Primary Production Relations in Plantations of *Thujopsis dolabrata* in the Noto Peninsula: Materials for the Studies of Growth in Forest Stands. 12.*

Taisitiroo SATOO**, Ken'itiroo NEGISI** and Kitokuroo YAGI***

CONTENTS

Abstract

A 28-year-old plantation with foliage leaf of 31.2 t in dry weight and 12.9 in leaf area index produced annually 11.3 t of dry matter, and a 25-year-old plantation with foliage leaf of 44.0 t in dry weight and 17.9 in leaf area index produced 19.2 t of dry matter annually, both as the aerial parts, all per hectare. A 38-year-old plantation had 31.9 t/ha of leaf dry weight and 12.9 of leaf area index. These large amounts of foliage leaf were due to long average life span of leaf but not to large annual production of leaf. Annual production of leaf was nearly the same as other conifers. Net production of trees within a stand was linearly proportional to leaf mass on them, but independent from the efficiency of leaf, net assimilation rate, except for trees of smaller dimensions. Net assimilation rates of these stands were lowest among coniferous forests. Net assimilation rate increased with dimension of trees such as D. B. H., height and leaf mass on tree, though not linearly. Leaf water content decreased with increasing D. B. H. and height of trees, both for the current year leaf and older leaf.

1. Introduction

Primary production relations in plantations of *Thujopsis dolabrata* (Cupressaceae) in Noto Peninsula were studied in the same way as the previous works. This species is extremely shade tolelant and comparison of its production relations with other

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* Contributions from JIBP-PT No. 182.

** Department of Forestry, Faculty of Agriculture, University of Tokyo.
東京大学農学部林学科

*** University Forest Experiment Station at Tanashi, Faculty of Agriculture, University of Tokyo.
東京大学農学部演習林田無試験地

conifers may be of importance in understanding some aspects of production relations. This species distributes widely in montane regions but planting of it is not common.

In Noto Peninsula it is planted widely with cuttings taken from young plantations, and three cultivars, different in leaf morphology and wood quality, are developed. Among three cultivars, "kusa-ate" is most widely used, and the plantations studied here belonged to it. Many of forests there are managed with selection system and regeneration is made by artificial layering of lower branches. Natural layering is also very common in natural forests of this species. However, in this study, even-aged forests were chosen to make easy the comparison with forests of other species studied by the author hitherto which are mostly even-aged, and also because forests of simple structure is favorable at the present stage of the study.

Field works were made in the summer of 1963. Dr. M. KATSUTA, Mr. T. MATUO and Mr. K. HANAZAKI joined in the field works. The authors are very grateful for their helps.

2. The forest studied

Studies were made on three plantations in Kooti, Anamizu-mati, Isikawa-ken. Anamizu-mati is on the middle part of the Noto Peninsula in Japan Sea. According to the mean for 30 year's record (1931-1960) at Wajima Observatory (37°32′N, 136°54′E), which is about 18 km north to Anamizu-mati, annual mean temperature was 12.7°C with maximum mean monthly temperature in August (24.7°C) and minimum in February (2.2°C). Annual precipitation was 2278 mm with heavy snow in winter. Frostless season was from April to late November. General descriptions of the plantations studied are given in Table 1, and distribution of D. B. H. of the three plots is compared in Fig. 1. The Plots I and II are similar but less light penetrated into forest floor of the Plot II. Development of undergrowth vegetation was very poor,

Table 1. General description of the stands.

Plot	I	II	III
Altitude (m)	ca 150	120	280
Slope	40°	30°	26°
Aspect	SE	SW	SW
Age	24-31	23-27	35-42
D. B. H. (cm)	9.42	9.19	15.56
Height (m)	8.68	7.44	12.19
Number of tree per ha	5584	6490	2760
Basal area (sq. m/ha)	42.17	47.33	55.97
Volume			
G/*g*	265.4	222.2	417.3
aD^b	260.5	232.6	415.0
Mean	263	227	416
Relative light intensity on forest floor	1.7-3.7	0.6	0.3-0.5

