Studies on the Production Structure of Forest (XVI)

Primary productivity of *Abies veitchii* forests in the subalpine zone of Mt. Fuji*

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Introduction

Generally speaking, there are four zones in the vertical distribution of plant communities in the Japanese Islands; the submontane, the montane, the subalpine and the alpine zones. The subalpine zone, lying between the montane zone and alpine zone or between the upper limit of montane zone and the forest line in the mountain region of central Japan, are represented by the forests consisting of evergreen coniferous species, such as *Abies veitchii, Abies mariesii, Picea jezoensis* v. *hondoensis, Tsuga diversifolia,* etc. mixed with deciduous ones, such as *Betula ermanii, Larix leptolepis,* etc.

The climatic condition in the subalpine zone, corresponds to that in the subarctic zone, is severe in general because of low temperature, cold wind, snowfall, etc., so the regeneration and tending of forest stands in this zone come to be important problems in forestry as the felling area in this zone spreads.

About twenty or more workers belonging to our Forest Experiment Station have carried out joint studies on the silvicultural treatments of the subalpine zone, which contains researches on the natural regeneration, the artificial regeneration, the forest dry matter productivity and the climatic condition.

This paper deals with the primary productivity of several forests of *Abies veitchii* which is one of the typical tree species in the subalpine zone of central Japan. The studies were performed as a part of the joint studies mentioned above.

The primary productivity in subalpine *Abies* forests has been studied by several workers. Especially, OSHIMA *et al.*[12], KUROIWA[6)~8)], KIMURA[2] and KIMURA *et al.*[3] have an interest in the peculiar structure of *Abies* forests on Mt. Shimagare, Nagano Prefecture, where all subalpine *Abies* trees in the forest aged about 100 years die in stripes naturally, and the next generation grows in the stripes of dead trees, and their ecological and physiological studies on the structure and productivity have been reported in series. Also, ASADA and AKAI[1] surveyed the productivity of many subalpine *Abies* forests in Nagano Prefecture from the viewpoint of silvics.

This article was read in part at the 78th and 79th Annual Meetings of Japanese Forestry

* Contributions from JIBP-PT No. 73.

Received December 4, 1969

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Society (1967 and 1968), and half of the investigation was reported in our previous paper[18].

Outline of fields and field work

The field works were carried out in 1966 and 1967 in the subalpine zone of the NNW slope of Mt. Fuji, Minami-Tsuru District of Yamanashi Prefecture, central Japan.

The general features of the NNW slope of Mt. Fuji are as follows:

The elevation from 1,400 to 1,500 m is the border between the montane or cool-temperate zone represented by *Fagus crenata* and the subalpine or subarctic zone. The subalpine zone reaches up to the forest line, lying at about 2,400~2,500 m above the sea level, with which the alpine or arctic zone represented by dwarf *Larix leptolepis, Betula ermanii* and others begins upwards.

The subalpine zone of this area is mostly covered with natural coniferous forests mainly consisting of *Abies veitchii, Tsuga diversifolia, Larix leptolepis, Abies mariesii*, etc. *Abies veitchii*, which sometimes distributes at 1,200 or 2,800 m altitude[21], is the most common species in this subalpine zone, but its large-sized pure stand is poorly developed though the small-sized one occurs with more frequency. The aged *Tsuga* forest seems to be in its climax stage and occupies a large area in this zone. *Larix* is the pioneer species which develops on the uncovered land originated in forest fire, degradation, clear cutting and others. *Abies mariesii* is not common on Mt. Fuji, a stand of which is found only in a limited area on the NNW slope. In the upper parts of the subalpine zone the evergreen conifer—moss community is the general type, and in the middle parts the evergreen conifer—*Cacalia adenostyloides*—moss community. The lower parts of it have communities showing more complexity in the construction[21].

The soil is inmature and of black volcanic ash origin, the depth of which is ordinarily from 40 to 50 cm. Under the soil layer there exists unweathered lava with the alternate sand- and gravel layers of basaltic matter, which disturbs the development of root system of trees.

Our object was to appraise the full or potential productivity of organic matter in *Abies veitchii* forests, so in June of 1966 and 1967, twenty stands, most of which were regarded as in the full density stage, were preliminarily surveyed along the Shoji route of Mt. Fuji (Table 1), and nine stands of them were investigated in detail in October of 1966 and 1967. The outline of nine stands are as follows:

Plots investigated in 1966

Plot 11: 24th Compartment of Imperial Gift Forest of Yamanashi Prefecture. NNW slope with a gentle gradient, consisting of *Abies veitchii* of medium size (10~25 cm in DBH), aged from 60 to 90 years, mixed with a few *Pinus pentaphylla, Tsuga diversifolia, Betula platyphylla* v. *japonica* and *Sorbus commixta*. The ground was entirely covered with moss.

Plot 14: 24th Compartment. SSW slope with 15° gradient, *Abies veitchii* aged from 40 to 70 years in pole stage (2~18 cm in DBH), growing mixed with a few suppressed *Tsuga diversifolia*; no ground vegetation could be found.

Plot 21: 23rd Compartment. Flat area, abandoned nursery, young and dense stage in small size (1~8 cm in DBH), aged about 25 years, growing mixed with no other species, no ground vegetation.

Table 1. Outline of preliminarily surveyed stands

Plot	Altitude	Age of released growth	Number of trees	Mean tree height	Mean height of main trees	Mean DBH	Basal area	Stem volume	Note
	m	yr	no./ha	m	m	cm	m^2/ha	m^3/ha	
11*	1,640	25	3179	13.6	14.9	15.5	64.77	515.6	
12	1,640		2806	14.2	14.7	16.6	64.46	526.8	
13	1,650		2311	12.6	13.5	15.6	47.57	360.0	
14*	1,700	25	9700	6.8	7.7	7.6	56.84	285.0	Cutting area of *Tsuga* forest
15	1,690		5700	11.1	13.4	12.0	83.43	655.3	Ditto
16	1,820		644	19.7	19.7	41.7	95.17	900.1	*Tsuga* reserve forest
17	1,730		12857	6.3	7.8	6.7	55.58	272.6	Wind break area
18	1,800		12500	7.5	7.8	7.2	60.13	316.7	Ditto
19A	1,940	12	15200	2.0		4.5**			Ditto
19B	1,940	12	41600	1.3		3.4**			Ditto
20	1,530	25	1669	9.9	9.9	14.9	29.59	166.9	Plantation
21*	1,530	25	19500	4.5	4.5	4.3	33.65	113.7	Abandoned nursery
22*	1,530	4	10^6	0.46		0.66**	37.0 **	12.2	Nursery
31	1,640		2218	11.2	15.0	16.2	64.94	568.4	
32*	1,660	60	1204	16.3	18.6	24.0	63.39	568.0	
33*	1,700	60	3814	10.1	12.4	12.8	58.03	340.8	Cutting area of *Tsuga* forest
34*	1,530	23	2076	8.5	8.5	13.1	29.28	138.0	Plantation
35	1,700		973	15.4	17.2	28.1	72.13	618.6	Cutting area of *Tsuga* forest
36	1,700		1380	14.3	14.7	25.3	76.65	588.6	
37*	1,530	25	12106	5.3	5.3	5.5	33.36	177.1	Abandoned nursery
38*	1,500	5	63×10^4	0.69		1.0**	54.9**	25.8	Nursery

Plot 11~22: surveyed in 1966, Plot 31~38: surveyed in 1977.
All plots except plot 16 were mainly consisted of *Abies veitchii*.
* : Plots surveyed in detail.
**: At stem base.

