PARTIAL DEFOLIATION AND GROWTH OF 5-YEAR-OLD RADIATA PINE

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ABSTRACT

Five-year-old trees of **Pinus radiata** D. Don were artificially defoliated by removing needles of various ages according to 19 treatments ranging from no removal to complete defoliation. Growth was followed for up to two years after defoliation. Removal of 3- to 4-year-old foliage in early spring generally did not cause significant losses in increment, but in combination with removal of 2- to 3-year-old foliage caused losses of up to 15 percent. Removal of 1- to 2-year-old foliage reduced height, basal area, and volume growth by 20, 43 and 51 percent respectively; in combination with removal of 2- to 3-year-old foliage, losses increased to 26, 63, and 70 percent. Removal of the current year's foliage as it was formed caused height, basal area, and volume growth losses of 53, 73 and 77 percent respectively over the two years. Growth was most severely reduced for trees defoliated in September, less so in December, and still less so for March or June treatments. Trees completely defoliated appeared to recover slowly, but further defoliation killed all the trees. Partial defoliations resulted in no mortality, but all treatments caused a drop in growth, the biggest with removal of the current year's foliage and the smallest with removal of 3- to 4-year-old foliage. An equation of the form of a slowly increasing parabola is presented to quantify volume increment losses in terms of degree of defoliation.

Although results here are quantitatively different from other studies they show also that, with severe partial defoliation, basal area and volume growth are reduced more than height growth.

INTRODUCTION

The growth of a tree depends directly on its foliage mass and on the photosynthetic efficiency of that foliage. Thus, growth can be markedly reduced when part of the crown is removed in a silvicultural treatment such as pruning, or as a result of fungal or insect attack. In evaluating the potential impact of an insect or fungal defoliator, it is important to be able to predict accurately what loss of increment will occur and how growth of different parts of the tree is affected by different intensities of defoliation. Although some information is available on the effect of degree of defoliation on stem growth (e.g., Austara, 1970), this is based on work with species other than *Pinus radiata* and in countries differing in climate from New Zealand. Applicability of these other studies to young *P. radiata* growing in New Zealand is questionable. Moreover, many of these studies have been concerned with removing a certain proportion of the tree crown from the base upwards, as in pruning trials, and have not been designed to investigate the effect of removing different age classes of foliage *per se.* The aim of this study was to determine the loss of height, basal area, and volume increment of young *P. radiata* trees defoliated to known and different intensities, in terms of various age classes of foliage. In the first part of the study, all the defoliation treatments were carried out at the beginning of the growing season and growth was followed over a period of 2 years; in the second part, the trees were defoliated at different seasons of the year and growth was followed for up to 18 months after defoliation. This approach was designed to provide information on what age of foliage needs to be preserved to prevent undue loss of growth of young *P. radiata* growing in New Zealand.

EXPERIMENT 1 — *Materials and Methods*

Nine defoliation treatments were carried out in early September 1966 on trees in a 5-year-old aerially sown stand of radiata pine (in Compartment 1250, Kaingaroa Forest) which had been thinned the previous year to a spacing of about 2.0 × 2.0 m.

The nine treatments were as follows:,

S0 Control; no needles removed.

S0-1 0- to 1-year-old needles removed as they were formed throughout the year, i.e., from September 1966 to September 1967.

S1-2 1- to 2-year-old foliage removed, i.e., needles produced during the 1965-66 growing season.

S2-3 2- to 3-year-old foliage removed, i.e., needles produced during the 1964-65 growing season.

S3-4 3- to 4-year-old foliage removed, i.e., needles produced during the 1963-64 growing season.

S1-2-3 1- to 2- and 2- to 3-year-old foliage removed, i.e., needles produced between September 1964 to September 1966.

S2-3-4 2- to 3- and 3- to 4-year-old foliage removed, i.e., needles produced between September 1963 and September 1965.

S*all,c* Complete defoliation and continued removal of any new needles.

S*all,6* Complete defoliation; new growth left for 6 months, then completely defoliated again.

The trees were defoliated by plucking off the needles, causing as little damage as possible. Where young soft tissue was encountered, the needles were cut off with scissors.

Only medium-sized trees, selected on the basis of total height, were included for defoliation; the variation in the height of the trees selected, however, still ranged from

170 to 285 cm. Six trees were allocated at random to each treatment. Growth was followed for 2 years after the partial defoliation treatments were applied, except for trees in the two complete defoliations, S*all,c* and S*all,6,* all of which had died before the end of the first year. These trees were felled 1 year after being defoliated.

At the start of the second growing season there was evidence of the presence of *Dothistroma pini,* and all trees were sprayed with cuprous oxide at the rate of 2.24 kg/ha active ingredient. Trees of the two complete defoliation treatments, S*all,c* and S*all,6,* were attacked by *Diplodia pinea,* probably at least partly as a result of being severely weakened by having been completely defoliated.

At the time when the partial defoliations were carried out, an additional 18 medium-sized trees were selected to determine the average distribution of foliage of different age classes within the tree crowns. Twelve of these trees were felled in September 1966, and six in September 1968; the latter date was the time of the final harvest. The foliage was stripped according to age class and the oven-dry weight of each age class of foliage was determined after being dried 48 h at 80°C. Although these foliage determinations were made in early September, some 0- to 1-year-old foliage was present, but it amounted to less than 5% of the total foliage mass. Many individual trees begin their "spring" flush prematurely in late autumn (April or May), and this growth flush is merely arrested during the winter months. The foliage of the premature spring growth was not included in the calculations of the percentage distribution of foliage by age classes presented in Table 1.

The main stems of the six trees harvested in 1968 were subdivided into 20-cm lengths to determine the age class distribution of foliage with percentage height (Fig. 1).

At the time that the defoliations were carried out, the heights of the trees were measured and the mid-points between branch clusters were marked on the main stem. The overbark diameters of these mid-points were measured with precision calipers and recorded, together with their heights above ground level. The trees were remeasured

TABLE 1—The proportions by weight of foliage of 5- and 7-year-old radiata pine at Kaingaroa

Foliage age class (yr)	Trees: 5-yr-old 1966 Dry wt ± s.e. (g)	Trees: 5-yr-old 1966 Percentage of total	Trees: 7-yr-old 1968 Dry wt ± s.e. (g)	Trees: 7-yr-old 1968 Percentage of total
0-1	—	—	—	—
1-2	31 ± 4	75	1449 ± 196	77
2-3	8 ± 1	20	399 ± 94	21
3-4	2 ± 1	5	39 ± 10	2

15 times during the 2 years after partial defoliation treatment. The average time between measurements was seven weeks. The times were somewhat shorter during the periods of rapid growth in spring and summer than during autumn and winter.