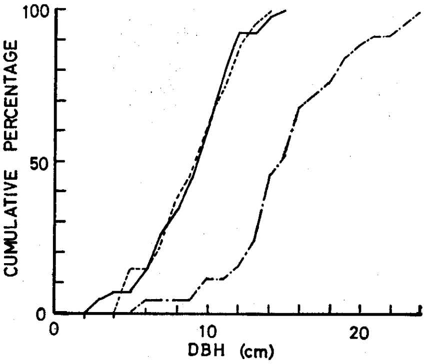

Fig. 1. Frequency distribution of d. b. h. of the three stands. Solid line: Plot I, dotted line: Plot II, broken line: Plot III.

as understood from the relative light intensity under canopy shown in Table 1.

3. Method

Method was in general the same as the previous works and not repeated here. For the Plot III, which was located on a rather remote site, sampling for growth in branch and separation of leaves of current and previous years were not made because of limited time. Undergrowth vegetation was too scarce to be studied, and study of roots was not made.

4. Biomass aboveground

For conversion of the values for sample trees into unit ground area basis, two methods were used: allometry using D. B. H. as the independent variable (aD^b) and the ratio of basal area to sum of cross-sectional area of sample trees (G/g). Discussions on these methods were already given (SATOO 1966, 1968, 1970). Constants for the allometric

Table 2. Constants of the allometric equation:
$\log W_{\mathrm{kg}} = b \log D_{\mathrm{cm}} - a$.

Plot	I		Ⅱ		Ⅲ	
	b	a	b	a	b	a
Volume (cu. dm)	2.6334	0.9657	2.4908	0.9168	2.2851	0.5871
Biomass						
Stem	2.3447	1.0674	2.2690	1.0821	2.2011	0.9081
Branch	3.1244	2.7810	2.6541	2.1476	2.7039	2.3439
Leaf	3.0684	2.3376	2.5280	1.6850	2.8889	2.4481
Leaf area (sq. m)	2.0703	1.7156	2.5249	1.0684	2.7893	1.7227
Net production						
Stem	4.4201	1.4717	3.1910	−0.1125	3.6818	1.1679
Branch	4.6401	2.3608	3.2753	0.8356		
Leaf	4.5565	4.4829	3.2711	3.4989		

Table 3. Biomass (t/ha).

Plot	I		Ⅱ		Ⅲ	
Method	G/g	aD^b	G/g	aD^b	G/g	aD^b
Stem	105.1	103.8	95.3	94.3	156.9	157.3
Branch	13.0	13.0	19.8	20.2	24.6	24.1
Leaf	32.2	30.1	44.5	43.6	32.1	31.7
Total	150.3	146.9	159.6	158.1	213.6	213.1
Leaf area (sq. m)	13.25	12.62	18.31	17.48	13.21	12.68
			Distribution (%)			
Stem	69.9	70.6	59.7	59.6	73.5	73.8
Branch	8.7	8.9	12.4	12.8	11.5	11.3
Leaf	21.4	20.5	27.9	27.6	15.0	14.9

equations are given in Table 2. The values per unit ground area by these methods agreed very well, as seen from Table 3.

The Plots I and III had almost the same amount of leaf, ca. 30 t/ha, but the Plot II had far more leaf, ca. 44 t/ha. These values are largest of the leaf mass so far reported, and about 10 times as larger in dry weight and about 3.5 times as larger in leaf area index than forests of *Larix leptolepis* which has the smallest amount of leaf among conifers so far reported. Leaf mass of coniferous forests in Japan was tabulated elsewhere (SATOO 1971). Such a large mass of leaf as these stands is not due to the large amount of leaf produced annually but to the longer life span of leaf. Annual leaf production was 3.6-4 t, ha for both the Plots I and II, as seen from Table 5. This value is almost equivalent to the leaf mass, or annual leaf production in this case, of *Larix leptolepis* stands (SATOO 1974b) which is a deciduous conifer. As seen from Fig. 2, leaf produced in the year of the study of the sample trees (Pl) was linearly proportional to total leaf mass (L) on them, and described as

Table 4. Percentage of annual leaf production to total leaf mass.