Plot 22: 23rd Compartment. Nursery, four years after transplanting of natural seedlings at 10 cm × 10 cm spacing, unthinned.

Plots investigated in 1967

Plot 32: 24th Compartment. NNW slope with a gentle gradient, consisting of relatively large sized *Abies veitchii* (10~45 cm in DBH), aged from 45 to 130 years, growing mixed with a few *Betula ermanii, Sorbus commixta, Pinus pentaphylla* and suppressed *Tsuga diversifolia.* The ground for the most part was covered with moss and few herbs such as *Cacalia adenostyloides, Maianthemum dilatatum*, etc.

Plot 33: 24th Compartment. SW slop with 10° gradient, middle-sized *Abies veitchii* (5~23 cm in DBH), aged from 40 to 55 years, mixed with a few *Sorbus commixta* and suppressed *Tsuga diversifolia*, moss ground vegetation. Many dead trees suggested that the canopy had rapidly opened in the last few years owing to some adverse condition or influence.

Plot 34: 23rd Compartment. A 23-year-old plantation of *Abies veitchii* (10~18 cm in DBH), flat area. Since the canopy closure had been completed a few years earlier and the leaf biomass came to the maximum, ground vegetation could not be found.

Plot 37: The same as Plot 21 (2~9 cm in DBH).

Plot 38: 25th Compartment. Nursery, five years after transplanting of natural seedlings at 10 cm × 10 cm spacing, unthinned.

The climatic conditions at these plots are presented in Table 2, calculated from the

Table 2. Climatic condition

Plot	Altitude	Mean temperature			Warmth index	Coldness index	Precipitation		
		Annual	May-Oct.	Nov.-Apr.			Annual	May-Oct.	Nov.-Apr.
	m	°C	°C	°C	month-°C	month-°C	mm/yr	mm/0.5yr	mm/0.5yr
14, 33	1,700	5.2	12.4	−2.0	44.5	−42.0			
32	1,660	5.4	12.6	−1.8	45.8	−40.8			
11	1,640	5.5	12.7	−1.7	46.7	−40.3	ca.2,000	ca.1,450	ca. 550
21, 22, 34, 37	1,530	6.2	13.3	−1.0	51.0	−36.8			
38	1,500	6.4	13.5	−0.8	52.2	−36.0			

Mean monthly temperature (°C)

Plot	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
14, 33	−6.9	−6.6	−2.7	4.9	7.4	12.1	16.6	17.2	13.6	7.6	3.0	−3.7
32	−6.6	−6.4	−2.5	5.1	7.6	12.3	16.8	17.4	13.8	7.8	3.2	−3.5
11	−6.5	−6.3	−2.4	5.3	7.7	12.4	17.0	17.5	13.9	7.9	3.3	−3.4
21, 22, 34, 37	−5.8	−5.6	−1.7	6.1	8.4	13.0	17.5	18.0	14.5	8.5	4.0	−2.7
38	−5.7	−5.4	−1.5	6.3	8.6	13.2	17.7	18.2	14.6	8.6	4.2	−2.6

data of meteorological stations at Shoji (820 m elevation, 11～12 km NW of the plots), Funatsu (860 m, 11～12 km NNE) and Top of Mt. Fuji (3,772 m, 6～8 km SE). The temperature at each plot was computed by the mean lapse rate of 0.54°C in summer half year and 0.62°C in winter half against 100 m elevation.

In the two preliminary surveys, the sample area of 20～400 m² suitable to the tree size of each plot, except the nursery plots, was delimited in each forest stand, and DBH and height of trees were measured.

The detail surveys were carried out in the nine plots afore-mentioned. After the measurement of light intensities both under the canopy and on the nearest open ground, ordinary eight sample trees per plot, of various size covering the whole range of DBH distribution given by tree census, were selected and felled one by one. After recording of DBH, height, clear length, crown diameter and height increment in the past of each sample tree, the fresh weights of stem bole, branches, current twigs, needles and current needles were separately weighed according to the stratified clip technique[11] of one meter depth per stratum. In the survey in 1966, the root systems of several sample trees of various sizes were dug out and weighed. In 1967, several root systems were also measured by us and afterwards, in November of the same year, Dr. N. Karizumi of Forest Experiment Station made an investigation into the roots which we left unmeasured.

The stem discs of each sample tree were taken at one meter intervals along the stem bole and at just below the lowest living branch for the stem analysis. The small samples of respective tree components in each plot were also taken for determinations of oven-dry weight and of leaf area.

Biomass

The small samples were carried to the laboratory and oven dried at 80°C to constant weights to obtain the conversion factors from fresh weight to dry weight.

All weight values in this paper are expressed in oven-dry unit.

The biomass on the plot area was estimated on the assumption that the rate in biomass of the total sum of sample trees per plot to that on the whole plot area is equal to the rate in respective basal areas. Namely,

$$y = y'G/G' \qquad \cdots\cdots\cdots\cdots(1)$$

where y and y' denote the total biomass on the plot area and that of the sample trees respectively, while the corresponding values of the sum of basal area are represented by G and G'.

The biomass at the end of the growing season (October) of the subalpine *Abies* stands studied is shown in Table 3 with other properties.

The values of root biomass in Plots 11, 14 and 21 were estimated as a root biomass per plot amounting to 30 per cent of the total biomass of both stems and branches per plot, summarizing the results of actual measuring in several sample trees, while in other plots the root biomass was given by direct measurement. The ratio of biomass in roots to that in both stems and branches per plot came to from 23 to 42 per cent except the high ratio in the nursery plots, Plots 22 and 38, at 64 and 48 per cent respectively.

The leaf area on one leaf side was calculated through the needle weight multiplied by the specific leaf area—rate of leaf area per unit leaf weight. The values of specific leaf area for current needles and other aged needles belonging to each plot were independently determined by the dot-grid method applied to photographically enlarged leaf forms. The values of specific leaf area in each plot are presented in Table 4. In Plot 34 the ratio was determined at each canopy stratum with the depth of one meter to find the vertical change

Table 3. Biomass and other properties

Plot no.			11	14	21	22	32	33	34	37	38
Number of trees		no./ha	3179	9700	19500	10^6	1204	3814	2076	12106	63×10^4
Mean tree height		m	13.6	6.8	4.5	0.46	16.3	10.1	8.5	5.3	0.69
Mean height of main trees		m	14.9	7.7	4.5		18.6	12.4	8.5	5.3	
Mean DBH		cm	15.5	7.6	4.3	0.66*	24.0	12.8	13.1	5.5	1.0*
Basal area		m^2/ha	64.77	56.84	33.65	36.95*	63.39	58.03	29.28	33.36	54.89*
Stem volume		m^3/ha	515.55	284.99	113.67	12.18	568.02	340.80	138.00	117.07	25.75
Oven-dry weight	Stem	t/ha	190.24	107.63	45.73	4.9	205.68	129.23	44.98	42.11	9.26
	Total branch	t/ha	15.69	15.48	8.67	1.8	32.26	16.94	17.01	13.61	3.45
	Current twig	t/ha	0.77	0.78	0.59	0.4	0.78	0.59	0.83	0.60	0.58
	Total needle	t/ha	16.70	17.61	13.95	5.5	18.79	13.31	21.30	18.27	7.29
	Current needle	t/ha	3.29	3.43	2.86	1.6	4.36	4.07	4.47	3.44	2.54
	Root	t/ha	61.78	36.93	16.32	4.3	54.24	40.56	25.88	17.48	6.05
	Whole plant	t/ha	284.40	177.65	84.67	16.5	310.97	200.04	109.17	91.47	26.05
Leaf area (one-side)	Total needle	ha/ha	8.2	9.7	8.1	5.5	10.6	7.8	12.8	10.9	7.7
	Current needle	ha/ha	1.6	1.9	1.9	1.5	2.6	2.6	3.0	2.7	2.9
	Aged needle	ha/ha	6.6	7.8	6.2	4.0	8.0	5.2	9.8	8.2	4.8
Relative light intensity		%	4.1	3.6	4.5		1.0	3.7	1.9	1.0	0.8
Light extinction coefficient		(ha/ha)	0.39	0.34	0.38		0.43	0.43	0.31	0.42	0.63
Specific pipe length		cm	148	120	164		168	114	156	150	

* : At stem base.

