Primary Production Relations in Plantations of Norway Spruce in Japan—Materials for the Studies of Growth in Stands. 8.*—

Taisitiroo SATOO

Contents

Abstract

Primary production relations of plantations of Norway spruce, *Picea abies*, in the Tokyo University Forests in Hokkaido and in Titibu were studied and compared with the reports from Europe, its natural habitat. The relationship between height and age of many plantations of this species in Japan was summarized from literature and graphically presented. Height growth of this species in Japan was not different from the height in SCHWAPPACH's yield table. Four stands of different site quality in Hokkaido were compared. Mass of stem and branch, and total aboveground biomass of spruce per unit area were linearly proportional to site index expressed as the height at 45th year, but it was not for leaf mass. Most part of aboveground biomass of these stands was of spruce and undergrowth was minimum, though percentage of undergrowth biomass was higher on the poorest site. Production of stem per unit ground area was linearly proportional to site index, but production of branch and leaf was not. Thus aboveground net production per unit ground area was larger on better sites but not linearly proportional to the site index. Except for the poorest site, about nine tenth of aboveground net production was by spruce and the rest was by the undergrowth. Percentage of production by undergrowth in the poorest stand was larger. About one tenth of the aboveground net production by spruce was branch for all stands studied, but the percentages of stem and leaf were variable by stand. On the medium sites, the percentage of produced matter used for reproduction of leaf mass was largest. Net assimilation rate was largest on the medium sites and smallest on the poorest site, while efficiency of leaf to produce stem wood was highest on the best site. Discussions were given on this respect. Influence of dominance of trees within a stand on production relations was studied in a

* Contributions from JIBP-PT No. 108.

plantation in Hokkaido. Net production was largest in dominant trees, but there were not much differences in net assimilation rate and the efficiency of leaf to produce stem wood among tree classes. In the plantation in Titibu which is located on a remote site and not thinned for a long years, compared with the plantations in Hokkaido, leaf mass per unit ground area was larger and branch mass was smaller. Aboveground net production per unit area was somewhat larger while net assimilation rate and efficiency of leaf to produce stem wood was fairly lower, presumably because of larger leaf mass. Distribution of produced matter into branch was far smaller, reflecting severe competition in this stand. Leaf mass of these stands was compared with 34 stands in Europe. Leaf mass of 6 plantations of this species in Japan was larger than the mean of European plantations. Leaf mass of these plantation was also larger than forests of black spruce in Canada and *Picea glehnii* in Hokkaido.

I. Introduction

Primary production relations in plantations of Norway spruce, *Picea abies*, were studied in Tokyo University Forests in Hokkaido and in Titibu. Of the plantations in Hokkaido, the influences of site quality and dominance of trees within a stand on primary production relations were mainly investigated, while, on the plantation in Titibu, only some aspects of primary production relations were studied for the comparison with those in Hokkaido.

Norway spruce is the most important species in European forestry, and production relations of the forests of this species were already studied by BURGER (1939a, b, 1941, 1962, 1963), MÖLLER (1945), VANSELOW (1951), TAMM and CARBONIER (1961), MARCHENKO and KARLOV (1962) SMIRNOV and ALEKSEEV (1967), DIETRICH (1968), DROST ZU HÜLSHOFF (1969, 1970) and TAMM (1969). There are some plantations of this species in North America, but studies of their production relations are not yet available. Comparison of primary production relation of forests of the same species planted in a country far away from its origin with those in its natural habitats may be of use for the understanding of its silvical and ecological natures, and it may also be of interest from the viewpoint of International Biological Programme.

A part of this study was already included in the author's synthesis (SATOO 1966, 1969). Field works of this study were made in 1957 by Mr. Y. MORI, Mr. Y. KONISI and Mr. A. OOGAWARA with cooperation of staff of the University Forests. The author wishes to express his sincere gratitudes to them.

II. Planting of Norway spruce in Japan

History of planting of this species, which is an exotic species to Japan, is rather old. According to MATUI (1965), in Hokkaido, it is said that seeds of this species were sawn in a nursery in Hokkaido as early as 1878, but there is no evidence about it. However, 55.5 hectares of plantations of this species, which were planted between 1907 and 1916, still exist. Summing up the figures in a table by MATUI (1965), total area of plantations of this species in Hokkaido is about 2,000 hectares, but according to KAWAGUCHI (1953) there are 5,431 hectares of plantations of this species in Hokkaido. Beside Hokkaido, there are 195 hectares of plantatious in other islands than Hokkaido of Japan, according to the census made by the Forestry Agency of Japanese Government (1956). This species has the largest area of plantations among the exotic species planted in Japan. It is planted mostly in Hokkaido and northern half of Honsyu (Hondo, the main island), but it is planted also in the island of Shikoku, southwestern Japan (SHIMODA and OCHI 1959). There are many reports and papers on the growth of this species in Japan. The relation between age and mean height of the plantations in Japan was summarized from these reports as well as censuses and graphically presented (SATOO 1958). This graph was revised by adding new data and shown as Fig. 1. As stand density was

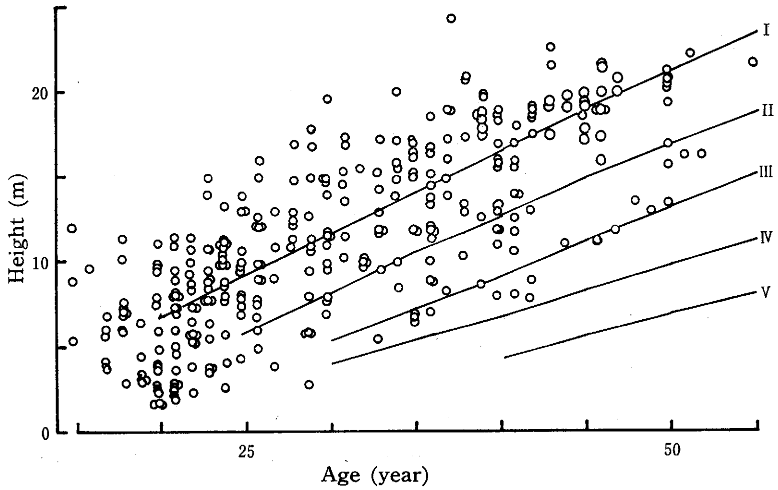

Fig. 1. Height growth of plantations of Norway spruce in Japan. Lines I, II, etc. are height on site class I, II., etc. of SCHWAPPACH's yield table.