Plot	I	II
Per tree		
Mean of sample trees	9.9	7.5
From the equation	11.2	8.7
Per unit ground area		
G/g	11.1	8.5
aD^b	12.6	9.1

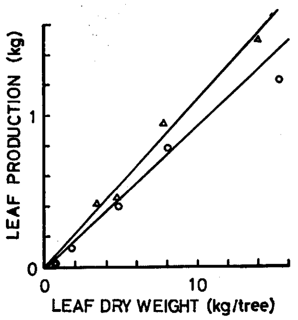

Fig. 2. Leaf production in relation to leaf dry weight of trees. Triangles: Plot I, circles: Plot II.

$$Pl=0.112\,L,\ r=0.98^{**}\ \text{for Plot I},$$

and

$$Pl=0.085\,L,\ r=0.99^{**}\ \text{for Plot II}.$$

Percentage of leaf mass newly produced was 11.2% for the Plot I and 8.5% for the Plot II. Assuming that the quotient obtained by dividing total mass of leaf by the leaf mass produced in a year gives mean life span of leaf, it was 9 years for the Plot I and 12 years for the Plot II, about 10 years in average. Similar values were obtained by use of leaf mass per unit ground area as shown by Table 5. The cause of the difference of the values between the two plots is not clear. It is reported that leaf mass of *Cryptomeria japonica* (SATOO 1966) and *Pinus densiflora* (HATIYA et al 1966) is larger on better site, but it is not probable that the Plot II is on a far better site than the Plot I. Both the two plots were located on the end of ridges, and height at 20th year of sample trees having cross-sectional area very close to the mean which was determined from stem analysis was 6.3 m for the Plot I and 5.4 m for the Plot II. Site quality could be a little better in the Plot I than II if tree height reflects it. The Plot II was a little younger than the Plot I, but it is not probable that this small difference in the age causes the difference in mean life span and mass of leaf. It was already discussed that the difference in leaf mass per unit ground area among different species is not due to the difference in annual leaf production but to the difference in mean life span of leaf (SATOO 1971). This trend among tree species seems to be also true for between the Plots I and II of the same species. Distribution of biomass among parts of tree was different among the plots, but distribution ratio to leaf was very high compared with other species of conifer (Table 3).

5. Net production aboveground

To convert the values of net production of the sample trees into the values per unit ground area of forest, two methods used for biomass estimation were also used here. Constants of allometric equations are given in Table 2. The estimates of net production per unit ground area of forest are shown in Table 5. The estimates by the two methods did not differ too much. Despite the enormous foliage, net production of these stands was not larger than forests of other conifers (SATOO 1971). It was already reported that with increasing leaf mass per unit ground area, production per unit leaf decreased as the results of mutual shading and aging of leaf (SATOO 1971). It is also possible that activities of leaves decline with age. Distribution of produced matter into parts of tree is shown in Table 5. Contrast to biomass, in the Plot II the distribution into branch and leaf was smaller and distribution into stem was larger than in the Plot I. One of the possible reason of this difference is higher stand density in the Plot II, but the difference in the stand density seems to be not large enough to result this large difference in distribution ratio. Distribution ratio did not show any relation to the dimensions of trees, though there were found close

Table 5. Aboveground net production (t/ha/year).

Plot / Method	I		II		III	
	G/g	aD^b	G/g	aD^b	G/g	aD^b
Stem	6.74	5.66	13.79	13.29	6.23	6.14
Branch	1.44	1.36	1.71	1.82		
Leaf	3.58	3.81	3.80	3.95		
Total	11.76	10.83	19.30	19.06		
		Distribution (%)				
Stem	57.3	52.3	71.4	69.7		
Branch	12.2	12.6	8.9	9.6		
Leaf	30.5	35.1	19.7	20.7		

relationships between the two among trees of stands of *Populus davidiana*, *Pinus densiflora*, and *Cinnamomum camphora* (SATOO 1966).