Table 4. Specific leaf area (Leaf area per unit leaf dry weight)

Plot	Current needles	Aged needles
	cm²/g	cm²/g
11	50	49
14	55	55
21	65	56
22	93	102
32	59.9	55.7
33	62.9	56.2
34	67.0	58.4
37 Dominant	78.9	55.2
Others	83.6	56.7
38	105.7	100.5

Plot 34		
Height of stratum	Current needles	Aged needles
m～m	cm²/g	cm²/g
9.2～9.9	43.7	—
8.2～9.2	50.9	46.5
7.2～8.2	56.5	52.8
6.2～7.2	62.0	51.5
5.2～6.2	62.7	52.4
3.2～5.2	81.6	60.1
1.2～3.2	93.7	65.1
Weighted mean	67.0	58.4

of the ratio and to check the values of the other plots.

The needle biomass is summarized as within the range from 13 to 19 t per ha in weight and from 8 to 11 in leaf area index (LAI) except Plots 33, 34 and nursery plots. The canopy of Plot 33 seemed to have opened in recent few years, so it carried a relatively small needle biomass, while that of Plot 34 was in the stage of the maximum needle biomass. But, the differences of biomass in current needles of Plot 33 from the others are relatively smaller than in whole needles. Accordingly, the ratio of current needles against whole needles in Plot 33, 0.31 t per t, is as high as that in the nursery plots, though that in other plots is 0.20 t per t in average. Kimura[2] reported this ratio at 0.19 t per t in a mature stand dominated by *Abies veitchii* in Mt. Yatsugatake, and also Kimura *et al.*[3] at 0.31 t per t in a young stand with 80 cm tree height in the same district.

Oshima *et al.*[12] studied in *Abies veitchii*—*A. mariesii* forests of Mt. Shimagare and found their total needle biomass within the range of from 8.6 to 12.1 t per ha. Kimura[2] estimated the needle biomass of a mature subalpine *Abies* forest to be 20.8 t per ha and Kimura *et al.*[3] that of a young stand of *Abies veitchii* to be 10.24 t per ha. Calculating from the data of 24 forests of *Abies veitchii* in Nagano Prefecture surveyed by Asada and Akai[1], their needle biomass comes to 16.2±5.0 t per ha in average.

Also, Shidei *et al.*[14] found the needle biomass of 19.1 t per ha in a middle-aged *Abies sachalinensis* in Hokkaidô. Tadaki and Hatiya[17], correcting the values given by Tadaki[16], summarized the leaf biomass of closed evergreen coniferous forests in Japan, excluding *Pinus* and *Cryptomeria* forests, as 16.0±4.5 t per ha in dry weight and from 5 to 10 in LAI based on the data of 47 stands. So the needle biomass in our subalpine *Abies* forests except the nursery plots seems to be within the reasonable range in evergreen coniferous forests.

The vertical distribution of the biomass per each plot is illustrated in Fig. 1. Though there are obvious differences in total biomass caused by the various stem biomass, a distinct difference can not be found among plots in the amount nor in the form of the distribution of canopy biomass except Plots 32 and 34; the depth of a stratum of the former is different from the other, and the canopy of the latter is just fully closed and not yet pruned naturally.

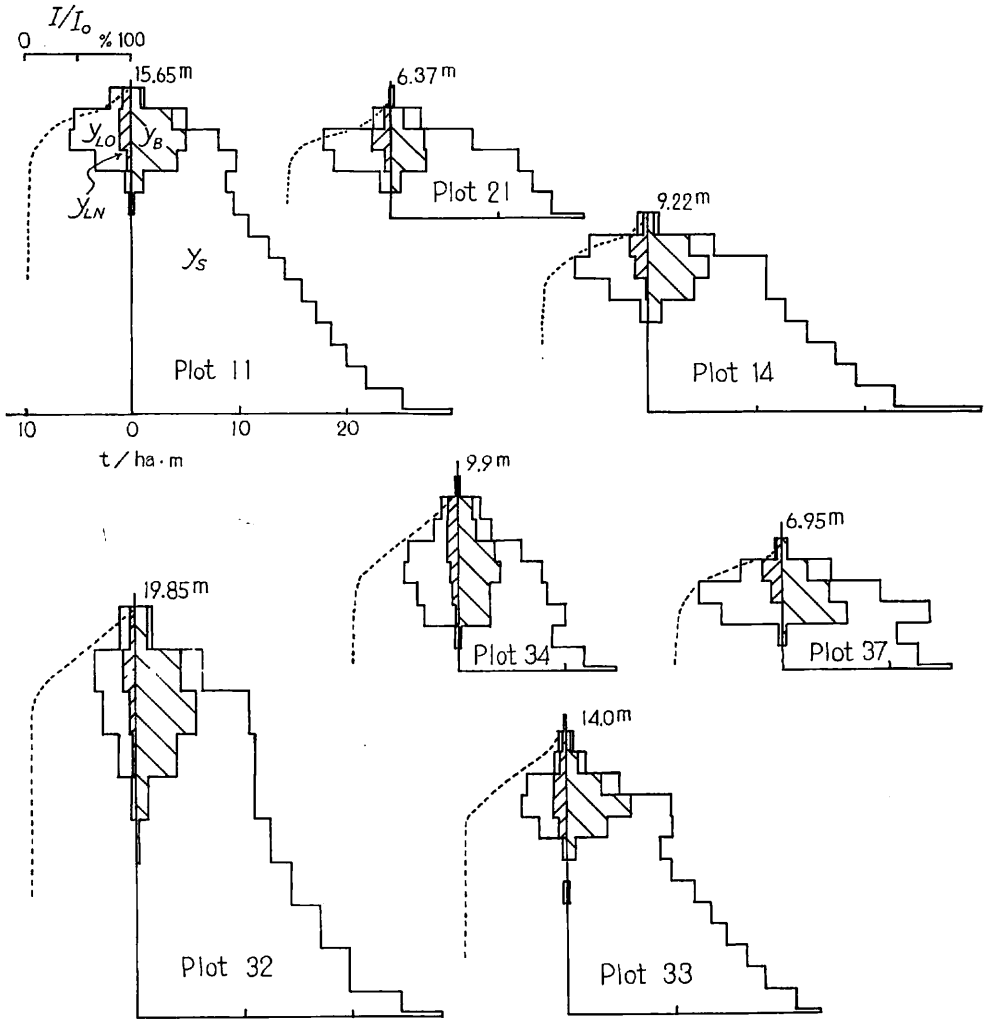

Fig. 1 Vertical distribution of biomass in stem (y_S), in branch (y_B), in current needle (y_{LN}) and in aged needle (y_{LO}) per plot. Dotted line expresses course of light attenuation along community profile estimated by Equation (2).

