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FOLIAGE BIOMASS OF DOUGLAS FIR IN A 53-YEAR-OLD PLANTATION

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ABSTRACT

Foliage biomass of five 53-year-old Douglas fir trees was assessed by regression analysis. The biomass of the measured tree components of total foliage, current-year foliage, twigs and branches were all most strongly correlated with tree stem diameter below the lowest living branch.

Needle retention was low, with only a trace of five-year old needles found and 67-82% of the total foliage held as current and one-year-old needles. Needle biomass was estimated at 7.8 tonnes dry wt/ha with an annual production of 2.6 tonnes dry wt./ha.

Predictive equations are developed which could be used to establish a current norm for foliage biomass of Douglas fir in northern Kaingaroa State Forest.

INTRODUCTION

Plantations of Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco, represent about 7% of the total exotic forest resource in New Zealand. Although the percentage is small it provides nearly 25% of current sawn timber exports (Fraser, 1978). Since 1969, however, growth rates of old trees have declined (Beekhuis, 1978), probably through intense competition and the effects of the pathogenic complex of the Swiss needle cast fungus, *Phaeocryptopus gaeumannii* (Rohde) Petrak, and lepidopterous defoliators (Cameron *et al.*, 1978).

The loss in yield resulting from a non-lethal level of tissue loss within a crop can be assessed by growth analysis and energy flow techniques (Bardner and Fletcher, 1974).

The quantitative assessment of foliage biomass recorded here is the basis of a continuing energy flow study, which will attempt to quantify the role of lepidopterous defoliators within the pathogenic complex affecting Douglas fir.

Study Area

Field work was undertaken in Comp. 1103 Kaingaroa State Forest; a high quality site for Douglas fir (Mountfort, 1978) and representative of Douglas fir silviculture. The stand was planted at approximately 2200 stems/ha in 1923 and thinned to 330 stems/ha in 1968/69. Canopy closure was approximately 75%, although patchy, with large open areas separating closely packed crowns, so that expansion of crowns appeared to be limited. Foliation of tree crowns was uniformly sparse.

Phaeocryptopus gaeumannii was found to be present in Kaingaroa in 1960 (Hood and Kershaw, 1973) and all Douglas fir in the forest is now heavily infected with the fungus. Recent epidemics of the looper *Selidosema suavis* were recorded in the forest in 1970 and 1972 (Alma, 1972).

METHODS

Stand character was determined by measuring diameter at breast height over bark (d.b.h.) and distance measurements of 100 trees by the point-centre-quarter method (Cottam and Curtis, 1956). Five trees from the more common d.b.h. size classes were felled. Felling and foliage sampling was done from 4-12 February 1976.

A tape was laid along the stem axis of the felled trees from the base to the tip. The canopy length was recorded as the distance from the lowest living branch to the tip of the mainstem leader. For each tree, d.b.h., the diameter at the base of the live

