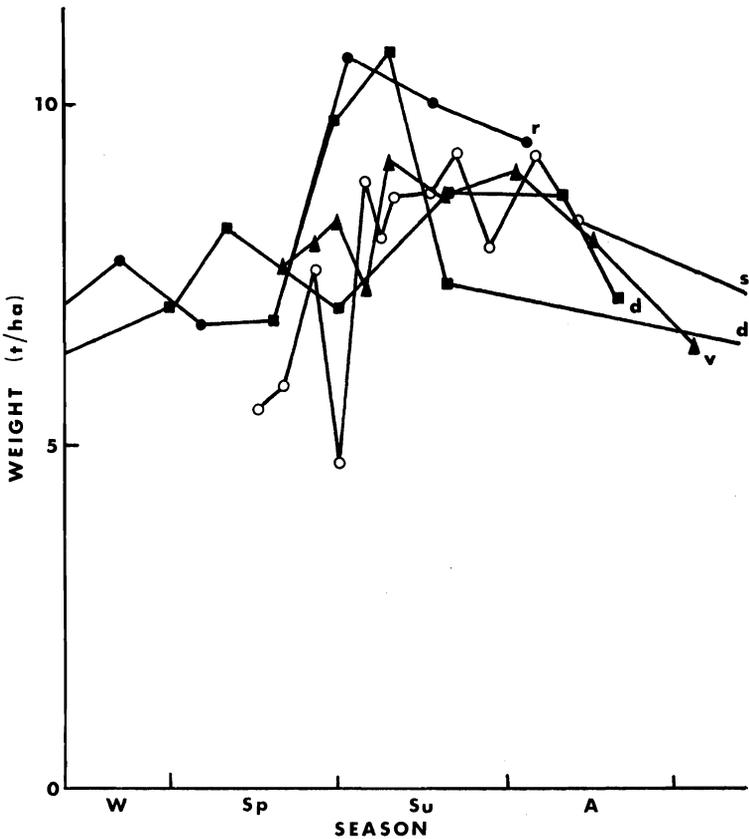


FIG. 6—Seasonal change in total foliage mass on stands of four species of pine (Key as for Fig. 4 plus s, *P. sylvestris* from Rutter 1966).

REFERENCES

- BEEKHUIS, J. 1965: Crown depth of radiata pine in relation to stand density and height. *New Zealand Journal of Forestry* 10: 42-61.
- BROWN, A. G. 1974: Comparison of early growth in radiata pines raised by cuttings from parents of different ages with that of seedling trees. *Australian Forestry Research* 6(3): 43-7.
- BURDON, R. D. 1971: Clonal repeatabilities and clone-site interactions in *Pinus radiata*. *Silvae Genetica* 20: 33-9.
- 1976: Foliar macronutrient concentrations and foliage retention in radiata pine clones on four sites. *New Zealand Journal of Forestry Science* 5: 250-9.
- EWERS, F. W.; SCHMID, R. 1981: Longevity of needle fascicles of *Pinus longaeva* (Bristlecone pine) and other North American pines. *Oecologia* 51: 107-15.
- HATIYA, K.; FUJIMORI, T.; TOCHIAKI, K.; ANDO, T. 1966: Studies on the seasonal variations of leaf and leaf-fall amount in Japanese red pine (*Pinus densiflora*) stands. *Bulletin of the Government Forest Experiment Station No. 191*: 101-13.

- JACKSON, D. S.; GIFFORD, H. H.; CHITTENDEN, J. 1976: Environmental variables influencing the increment of *Pinus radiata*: (2) Effects of seasonal drought on height and diameter increment. **New Zealand Journal of Forestry Science** 5: 265-86.
- KISHCHENKO, I. T. 1978: Seasonal growth of pine needles in different forest types of southern Karelia. **Lesovedenie No. 2**: 29-32.
- KNIGHT, P. J. 1978: Foliar concentrations of ten mineral nutrients in nine *Pinus radiata* clones during a 15-month period. **New Zealand Journal of Forestry Science** 8: 351-68.
- MADGWICK, H. A. I. 1968: Seasonal changes in biomass and annual production of an old-field *Pinus virginiana* stand. **Ecology** 49: 149-52.
- 1981: Above-ground dry-matter content of a young close-spaced *Pinus radiata* stand. **New Zealand Journal of Forestry Science** 11: 203-9.
- MADGWICK, H. A. I.; JACKSON, D. S.; KNIGHT, P. J. 1977: Above-ground dry matter, energy, and nutrient contents of trees in an age series of *Pinus radiata* plantations. **New Zealand Journal of Forestry Science** 7: 445-68.
- MADGWICK, H. A. I.; WHITE, E. H.; XYDIAS, G. K.; LEAF, A. L. 1970: Biomass of *Pinus resinosa* in relation to potassium nutrition. **Forest Science** 16: 154-9.
- MAILLETTE, L. 1982: Needle demography and growth pattern of Corsican pine. **Canadian Journal of Botany** 60: 105-16.
- ORLOV, A. Ya. 1980: Dynamics of needle mass in pine stands. **Lesovedenie No. 1**: 34-41.
- RUTTER, A. J. 1957: Studies in the growth of young plants of *Pinus sylvestris* L. 1. The annual cycle of assimilation and growth. **Annals of Botany N.S.** 21: 399-426.
- 1966: Studies on the water relations of *Pinus sylvestris* in plantation conditions. IV. Direct observations on the rates of transpiration, evaporation of intercepted water, and evaporation from the soil surface. **Journal of Applied Ecology** 3: 393-405.
- SATOO, T. 1971: Primary production relations of coniferous forests in Japan. Pp. 191-205 in Duvigneaud, P. (Ed.) "Productivity of Forest Ecosystems". Proceedings of the Brussels Symposium, 1969. UNESCO, Paris.
- SHERRY, S. P. 1947: The potentialities of genetic research in South African forestry. British Empire Forestry Conference, Great Britain, 1947. 11 p.
- SMITH, W. H.; NELSON, L. E.; SWITZER, G. L. 1971: Development of the shoot system of young loblolly pine. II. Dry matter and nitrogen accumulation. **Forest Science** 17: 55-62.
- SWEET, G. B. 1973: The effect of maturation on the growth and form of vegetative propagules of radiata pine. **New Zealand Journal of Forestry Science** 3: 191-210.
- WILL, G. M. 1958: Nutrient return in litter and rainfall under some exotic-conifer stands in New Zealand. **New Zealand Journal of Agricultural Research** 2: 719-34.