Growth in height, basal area, and volume of the six trees per treatment was calculated over the 2-year period following defoliation. Stem volume was obtained by summing the volumes of sections using Smalian's formula (Spurr, 1952).

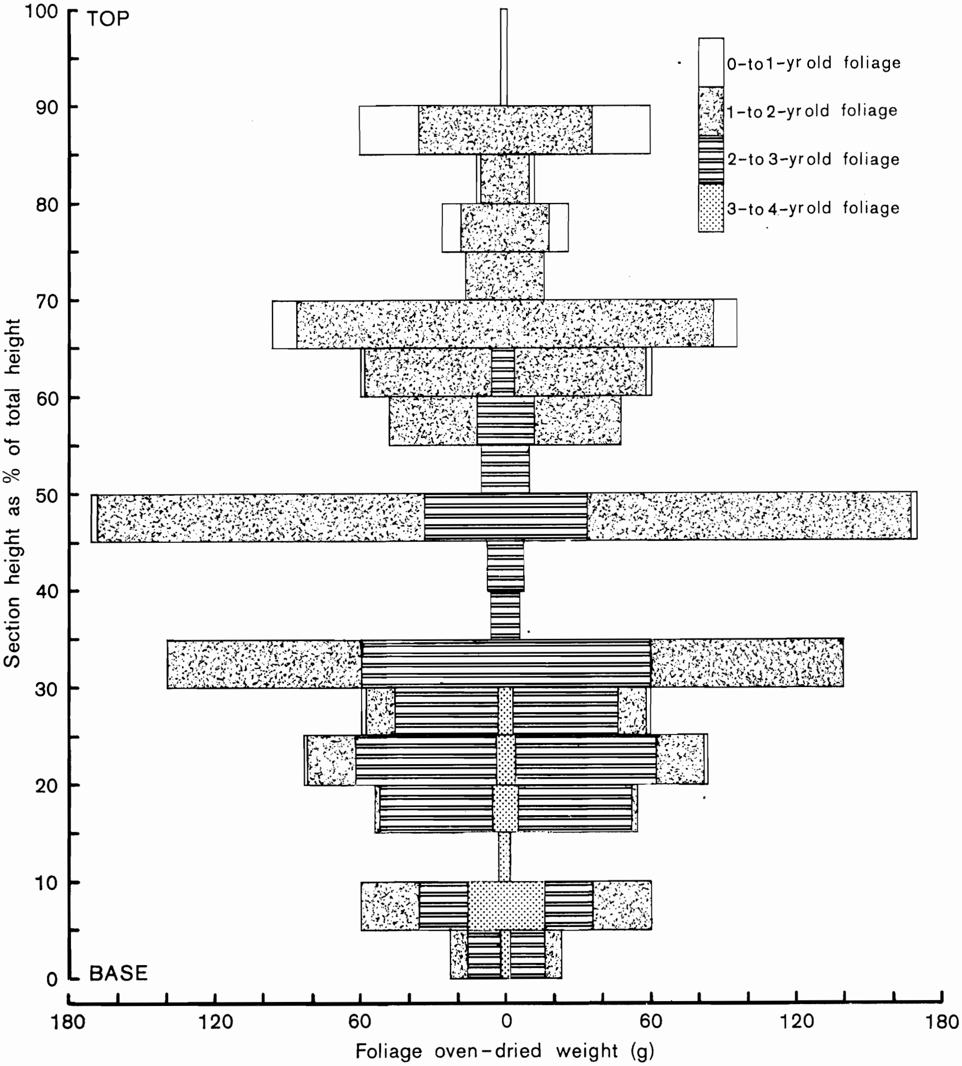


FIG. 1—Distribution of foliage by age classes within the crown.

Individual treatment means were adjusted by analyses of covariance (straight line model assumed) to compensate for differences in initial size, and treatment differences were then compared using Scheffé's method (Freese, 1967). The values plotted in Figs. 2-4 inclusive are also adjusted by covariance.

EXPERIMENT 1—*Results*

Height increment

In the first year after defoliation, no difference in height growth after adjustment by covariance could be detected among *S0, S3-4,* and *S2-3-4* (Table 2). The treatment *S2-3* did not result in a height increment significantly less than that for *S2-3-4,* but it was different from *S0* and *S3-4.* Heights of *S0-1* and *S1-2* did not differ significantly from each other, and were approximately 37% less than that of *S0.* Of the three remaining treatments, height growth of *S1-2-3* was significantly greater than that of both S*all,c* and S*all,6,* which in turn did not differ one from the other.

In the second year, height increments of *S0* and *S2-3-4* could not be separated but that of *S3-4* was significantly less than both, having 16% less height growth than *S0* (Table 2). Treatments *S1-2, S2-3, S3-4* and *S1-2-3* formed a tightly knit group, which showed a substantially greater amount of height growth than *S0-1* which had only 26% of the height growth of *S0.* Trees in the complete defoliation treatments were all dead by the second year.

For both years together, no difference in total height increment could be detected among *S0, S3-4,* and *S2-3-4.* Height increment of *S2-3* was only 75% of *S0* (Table 2), a significant reduction, but that of *S2-3* did not differ significantly from either *S3-4* or *S2-3-4* and it was not significantly greater than that of *S1-2* over the 2 years.

These same differences are depicted graphically in Fig. 2 which shows intra-seasonal trends also. The pattern of growth is upset only for *S0-1,* the growth of which was not in any way impaired until 5 months after the defoliation, and for *S2-3* which showed a sudden decline about 15 months after the defoliation.

TABLE 2—Mean height growth ($\Delta\bar{h}_i$) of the defoliation treatments during October 1966-67, 1967-68, and 1966-68 expressed in cm and as a percentage of S_0 for these periods

1966 to 1967 Treatment	$\Delta\bar{h}_i$ (cm)	$\times \frac{100}{S_0}$	1967 to 1968 Treatment	$\Delta\bar{h}_i$ (cm)	$\times \frac{100}{S_0}$	1966 to 1968 Treatment	$\Delta\bar{h}_i$ (cm)	$\times \frac{100}{S_0}$
S_{3-4}	139	105	S_0	236	100	S_0	368	100
S_0	132	100	S_{2-3-4}	229	97	S_{2-3-4}	352	96
S_{2-3-4}	126	95	S_{1-2}	198	84	S_{3-4}	331	90
S_{2-3}	118	89	S_{2-3}	194	82	S_{2-3}	313	85
S_{0-1}	97	63	S_{3-4}	191	81	S_{1-2}	294	80
S_{1-2}	95	62	S_{1-2-3}	190	80	S_{1-2-3}	272	74
S_{1-2-3}	78	59	S_{0-1}	61	26	S_{0-1}	156	42
$S_{all,6}$	22	17						
$S_{all,c}$	13	10						

Vertical line indicates treatments not different at the 5% significance level.