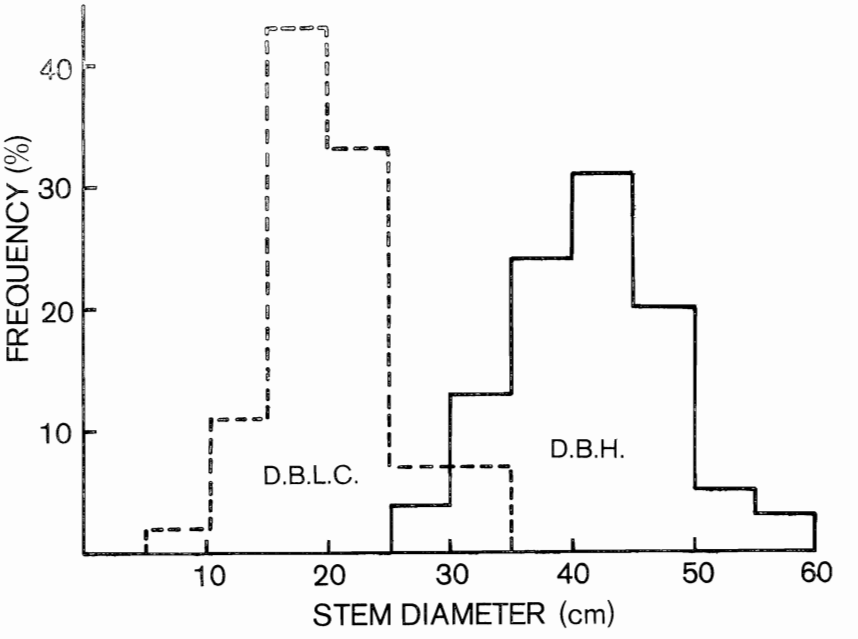

FIG. 1—The frequency of stem diameter classes within Cpt. 1103 Kaingaroa Forest.

crown (d.b.l.c.), the position and the diameter above the basal swell of all live branches and the position and length of all "epicormics" were recorded. Epicormics are defined here as short secondary branches arising from the main stem. Dead branches were ignored. The tree crown was marked off into ten equal sections and a branch, undamaged by felling and nearest the centre of each section, was taken from each. The cardinal aspect of the selected branches depended on the position of the tree after felling and was essentially random. All sections of branch bearing foliage were then removed from the sample branches and sorted into current-, one-, two-year-old etc. age classes. Ten epicormic shoots from each of three trees were removed at random and treated similarly. All of the removed material was oven dried at 105°C to a constant weight (2 days) and then separated into foliage and twigs before weighing. The wet weight of stripped sample branches (excluding foliage-bearing twigs) was recorded and weighed sub-samples were oven dried and reweighed to determine moisture content. Sub-samples of 50 whole needles were taken from crown levels 1,3,5,7 and 9 from the dried foliage of each of the sample trees. The resulting data was subjected to an analysis of variance, followed by Student-Newman-Keuls range test, for between-tree differences, and Least Significant Differences were estimated for the means of needle-age weights and needle-crown-level weights.

The percentage of needle retention on the sample branches of three trees was assessed visually by an experienced observer.

Discs were cut from the stem of the felled trees at the stump and below the lowest living branch. Ring widths of each disc were measured along four radii and averaged.

In September the d.b.l.c. of 60 trees in the same stand were measured using an 8 in. Barr and Stroud FP 15 optical dendrometer.

Calculations involved linear and/or logarithmic regressions to arrive at whole tree biomass. Meyer's (1941) correction

$$W = e^{\bar{w}} + \tfrac{1}{2}s^2$$

was used in all logarithmic regression equations to lessen the bias of estimated weights. (W is the corrected weight, $\bar{w}$ is the estimated weight from the regression and s^2 is the residual mean square).

RESULTS

The point-centre-quarter method of stand assessment revealed an approximately normally distributed range of d.b.h. size classes with an arithmetic mean of 41.5 cm and a stand density of 330 stems/ha. The dendrometer measurement of d.b.l.c. also approximated to a normally distributed size-class range with an arithmetic mean of 20.2 cm.

The dimensions of the felled trees are shown in Table 1. In Table 2 are the regression equations calculated from the sample branch data. The high values of the coefficients of determination for branches in the central crown region, which carry the bulk of a tree's foliage (Fig. 2), confirms that the degree of foliation of the five sampled trees was essentially the same and sample branch data could be combined. For relating foliage and twig dry weight to branch diameter, logarithmic transformations of the data were necessary to obtain linearity. The correlation between foliage biomass

TABLE 1—Dimensions of the five trees felled for analysis

Tree No.	Height m	Crown length m	d.b.h. cm	d.b.l.c. cm	Branches (no. excluding epicormics)
1	32.0	9.0	34.0	15.8	161
2	33.0	14.0	36.5	21.2	160
3	32.0	10.5	43.5	18.6	157
4	35.0	13.0	47.0	24.8	155
5	38.5	14.5	53.0	25.4	173

TABLE 2—Regression equations derived from the combined data of sampled branches and epicormics removed from the felled trees