The specific pipe length was calculated in each plot, which expresses the proportionality constant in the direct relation of the total weight of both stems and branches contained in a horisontal stratum to the weight of leaves appearing in and above that stratum. The specific pipe length was proposed by Shinozaki *et al.*[15] who supposed that the stems and branches in a certain horizon of a plant community were supporting, both mechanically and functionally, not only the foliage in the same horizon but also all the foliage occurring in higher horizon. The values of it, having the dimension of length, were calculated as shown in Table 3, among which the value of Plot 33 was exceptionally small because of its open canopy.

The course of light attenuation along the community profile was estimated by Beer-Lambert's formula[11];

$$I/I_0 = \exp(-KF) \qquad \cdots\cdots\cdots(2)$$

and shown by dotted lines in Fig. 1, where I_0 and I denote the incident light intensity and the light intensity under the leaf area F respectively, and K the extinction coefficient. From the values of relative light intensity I/I_0 under the canopy measured before felling of sample trees, K was calculated at 0.39 (ha per ha) in average of seven forest plots with the range of from 0.31 to 0.43.

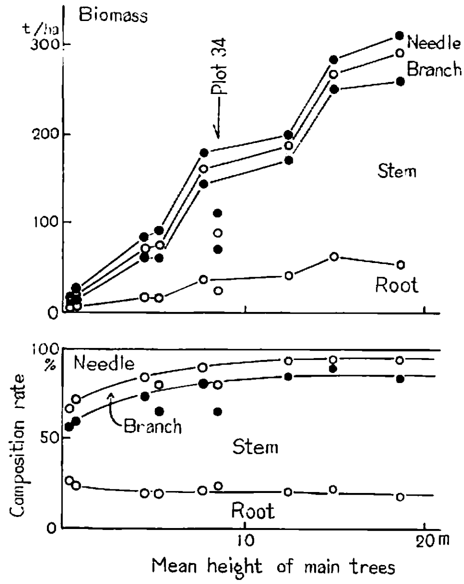

Fig. 2　Increase of biomass and change of composition rate with increasing of mean height in main trees.

The total biomass of stand increases with the forest growing. Fig. 2 shows the course of biomass increasing with the growth stage expressed by the mean height of trees composing main canopy. The increase of total biomass of forest is mainly caused by that of stems. The percentage in stem biomass against the total biomass becomes larger, while on the contrary, that in needle and branch biomass becomes smaller with increasing mean tree height. Plot 34 is somewhat dissimilar to those plots because it is a plantation. Having a much lower initial density than the other natural or semi-natural plots, Plot 34 has been grown under unclosed canopy till a few years ago, so the total biomass is smaller, while the percentage of branches and needles against the total biomass is larger comparing with the progress of biomass increase in natural stands.

Stem increment

The stem volume increment including stem bark in recent one year per plot was estimated as the total amount of stem increment of sample trees, determined by stem analysis, multiplied by the rate of G/G' in Equation (1) and shown in Table 5.

Table 5. Stem volume increment (with bark) in the recent one year

Plot	Stem volume (A)	Increment (B)	(B)/(A)
	m³/ha	m³/ha/yr	1/yr
11	515.55	18.81	0.036
14	284.99	21.69	0.076
21	113.67	23.06	0.203
22	12.18		
32	568.02	13.97	0.025
33	340.80	10.58	0.031
34	138.00	21.97	0.122
37	117.07	15.50	0.132
38	25.75		

The average values of leaf efficiency in stem increment or the stem increment per unit leaf weight per year came to 1.06 dm³ per kg needles per year, with the wide range of from 0.74 to 1.65 dm³ on volume basis and 0.40 kg per year with the range from 0.27 to 0.99 kg on dry weight basis.

As Tadaki and Shidei[20], and Tadaki[16] have suggested, there is an obvious difference between the vertical distribution of the horizontal strata having larger leaf biomass and that of those having larger stem increment; and the amount of stem increment is nearly the same at any height under the horizon

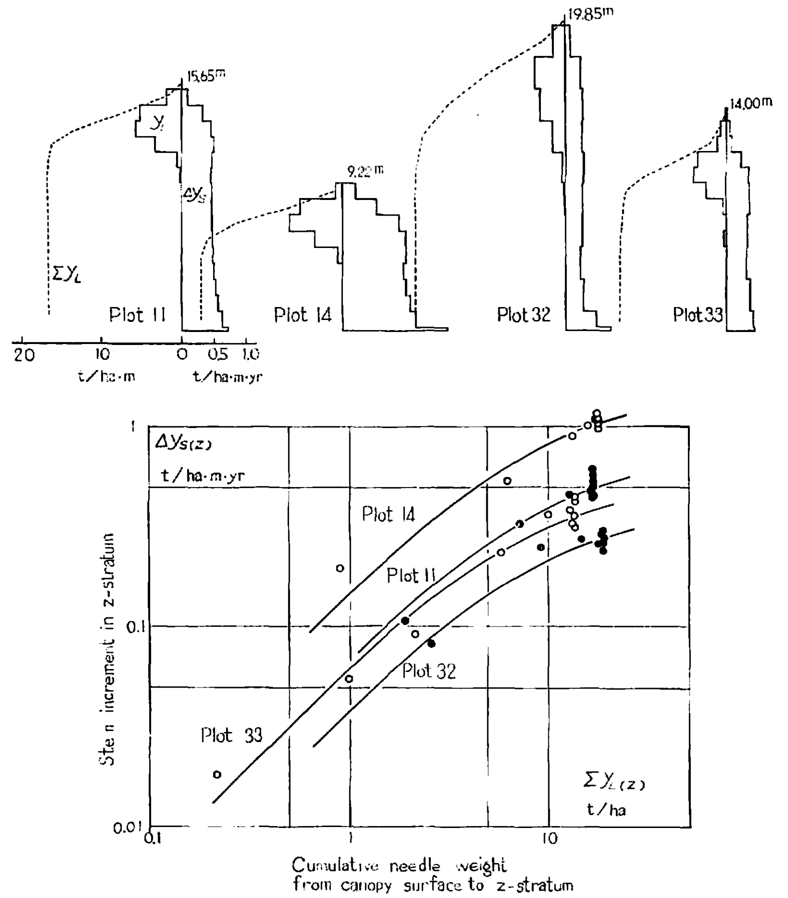

Fig. 3 Vertical distribution of stem increment per year per plot (Δy_S) in relation to that of needle biomass (y_L) and of cumulative needle weight (Σy_L), and relation between stem increment in a certain horizontal stratum z ($\Delta y_{S(z)}$) and cumulative needle weight from canopy surface to z-stratum ($\Sigma y_{L(z)}$) approximated as Equation (3).

where the canopy is closed, whereas it decrease upwards above that horizon. And they have also suggested that there is some clear relation between the stem increment in a certain horizontal stratum and the cumulative leaf amount which expresses the leaf biomass appearing in and above that horizontal stratum.

The situations afore-mentioned in typical four plots are illustrated in Fig. 3, in which the annual stem increment is expressed on dry weight basis. The relation between the stem weight increment in a horizontal stratum z, $\Delta y_{S(z)}$, and the cumulative needle weight from the canopy surface to z-level, $\Sigma y_{L(z)}$, can be approximated from the following formula[18],

$$1/\Delta y_{S(z)} = A/\Sigma y_{L(z)} + B \qquad \cdots\cdots (3)$$

where A and B are the constants.

Net productivity

There are two methods to estimate the net production figure based on the biomass measuring[4]. The first one is

$$\Delta P_n = \Delta y + \Delta L + \Delta G \qquad \cdots\cdots\cdots(4)$$

where ΔP_n, Δy, ΔL and ΔG denote the net production during the period $t_1 \sim t_2$, the difference of biomass between t_1 and t_2, the amount of loss by death during the period and that by animal grazing respectively.