Sources: ANDO et al. 1963, ASAHI 1951 a & b, ASAYA 1953, KAMATA 1949, KAWADA & YAMAJI 1949, KAWAGUCHI 1953, KAWAGUCHI & YOKOYAMA 1962, MAEDA 1949, MATUI 1966, 1967, MATUI & YOKOYAMA 1950, MATUI et al. 1967, SAITO et at. 1962, SATO 1964, SATO & SAWAFUJI 1953, SHIMODA & OCHI 1959, SUGANO et al. 1967, SUMITA 1943, TADA 1956, TAKAHASHI 1954, YOSHIMURA 1967, YUASA 1950, Anonym. 1953, Anonym. 1956.

very variable among individual stands, only height was shown. To compare with the growth in its natural habitats, heights in the yield table by SCHWAPPACH (1929) are also shown. Height growth of this species in Japan is not different from the one in its natural habitats.

III. Influence of site quality on production relations

1. Plantations studied

The plantations studied belong to the compartment 76 of the University Forest which is situated at almost the center of Hokkaido. Longitude and Latitude of Nisitappu Forest

Office, about 2.5 km east of the plantations, is 142°26′40″ E and 43°12′50″ N, respectively. Mean of the recent 10 years at Nisitappu Forest Office (altitude 260 m) of annual mean temperature was 6.7℃, and the maximum and minimum monthly mean temperatures were 20.8℃ in August and −8.9℃ in January, respectively. Mean annual precipitation was 1200 mm. Frost-free season was between May and September, but annual fluctuation was rather large. The plantations studied were located about 100–150 m higher than the observatory. From ASAHI's (1951) 6 plots for soil survey in the plantations, stands equivalent to site class 3, 4, and 5 were used here and named stands A, B, and C, respectively. The soil of these stands was described in details in ASAHI's paper (1951).

Table 1. General description of the stands studied

Locality		Hokkaido				Titibu
Stand		A	B	B′	C	
Slope		ca 20°	ca 25°	ca 28°	ca 25°	ca 30°
Aspect		E	S E	S E	S	S E
Age		47	46	46	45	39
Number of trees	/ha	488	756	756	914	2240*
Height	m	23.5	18.3	18.3	15.6	16.5
Height at 45th year		23.2	17.9	18.0	15.6	—
DBH	cm	29.1	20.0	20.5	17.3	17.2
Basal area	sq. m/ha	33.78	24.90	26.13	21.42	52.56

* Plus 570 dead trees

In addition to these stands, a stand showing growth very close to the stand B was used as stand B′. Base rock is sand stone of tertiary but is covered by a layer of volcanic ash about 12 cm deep. According to ASAHI's (1963) classification, the soil belongs to brown forest soil. These stands were planted in 1911, 1912, 1913, and 1912, respectively, after a forest fire. Provenance of the seeds is not known. Thinning was made in 1920 and 1942. General description of the plots are given in Table 1.

2. Methods

Sample plots, each 40×40 m, were selected from the stands A, B, B′, and C so that they represent each stand and that there are no openings of the canopy. After measuring diameter breast high of all trees in the plots, 5 sample trees were cut from each plot. After measuring height and clear length, discs were collected from the stems of sample trees at heights of 0.0, 0.3, 1.3 m and then at every 2 m, for annual ring analysis. From the lowest living branch upwards, samples of branches were taken from every 5th branches. After recording the height of the base and the length, leaves were stripped off from the branches, separated into leaves of the current year (new leaves) and old leaves, and weighed. Leaves of each group were mixed thoroughly and samples for dry weight were taken. After weighing separately new shoots and old branches, discs were taken from the samples of branches at their base, 0.1 m from the base, and then at every 0.5 m, and annual ring analysis was made. Samples for dry weight determination were also taken. Other branches were separated into leaves and branches, and weighed. The weights of parts newly formed and older ones were estimated from the ratio given by the samples. In each sample plot, 5 subplots, each 1×1 m, were clipped clearly and dry weights of annual and perennial ground vegetation were separately determined. In the plot C, as there were some broad leaved trees beneath the canopy of spruce, they were sampled and dry weight was determined separately for leaves, branches and stems, and discs were taken from stems and branches to determine the growth rate in cross sectional area which was used for the estimation of wood production. Underground parts were not sampled.

3. Biomass aboveground

A. Tree layer of spruce.

The value per hectare was estimated by multiplying the sum of value of the sample trees with the ratio of basal area to the sum of cross-sectional area of sample trees. This method is simplest and the error of estimates is not larger than other methods (SATOO 1968).

A-1. Stem and branch

Volumes of stem and branch are shown in Fig. 2. The volume of stem was less in the inferior sites, despite the larger number of trees per unit area in them. If the volume of trees already harvested by thinnings is added, the differences must be larger, but the volume of timber harvested by thinnings is not known. Amount of branch was also smaller on the inferior sites. It is known that amount of branch is smaller in stands with larger number of trees per unit area of ground among the stands of the same age because of severe competition and subsequent self pruning (SATOO et al 1955). However, in this case, the smaller amount of branch on the inferior sites, which have larger number of trees per unit ground area, is not caused by severe self pruning due to competition: there were minimum differences in the average live crown length among the plots and live crown ratio was higher on the inferior sites (Table 2). Live crown ratio indicates that competition was less on

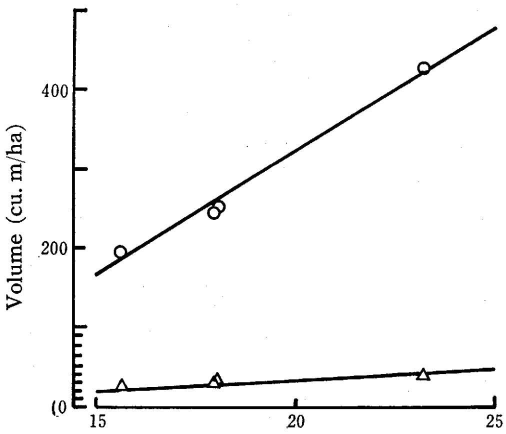

Fig. 2. Volume of stems and branches of stands in relation to site quality expressed as the height at 45th year.
circles: stems, triangles: branches