	$Y = a + bx$				
Y (g)	a	b	x(cm)	RMS	R^2
Ln Foliage Section 1	1.270	2.88	Ln Branch Diameter	1.702	0.34
" 2	—0.186	3.903	"	1.178	0.56
" 3	2.827	2.264	"	0.145	0.85
" 4	1.610	3.189	"	0.109	0.92*
" 5	2.756	2.484	"	0.057	0.96**
" 6	2.712	2.728	"	0.015	0.98***
" 7	3.323	1.956	"	0.089	0.92**
" 8	2.729	2.632	"	0.096	0.92**
" 9	3.403	1.398	"	0.604	0.53
" 10	2.280	1.366	"	0.157	0.66
Ln Foliage Overall	2.789	2.180	"	0.489	0.76***
Ln Current-year foliage	2.091	1.856	"	0.533	0.67***
Ln Twig weight	2.062	1.972	"	0.380	0.76***
Ln Branch weight	2.664	3.317	"	0.115	0.94***
Ln Epicormic foliage	—1.223	0.080	Epicormic length	0.618	0.66***
Ln Epicormic Twig Wt.	—2.340	0.010	"	0.305	0.85***

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

and branch diameter was less reliable for the upper and lower 20% of the canopy than for the central canopy region. Since the residual mean squares appeared to be related to the position in the crown, and as differences between the equations for the different crown sections were real, the separate regression equations were used to estimate the foliage dry weight for each crown section. A logarithmic transformation of the dry weight of epicormic foliage and wood was positively correlated with epicormic length.

Foliage and branch biomass of the five sample trees (Table 3) was estimated using the regression equations of Table 2 and the recorded measurements of branch diameter

and position. For each crown section the weight of foliage in each age class was estimated by using the age-class percentages found on the sample branch from that section. This revealed that the bulk, 67-82%, of the foliage was held as current- and one-year-old needles. Four of the five trees sampled held a greater dry weight of one-year-old than current-year needles.

Weighed sub-samples of needles showed that individual needles from trees 3 and 4 were significantly heavier than those of trees 1,2 and 5 (Table 4). A comparison of needle weight with age over all trees showed that dry weight per needle was significantly less for current-year needles than older needles. Dry weight per needle tended to

TABLE 3—Foliage biomass (kg dry weight) of the five sample trees derived from the regression equations of Table 2, and branch and epicormic data collected in the field. Percentage of total foliage for each category in parenthesis

Biomass	Sample Tree Number				
	1	2	3	4	5
Current-year Foliage	4.7 (33)	8.5 (32)	7.7 (43)	13.1 (35)	12.3 (31)
One-year "	4.8 (34)	10.1 (38)	6.9 (39)	14.9 (39)	15.7 (40)
Two-year "	3.0 (21)	5.8 (22)	2.9 (16)	7.3 (19)	7.9 (20)
Three-year "	1.4 (10)	2.1 (8)	0.5 (3)	2.3 (6)	2.8 (7)
Four-year "	0.2 (1)	0.3 (1)	trace	0.2 (<1)	0.4 (1)
Five-year "	trace	trace	0	0	0
Total Foliage	14.3	27.1	18.1	38.2	39.7
Twigs	5.1	8.8	6.8	38.7	44.5
Branches	31.1	67.8	44.5	113.3	120.2

TABLE 4—Analysis of the dry weights of 100 50-needle sub-samples of four ages taken from the five sample trees at five crown levels

	Analysis of Variance			
	SS	DF	MS	F
Total	0.23626	99		
Trees	0.13407	4	0.03352	39.471***
Crown Levels	0.01247	4	0.00312	3.674**
Needle Ages	0.01499	3	0.00499	5.884***
Residual	0.07473	88	0.00085	

Table of Means

	1	2	3	4	5	
Trees	0.13031	0.14928	0.22062	0.21037	0.14721	
Crown Levels	0.15229	0.17186	0.18178	0.18333	0.16854	(LSD = 0.01534)
Needle Ages	0.15143	0.17198	0.18134	0.18149		(LSD = 0.01372)

** P <0.01 *** P <0.001

(Lines on the same level link means which are not significantly different from each other at the 5% level.)

increase with needle age. Needles from the lowest crown level weighed significantly less than those from the four higher crown levels examined. Needles tended to be heaviest in the central crown region.