The second one is

$$\Delta P_n = y_N + \Delta L_N + \Delta G_N \qquad \cdots\cdots\cdots(5)$$

where y_N, ΔL_N and ΔG_N stand for the biomass newly produced during the period $t_1 \sim t_2$ at t_2, the loss by death during the period out of newly produced matter and that by grazing respectively.

The second method was used for the present investigation. Since ΔL_N and ΔG_N were usually supposed to be considerably smaller than y_N, they were disregarded and y_N was divided into several tree components,

$$\Delta P_n \fallingdotseq y_{NS} + y_{NB} + y_{NL} + y_{NR} \qquad \cdots\cdots\cdots(6)$$

where *S*, *B*, *L* and *R* added as suffix denote the tree components; stem, branch, leaf (needle) and root respectively.

The determination of y_{NS} is possible by the method of stem analysis. The obtained values of the volume increment were converted into dry weight multiplying the average dry weight—volume ratio.

To estimate the amount of y_{NB}, naturally including not only the amount of current twigs but also that of increment in aged branches, the relation between the branch weight per tree and the stem volume inside its crown which indicates the stem volume above the lowest living branch was employed[18]. On the assumption that the situation of the afore-mentioned relation did not change within a short period, the amount of newly produced branches per tree could be determined as the difference of the branch weights between at present and at the end of the preceding growing season, the latter being calculated by applying the stem volume *in the preceding year* above the lowest living branch *at present*. The value of y_{NB} was given as the total sum of the values of single trees. This method is based on the consideration that the amount of branch fall in the crown above the *present* lowest living branch may be fairly small during the recent one year.

The amount of y_{LN} was here regarded as to be equal to the biomass of current needles at the time of investigation, though KIMURA[3] reported that about 15 per cent of current needles of young *Abies veitchii* was shed during the same growing season, and KUROIWA[7] suggested that the needle weight of *Abies veitchii* increased about 0.05 g dry weight per 100 cm^2 leaf area per year.

since the direct determination of y_{NR} was difficult, its estimation was made on the assumption that the rate of newly produced biomass against the whole biomass in under ground parts was equivalent to that in above ground woody parts.

In nursery plots, the branch fall was scarcely observed, so y_{NS} and y_{NB} in total was estimated as the difference between the biomass at present and that at the end of the last growing season. The former was calculated from the relation of stem and branch weight to D^2H per tree (*D*: diameter at stem base, *H*: height of seedling), while the latter by the same relation of D^2H at the end of the last growing season replaced by D^2H at present. The estimations of their y_{NL} and y_{NR} were carried out in the same procedures of the forest plots

Table 6. Estimates of net production

Plot no.		11	14	21	22	32	33	34	35	38
										t/ha/yr
Current products	Stem	6.9 (48)	8.2 (49)	9.5 (51)	4.1 (49)	5.0 (40)	4.1 (36)	7.2 (36)	5.3 (36)	4.1 (48)
	Branch	1.7 (11)	2.1 (13)	2.5 (14)		1.8 (14)	1.4 (13)	3.7 (19)	3.2 (22)	
	Root	2.6 (18)	3.1 (18)	3.6 (20)	2.7 (32)	1.6 (12)	1.5 (14)	4.5 (23)	2.7 (18)	2.0 (23)
	Needle	3.3 (23)	3.4 (20)	2.9 (15)	1.6 (19)	4.4 (34)	4.1 (37)	4.5 (22)	3.4 (24)	2.5 (29)
Net production		14.5 (100)	16.8 (100)	18.5 (100)	8.4 (100)	12.8 (100)	11.1 (100)	19.9 (100)	14.6 (100)	8.6 (100)

Figures in parentheses indicate the relative values.

afore-mentioned.

Thus the net production figure in each plot was determined as shown in Table 6.

Gross production

The value of the gross production is given as the total sum of the net production and the consumption by respiration. The rough estimates of dry matter loss due to the respirations of needles and of woody organs were separately calculated from certain available data.

According to the observation by Kuroiwa[7], the respiratory rate in current needles of dominant and intermediate trees in young *Abies veitchii* stand in Mt. Shimagare averaged 0.98 mg CO_2 and in aged needles 0.75 mg CO_2 per g dry weight of needles per hour at 15°C in summer.

Pisek and Winkler[13] reported that the respiratory rate of *Picea excelsa* at high altitude reached a maximum in summer to be about twice as large as that in the other seasons; here, the rate of *Abies veitchii* in seasons other than summer was assumed to be one-half of Kuroiwa's rate.

From those rates and the monthly temperatures shown in Table 2, and assuming the temperature coefficient of respiratory activity $Q_{10} = 2$, the loss of dry matter due to needle respiration in each plot was calculated by the usual procedure, in which the conversion coefficient from respired CO_2 to the dry matter was accounted as 0.614, regarding the average composition of plant material as $(C_6H_{12}O_5)_n$.

In the case of our investigation, the seasonal change of needle biomass was unconfirmed, so the needle biomass as the base of the calculation of respiratory loss was assumed that the amount of aged needles did not change through the growing season and the current needles existed from June onward unchanging their biomass.

The respiratory loss in woody components—stem, branch and root—was roughly estimated by the indirect method suggested by Shidei *et al.*[14]:

The gross production ΔP_g is defined as the sum of the net production ΔP_n and the respiratory consumption ΔR;

$$\Delta P_g = \Delta P_n + \Delta R. \qquad \cdots\cdots(7)$$

This relation can be derived as in the following:

$$A \cdot y_L = \Delta P_n + (r_L \cdot y_L + r_C \cdot y_C), \qquad \cdots\cdots(8)$$

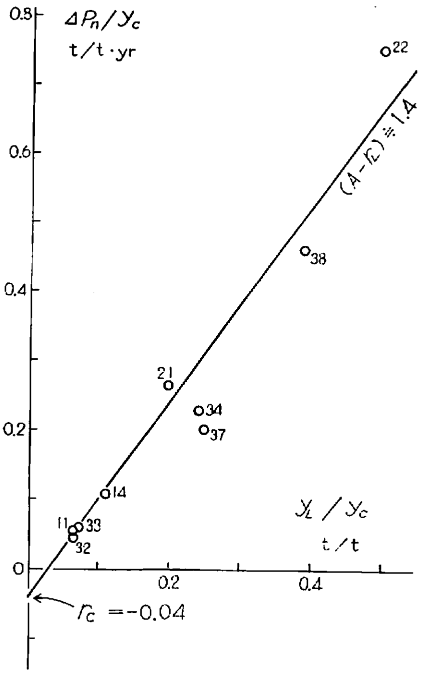

Fig. 4　Estimation of average respiratory rate in wood (r_C) and average net assimilation rate in needle (A-r_L) according to Equation (10). Figures added to the circles indicate the plot number.

where A is the average gross assimilation rate, y_L the leaf biomass, y_C the biomass of woody components, and r_L and r_C the average respiratory rate in leaves and in woody components respectively.

Then, the Equation (8) is reformed as

$$\Delta P_n = (A - r_L) y_L - r_C \cdot y_C \,, \qquad \cdots\cdots\cdots (9)$$

$$\Delta P_n / y_C = (A - r_L) y_L / y_C - r_C \,, \qquad \cdots\cdots\cdots (10)$$

where $(A - r_L)$ represents the average net assimilation rate in leaves.

When we illustrate the relation between $\Delta P_n / y_C$ and y_L / y_C, a linear relationship is expected, and $(A - r_L)$ and r_C are respectively given as the inclination of the regression line and the interception of longitudinal axis.