Table 2. Crown

Plot	Height at 45th year m	Height m	Length of live crown m	Live crown ratio %
A	23.2	23.5	11.0	47
B	17.9	18.3	11.2	61
B′	18.0	18.3	11.2	61
C	15.6	15.6	10.8	69

the inferior sites. To show the relations quatitatively, site index was expressed as the height at 45th year. As shown by Fig. 2, volume per hectare of stem (Vs cu. m) and branch (Vb cu. m) was linearly proportional to the site index expressed by the height at 45th year (H^* m), and described as

$$Vs = 31.7\,H^* - 312.92 \quad \text{and}$$

$$Vb = 2.59\,H^* - 16.85.$$

With increase of 1 meter of height at 45th year, stem volume increased by 31.7 cubic meters and branch volume increased by 2.6 cubic meters.

A-2. Leaf

Amount of leaf per hectare is shown in Table 3. The plots B and B′, which are almost equal in site index, showed similar values, but there was no clear relationship with the site quality: plot A which is on the best site had largest amount of leaf but the plot C which is on the poorest site had larger amount of leaf than tha plots B and B′. Amount and percentage of current year leaf were largest in the plots B and B′, and least in the plot C which is on the poorest site. The difference in the amount of leaf by plot was larger when old and new leaf were compared separately than when total leaf was compared. In the total leaf, minumum value was 77% of the maximum, while it was 47% in new leaf and 64% in old leaf of the maximum. The plots having more new leaf had less old leaf. This trend was found among stands of *Pinus densiflora* of similar age having similar total amount of leaf, and it was presumed that if larger amount of leaf is produced newly larger part of older leaf dies because of deficient light (SATOO 1966). MÖLLER reported that the influence of site quality on the amount of leaf per unit area of forest was not found on forests of European beech and Norway spruce, but KITTREDGE (1944) suggested that there are more leaves on better site. The author (1967 and 1969) reported that amount of leaf on a unit ground area of plantations of *Cryptomeria japonica* was larger on better sites. HATIYA et al (1966) also reported that amount of leaf per unit ground area was larger on better sites of *Pinus densiflora*. In these spruce stands, no relationship was recognized between site quality and amount of leaf per unit ground area, though size of the samples was not large enough.

Table 3. Leaf biomass (t/ha)

Plot	A	B	B′	C
New leaves	3.37	4.54	4.69	2.19
Old leaves	15.27	9.83	9.98	14.72
Total	18.64	14.37	14.67	16.91
Percentage of new leaves	18.1	31.6	32.0	12.9

A-3. Biomass

The volumes of stem and branch were converted into dry weights using TRENDELENBURG's (1939) mean bulk density of wood of Norway spruce, 0.488, and,

Table 4. Biomass of the tree layer (t/ha)

Plot	A	B	B′	C
Height at 45th year	23.2	17.9	18.0	15.6
Stem	208.56	119.26	123.20	94.05
Branch	16.73	14.11	18.47	12.19
Stem+branch	225.29	133.37	141.67	106.24
Leaf	18.64	14.37	14.67	16.91
Total	243.93	147.74	156.34	123.15

together with dry weight of leaf, biomass per hectare is shown in Table 4. Biomass per hectare (W t) was linearly proportional to the height at 45th year (H^* m) as

$$W_t = 16.3\,H^* - 137.0$$

With increase of 1 meter of height at 45th year, aboveground biomass of the tree layer increased by about 16 tons (Fig. 3). As seen from Table 4, the difference in biomass is mainly due to the differences in the amount of stem. If the difference in bulk density of wood by site quality was taken into account, the difference must be still larger. According to SCHMIDT (1953), bulk density of wood of Norway spruce is lower on poorer sites.

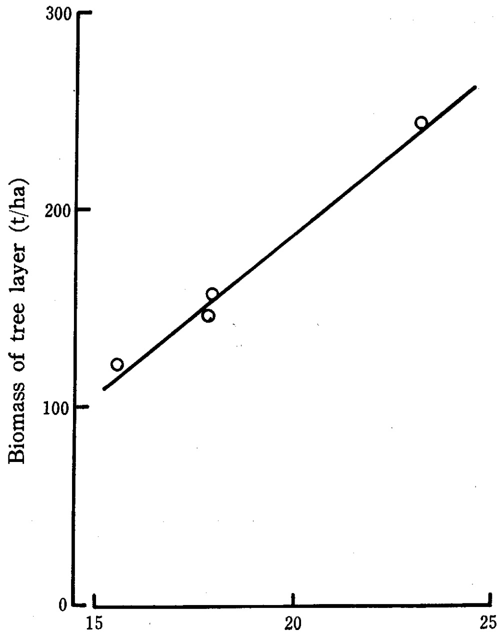

Fig. 3. Biomass of tree layer (aboveground only) of stands in relation to site quality.

B. Undergrowth

B-1. A layer of broadleaved trees beneath the canopy.

In the plots A, B, and B′, this layer was negligible, but in the plot C there were many trees belonging to this layer; 125 trees of diameter breast high between 2 and 3.5 cm and 62 trees of between 3.5 and 5 cm, per hectare. Important species were *Magnolia obovata*, *Acer mono*, *Kalpanox pictus* and *Styrax abassia*. Aboveground biomass of this layer is shown in Table 5.

B-2. Ground vegetation

Ground vegetation consisted of many species of annual as well as perennial herbs, vines and saplings of trees. As shown in Table 5, the amount of ground vegetation did not differ too much among the plots.