The distribution of needles within the crown was essentially the same for the five trees sampled, and parallels Silver's (1962) observation that younger foliage predominated in the upper crown and older foliage predominated in the lower crown, while a well-defined maximum weight for each age class was found in the mid-crown region (Fig. 2). The top 10% of the crown is sparsely needled and holds less than 1% of the total leaf biomass.

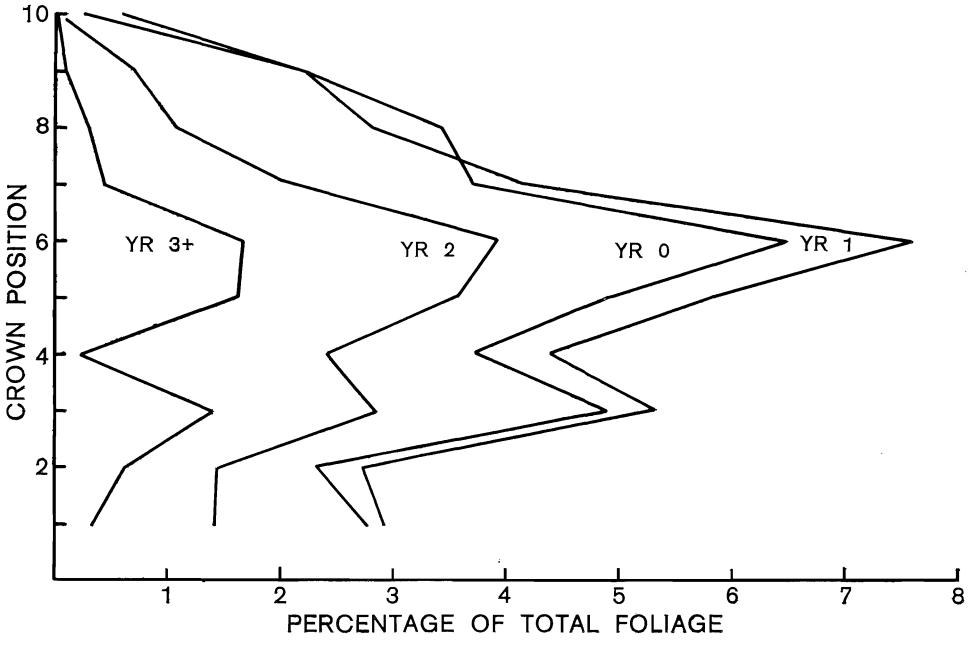

FIG. 2—The distribution of foliage biomass by age and position within the crowns of the five trees sampled.

Visual assessment of needle retention revealed that about 7% of current needles had already been lost — about 14 weeks after bud-break — (Fig. 3) and that the loss appeared to be very evenly distributed throughout the crown.

Table 5 shows the regression equations for the biomass of various plant components on easily measured tree parameters. In estimating foliage, twig and branch biomasses, d.b.l.c. was far superior to either d.b.h. or d.b.h.^{2} × height (H).

The stand weight of a given tree component can be estimated from the product of the number of trees in the stand and the estimated average tree weight of that component (Swank and Schreuder, 1974). For Compartment 1103 stand foliage biomass was calculated at 7.8 tonnes/ha*.

A five-yearly summary of annual area increment at stump height (Fig. 4) shows

* All biomass results given here are in terms of oven-dry weight.