6. Efficiency of leaf

6-1. Efficiency of leaf in net production: net assimilation rate

Net production of sample trees (P kg) was linearly proportional to the leaf mass on them, and described for leaf dry weight (L kg) as

$$P=0.384\,L,\ r=0.97^{**}\ \text{for the Plot I,}$$

and

$$P=0.454\,L,\ r=0.94^{**}\ \text{for the Plot II.}$$

For leaf area (F sq. m) as

$$P=0.0933\,F,\ r=0.95^{**}\ \text{for the Plot I,}$$

and

$$P=0.1105\,F,\ r=0.99^{**}\ \text{for the Plot II.}$$

Fig. 3 shows these relationships. The constants of these equations mean net production per unit leaf and represent the efficiency of leaf, net assimilation rate. Mean values of net assimilation rate of each sample tree and net assimilation rate calculated by dividing net production per unit ground area of forest by leaf mass per unit ground area are also shown in Table 6. For both the plots and in both presentation of leaf mass, mean values for sample trees were smallest and the values derived from the equations were largest. Net assimilation rates

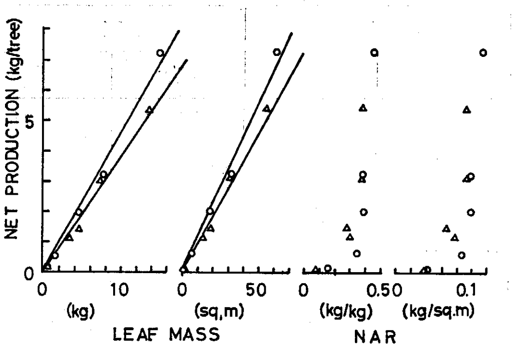

Fig. 3. Relationships between net production and leaf mass or net assimilation rate. See the explanation of Fig. 2.

Table 6. Net assimilation rate (aboveground).

Plot \ Basis	Leaf dry wt. (kg/kg)		Leaf area (kg/sq. m)	
	I	II	I	II
Per tree				
Mean of sample trees	0.304	0.367	0.0739	0.0893
From the regression	0.384	0.454	0.0933	0.1105
Per stand				
G/g	0.365	0.438	0.0888	0.1054
aD^b	0.360	0.437	0.0858	0.1090

of coniferous forests were tabulated in a previous paper (SATOO 1971). Net assimilation rates of these stands were the lowest among coniferous forests. Net assimilation rate was larger in the Plot II which had larger leaf mass and larger net production, by any of the methods used. This result does not agree with the trend found among natural forests of *Abies veitchii* (SATOO 1971). As seen from Fig. 3, though among trees of lower net assimilation rate net production increased with increasing net assimilation rate, among trees of higher net assimilation rate net production was independent from net assimilation rate. This trend was also found among trees in a stand of *Abies sachalinensis* (SATOO 1974c), but not among trees in stands of *Larix leptolepis* (SATOO 1971), *Pinus densiflora* (SATOO 1968b), and *Betula maximowicziana* (SATOO 1970).

The relationships between net assimilation rate and dimensions of trees are shown

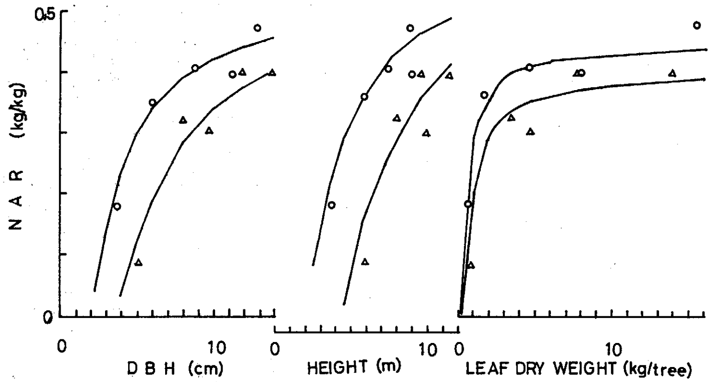

Fig. 4. Relationships between net assimilation rate and dimensions of trees. See the explanation of Fig. 2.

in Fig. 4. Though net assimilation rate (E kg/kg/year) increased with increasing D.B.H. (D cm), height (H m) and leaf mass (L kg), it was not proportional to dimensions but seemed to have a sort of asymptote. Net assimilation rate of trees was expressed as a function of reciprocal of a dimension, as described as: for D.B.H.