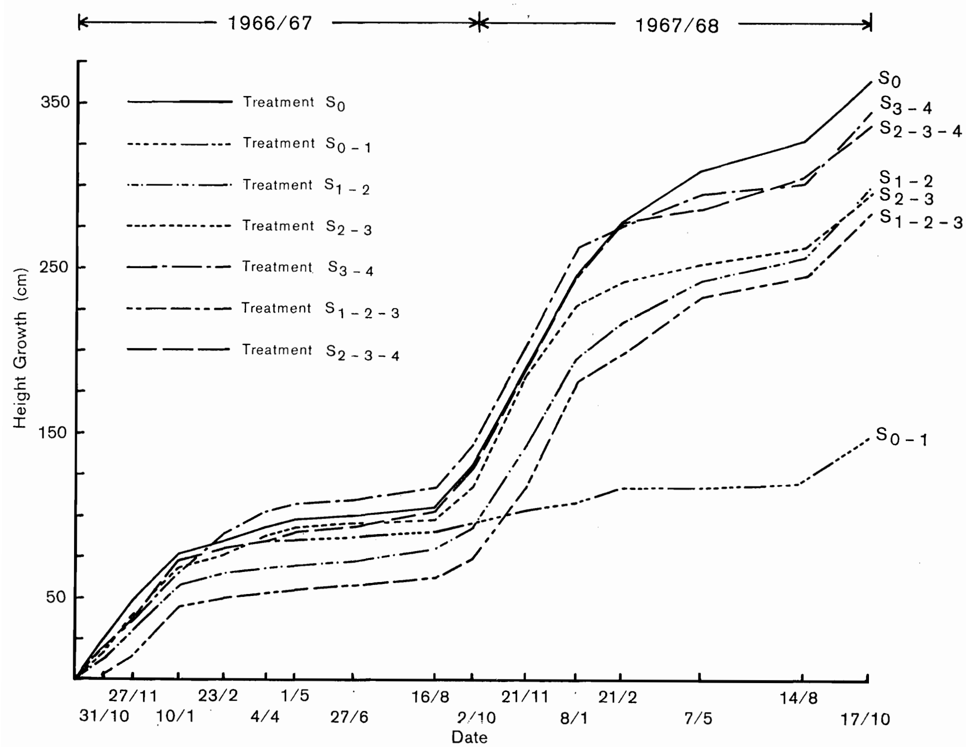


FIG. 2—Effect of September partial defoliation treatments on height growth.

Basal Area Increment

In the year after defoliation, only S*2-3* grew the same in basal area as the control, S*0* (Table 3). Basal areas of S*3-4* and S*2-3-4* were about 15% less than that of S*0*, a difference which was statistically significant at the 5% level. Treatments S*0-1* and S*1-2* formed the next group in descending order with losses of about 50% and these were very highly significantly different from each of S*0*, S*2-3*, S*3-4*, and S*2-3-4*. Treatment S*0-1* showed no loss in basal area growth until 5 months after the defoliations, and from then on showed little gain (Fig. 3). Basal area increment for S*1-2-3* was very much lower than for any of those treatments just mentioned, S*all,6* was even lower, and finally S*all,c* showed almost no growth in basal area at all.

In the second year, basal area increments of S*2-3-4*, S*2-3*, and S*3-4* were not significantly different from that of S*0*. Compared with S0, S*1-2* showed a highly significant loss of about 40%, S*1-2-3* of more than 50%, and S*0-1* of more than 80%.

Over both years there was no significant difference in basal area growth among S*0*, S*2-3*, S*3-4*, and S*2-3-4*, but that for S*1-2* was almost 40% lower than that of S*0* and those for S*1-2-3* and S*0-1* were approx. 60 and 70% lower.

TABLE 3—Mean basal area increments ($\Delta\bar{g}_i$) of the defoliation treatments during October 1966-67, 1967-68, and from October 1966 to 1968 expressed in cm^2 and as a percentage of S_0 for these periods

1966 to 1967			1967 to 1968			1966 to 1968		
Treatment	$\Delta\bar{g}_i$ (cm^2)	$\times \frac{100}{S_0}$	Treatment	$\Delta\bar{g}_i$ (cm^2)	$\times \frac{100}{S_0}$	Treatment	$\Delta\bar{g}_i$ (cm^2)	$\times \frac{100}{S_0}$
S_0	17.86	100	S_{2-3-4}	38.48	109	S_{2-3-4}	53.48	100
S_{2-3}	17.17	96	S_0	35.37	100	S_0	53.23	100
S_{3-4}	15.43	86	S_{2-3}	33.84	96	S_{2-3}	51.01	95
S_{2-3-4}	15.00	84	S_{3-4}	31.98	90	S_{3-4}	47.41	89
S_{0-1}	8.56	48	S_{1-2}	21.96	62	S_{1-2}	30.25	57
S_{1-2}	8.29	46	S_{1-2-3}	15.35	44	S_{1-2-3}	19.54	37
S_{1-2-3}	4.01	22	S_{0-1}	5.69	16	S_{0-1}	14.25	27
$S_{all,6}$	2.18	12						
$S_{all,c}$	0.36	2						

Vertical line indicates treatments not different at the 5% significance level.