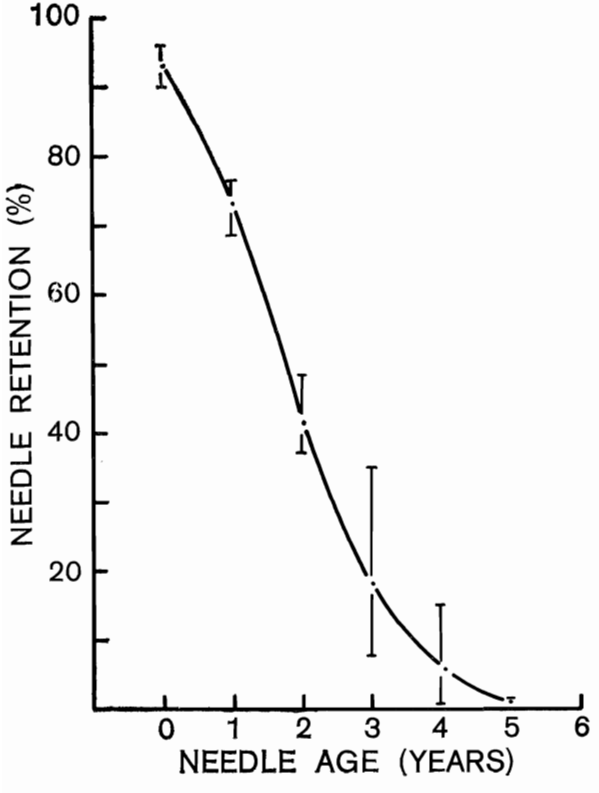

FIG. 3—The visual assessment of needle retention for each age class.

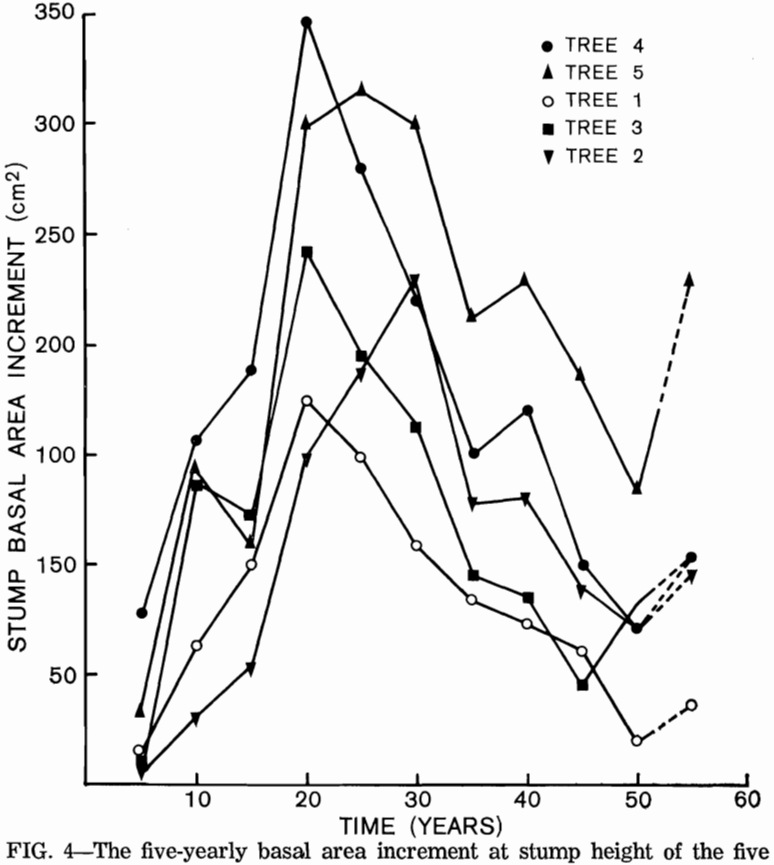

FIG. 4—The five-yearly basal area increment at stump height of the five sample trees.