In the case of this investigation, we could determine the value of r_C around 0.04 t per year and $(A - r_L)$ seemed to come to about 1.4 t per t per year as shown in Fig. 4.

Then, the gross production figure in each plot can be determined as the total sum of net production, respiratory consumption in needles and that in woody components as presented in Table 7.

Table 7.　Estimates of gross production

Plot no.		11	14	21	22	32	33	34	37	38
										t/ha/yr
Net production		14.5 (32)	16.8 (38)	18.5 (47)	8.4 (53)	12.8 (26)	11.1 (31)	19.9 (38)	14.6 (35)	8.6 (45)
Respiration	Current needle	4.3 (9)	4.4 (10)	3.9 (10)	2.2 (14)	5.7 (12)	5.2 (15)	6.1 (12)	4.7 (11)	3.5 (18)
	Aged needle	16.5 (36)	17.0 (38)	14.2 (36)	5.0 (31)	18.3 (38)	11.5 (33)	22.3 (43)	19.7 (47)	6.4 (33)
	Woody organ	10.7 (23)	6.4 (14)	2.8 (7)	0.4 (2)	11.7 (24)	7.5 (21)	3.5 (7)	2.9 (7)	0.8 (4)
Gross production		46 (100)	45 (100)	39 (100)	16 (100)	49 (100)	35 (100)	52 (100)	42 (100)	42 (100)

Figures in parentheses indicate the relative values.

Energy efficiency

The total amount of the incident solar radiation is 125×10^3 cal per cm^2 through a year and is 70×10^3 cal per cm^2 during the period from May to October corresponding to the growing season, according to the observation by Meteorological Station at Iida, located on the same latitude in spite of the long distance of 70 km or more away from the area we worked.

Based on those figures, the efficiency of energy fixation (LINDEMAN's ratio) was calculated

Table 8. Energy efficiency

Plot no.	11	14	21	22	32	33	34	37	38
For net production									
Whole year	0.005	0.006	0.006	0.003	0.004	0.004	0.007	0.005	0.003
Growing season*	0.009	0.010	0.011	0.005	0.008	0.007	0.012	0.009	0.005
For gross production									
Whole year	0.015	0.015	0.013	0.005	0.016	0.012	0.017	0.014	0.006
Growing season*	0.027	0.027	0.024	0.010	0.029	0.021	0.031	0.025	0.011

* From May to October.

for both net and gross production figures as given in Table 8. It seems that the efficiency of the growing season in subalpine *Abies* forests comes to around 0.9 per cent for the net production and 2.6 per cent for the gross production in average.

Discussion

The net productivity in a mature subalpine forest dominated by *Abies veitchii* at about 2,250 m above the sea level was estimated at 11.1 t per ha per year by Kimura[2] and that in a young forest at the same situation 7.4 t per ha per year by Kimura *et al.*[3] Also, Asada and Akai[1] reported a wide range of net productivity of *Abies veitchii* forests in Nagano Prefecture as from 7.6 to 19.7 t per ha per year.

Besides, Shidei *et al.*[14] found a fairly high net productivity, about 21 t per ha per year, in a *Abies sachalinensis* forest of Hokkaido at the prime of its life, and Möller[9] estimated a maximum net productivity of *Picea abies* in a forest in Denmark at 18.0 t per ha per year.

According to the summarization of Tadaki and Hatiya[17], the net productivity of 46 evergreen coniferous forests in Japan, excluding *Pinus* and *Cryptomeria* forests, averaged 13.5±4.2 t per ha per year.

Therefore, not only may the annual net productivity of our forests, from 11 to 20 t per ha per year, be considered as normal as that of subalpine coniferous forests, but also the productivity in subalpine forest where cool temperature and severe climatic conditions prevail seems to be not so low as commonly believed.

The gross production figures of our forests, from 35 to 52 t per ha per year, are unreliable because of rough estimates in respiratory loss, but they are similar to those of a mature subalpine *Abies* forest estimated at 40 t per ha per year by Kimura *et al.*[3], and of a middle-aged *Abies sachalinensis* forest estimated by Yoda *et al.*[22] from 35 to 40 t per ha per year in respiration with from 20 to 24 t per ha per year in net production. On the other hand, there is a big difference in gross production between ours and a *Picea abies* forest in Denmark estimated by Möller[9] at 26.5 t per ha per year as the total of 18.0 t in net production and 8.5 t in respiration. The difference originates mainly from the difference of respiratory loss attributable to the latitude and temperature condition.

Kira *et al.*[4] and Kira and Shidei[5] found the proportional relation between the gross productivity of several broad leaf forests and the length of growing season in months multiplied by the leaf area index, and Tadaki *et al.*[19], adding some other data, confirmed this relation.

In the case of our subalpine coniferous forests, the relations were tentatively plotted on the picture as illustrated in Fig. 5. The linear relationship is not well confirmed by the

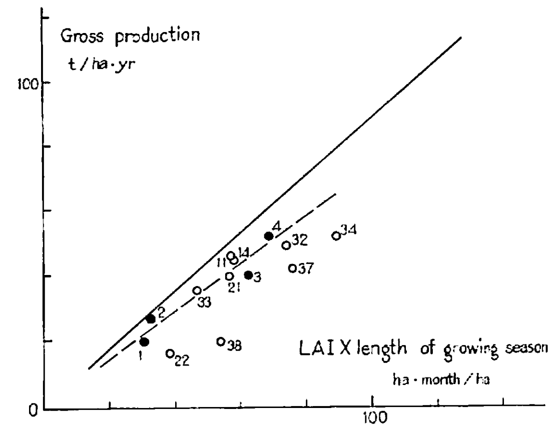

Fig. 5 Correlation between gross production, leaf area index (LAI) and length of growing season. Solid line denotes the relation in broad leaved forests given by KIRA *et al.*[4] and broken one the relation in subalpine coniferous forests, the latter is tentatively drawn as 80 per cent of the value in former. 1: Young *Abies veitchii* forest of Mt. Shimagare[3], 2: *Picea abies* forest of Denmark[9], 3: *Abies veitchii* forest of Mt. Yatsugatake[2], 4: *Abies sachalinensis* of Hokkaido[22], Open circles: Present investigation, figures added to the circles indicate the plot number.

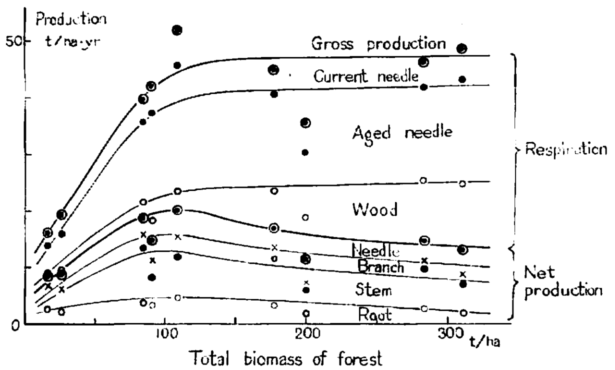

Fig. 6 Graphic presentation of annual dry matter productivity in *Abies veitchii* forests in relation to total biomass.

plotted points of subalpine coniferous forests, but the relation of subalpine conifers distinctly differs from that of broad leaf forests given by KIRA *et al.*[4]; less than 80 per cent of that of broad leaf forests. This fact shows that a production activity of unit leaf amount in conifers is inferior to that in broad leaf trees.

The primary productivity of *Abies veitchii* related to forest developing is graphically presented in Fig. 6. Here, the productivity is given in relation not to the stand age, but the total biomass of forest, because of the difficulties in deciding the age of natural forests and in estimating the effect of soil conditions. As most of the forests employed to illustrate the picture are in the full density stage, the full productivity of the subalpine *Abies* forests in the area we worked can be read from the picture.