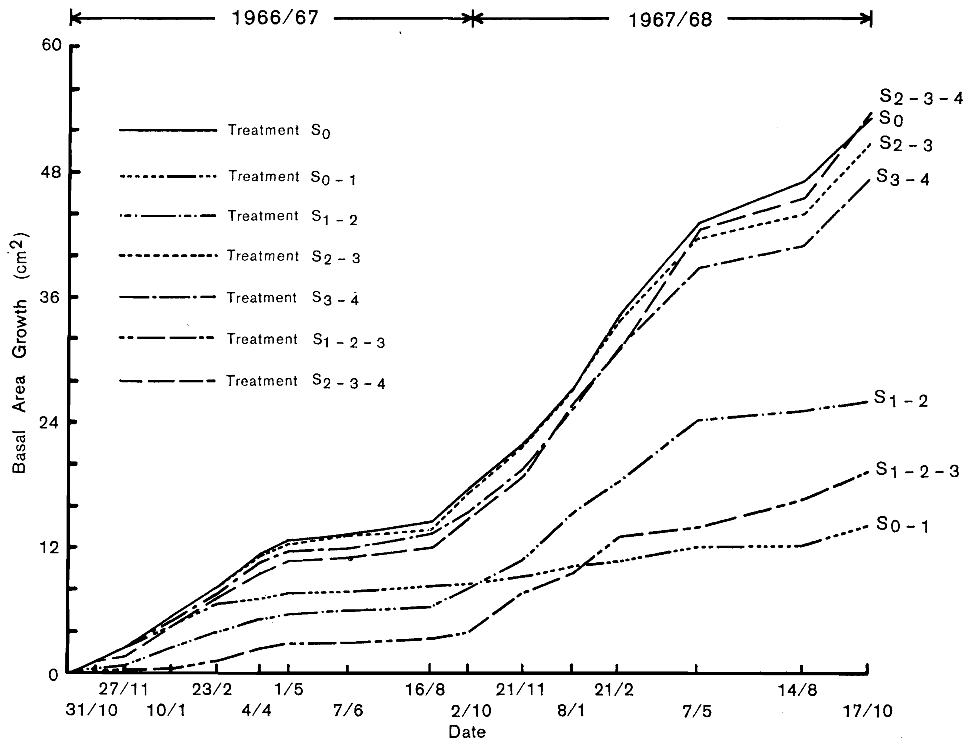


FIG. 3—Effect of September partial defoliation treatments on basal area growth.

Volume Increment

Volume increment in the first year after defoliation was the same for *S0, S3-4,* and *S2-3,* but that for *S2-3-4* was nearly 20% less than for *S0,* a reduction significant at the 5% level (Table 4). Treatments *S1-2* and *S0-1* had each 50%, and *S1-2-3* nearly 80%, less volume increment than *S0,* while *Sall,6* and *Sall,c* put on negligible volume increment before dying.

In the second year after defoliation, only *S3-4* increased as much in volume as *S0* (Table 4). Treatment *S2-3-4* was nearly 15%, *S2-3* more than 30%, *S1-2* more than 50%, *S1-2-3* nearly 70%, and *S0-1* 85% less than *S0.* These were all significantly different from *S0* and from each other.

TABLE 4—Mean volume increments ($\Delta \bar{v}_i$) of the defoliation treatments during October 1966-67, 1967-68, and from October 1966 to October 1968 expressed in cm^3 and as a percentage of S_0 for these periods

1966 to 1967			1967 to 1968			1966 to 1968		
Treatment	$\Delta \bar{v}_i$ (cm^3)	$\times \frac{100}{S_0}$	Treatment	$\Delta \bar{v}_i$ (cm^3)	$\times \frac{100}{S_0}$	Treatment	$\Delta \bar{v}_i$ (cm^3)	$\times \frac{100}{S_0}$
S_0	470	100	S_0	1317	100	S_0	1787	100
S_{3-4}	468	100	S_{3-4}	1252	95	S_{3-4}	1720	96
S_{2-3}	438	93	S_{2-3-4}	1134	86	S_{2-3-4}	1521	85
S_{2-3-4}	387	82	S_{2-3}	902	68	S_{2-3}	1340	75
S_{1-2}	234	50	S_{1-2}	633	48	S_{1-2}	867	49
S_{0-1}	218	46	S_{1-2-3}	433	33	S_{1-2-3}	534	30
S_{1-2-3}	101	21	S_{0-1}	197	15	S_{0-1}	415	23
$S_{all,6}$	29	6						
$S_{all,c}$	16	3						

Vertical line indicates treatments not different at the 5% significance level.

Over the 2-year period, differences from the control were the same as for 1967-68 in both relative order and proportional magnitude except for *S0-1,* the mean volume increment for which was not significantly less than that for *S1-2-3.*

The intra-seasonal trends were again relatively unaltered except for *S0-1,* even for drastic defoliation treatments such as *S1-2-3* (Fig. 4). Volume growth for *S0-1* again remained similar to that of the control, *S0,* and other treatments until 5 months after defoliation when it became less.

EXPERIMENT 2 — *Material and Methods*

Growth was similarly monitored on a further series of nine defoliation treatments between June 1966 and October 1967 in the same compartment but in a block of trees one year younger than those in Experiment 1. The nine treatments were:

C0 Control: no needles removed.

D0-1 0- to 1-year-old needles removed in December 1966, i.e., needles produced from September 1966 to December 1966, and foliage subsequently formed until September 1967.

D*1* + needles 1 year old and older removed in December 1966, i.e., all foliage formed before the 1965-66 growing season was removed.

D*all,c* Complete defoliation in December 1966 and continued removal of any new needles.

M*0-1* 0- to 1-year-old needles removed in March 1967, i.e., needles produced from September 1966 to March 1967, and foliage subsequently formed until September 1967.

M*1* + Needles 1 year old and older removed in March 1967, i.e., all foliage formed before the 1965-66 growing season was removed.

M*all,c* Complete defoliation in March 1967 and continued removal of any new needles.

J*0-1* 0- to 1-year-old needles removed in June 1967, i.e., needles produced from September 1966 to June 1967, and foliage subsequently formed until September 1967.

J*1* + Needles 1 year old and older removed in June 1967, i.e., all foliage formed before the 1965-66 growing season was removed.

J*all,c* Complete defoliation in June 1967 and continued removal of any new needles.