TABLE 5—Logarithmic regression equations relating dry weight biomass of the sample trees (Table 3) to whole-tree parameters. Ln Y = a + b. ln x

Y kg	a	b	x d.b.h. (cm) H (m)	RMS	R^2
Total Foliage	— 3.8636	1.8965	d.b.h.	0.1143	.58
"	— 6.0093	0.8394	$(d.b.h.)^2.H$	0.0986	.64
"	— 3.6002	2.2501	d.b.l.c.	0.0036	.98***
Current-year foliage	— 3.0986	1.3943	d.b.h.	0.0469	.64
"	1.0193	0.6107	$(d.b.h.)^2.H$	0.0403	.69
"	— 2.6735	1.5781	d.b.l.c.	0.0001	.98***
Twigs	— 15.3404	4.8020	d.b.h.	0.3589	.74
"	— 20.5623	2.1063	$(d.b.h.)^2.H$	0.2785	.79*
"	— 11.8034	4.7527	d.b.l.c.	0.1741	.87*
Branches	— 5.4815	2.5846	d.b.h.	0.1637	.64
"	— 8.3163	1.1359	$(d.b.h.)^2.H$	0.1392	.69
"	— 4.6919	2.9248	d.b.l.c.	0.0033	.98***

* $P < 0.05$ *** $P < 0.001$

that the five sample trees in this stand have been continually changing in their status through 50 years of growth. An increase in the annual area increment can be found in the growth of recent years.

DISCUSSION

This study was made in mid-summer, rather than at the end of the growing season as suggested by Newbould (1968), to determine the foliage biomass available to peak population levels of insect defoliators. Populations of *Selidosema suavis,* a major geometrid defoliator of Douglas fir, are usually greatest from November to December and from March to April in Kaingaroa. The early sampling date probably accounts for the lower weight per needle, and total needle weight, of current-year needles when compared with one-year-old needles. The recorded increase in weight with needle age may be due to leaf maturation processes or the preferential loss of smaller needles from older shoots.

Regression analyses based on a small sample of trees, which are felled and weighed, are probably the most practical method for determining forest biomass. Predictive equations relating component biomass to some easily measured parameter may then be used to measure other trees or extrapolated to obtain stand biomass.

Hall (1965) and Shinozaki *et al.* (1964) found d.b.l.c. to give the best estimate of crown biomass for a number of tree species, although Hall found that for red pine the correlation between stem diameter and foliage supported at that point, increased within the crown from the base to the apex. Shinozaki's conclusions led him to propose the "pipe model theory" which considers a given leaf area to be supported by a unit thickness of vascular and supporting tissue. Larson (1963) suggests that as wood production is dependent on leaf activity, it usually increases with foliage biomass, from the apex to the base of the live crown. Thus the stem diameter at the base of the live crown, although an historical record, is normally closely correlated with the crown it supports and is a measurement that should be used when estimating foliage biomass.

What is more, the relationship should remain constant, in constant conditions, whereas that between d.b.h. and foliage biomass is continually changing. The difference between the correlation of foliage biomass with d.b.l.c. and d.b.h. in this study is probably due to the changing status of individual trees following thinning, the death of competing trees and possibly a differing susceptibility to inclement weather and new pathogenic agents. The historical record of the stump is approximately 25 years removed from that of the crown base and therefore a less reliable indicator of foliage biomass. Clearly stand foliage biomass estimates based on "mean tree" d.b.h. or basal area, as used in some plantation biomass studies (Peterken and Newbould, 1966), could involve considerable error.

The brief needle retention of Douglas fir in Kaingaroa (5-year-old max.) differs markedly from that recorded in other studies. In Southland, New Zealand 12-year-old needles are commonly found (J. D. Slater-Hayes, pers. comm.). Silver (1962) and Dice (1970) found 10- and 8-year-old needles respectively in American north-western states. The needle retention curve for Kaingaroa (Fig. 3), which shows the loss of about 80% of 3-year-old needles, indicates that the defoliator epidemics of 1970 and 1972 were not necessarily responsible for the disappearance of the older needles. Instead, the poor retention of needles may be attributable to the combined effects of competitive stress, the needle-cast fungus and normal insect defoliation.