$$E=0.565-2.27\frac{1}{D},\ r=-0.84^{*}\quad \text{for the Plot I,}$$

and

$$E=0.548-1.27\frac{1}{D},\ r=-0.98^{**}\quad \text{for the Plot II;}$$

for height

$$E=0.689-3.29\frac{1}{H},\ r=-0.90^{*}\quad \text{for the Plot I ,}$$

and

$$E=0.626-1.62\frac{1}{H},\ r=-0.97^{**}\quad \text{for the Plot II;}$$

and for leaf mass

$$E=0.394-0.201\frac{1}{L},\ r=-0.96^{**}\quad \text{for the Plot I ,}$$

and

$$E=0.450-0.157\frac{1}{L},\ r=-0.99^{**}\quad \text{for the Plot II .}$$

Net assimilation rate of trees of *Cinnamomum camphora* showed different pattern in the relation to these dimensions (SATOO 1968a).

6-2. Efficiency of leaf to produce stem wood

As shown by Fig. 5, stem wood production of the sample trees (Ps kg) of the Plots I and II was linearly proportional to their leaf mass and described for leaf dry weight (L kg) as

$$Ps=0.228\,L,\ r=0.99^{**}\quad \text{for the Plot I ,}$$

and

$$Ps=0.333\,L,\ r=0.90^{*}\quad \text{for the Plot II;}$$

and for leaf area (F sq. m) as

$$Ps=0.554\,F,\ r=0.99^{**}\quad \text{for the Plot I ,}$$

and

$$Ps=0.810\,F,\ r=0.99^{**}\quad \text{for the Plot II .}$$

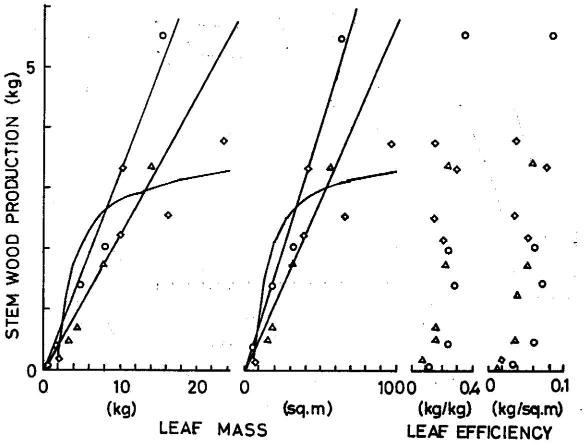

Fig. 5. Relationships between stem wood production and leaf mass or leaf efficiency. Triangles: Plot I, circles: Plot II, squares: Plot III.

However, in the Plot III, though stem wood production increased with increasing leaf mass, it was not linearly proportional but had an asymptote and described as

$$Ps=3.55-7.39\frac{1}{L},\ r=-0.92^{**}$$

and

$$Ps=3.55-30.7\frac{1}{F},\ r=-0.93^{**}.$$

It is not clear why there is a difference in trend among the plots, compared with the Plots I and II, the Plot III is older and on a rather drier site. Stem wood production per unit leaf mass, or the "efficiency of leaf to produce stem wood" was determined from the equation for the Plots I and II, and also dividing stem wood production by leaf mass per tree and per unit ground area of forest for all the plots and shown in Table 7. For both the Plots I and II, and in both weight and area basis, the values derived from the equation were largest and mean values of sample trees were smallest, as in case of net assimilation rate. Among the three plots, the Plot II had highest efficiency and the difference between the Plots I and III was minimum. For all plots, though among trees with lower efficiency of leaf the stem wood production increased with the efficiency of leaf, among trees with higher efficiency of leaf the effect of leaf efficiency on stem wood production was not clear. Fig. 6 shows the relations of the efficiency of leaf to produce stem wood of the sample trees to the dimensions of trees. In the Plots I and II, though the efficiency of leaf (Es) increased with D.B.H. (D cm), height (H m) and leaf mass (L kg), it was not linearly proportional to the dimensions but seemed to have asymptotes, and described for D.B.H. as

Table 7. Efficiency of leaf to produce stem wood.