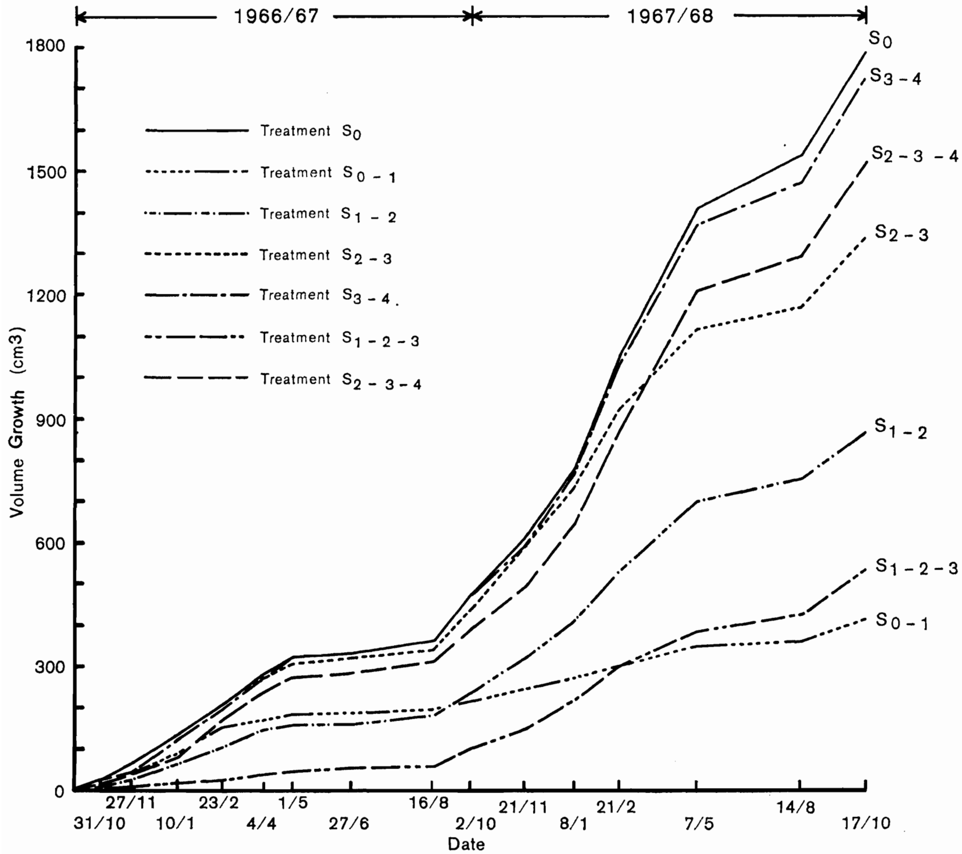


FIG. 4—Effect of September partial defoliation treatments on volume growth.

Thus, the same three defoliation treatments were repeated on three different occasions to give nine defoliation treatments altogether. Again six trees were allocated at random to each of the treatments, and a further six trees were left undefoliated to serve as controls.

Height and diameter at the mid-points between all branch clusters were measured as in Experiment 1 and remeasured every seven weeks or so from June 1967 to October 1968. Growth in height, basal area, and volume was calculated over this period as in Experiment 1 and, similarly, treatment means from June 1967 to August 1968 were adjusted by analyses of covariance.

EXPERIMENT 2 — *Results*

All the trees completely defoliated, whatever the season, died soon after treatment and are omitted, therefore, from subsequent analysis. The remaining treatments follow the same order in their means for height, basal area, and volume increments (Table 5). All defoliations in which current year's foliage (0- to 1-year-old) was removed depressed growth more than did defoliation of 1-year-old and older foliage, and these treatments in turn grew less than the undefoliated controls. Moreover, defoliations in December had more effect than those in March which in turn had more effect than the defoliations in June, except that J*0-1* and M*0-1* are reversed.

Results from September defoliations in Experiment 1 are included in Table 6 along with their nearly comparable counterparts in Experiment 2. This can be considered as forming an earlier series in a continuum of 3-monthly defoliations, except that the September ones are on trees one year older and S*1-2-3* is not exactly the same as D*1*+, or M*1* +, or J*1* +, because in the latter group 3- to 4-year-old foliage was also removed.

The intra-seasonal growth trends from June 1967 to August 1968 in height, basal area, and volume are shown in Figs. 5, 6, and 7, respectively. These patterns of growth are substantially the same for all the defoliation treatments analysed.

DISCUSSION

Wood (1974) examined the spatial distribution of foliage of various ages within the crown of a 5.3-m tall radiata pine sapling growing near Canberra, Australia; the tree was planted 6½ years previously and the average height of the dominants in the stand was about 8 m. Generally there is close agreement in the distribution of foliage between the two studies, except that Wood noted that the 1- to 2- and 2- to 3-year-old foliage classes accounted for 44 and 38% of the total crown foliage, while we found they comprised 77 and 21% respectively of the total crown. The tree Wood examined was about one year older than those in our study and he observed that crown closure was occurring, whereas the trees in our study had rapidly expanding crowns and crown closure had not occurred. Wood noted the presence of 4- to 5-year-old foliage, but the trees in our study obviously had made very little growth over the first 2 years after the stand was established from aerially sown seed and we were not able to detect the presence of foliage of this age.

Overseas studies (e.g., O'Neil, 1962) have shown that trees completely defoliated once may die, but mortality appears to vary markedly depending upon the season of the year in which the trees were defoliated. In this study trees of treatments S*all,c,* D*all,c,* M*all,c,* and J*all,c* were completely defoliated and new leaf growth was removed almost

TABLE 5—Mean height growth ($\Delta\bar{h}_i$), mean basal area growth ($\Delta\bar{g}_i$), and mean volume growth ($\Delta\bar{v}_i$) of the seasonal defoliation treatments during 1967-68 expressed in cm, cm², and cm³ respectively and also as percentages of C_0 from 1967 to 1968

Treatment	$\Delta\bar{h}_i$ (cm)	$\times \frac{100}{C_0}$	$\Delta\bar{g}_i$ (cm²)	$\times \frac{100}{C_0}$	$\Delta\bar{v}_i$ (cm³)	$\times \frac{100}{C_0}$
C_0	216		20.26		663	
J_{1+}	201	93	19.77	98	588	89
M_{1+}	188	87	18.03	89	578	87
D_{1+}	142	66	17.81	88	549	83
M_{0-1}	74	34	6.16	30	146	22
J_{0-1}	61	28	4.70	23	101	15
D_{0-1}	55	26	2.98	15	82	12

Vertical lines indicate treatments not different at the 5% significance level.

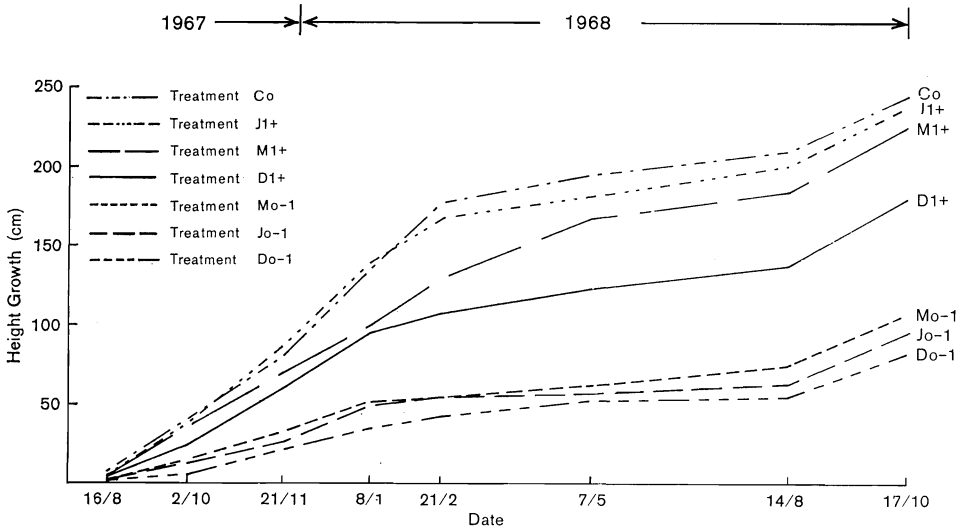


FIG. 5—Effect of season and degree of partial defoliation on height growth.