The loss of older needles resulted in 67-82% of the total foliage biomass being held as current and one-year-old needles, whereas Silver (1962) and Dice (1970) respectively recorded 51% and 46% for the same category. However net photosynthetic rates of needles declines with age to a point where needles 4-5 years old have half the rate of current needles (Mitchell, 1975), so that the loss of old needles may not be as debilitating as the proportional loss in biomass would indicate.

The distribution of foliage biomass within the crown of the sample trees differed from Dice's (1970) observations. He found that the maximum foliage biomass was held low in the crown, at a point equivalent to section three rather than at section six as in this study. Woodman (1971) found that maximum mean daily photosynthetic rates occur at a level comparable with section six. His "zones of relative assimilative efficiency" correspond closely with the zones of foliage density observed on the trees of this study.

Turner and Long (1975), after studying a variety of stands, suggest that for Douglas fir in N.W. America stand foliage biomass increases to a maximum, which coincides with crown closure, then levels at a value of 10-12 tonnes/ha. Grier *et al.* (1974) calculated foliage biomass at 8.9 tonnes/ha for a 450-year-old stand in the same region. Burger (1935) estimated foliage biomass at 11-17 tonnes/ha for 20- to 41-year-old plantations of Douglas fir in Switzerland. Annual foliage production was estimated at about 2.2 tonnes/ha (Turner and Long, 1975) and almost 2 tonnes/ha (Dice, 1970) in N.W. America.

In Kaingaroa Forest, although needle retention is brief, Compartment 1103 supports approximately 7.8 tonnes/ha of foliage and has an annual production of about 2.6 tonnes/ha of foliage. The annual foliage production figure does not take into account the increase in needle weight with age nor the estimated loss of about 7% of the current year needles prior to sampling. After correction for canopy closure, total foliage

biomass/ha was similar to that recorded for Douglas fir in other areas. Kaingaroa trees held most of their foliage as current and one-year-old needles which are probably photosynthetically more efficient than older needles. The foliage turnover and d.b.h. growth rate of the Kaingaroa trees is approximately twice that recorded for a variety of stands in N.W. America.

The figures for Douglas fir in Kaingaroa can also be compared with those of 9.3 tonnes/ha of foliage and 4.0 tonnes/ha annual foliage production for a 22-year-old stand of *Pinus radiata* from the same area (Madwick *et al.,* 1977).

The slight differences in published predictive equations (Burger, 1935; Dice, 1970; this report) for total foliage biomass of Douglas fir using d.b.h. measurements may have arisen from site, silvicultural and size-class differences of the sampled trees. Dice (1970) studied trees averaging 15 cm d.b.h., Burger's (1935) trees ranged from 6-46 cm d.b.h. while those in this study ranged from 34-53 cm d.b.h. The differences may also reflect the degree of defoliation caused by *P. gaeumannii.* Boyce (1940) states that Douglas fir in N.W. America is apparently unaffected by the fungus, but says infected Swiss trees retain their foliage for about five years. The loss, by Swiss and Kaingaroa trees, of older needles would alter the wood production to leaf biomass ratio. Similarities in the predictive equations on the other hand indicate, as Kittredge (1948) suggests, that with species and site defined, leaf weight may be predicted using a standard regression equation regardless of tree crown class or stand density.

The high coefficients of determination for equations developed herein based on d.b.l.c. lend support to Shinozaki's theory of a causal relationship between stem tissue and the foliage biomass it supports. The stem measurement however is an historical record of growth and the correlation with foliage biomass may vary from year to year and from tree to tree, depending on the degree of defoliation sustained through *P. gaeumannii* and insect attack. In a stable environment such predictive equations should remain constant. Those developed here are used to establish the current norm for foliation and are complemented by measurements of d.b.l.c. and litterfall.

The increased basal area increment since 1972 is interpreted as a response to thinning and must be due, in part, to an increase in canopy weight and/or an increase in the functional capacity of the canopy. Growth increases are occurring in spite of infection with *P. gaeumannii* and moderate defoliation by insects (cf. Bunn and James, 1978). The thinning of mature stands increases individual tree growth and may well increase wood production per unit foliar weight (Burger, 1973; Van Laar, 1973).

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