Plot \ Basis	Leaf dry wt. (kg/kg/yr.)			Leaf area (kg/sq. m/yr.)		
	I	II	III	I	II	III
Per tree						
Mean of sample trees	0.165	0.256	0.188	0.0393	0.0625	0.0458
From the regression	0.228	0.333		0.0554	0.0810	
Per stand						
G/g	0.209	0.310	0.194	0.0499	0.0753	0.0472
aD^b	0.188	0.305	0.194	0.0448	0.0745	0.0484

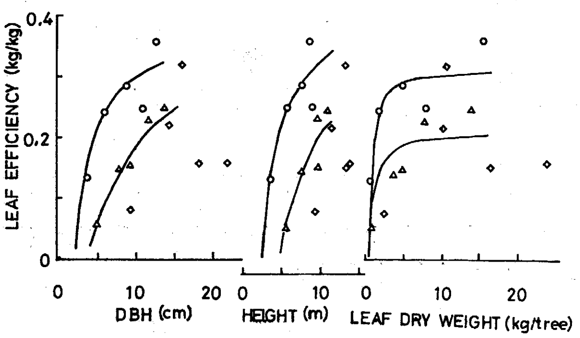

Fig. 6. Relationships between stem wood production per unit leaf and dimensions of trees. See the explanation of Fig. 5.

$$Es=0.345-1.57\frac{1}{D},\ r=-0.97^{**} \text{ for the Plot I},$$

and

$$Es=0.389-0.924\frac{1}{D},\ r=-0.88^{*} \text{ for the Plot II;}$$

for height as

$$Es=0.398-2.00\frac{1}{H},\ r=-0.92^{*} \text{ for the Plot I},$$

and

$$Es=0.441-0.116\frac{1}{H},\ r=-0.88^{*}\quad \text{for the Plot II;}$$

and, for leaf dry weight as

$$Es=0.214-0.112\frac{1}{L},\ r=-0.90^{*}\quad \text{for the Plot I},$$

and

$$Es=0.319-0.122\frac{1}{L},\ r=-0.97^{**}\quad \text{for the Plot II}.$$

In the Plot III such clear trends were not recognized.

In the Plots I and II, similar relationships were found between production and leaf mass as well as leaf efficiency for both net production and stem wood production. This similarity was due to the fact that distribution ratio to stem was not different systematically among trees in the plots. "Efficiency of leaf to produce stem wood" is the product of net assimilation rate times distribution ratio into stem (SATOO 1974a).

In the Plots I and II, not only stem wood production but also production of leaf and branch was linearly proportional to leaf mass. The relation between leaf production and leaf mass was already described for leaf dry weight. The relationship between leaf production (Pl kg) and leaf area (F sq. m) was described as

$$Pl=0.0272\,F,\ r=0.98^{**}\quad \text{for the Plot I},$$

and

$$Pl=0.0208\,F,\ r=0.99^{**}\quad \text{for the Plot II}.$$

The relationship between branch production (Pb kg) and leaf mass was described for leaf dry weight (L kg) as

$$Pb=0.043\,L,\ r=0.98^{**}\quad \text{for the Plot I},$$

and

$$Pb=0.036\,L,\ r=0.99^{**}\quad \text{for the Plot II;}$$

and for leaf area (F sq. m) as

$$Pb=0.0105\,F,\ r=0.97^{**}\quad \text{for the Plot I},$$

and

$$Pb=0.0089\,F,\ r=0.99^{**}\quad \text{for the Plot II}.$$

Thus production of each part of the aerial part is linearly proportional to leaf mass. It means that distribution ratios are rather stable within plots.

7. Water content of leaf

As shown by Fig. 7, both in new and old leaf, water content decreased with

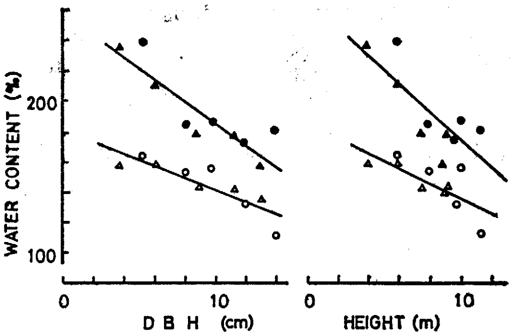

Fig. 7. Leaf water content in relation to dimensions of trees.