TABLE 6—Mean height, basal area, and volume increments for seasonal defoliations of 0- to 1-year-old foliage and foliage 1 year old and older expressed as percentages of their corresponding controls

Season of defoliation	Growth as percentage of control					
	0—1 defoliation			1+ defoliation		
	$\Delta\bar{h}_i$	$\Delta\bar{g}_i$	$\Delta\bar{v}_i$	$\Delta\bar{h}_i$	$\Delta\bar{g}_i$	$\Delta\bar{v}_i$
September	16	12	14	83	41	30
December	26	15	12	66	88	83
March	34	30	22	87	89	87
June	28	23	15	93	98	89

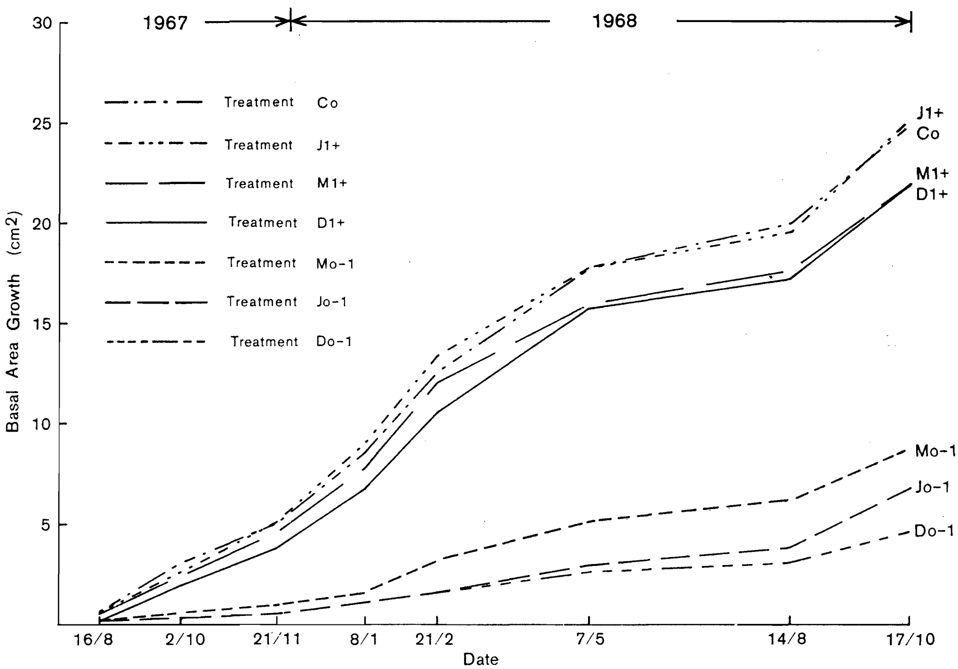


FIG. 6—Effect of season and degree of partial defoliation on basal area growth.

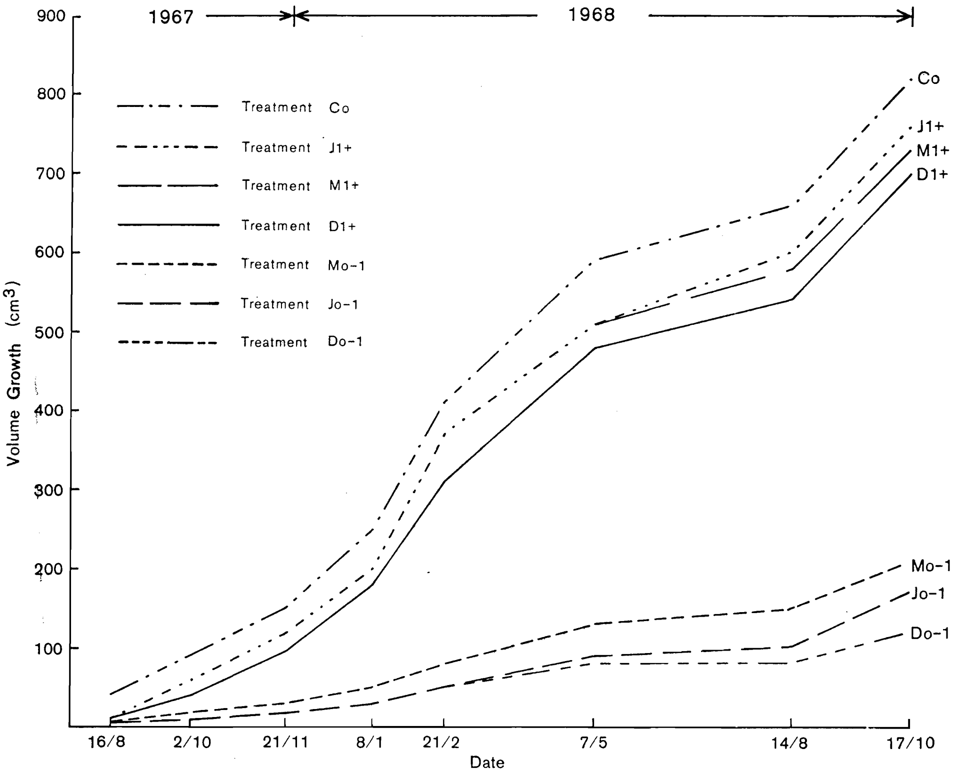


FIG. 7—Effect of season and degree of partial defoliation on volume growth.

as soon as it was formed, but all these trees died 3-4 months after the first defoliation. All trees in S*all,6* also survived the first complete defoliation and appeared to be recovering slowly. When these trees were defoliated a second time 6 months later, all quickly succumbed. Bamber and Humphreys (1965) reported that exhaustion of starch reserves was the probable cause of death of *Eucalyptus* spp. repeatedly defoliated by insects and this is suspected to be the cause of death in these treatments too. There was negligible increment in these treatments and the rest of this discussion will be confined to the other partial defoliation treatments.