The net productivity reaches a climax at about 100 t per ha of the total biomass—mean height of dominant trees around 5 m—which appears at stand age about 30 years in a closely regenerated stand on a sunny area of ordinary site conditions in the subalpine zone of Mt. Fuji. The variation in needle biomass having the same pattern as in net production, the peaks of variations of both patterns almost corresponds to each other.

In gross productivity a rapid increase up to the biomass of about 100 t per ha is followed by a relatively constant stage up to 300 t per ha of total biomass, in which the net productivity decreases and the respiratory loss in woody components increases with increasing of the total biomass. We could not find a clear maximum of gross production as MÖLLER *et al.*[10] found in the plantations of *Fagus sylvatica.*

Acknowledgement

We wish to express our gratitude to Dr. M. KUSAKA of the Government Forest Experiment Station, leader of the project on the silvicultural treatments of the subalpine zone; to the late Dr. A. ANDO, Mr. A. ENDO, Mr. T. FURUKOSHI and other staff members of Yamanashi Prefectural Forest Experiment Station who gave us their kind cooperation for the field works, and to Dr. N. KARIZUMI, Government Forest Experiment Station, who cooperated with us through the investigation of root systems. Our thanks are also due to Mr. Y. AOYAGI, Mr. H. HIRAIDE, Mr. S. SATO, Mr. K. KAMIJIMA and other staff members of Yoshida Forest Office of Yamanashi Prefecture who afforded us many facilities for the investigation.

Summary

Seven forests and two nurseries of *Abies veitchii*, located in the subalpine zone of Mt. Fuji, were investigated on their primary productivities in the fall of 1966 and 1967. There were few significant differences among the canopy layers of forests in biomass and in vertical distribution of the organs, in spite of the large differences in the whole biomass. Leaf area index of the seven forests, 8～11, led to the coefficient of light extinction 0.31～0.43/LAI. Net production as the sum of the biomass newly produced during the recent one year was estimated at 11.1～19.9 t per ha per year for the seven forest plots and 8.4～8.6 t per ha per year for the nurseries. Tentative estimate of annual respiratory loss was made and gross production was roughly estimated at 35～52 t per ha per year for the forest plots and 16～19 t per ha per year for the nurseries, which correspond to 1.2～1.7 per cent and 0.5～0.6 per cent of the fixation of solar energy for the whole year respectively. The variation of primary productivity in *Abies veitchii* forest relating to increase of the whole biomass is graphically presented.

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Appendix Ⅰ. Distribution of DBH

DBH	Number of trees						
cm	Plot 11	Plot 14	Plot 21	Plot 32	Plot 33	Plot 34	Plot 37
1		1*	2				
2		2, 4*	7	1*			4
3		1, 1*	5	1*	1		1
4	1*	5	4		1*		2
5		7	8		1		5
6		3	8		2, 1°		4
7	2	7	2		2, 1°		3
8		1	2	2*	2		5
9		6		1	1		2
10	2°	2		1°	2	4	
11	1	5			2	2	
12	1°	2			2, 1°	1	
13		1		1	2	2	
14	2	2		1°	4	2	
15	5	4			3	1	
16	3			1	2	3	
17	1				1	1	
18	1, 1*, 1°	1		2	1	1	
19	5				3		
20	3				1		
21	2			3, 1*	1		
22				2	3		
23					1		
24				1			
25				1			
26							
27				2			
28				5			
29				1			
30				2			
31				4			
32				4			
35				1			
36							
37				1			
40				1			
46				1			
Sum	25 2* 4°	49 6*	39	34 5* 2°	37 1* 3°	17	26
Plot area m^2	97.5	56.7	11.5	340.6	107.5	81.9	11.5

*: Coniferous tree other than *Abies veitchii*, °: Broad leaved tree.

Appendix Ⅱ-1. Sample trees in Plot 11

Tree no.	11-9	11-10	11-11	11-12	11-13	11-14	11-15	11-16
H	15.65	14.35	15.55	14.61	13.48	15.15	14.61	12.20
D	23.0	18.0	17.0	13.6	14.8	19.4	17.3	12.5
ΔH	19	15	15	17	12	20	11	0
w_S	125.444	72.266	67.898	46.284	48.211	89.209	65.630	33.683
w_{BO}	9.522	6.999	3.913	2.992	5.787	8.385	3.625	1.794
w_{BN}	0.937	0.239	0.317	0.110	0.098	0.355	0.142	0.020
w_{LO}	10.054	5.672	4.018	2.781	3.672	7.985	3.430	1.059
w_{LN}	3.057	1.161	1.319	0.595	0.603	1.858	0.756	0.138
w_R								
v_S	339.956	195.843	184.005	125.431	130.652	241.760	177.860	91.282
Δv_S	13.963	9.799	4.375	3.657	4.760	12.110	3.000	2.569

Notations: H: tree height in m, D: DBH in cm, ΔH: height increment in recent one year in cm/yr, w: oven dry weight in kg, S: stem, BO: aged branch, BN: current branch, LO: aged needle, LN: current needle, R: below ground part, v_S: stem volume in dm^3, Δv_S: stem volume increment including bark increment in recent one year in dm^3/yr.

Appendix Ⅱ-2. Sample trees in Plot 14

Tree no.	14-1	14-2	14-3	14-4	14-5	14-6	14-7	14-8
H	6.95	7.66	9.00	5.80	3.65	8.38	7.40	9.22
D	6.8	7.6	11.1	5.0	2.8	9.6	6.3	14.8
ΔH	48	14	22	0	0	15	7	20
w_S	6.013	9.094	17.888	2.471	0.732	13.403	6.856	34.405
w_{BO}	0.487	0.753	2.431	0.142	0.042	1.924	0.868	5.761
w_{BN}	0.017	0.038	0.121	0.007	+	0.131	0.033	0.312
w_{LO}	0.543	0.930	2.452	0.199	0.042	2.162	0.744	4.903
w_{LN}	0.089	0.242	0.578	0.031	0.002	0.480	0.161	1.309
w_R	1.955		6.132		0.232			
v_S	15.804	23.545	45.756	6.760	1.862	35.375	18.200	93.294
Δv_S	0.432	1.296	4.844	0.273	0.090	2.967	0.526	7.881

Appendix Ⅱ-3. Sample trees in Plot 21

Tree no.	21-17	21-18	21-19	21-20	21-21	21-22	21-23	21-24	21-25	21-26
H	6.37	5.79	5.18	5.17	4.42	3.87	3.61	1.71	2.46	4.42
D	7.9	5.9	5.3	4.9	4.0	2.9	2.4	1.3	2.0	3.6
ΔH	59	44	56	45	25	27	1	0	0	11
w_S	7.319	4.132	2.776	2.597	1.451	0.823	0.405	0.123	0.274	1.238
w_{BO}	1.554	0.680	0.526	0.356	0.223	0.103	0.038	0.029	0.077	0.147
w_{BN}	0.109	0.050	0.034	0.048	0.010	0.007	0.005	0.000	0.001	0.010
w_{LO}	2.219	0.939	0.657	0.500	0.275	0.167	0.066	0.026	0.076	0.203
w_{LN}	0.536	0.212	0.180	0.202	0.061	0.040	0.023	0.001	0.005	0.060
w_R	2.790	.				0.304		0.042	0.093	0.330
v_S	17.849	10.428	6.792	6.563	3.776	2.039	1.076	0.291	0.732	2.992
Δv_S	4.382	2.216	1.394	1.149	0.649	0.272	0.042	0.010	0.017	0.528