C. Biomass aboveground

Biomass aboveground of these stands is shown in Table 6. Biomass was larger in better sites

Table 5. Biomass of undergrowth (t/ha)

Plot	A	B	B′	C
Shrub layer				
Leaf	0	+	+	0.03
Branch	0	+	+	0.10
Stem	0	+	+	0.24
Total	0	+	+	0.37
Ground vegetation				
Annual	0.22	0.04	0.04	0.02
Perennial	1.40	1.32	1.32	1.20
Total	1.62	1.36	1.36	1.22

Table 6. Biomass aboveground (t/ha)

Plot	A	B	B′	C
Tree layer	243.93	147.74	156.34	123.15
Shrub layer	0	0	0	0.37
Ground vegetation	1.62	1.36	1.36	1.22
Total	245.55	149.10	157.70	124.74

Table 7. Distribution of biomass (%)

Plot	A	B	B′	C
Height at 45th year	23.2	17.9	18.0	15.6
Tree layer	99.3	99.1	99.1	98.8
Undergrowth	0.7	0.9	0.9	1.2
Within tree layer				
Stem	85	80	79	76
Branch	7	10	12	10
Leaf	8	10	19	14

Table 8. Net production

Plot	A	B	B′	C
Spruce				
Volume (cu. m/ha)				
Branch	2.00	2.40	2.68	1.72
Stem	16.48	11.70	11.69	8.83
Total	18.48	14.09	14.37	10.55
Dry matter (t/ha)				
Branch	0.98	1.17	1.29	0.84
Stem	8.04	5.70	5.67	4.31
Branch+stem	9.02	6.87	6.96	5.15
Leaf	3.37	4.54	4.69	2.19
Total	12.39	11.41	11.65	7.34
Undergrowth (t/ha)				
Annual	0.22	0.04	0.04	0.02
Perennial	1.40	1.32	1.32	1.20
Shrub				
Leaf	0	+	+	0.03
Branch	0	+	+	0.01
Stem	0	+	+	0.13
Total	1.62	1.36	1.36	1.39
Grand total	14.01	12.77	13.01	8.73

mainly due to larger mass of stem and branch of spruce.

D. Distribution

As seen from Table 6, most part of biomass aboveground of these stands was of spruce, and ground vegetation was rather negligible. Distribution of biomass among aerial parts of spruce is shown by Table 7. Distribution to the stem was higher on the better sites.

4. Aboveground net production

A. Tree layer of spruce

Volume increment in stem and branch was shown in Table 8. Increment in stem was larger in the better sites while it was not always so in branch. As seen from Fig. 4, increment in stem (ΔVs cu. m) was linearly proportional to the height at 45th year (H^* m), as

$$\Delta Vs = 0.996\ H^* - 6.425.$$

With increase of 1 meter of height at 45th year increment in stem volume increased by 1 cubic meter. It was reported that increment in stem volume of plantations of *Cryptomeria japonica* increased with site index which was expressed as the ratio of actual height to the height in corresponding regional yield tables (SATOO 1967). However, this trend was not found for the increment in branch and leaf. By converting the volume increment of stem and branch into dry weight with bulk density, 0.488, and adding the dry weight of current year leaf to them, annual dry matter production (aboveground) per hectare in Table 8 is given. Dry matter production was larger on better sites but it was not linearly proportional to the site index. Production of branch and leaf was largest in the medium sites.

B. Undergrowth

Ground vegetation consisted of many species. As aerial parts of perennial herbs found there also die every year, biomass of them was regarded as the products of the year and added to annual herbs. Small broadleaved trees were not found at all in the plot A and in the plots B and B′ to be of any importance, but in the plot C there were small broadleaved trees as many as 187 trees per hectare underneath the canopy. As they were all deciduous, leaf biomass was considered as the product of the year. Production of branch and stem was estimated by multiplying the biomass with the relative rate of growth in cross-sectional area of the samples, separately for trees above and below 3.5 cm in diameter breast high. Dry matter production by the undergrowth is also shown in Table 8.

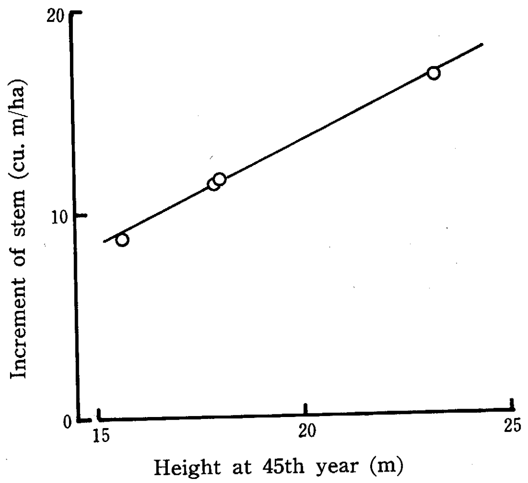

Fig. 4. Increment of stem of stands in relation to site quality.

Table 9. Distribution of produced matter (%)

Plot	A	B	B′	C
Within spruce tree layer				
Stem	65	50	49	59
Branch	8	10	11	11
Leaf	27	40	40	30
Aboveground				
Spruce	88	90	90	84
Undergrowth	12	10	10	16

C. Distribution of produced matter.

Table 9 shows the ratio of distribution of dry matter produced by these spruce stands. Except for the plot C, which is on the poorest site, about nine tenth of dry matter was produced by the spruce tree layer, and about one tenth by undergrowth. In the plot C, where there were some small broadleaved trees underneath the canopy, percentage of production by the undergrowth was greater than the other plots. About one tenth of dry matter produced by the tree layer of spruce was distributed into branch production in all four plots, but the distribution ratios into stem and leaf were variable with plots: distribution into stem wood production was smallest and distribution into reproduction of leaf was largest in the plots B and B′ which are medium in site quality.