	Current year leaf	Old leaf
Plot I	Filled triangles	Open triangles
Plot II	Filled circles	Open circles

increasing D. B. H. and height of trees, and there was no difference between the Plots I and II. The variation of water content was larger in new leaves than old ones. This trend presumably reflects the fact that larger trees have more sun leaves than smaller suppressed ones. Similar trends were recognized among trees in a stand of *Cinnamomum camphora* (Satoo 1968a).

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** in Japanese only, title is tentative translation from the original by the present author.

(*Received April 1, 1972*)

能登半島のアテの植栽林の物質生産

—林分生長論資料12—

佐藤大七郎
根岸賢一郎
八木喜徳郎

あらまし

1haあたり31.2t (LAI: 12.9) および44.0t (LAI: 17.9) の葉をもつた林は，それぞれ，1年1haあたり11.3tおよび19.2tの乾物を生産した。もうひとつの林は1haあたり31.9t (LAI: 12.9) の葉をつけていた。これらのきわめて多量の葉をつけていることは，葉の平均寿命がながいためであつて，年々の葉の生産量がおおいためではなかった。年々の葉の生産量はほかの針葉樹の林とかわらなかった。林のなかのひとつひとつの木の純生産量は，劣勢木をのぞくと，そのつけている葉の量に比例し，葉の能率 (NAR) とは関係がなかった。葉の能率は針葉樹の林のなかでもつともひくかつた。あるおおきさまでの木では，樹高，胸高直径，葉の量とともに葉の能率がましたが，それよりおおきな木ではあまりまさなかった。葉の含水率は，古い葉でも新しい葉でも，樹高と胸高直径がおおきいほどすくなかった。

Appendix 1. Sample tree data.

Plot	Tree	D. B. H. (cm)	Height (m)	Volume (cu. m)	Biomass (kg)			Leaf area (sq. m)	Production (kg)		
					Stem	Branch	Leaf		Stem	Branch	Leaf
I	1	5.2	5.8	0.00814	4.12	0.23	0.65	2.67	0.04	0.01	0.02
	2	8.0	7.8	0.02656	10.41	1.53	3.43	14.09	0.50	0.19	0.43
	3	9.7	9.9	0.04415	19.86	2.28	4.66	19.15	0.72	0.23	0.47
	4	11.8	9.5	0.06140	24.42	3.06	7.73	31.78	1.72	0.38	0.96
	5	13.8	11.2	0.10988	40.24	5.13	13.90	57.16	3.38	0.56	1.51
II	6	3.7	3.8	0.00315	1.60	0.21	0.61	2.50	0.08	0.01	0.02
	7	6.0	5.8	0.01043	4.80	0.97	1.73	7.13	0.43	0.07	0.13
	8	8.7	7.4	0.02657	11.59	2.19	4.87	20.02	1.40	0.18	0.41
	9	11.2	9.0	0.04497	20.07	4.14	8.09	33.26	2.03	0.41	0.81
	10	12.8	8.8	0.06793	26.21	6.12	15.37	63.21	5.56	0.50	1.24
III	11	9.6	9.7	0.04440	17.77	1.96	2.18	8.98	0.18		
	12	14.6	11.7	0.12011	44.42	7.51	10.03	41.23	2.24		
	13	16.2	13.2	0.16047	61.19	7.34	10.47	43.04	3.35		
	14	18.3	13.4	0.19085	71.36	12.67	16.27	66.91	2.57		
	15	22.0	14.2	0.29612	110.43	18.29	23.53	96.76	3.79		

Appendix 2. Stand table.

D. B. H.	Number of tree per ha			D. B. H.	Number of tree per ha		
	I	II	III		I	II	III
3	260			14	260	240	552
4	130	962		15	130		221
5	0	0		16			442
6	390	481	110	17			110
7	649	0	0	18			110
8	390	962	0	19			221
9	649	721	0	20			110
10	909	962	221	21			110
11	1039	721	0	22			0
12	779	962	110	23			110
13	0	481	221	24			110