Appendix II-4. Sample trees in Plot 32

Tree no.	32-1	32-2	32-3	32-4	32-5	32-6	32-7	32-8
H	19.85	19.20	18.85	18.00	18.80	17.65	14.08	7.65
D	40.0	31.5	30.0	28.0	25.0	21.0	15.5	8.5
ΔH	22	17	10	10	10	14	16	1
w_S	457.336	248.937	209.769	201.475	166.776	103.179	44.426	9.240
w_{BO}	96.573	25.966	33.017	32.040	17.750	8.416	6.313	0.493
w_{BN}	2.100	1.005	0.644	0.641	0.639	0.331	0.083	0.002
w_{LO}	36.137	16.075	14.988	14.455	8.903	5.578	4.505	0.517
w_{LN}	8.664	6.166	4.440	4.615	3.729	2.157	0.739	0.022
w_R	132.649	66.235	49.107	48.077	36.444	24.239	16.897	6.418
v_S	114.089	687.668	635.660	519.266	475.145	305.262	138.396	24.508
Δv_S	30.420	17.706	7.643	14.215	15.416	6.118	5.165	1.222

Appendix II-5. Sample trees in Plot 33

Tree no.	33-40	33-23	33-10	33-36	33-7	33-37	33-3	33-28
H	11.70	14.00	11.46	10.80	6.71	11.66	11.78	6.48
D	11.0	23.0	16.0	13.5	8.0	13.0	19.0	6.5
ΔH	9	18	11	15	2	21	18	9
w_S	23.397	98.395	43.154	31.649	6.986	34.630	59.145	4.272
w_{BO}	1.160	11.997	4.557	3.539	0.727	6.540	9.099	0.535
w_{BN}	0.089	0.670	0.135	0.094	0.007	0.109	0.278	0.004
w_{LO}	1.331	6.793	2.943	2.142	0.492	2.030	5.483	0.356
w_{LN}	0.599	3.741	1.150	0.814	0.064	0.859	2.214	0.047
w_R	4.566	31.234	16.091	9.220	3.611	10.076	18.284	1.579
v_S	60.149	243.553	119.542	81.780	19.682	87.007	172.933	10.765
Δv_S	0.971	10.592	1.811	1.565	0.318	3.352	6.002	0.092

Appendix II-6. Sample trees in Plot 34

Tree no.	34-2	34-10	34-8	34-14
H	9.00	7.25	9.23	9.90
D	12.4	9.6	15.5	17.0
ΔH	75	55	40	65
w_S	19.346	10.554	29.348	34.288
w_{BO}	5.730	4.600	10.437	12.885
w_{BN}	0.244	0.067	0.659	0.745
w_{LO}	6.053	4.911	10.710	13.324
w_{LN}	1.542	0.651	3.344	3.766
w_R	14.071	4.608	15.102	20.043
v_S	58.270	30.156	94.976	103.585
Δv_S	10.717	4.865	14.085	16.028

Appendix II-7. Sample trees in Plot 37

Tree no.	37-13	37-3	37-14	37-24	37-7	37-17	37-19	37-25
H	5.65	4.25	5.38	2.87	5.20	6.40	6.20	6.95
D	4.9	3.8	5.4	1.9	5.0	7.8	7.1	8.7
ΔH	51	13	10	0	36	48	45	60
w_S	2.546	1.558	2.708	0.306	2.144	5.860	5.038	7.898
w_{BO}	0.489	0.213	0.551	0.060	0.376	1.221	1.243	4.516
w_{BN}	0.039	0.007	0.055	0.000	0.010	0.084	0.050	0.157
w_{LO}	0.626	0.297	0.710	0.053	0.504	1.550	1.511	4.634
w_{LN}	0.203	0.045	0.272	0.001	0.074	0.517	0.317	0.863
w_R	0.777	0.546	0.886	0.150	0.827	2.137	1.756	4.568
v_S	6.680	3.381	7.620	0.935	6.128	17.403	13.802	22.061
Δv_S	0.722	0.260	0.700	0.016	0.783	2.385	1.984	3.476

森林の生産構造に関する研究（XVI）

富士山亜高山帯におけるシラビソ林の一次生産

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摘　　要

共同研究として行なわれた"亜高山帯の造林"の一部として，1966～1967年に富士山北西斜面の亜高山帯でシラビソ林の物質生産をしらべた。

あらかじめ概況調査した約20個のプロット（Table 1）の中から，9個のプロットを選んで精密測定した。層別刈取法によって，幹，枝，当年枝，葉，当年葉，根とわけて生重量を測定，これを乾重量に換算した。幹は樹幹析解した。ha あたりの現存量は断面積配分法によって推定した（Table 3）。その垂直的分布は Fig. 1 に示した。林分の生育が進むにつれて現存量は増加するが，葉や枝の，量や垂直分布の形はあまり変化せず，幹の量が増加する（Fig. 2）。林分の葉量は乾重量で 13～19 t/ha，葉面積指数は 8～11であり，葉の吸光係数は 0.31～0.43（ha/ha）と計算された。

幹増加量（樹皮を含む）は Table 5 のとおりで，葉の幹生産能率は葉乾重 1 kg あたり年間 0.74～1.65 dm^3 幹材積となる。これを幹の乾重成長になおすと 0.27～0.69 kg である。幹成長量の垂直的配分をしらべると，林冠内では下層ほど成長が大きくなるのに対し，林冠層より下の部分では，層ごとの幹成長量の差はめだたなくなる。この現象は，林冠最上層より順次葉量を合計した量――積算葉量と密接な関係をもっている（Fig. 3）。

純生産量は，当年生産部分の総計として求めた。幹生産量は樹幹析解により，枝生産量は，樹冠内幹材積と枝との回帰線を利用して，1年前の枝現存量を求め，これと現在の現存量の差を生産量と認める方法で，また根生産量は，地上部材部の生産率から換算して求め，これに当年葉現存量を加えて純生産量とした結果（Table 6），7個の林分プロットで 11.1～19.9 t/ha・年，2個の苗畑プロットで 8.4～8.6 t/ha・年となった。

総生産量は，別途報告されているシラビソの葉の呼吸率と気温の変化，および図（Fig. 4）を用いて推定した材部の呼吸率から計算した呼吸による消費量と純生産量の合計として求めた（Table 7）。その結果，総生産量は，林分プロットで 35～52 t/ha・年となった。

純生産量および総生産量に対する年間，および生育期間内のエネルギー効率（Table 8）は，純生産量に対して年間0.4～0.7%，生育期間0.7～1.2%，総生産量に対して，それぞれ，1.2～1.7%，2.1～3.1%と計算された。

1969年12月4日受理

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純生産量を他の亜高山帯針葉樹林のデータと比較すると，ほぼ常識的な値であったが，これらは，一般の針葉樹林の値とくらべてもそんなに小さくない。亜高山帯の物質生産力は，その気象条件などから考えられるほど低くはないようである。

総生産量について広葉樹林と比較すると，葉面積と生育期間長をかけ合わせた指数でくらべる場合，80%以下となる(Fig. 5)。つまり，葉の生産能率という点では，針葉樹林は広葉樹林に劣っている。

シラビソ林の現存量増加に対する生産量の変化を図化してみたが (Fig. 6)，純生産量は現存量 100 t/ha あたりで最大となるのに対し，100 t/ha 以上の現存量では純生産量が減少する代わりに，材の呼吸量が増加し，現存量 100 t/ha から 300 t/ha ぐらいまでは，総生産量にはあまり変化はないようである。