5. Efficiency of leaf

Production efficiency of leaf, or net assimilation rate, is shown in Table 10. Production efficiency of leaf was rather higher in the plots B and B′ which are medium in site quality than in the plot A which is on the richest site among the plots. This indicates that the highest rate of net production in the plot A was caused by the larger amount of leaf rather than the efficiency of leaf. In the plot C which is on the poorest site, net assimilation rate was lowest; the lower rate of net production by the plot C is due to lower efficiency of leaf though it had larger amount of leaf than the plots B and B′. It is supposed that the higher net assimilation rate of the plots B and B′ is due to higher

Table 10. The efficiency of leaf

Plot		A	B	B′	C
Height at 45th year	m	23.2	17.9	18.0	15.6
Leaf mass	t/ha	18.64	14.37	14.67	16.91
Dry matter production	t/ha	12.39	11.41	11.65	7.34
Stem wood production	cu. m/ha	16.48	11.70	11.69	8.83
Net assimilation rate	g/kg/yr	665	794	794	434
Efficiency of leaf to produce stem wood	ml/kg/yr	884	814	797	522
Net assimilation rate	g/kg/day	1.8	2.2	2.2	1.2
Net assimilation rate May~Sept.	g/kg/day	4.3	5.3	5.2	2.9

percentages of new leaf in their foliage. It was reported that photosynthetic rate of new leaf of white spruce was higher than older one (CLARK 1961). Net assimilation rate per day was 1.2–2.2 g/kg as a mean throughout the year and 2.9–5.2 g/kg if photosynthesis is active only in the frost-free season from May to September. Those values are far lower than other plants. Net assimilation rates of conifer forests are tablulated in the author's recent synthesis (SATOO 1969). Net assimilation rate of Norway spruce is rather lower even among forests of coniferous species.

In forestry, it is rather more general to give the efficiency of leaf to produce stem wood expressed as stem wood production per unit amount of leaf. This efficiency, as seen from Table 10, decreased with decreasing site index. This trend is different from the trend in net assimilation rate: net assimilation rate was higher in the plots B and B′ than the plot A whereas leaf efficiency for stem wood production was higher in the plot A than in the plots B and B′. The efficiency of leaf to produce stem wood is the product of net assimilation rate times distribution ratio to the stem. This difference in the trends between net assimilation rate and leaf efficiency in stem wood production was caused by higher distribution ratio to stem wood production in the plot A than the plots B and B′; in the plots B and B′, produced matter was allotted in higher percentages to the reconstruction of the crown. In the plot C, distribution ratio to stem wood production was higher than in the plots B and B′, but very low net assimilation rate in this plot resulted lower efficiency of leaf to produce stem wood. For the plantations of *Cryptomeria japonica* it was found that leaf efficiency in stem wood production increased with increasing site index (SATOO 1967).

IV. The influence of dominance of tree within a stand on the efficiency of leaf

From the plot B′, each 5 sample trees from dominant, average, and suppressed trees were selected and the efficiency of leaf was compared. Mean values of dimensions of each tree classes are given in Table 11. Dry matter production per tree is shown in Table 12. Dry matter production was largest in dominant and smallest in suppressed trees, as expected, but net assimilation rate and the efficiency of leaf to produce stem wood were not much different among tree classes: average trees had slightly higher efficiency of leaf. Thus, the difference in net production by tree class was mostly due to the difference in their leaf mass.

Table 11. Mean values for sample trees of each tree class

		Dominant	Codominant	Suppressed
Height	m	19.9	18.3	16.7
DBH	cm	25.2	20.5	15.5
Stem dry weight	kg	245.8	162.9	80.8
Branch dry weight	kg	57.4	30.3	16.1
Leaf dry weight	kg	36.0	19.4	10.3
New leaf	kg	8.1	6.2	2.6
Old leaf	kg	27.9	13.2	7.7
Dry weight of top	kg	339.2	212.6	107.5

Table 12. Dry matter production and efficiency of leaf of trees of different dominance in a stand

		Dominant	Codominant	Suppressed
Dry matter production				
Stem	kg/tree	12.9	7.5	3.7
	(%)	(52.6)	(48.7)	(50.7)
Branch	kg/tree	3.5	1.7	1.0
	(%)	(14.3)	(11.0)	(13.7)
Leaf	kg/tree	8.1	6.2	2.6
	(%)	(33.1)	(40.3)	(35.6)
Aboveground	kg/tree	24.5	15.5	7.2
Net assimilation rate	g/kg/yr	681	813	706
Efficiency of leaf to produce stem wood	ml/kg/yr	734	828	738

V. A plantation in Titibu

1. The plantation

The plantation studied belongs to the compartment 3-A-12 of Tokyo University Forest in Titibu and was situated upstream of Ootigawa which is a branch of Arakawa. Altitude is 1,030 m. Longitude and latitude of Totimoto Forest Office, about 11 km west of the plantation, are 138°51′ E and 35°56′ N, respectively. According to the data from Mitumine Forest Meteorological Observatory (cited by SUMITA (1943), now not existing) which was the nearest observatory situated about 7 km northwest of the plantation and at similar elevation, annual mean temperature was 8.4℃, monthly mean temperature was highest in August (23.3℃) and lowest in January (−6.7℃), and annual precipitation was about 1900mm. The temperature is similar to the plantations in Hokkaido but rainfall is more abundant. The soil is clay-loam belonging to brown forest soil. This plantation was planted in 1919 and weed trees were cleared in 1933, but no tending was made after then because of its remoteness. There were many trees dead, still standing and fallen, presumably because of competition, as shown by Table 1. General description of this stand is given in Table 1. SUMITA (1943) reported about growth of this plantation together with other plantations of this species in this University Forest.

2. Method

Six sample trees were cut from a sample plot, 25 m×40 m, and measured with the same method as the plots in Hokkaido. Undergrowth was so few that they were not measured. Underground parts were not studied.

3. Biomass aboveground

Biomass of the tree layer of this stand is shown in Table 13. Compared with the plantations in Hokkaido (Table 4), leaf biomass of this stand was larger and stem and branch biomass was smaller. Percentage of branch biomass in total aboveground biomass of the tree layer was only 4% while it was 7～14% in the stands of Hokkaido. As thinning had not been made for long years and there were many dead trees, it is probable that this stand had already attained its full density, and, as a result of severe competition among trees, self pruning is made to such an extent that branch biomass is so small. It is reported that in a spacing experiment of *Pinus densiflora*, provided that other conditions were similar, percentage of branch biomass in total biomass was smaller in denser stand (SATOO et al 1955).

Table 13. Biomass and production of the tree layer of a Norway spruce plantation in Titibu

	Biomass		Production	
	t/ha	%	t/ha	%
Stem	188.54	60	8.51	85
Branch	8.57	6	0.90	4
Leaf	23.93	34	4.51	11
Total	221.04		14.23	

4. Aboveground net production

Net production and distribution of produced matter into parts of tree are given in Table 13. Aboveground net production was a little larger than the plot A of Hokkaido which is on the best site and had largest production. Compared with the plot A of Hokkaido, production of stem and leaf was larger and branch production was smaller in this stand. Distribution ratios were similar to those of the plot A of Hokkaido, though distribution into leaf was larger and into branch was smaller.