Increment in height was substantially affected only by the more severe defoliation treatments, when current and 1- to 2-year-old foliage was removed (Table 2). Furthermore, whereas height growth in S*1-2* and S*1-2-3* was depressed immediately after defoliation, that for S*0-1* proceeded until the following February as though defoliation had not occurred, after which time there was only a very small increase in height.

These results for radiata pine indicate that although height growth is dependent partly on the food reserves assimilated previously, current photosynthetic production makes a major contribution to height growth. In contrast Larson (1964b) in a study with 5-year-old red pine observed that internode extension depended primarily on food reserves. However it is very difficult to compare these two studies since the trees used by Larson were considerably smaller than those used in our study and he followed growth for 3 months only. In our study, by removing current foliage (S*0-1*), height growth in the first year was reduced by 40%. In the following year with no 1- to 2-year-old foliage, with depleted food reserves, and with a reduced amount of new foliage as a consequence of the original treatment, height growth was reduced by over 70%. In contrast, by removing 1-year-old foliage (S*1-2*) height growth was reduced by 40% the first year, but was reduced less than 20% in the second year as new foliage production and, presumably, food reserves were not reduced to the same extent as in S*0-1*.

Foliage over 2 years of age had only a slight effect on height growth; it constituted about 25% of the existing foliage at time of defoliation (Table 1) but it occurred only on the lower two-thirds of the tree, and this may account for its relatively small effect on height increment. Nevertheless, S2-3 presents something of an anomaly in that its height increments in both years were significantly less than those of S*0,* although no different from those of S*3-4* and S*2-3-4,* both of which had height increments similar to that of the control at the 5% significance level.

Although height increments for S*1-2* and S*1-2-3* were about the same in both years, basal area increments were about 20% less for trees of S*1-2-3*. Thus, basal area increment was affected more by reductions of foliage mass than was height increment. This was further illustrated by a much greater reduction in basal area increment than in height increment when 0- to 1-year-old and 1- to 2-year-old foliage was removed. The same was true for volume increment, except that where taper was increased (e.g., S*2-3*), volume increment was depressed proportionally more than basal area increment.

Some defoliation treatments showed different effects on basal area and volume growths. The relative amounts of diameter growth at various heights up the stem (Rook and Whyte, 1973: Fig. 5, obtainable from editor on request) show, generally, that more severe partial defoliation treatments, e.g., S*0-1* and S*1-2-3,* resulted in less stem taper, with diameter growth being inhibited more at the base of the tree than at the top (Treatment S*2-3* was somewhat unusual, especially in the latter part of the second year after defoliation, when a greater amount of growth was taking place towards the base of the tree than at the top, resulting in a greater stem taper).

Changes in stem taper due to diameter growth being relatively more depressed at the base of severely defoliated trees are well documented (Larson, 1964a). Most previous work reported results of pruning trials where the lower crown was removed, but in our study the more severe defoliation treatments involved removal of the upper crown as in S*0-1* or S*1-2*. The only treatment which showed an increased taper was S*2-3*, and this treatment showed an anomalous reduction in height growth. Larson (1964a) noted that a markedly different pattern of growth can occur if the terminal bud is damaged. Three of the six trees of S2-3 showed a dramatic falling off in height growth towards the end of the second year after defoliation, although no damage to the terminal buds was observed; no reason is known for this reduction in height growth. In S*0-1*, there was a high rate of bud mortality on both the main stem and on branches, particularly in the upper part of the crown; terminal buds of five of the six trees in this treatment died, mainly at the beginning of the second year. Bud death, however, did not appear to alter otherwise the distribution of growth within the stem.

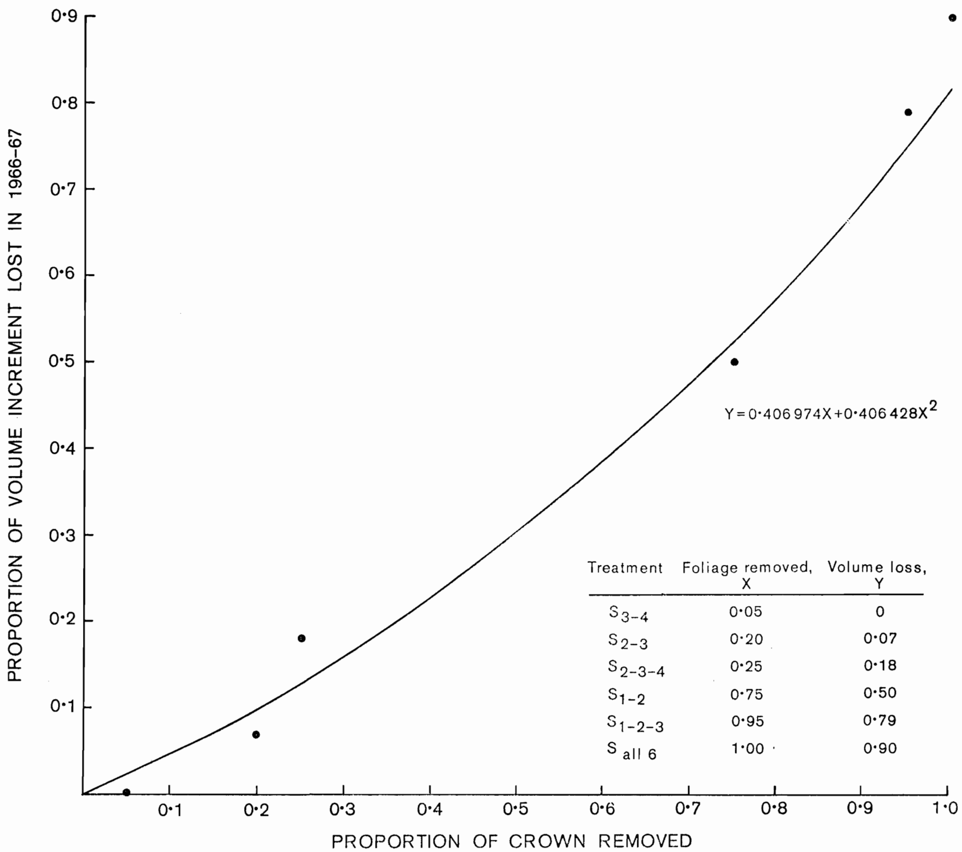
There was comparatively little difference between growth reductions caused by the March and June defoliations, but the December defoliations invariably caused greater reductions, although these were not always statistically significant. Generally, September defoliations cause the most severe reduction in growth. The only important exception was for height increment following removal of 1- to 2- and 2- to 3-year-old foliage, which was 83% of the control (Table 6), which appears anomalously high. However for the whole 2-year period, height increment over the first 12 months immediately after defoliation in September 1966 was 59% of the control and over the second 12 months was 80% of the control (Table 2). In the seasonal defoliation treatments, growth was being compared from June 1967 to August 1968, thus with a varying lag from the time of defoliation. For the September defoliation this lag represented virtually a complete growing season, and so this could account for the high figure of 83%. Unfortunately, no control trees in Experiment 2 were measured until March 1967, so that it is not possible to compare growth over a 12-month period immediately following the December defoliations and thus clarify this issue.