5. Efficiency of leaf

Net assimilation rate of this stand was 594 g/kg/year. Compared with the stands in Hokkaido, this value was smaller than the plots A, B, and B′, and larger than the plot C. The high rate of net production by this stand is due to large amount of leaf but not to efficiency of leaf. The efficiency of leaf to produce stem wood of this stand was 733 m*l*/kg/year. This value was also smaller than the plots A, B, and B′ and larger than the plot C of Hokkaido.

VI. Comparison with other forests of Norway spruce

As seen from Fig. 1, Norway spruce planted in Japan has height growth comparable to the one in a German yield table. Primary production relations of the forests of this species in Europe were reported by many authors (BURGER 1939 a, b, 1941, 1952, 1953; MÖLLER 1945; VANSELOW 1959; TAMM and CARBONIER 1961; MARCHENKO and KARLOV 1962; SMIRNOV and ALEKSEEV 1967; DIETRICH 1968; DROSTE zu HÜLSHOFF 1969, 1970 and TAMM (1969). YOSHIMURA (1967) reported primary production relations of this species planted in Kyoto, Japan. However, except YOSHIMURA (1967) and DROSTE zu HÜLSHOFF (1969, 1970), these papers dealt only with biomass or biomass and stem growth, but not net production. Net aboveground production by a plantation of this species in Kyoto was 14.73 t/ha/year. This value is larger than those reported here, but as YOSHIMURA himself wrote, his sample trees included trees in the border of forest and there is a possibility of overestimation. Recently DROST zu HÜLSHOFF (1969, 1970) reported net aboveground production of a 76-year-old forest of this species in Germany as 15.51 t/year. There are data for biomass of 34 stands in Europe and 6 stands in Japan, including 5 stands in this paper, of this species. However, biomass of stem is rather a function of age of stands, and branch biomass is affected by age and density of stands, only leaf biomass is compared here. In Fig. 5 is shown the frequency distribution of leaf biomass of 42 stands of spruces, including 40 Norway spruce stands and 2 stands of other spruces. Leaf biomass of the plantations studied here was larger than those reported from Europe. Mean of leaf mass of 34 stands in Europe was 13.5 t/ha. Stem wood production per unit weight of leaf, or efficiency of leaf to produce stem wood, of the plantations studied here was smaller than those reported from Europe, presumably because of larger leaf mass.

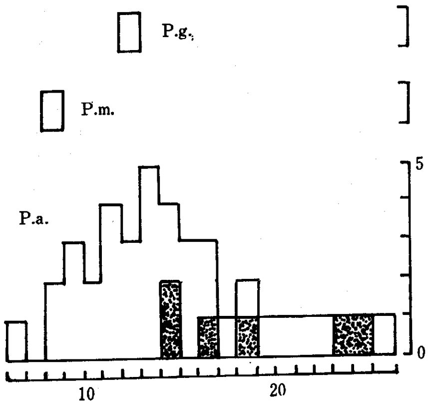

Fig. 5. Leaf biomass of forests of spruces.

Dotted squares are plantations in Japan.

Sources: *P. abies* (P.a.): BURGER 1939 a & b, 1941, 1952, 1953. DROSTE zu HÜLSHOFF 1969, DIETRICH 1968, MARCHENKO & KARLOV 1962, MÖLLER 1945, SMIRNOV & ALEKSEEV 1967, TAMM 1969, TAMM & CARBONIER 1961, YOSHIMURA 1967, and this study.
P. mariana (P. m.): WEETMAN & HARLAND 1964.
P. glehnii (P. g.): Joint Studies of Universities.

RODIN and BAZILEVICH (1965) collected Russian data of biomass and production of this species from mostly published sources and summarized in a table, but in these data production and biomass of spruce and other trees and shrubs in the stands were not separately shown and could not be used here.

VII. Comparison with forests of other spruces

As for the production relations of spruce other than this species, there is a study by WEETMAN and HARLAND (1964) on a black spruce forest. Data were collected on a forest of *Picea glehnii* by the Joint Studies of Four Universities in which the present author took part. Leaf biomass of the black spruce forest (WEETMAN and HARLAND 1964) was 8.6 t/ha which is smaller than the value of most of Norway spruce stands reported, as seen from Fig. 5. Leaf biomass of a young natural regeneration of *Picea glehnii*, mixed with some *Abies sachalinensis* trees, was 12.32 t/ha which is similar to those of Norway spruce. Net aboveground production by this *Picea glehnii* stand was; stem: 4.61 t/ha, branch: 0.54 t/ha, and leaf: 2.28 t/ha, thus, aboveground: 7.44 t/ha. This value is similar to the plot C of the Norway spruce plantations in Hokkaido.

Reference

ANDO, A., KOJIMA, T., & BABA, K. 1963. (Soil properties and tree growth. 12. A 36-year-old plantation of Norway spruce). Trans. 72nd Mtg., Jap. For. Soc. (1962). 133–135.**

ASAHI, M. 1951 a. Edaphological study on Norway spruce (*Picea excelsa* LINK.) plantations in Tokyo University Forest, Hokkaido. Bull. Tokyo Univ. For. **41**, 1–31.*

——— 1951 b. (Reappraisal of Norway spruce as species for planting in Hokkaido.) Hoppo Ringyo **3**: 12–13.**

——— 1963. Studies on the classification of forest soils in the Tokyo University Forest, Hokkaido. Bull. Tokyo Univ. For. **58**, 1–132.*

ASAYA, T. 1953. On the structure of planted forest stand formation, *Larix kaempferi* SERG., *Abies sachalinensis* MAST., and *Picea excelsa* LK., and the comparison of those growth in Kitami district. Trans. 62nd Mtg., Jap. For. Soc. (1952), 73–75.*

BURGER, H. 1939 a. Der Kronenaufbau gleichalteriger Nadelholzbestände. Mitteil. Schweiz. Anst. Forstl. Versuchsw. **21**: 1–57.

——— 1939 b. Baumkrone und Zuwachs in zwei hiebsreifen Fichtenbeständen. Mitteil. Schweiz. Anst. Forstl. Versuchsw. **21**: 145–176.

——— 1941. Holz, Blattmenge und Zuwachs. V. Fichten und Föhren verschiedener Herkunft auf verschiedener Kulturorten. Mitteil. Schweiz. Anst. Forstl. Versuchsw. **22**: 10–62.

——— 1952. Holz, Blattmenge und Zuwachs. 12. Fichten im Plenterwald. Mitteil. Schweiz. Anst. Forstl. Versuchsw. **28**: 109–156.

——— 1953. Holz, Blattmenge und Zuwachs. 13. Fichten in gleichalterigen Hochwald. Mitteil. Schweiz. Anst. Forstl. Versuchsw. **29**: 38–130.

CLARK, J. 1961. Photosynthesis and respiration in white spruce and balsam fir. Tech. Bull. State Univ. Coll. For. Syracuse Univ. **85**, pp. 72.

DIETRICH, H. 1968. Untersuchungen zur Nährstoffdynamik eines Fichtenbestandes. Arch. Forstwes. **17**: 391–412.

DROSTE ZU HÜLSHOFF, B. von 1969 a. Struktur und Biomasse eines Fichtenbestandes auf Grund einer Dimensionsanalyse an oberirdischen Baumorganen. Diss. München. SS. 222.

——— 1970. Struktur, Biomasse und Zuwachs eines älteren Fichtenbestandes. Forstw. Cbl. **89**: 162–171.

HATIYA, K., TOCHIAKI, K., & NARITA, T. 1966. (Analysis of growth in natural forests of *Pinus densiflora*: relations between site quality and growth.) Transact. 76th Mtg., Jap. For. Soc. (1965), 161–162.**

KAMATA, T. 1949. (Growth of plantations in southern Hokkaido.) Hoppo Ringyo **1**: 108–109.**

KAWADA, M., & YAMAJI, K. 1949. On the plantation of spruce (*Picea excelsa* LINK.) at the foot-mountain hill region in Gumma Prefecture, central Honshu. Bull. Govt. For. Expt. Sta. **41**, 63–84.*

KAWAGUCHI, M. 1953. (Growth of exotic trees.) Hoppo Ringyo **5**: 121–122.**

———, & YOKOYAMA, H. 1962. (Growth of Norway spruce). Bull. Kosyunai Tree Breeding Station **1**, 123–171.**

KITTREDGE, J. 1944. Estimation of amount of foliage of trees and shrubs. J. For. **42**: 905–912.

MAEDA, Y. 1949. (Growth of Norway spruce). Hoppo Ringyo **1**: 40–42.**

MARCHENKO, A. I., & KARLOV, E. M. 1962. Mineral 'nwi obmen v elovwi lesakh severnoi taigi i lesotundrwi Arkhangel 'skoi Obrasti. Pochvovedenie No. 7, 52–66.

MATUI, Z. 1965. Historical development of afforestation and silviculture in Hokkaido. Bull. Govt. For. Expt. Sta. **175**, 1–143.*

——— 1966. Historical and silvicultural research for each species of plantation in Hokkaido. Bull. Govt. For. Expt. Sta. **189**, 1–160.*

——— 1967. Stand structure and growth of each plantation of native and exotic tree species in Nopporo Experimental Forest. Bull. Govt. For. Expt. Sta. **207**, 69–163.*

———, & YOKOYAMA, C. 1960. (Growth of Norway spruce plantations). Proc. Mtg. 1949, Sapporo Branch, Govt. For. Expt. Sta. 71–77.**

———, et al. 1967. Survey of the stand structure and growth of each plantation of native and exotic tree species in Nopporo Experimental Forest. Bull. Govt. For. Expt. Sta. **202**, 133–213, **205**, 1–233.*

MÖLLER, C. M. 1945. Untersuchungen über Laubmenge, Stoffverlust und Stoffproduction des Waldes. Forstl. Forsøgsv. Danmark **17**: 1–287.

RODIN, L.E., & BAZILEVICH. 1965. Production and mineral cycling in terrestrial vegetation. (Engl. transl., pp. 288, Oliver & Boyd, Edinburgh & London, 1967).

SAITO, Y., et al. 1962. (Growth of Norway spruce plantations in the University Forest at Tomakomai). Proc. Mtg., Hokkaido Branch, Jap. For. Soc. **11**, 1–7.**

SATO, O. 1964. Researches on the growth of exotic trees in Tokyo University Forest at Chichibu. Misc. Inform. Tokyo Univ. For. **15**, 105–120.**

SATO, T., & SAWAFUJI, M. 1953. On the growth of European larch, Jack pine, and Norway spruce in Iwate District. Trans. 62nd Mtg., Jap. For. Soc. (1952), 50–52.*

SATOO, T. 1958. (Norway spruce). In: Sooki Ikusei Ringyo (Sinrin Sigen Taisaku Sookyoogikai, ed.) pp. 129–141. Sangyo Tosyo, Tokyo.**

——— 1966. Production and distribution of dry matter in forest ecosystems. Misc. Inform. Tokyo Univ. For. **16**, 1–15.

——— 1967. Efficiency and quantity of leaves of closed stands of *Cryptomeria japonica* as influenced by site quality. 14th IUFRO-Congress, Münich, Papers **2**, 395–404.

——— 1968. Primary production relations in woodlands of *Pinus densiflora*. In: Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. (H.E. YOUNG, ed.) pp. 52–80. Univ. Maine Press, Orono.

——— 1969. Primary production relations in coniferous forests in Japan. A paper distributed at "Symposium on the Productivity of the Forest Ecosystems of the World", Bruxelles. pp. 28+15.

———, NAKAMURA, K., & SENDA, M. 1955. Materials for the studies of growth in stands. 1. Young stands of Japanese red pine of various densities. Bull. Tokyo Univ. For. 48, 65–90.*

———, & SENDA, M. 1966. Materials for the studies of growth in stands. 6. Biomass, dry matter production and efficiency of leaves in a young *Cryptomeria* plantation. Bull. Tokyo Univ. For. **62**, 117–146.*

SCHMIDT, H. 1953. Kronen- und Zuwachsuntersuchungen an Fichten des bayerischen Alpenvorlandes. Forstwiss. Cbl. **72**: 276–286.