Where the 0- to 1-year-old needles were removed as in S*0-1*, the fascicle buds in the top 15 cm or so of the undefoliated part of the stem flushed, and many produced shoots 6-10 cm long in the 2 years after defoliation. Where defoliation in the basal part of the crown was very severe (75% or greater), many of the trees produced epicormic shoots on the bole and branches in the lower defoliated part of the crown. The occurrence of epicormic shoots in S*1-2* and S*1-2-3* appeared to be associated with loss of height growth; if the defoliation treatment was sufficiently severe to reduce height growth significantly, fascicle buds developed—possibly in reaction to a reduced hormone production by the apical meristem.

Kramer and Kozlowski (1960), after reviewing work on the effect on growth of pruning live branches, indicated that as a general rule approximately one-third of the live crown can be removed without affecting diameter growth and approximately two-thirds without significantly affecting height growth. Our study does not fully agree with this statement as all the defoliation treatments caused some reduction of growth over the 2 years after defoliation (Tables 2-6), although not all the growth rates were significantly different from those of undefoliated trees. However in our defoliation treatments we removed single age classes of foliage from branches over the entire length of the bole, while in pruning studies complete branches are removed from the base of the crown. So, different parts of the crowns are being removed. In our study defoliation of 2- to 3- and 3- to 4-year-old foliage in which less than 25% of the lower crown was removed, appeared to inhibit height, basal area, and volume growth only slightly and approximately to the same extent. This uniform reduction in growth within the stem possibly resulted from the roots being deprived of some assimilates by the defoliation of part of the lower crown but there are no data from this investigation to substantiate this claim. The more severe defoliation treatments in which more than 75% of the crown was removed resulted in relatively less basal area and volume growth than height growth, which is in general agreement with other studies (Kulman, 1971).

As an indication of the size of losses in volume increment to be expected in the growing season after a given reduction in foliage mass in early spring, an equation has been derived from the limited amount and limited nature of the results from this investigation. The ratio of volume increment for each of six defoliation treatments to volume increment of the control (S*0*) during the 1966-67 growing season (Y) has been related to the corresponding mass of foliage removed (X), also expressed as a ratio of the control. Treatments S*0-1* and S*all,c* were excluded as they both involved continual defoliation throughout the year, in contrast to the others (except for S*all,6*) where defoliation occurred only once, in September. Treatment S*all,6* was included as there was hardly any further growth after the second defoliation in March 1967, and a reasonable adjustment for this could be made. Four least-squares models were examined: $Y = b_0 + b_1X$; $Y = aX^bc^x$; $Y = b_0 + b_1X + b_2X^2$; and $Y = b_1X + b_2X^2$. The last provided the best overall fit and it is shown in Fig. 8 along with the relevant basic data. The trend is a slowly increasing parabola conditioned to pass through the origin, the shape of which seems to agree with results of studies of photosynthesis of radiata pine around this age (Wood, 1969; Rook and Brown, in prep.). These authors, too, have shown that 1- to 2-year-old foliage is photosynthetically more efficient than 3- to 4-year-old foliage.

Difficulties arise when a quantitative comparison, of the differences in response to defoliation of *P. radiata,* is attempted between this and other studies. Time of defoliation, parts of the crowns defoliated, age of tree, growing conditions, and species all differ. Austara (1970) found that a 50% defoliation caused markedly less reduction in diameter growth in *Pinus patula* Schlecht. et Cham. than would be predicted from our study with *P. radiata,* although the reduction in height growth was similar. O'Neil (1962) observed smaller reductions in height and basal area growth in *Pinus banksiana* Lamb. in Canada from the removal of 1- to 2-year-old foliage than we found with *P. radiata,* although both studies showed similar results from the removal of 2- to 3-year-old foliage. Linzon (1958) observed that height growth was reduced by 80-90% during the first year, and 10-40% during the second year after defoliation of the new foliage of *Pinus strobus* L. (aged 20 years). In our study, removal of the current year's



Treatment	Foliage removed, X	Volume loss, Y
S_{3-4}	0·05	0
S_{2-3}	0·20	0·07
S_{2-3-4}	0·25	0·18
S_{1-2}	0·75	0·50
S_{1-2-3}	0·95	0·79
$S_{\text{all 6}}$	1·00	0·90

FIG. 8—Proportion of possible current annual volume increment lost (Y) as a function of the proportion of the mass of foliage removed (X) in spring.

foliage caused a 37 and 74% reduction in height growth during the first and second growing seasons respectively. This comparison shows clearly the limited applicability of results from a study on one site with one species and age of tree, to another species and age of tree in another environment.

CONCLUSIONS

1. Severe defoliations, where all foliage was removed continually, killed young radiata pine in a few months.
2. The most severe partial defoliation involving a single age class of foliage was one where only new foliage was continually removed. This did not affect height, basal area, or volume increments until 3-5 months after defoliation, but then depressed all increments severely.
3. The next most severe defoliation involving a single age class of foliage was where 1- to 2-year-old foliage was removed, i.e., approx. 75% of the live crown at the beginning of the growing season was removed. Removal of 2- to 3-year-old foliage

in addition to 1- to 2-year-old foliage significantly reduced height, basal area, and volume growth further.

4. Removal of foliage older than 2 years of age had little effect on growth (but results of *S2-3* are anomalous).
5. The pattern of intra-seasonal increment was affected only when current foliage was removed.
6. Severe defoliation, in which more than 75% of the crown was removed, resulted in less basal area and volume growth than height growth.
7. Growth reductions were most severe for defoliations carried out in September, for December less so, and for March and June less and similar.
8. In contemplating prophylactic measures it seems best in the long run to ensure the good health of current foliage as the top priority.

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