SCHWAPPACH. 1929. Ertragstafeln der wichtigeren Holzarten in tabellarischer und graphischer Form. Neumann-Neudamm. SS. 74.

SHIMODA, M., & OCHI, K. 1959. On some foreign species in Shikoku District. 1. Bull. Govt. For. Sta. **114**, 207–222.*

SMIRONOV, V. V., & ALEKSEEV, V. I. 1967. Produktivnost' nadzemnoi chesti 75-letnego elovogo drevestoya. Rast. Resursy **3**: 505–513.

SUGANO, T., TANIGUCHI, M., & MAEDA, Y. 1967. (Structure and growth of a Norway spruce plantation at Tomakomai). Proc. Mtg. Hokkaido Branch, Jap. For. Soc. **16**, 12–15.**

SUMITA, Y. 1943. (Planting Norway spruce in the University Forest in Titibu.) Misc. Inform. Tokyo Univ. For. **5**, 23–34.**

TADA, H. 1956. (Growth of plantations on soils of volcanic sand origin in Kanayama district.) Kantairin 54, 11–21.**

TAMM C. O. 1969. Site damages by thinning due to removal of organic matter and plant nutrients.

In: Thinning and Mechanization (Ager, B.H. & Fries, J., ed.) 175–179. Stockholm.

———, & CARBONIER, C. 1961. Växtnäringen som skoglig produktionsfaktor. Kungl. Skogs- och Lantbruksakademiens Tidskr. **100**: 95–124.

TAKAHASHI, N. 1954. (Norway spruce). In: Kitai sareru gaikoku zusyu. I, 22–35.**

TRENDELENBURG, R. 1939. Das Holz als Rohstoff. J.F. Lehmans Verl., Berlin/München.

VANSELOW, K. 1951. Kronen und Zuwachs der Fichte in gleichaltriger Reinbeständen. Forstwiss. Cbl. **70**: 705–719.

WEETMAN, G.F., & HARLAND, R. 1964. Foliage and wood production in unthinned black spruce in northern Quebec. For. Sci. **10**: 80–88.

YOSHIMURA, K. 1967. Growth and biomass of Norway spruce forest in Ashu Experimental Forest. Bull. Kyoto Univ. For. **39**, 27–34.*

YUASA, M. 1950. (Growth of Norway spruce plantation in northern Hokkaido). Proc. Mtg. 1949, Sapporo Branch, Govt. For. Expt. Sta. 31–37.**

ANONYMOUS. 1953. (Present states of plantations in Hokkaido). Hokkaido Kokuyuurin Kyogikai, Sapporo. pp. 217.**

——— 1956. (A census of existing plantations of exotic trees). Forestry Agency, Japanese Govt. mimeo. pp. 73.**

* in Japanese with English summary

** only in Japanese

Titles in parentheses are tentative translation from Japanese original titles by the present author.

日本に植えられたヨーロッパトウヒ林の物質生産
—林分生長論資料 8—

佐　藤　大　七　郎

あ　ら　ま　し

東京大学農学部附属　北海道　および　秩父　演習林に　造林された，ヨーロッパトウヒの林について，物質生産に　関係ある　コトガラを　しらべ，これを，原産地の　ヨーロッパのものと　くらべた。日本に　造林された　ヨーロッパトウヒの　樹齢と　平均樹高の　関係を，おおくの　資料から　もとめて，ひとつの　図に　まとめ，ドイツの　収穫表の　樹高と　くらべた。日本に　造林された　この樹種の　樹高生長は，ドイツにおけるものと　ことならないようだ。北海道の，地位のちがう　4林分を　くらべると，単位面積あたりの，トウヒの，幹と　枝の　量，地上部全体の　乾物重は，45年生のときの　樹高で　あらわした，地位指数に　比例して　おおかったが，葉の量は　かならずしも　そうではなかった。これらの　林にある　植物現在量の　大部分は　トウヒで，下ばえの　わりあいは　わずかだった。単位面積あたりの　幹の生長量は　地位に　比例して　おおかったが，枝と　葉では　かならずしも　そうでは　なかった。その結果，単位面積あたりの，地上部の　純生産量は，地位の　たかいところほど　おおかったが，地位指数と　比例する　わけでは　なかった。地位の　最も　低い　林を　のぞいて，地上部の　生産量の　およそ　9割が　トウヒに　よるもので，ノコリが　下ばえに　よるものだった。地位の　最も　低い　林では　下ばえに　よるものの　ワリアイが　もっと　おおかった。トウヒの　生産した　ものの　およそ　1割が　枝だったが，幹と　葉の　しめる　ワリアイは　林によって　ことなって　いた。中ぐらいの　地位の　ところでは，葉の　再生産に　つかわれる　ワリアイが　おおかった。NAR (純同化率) は　中ぐらいの　地位の　ところが　最も　大きく，地位の　低い　ところが　最も　すくなかった。葉の　単位量あたりの　幹の材の生産量，いわゆる　幹を　生産する　葉の　能率は，地位が　高いほど　高かった。NAR と幹を　生産する　葉の　能率との　関係について　考察した。ひとつの　林の　なかでの，優勢木，なみの木，劣勢木を　くらべると，純生産量は　優勢な　木ほど　おおかったが，NAR と幹材生産能率とは　木の　優劣によっては　あまり　ちがわなかった。奥地に　あって　ながく間伐を　おこなっていない　秩父の　林　では，北海道の　ものにくらべると，単位面積あたりの　葉の量は　おおく，枝の量は　すくなかった。地上部の　純生産量は　北海道の　地位のたかい区の　ものよりも　やや　おおかったが，NAR と　幹を　生産する　葉の　能率は　それよりも　かなり　すくなかった。生産物の　枝への　分配は　いちじるしく　すくなかった。ヨ

ーロッパの　34林分と　葉の量を　くらべたが，日本に　造林された　林の　葉の量は　すべて　その平均より　おおかった。カナダの Black spruce 林　および　北海道の　アカエゾマツの　林に　くらべると，これらの　ヨーロッパトウヒの　葉の量は　かなり　おおかった。