Primary Production Relations of a Young Stand of *Metasequoia Glyptostroboides* Planted in Tokyo: Materials for the Studies of Growth in Forest Stands. 13.*

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Abstract

On a 17-year-old closed stand of *Metasequoia glyptostroboides* in an arboretum near Tokyo, biomass and production were measured. The measurements included root and ground vegetation, and the value of net production was corrected for leaffall during the growing season. With leaf mass of 4.3 t/ha and leaf area index of 8.5, the tree layer produced annually 16.2 t/ha of dry matter as the aerial part. If the correction for leaffall was not made, net production was underestimated by about 4%. With leaf mass of 0.4 t/ha and leaf area index of 1.0, the ground vegetation produced 0.95 t/ha of dry matter as the aerial part. Leaf dry weight of this stand was within the range of variation of leaf mass of *Larix leptolepis* stands, another deciduous conifer, but leaf area index was far larger than it, reflecting larger specific leaf area. Net production by trees within the stand was dependent on leaf mass on them, but independent from the efficiency of leaf, net assimilation rate. Relative growth rate of branch, leaf water content, and specific leaf area changed systematically with the depth in the crown canopy. The relationships between leaf mass and average life span of leaf and between net assimilation rate and leaf mass of the stands, of different species of conifer, which were reported previously, did not change by the addition of the values for this species.

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1. Introduction

In a previous paper (SATOO 1971), in which production relations of coniferous forests of Japan were synthesized, the author pointed out that, the amounts of leaf per unit ground area of forest stands of different species are proportional to average life span of their leaf but independent of annual leaf production, and that annual net assimilation rate, or efficiency of leaf to produce dry matter, of forest stands is reversely proportional to the amount of leaf per unit ground area of stands on a double logarithmic scale. However, when the synthesis was made, data available for deciduous conifer were only for *Larix leptolepis*. To ascertain these findings by use of data of another deciduous coniferous species, production relations were studied on a closed stand of *Metasequoia glyptostroboides*.

After the field works of this study were made, a report on biomass and dry matter production of stands of this species was published by SAITO et al. (1970).

Field works and a part of processing of the samples were made with help of Mr. K. YAGI and the staff of Tanasi Experimental Field of Tokyo University Forest. Measurements of root systems of the tree layer were made by Dr. N. KARIZUMI and his crew of Government Forest Experiment Station. The author would like to appreciate their cooperation. Details of the measurements of root systems will be published by Dr. KARIZUMI.

2. The stand

Two of the young seedlings of this species, which were sent from U.S.A, where seeds brought from continental China were sawn, were planted in Tanasi Experimental Field, west to the city of Tokyo, after growing them in a greenhouse. Cuttings were taken from them in 1953, and rooted cuttings were planted in the arboretum of the Experimental Field. The two clones were not separately planted. When the field works were made, the plantation was 17-year-old. The total area of the stand was about 600 sq. m. The sample plot, which had an area of 251 sq. m., was set so that the outermost rows of the trees were not included in it and that the border line of it passed through the middle of the rows of trees. General description of the stand is given as Table 1. Though stand density was not high, crown was fully closed and lower branches were already dead and shed. Variation in diameter, height and clear length among trees was rather large.

Table 1. General description of the stand.

Age		17
D. B. H.		20.2
Height of average tree	m	14.7
Basal area	sq. m	23.69
Number of tree per hectare		753
Clear length	m	4.2

Since the aerial parts of the ground vegetation were all clipped off at the ground level for another experiment (SASA and SATOO 1968) two years previously, the ground vegetation was made of sprouts from roots or from rhizomes or seedlings younger than 2 years. Important species were: *Celtis sinensis* var. *japonica*, *Lonicera japonica*, *Pleioblastus chino*, and *Carex alterniflora*. There were some annual plants, mostly those found in adjacent fields and roadside, but their number was very few. Soil is silty loam of volcanic ash origin (Kanto-loam) and very deep.

3. Method

Aerial parts of all ground vegetation were clipped at the ground level on five 1×1 m subplots set at the center of the plot. As all plants were lower than 50 cm, they were not separated into strata. They were weighed separately for leaf and non-photosynthetic tissues for each species of each subplot. Samples for conversion of fresh weight into dry weight and into leaf area and for relative growth rate of woody parts were collected. Dry weight was determined by usual method and leaf area was determined with a photoelectric device (MURATA and HAYASHI 1967).

After measuring diameter breast high of all trees in the plot, five sample trees were selected so that trees representing the largest, the smallest and the average trees are included and that two neighbouring trees are not cut. After felling, height was measured and trees were separated into layers at the heights of the ground level (0.0 m), 0.3 m, 1.3 m, 3.3 m, and then at every 2 m. For every layer, stem, branch, and leaf were separated, weighed, and sampled. Branch was separated further into new shoot, old branch larger than 1 cm in diameter, and smaller than 1 cm. Samples were collected for conversion of fresh weight and volume into dry weight of stem, branch and leaf, into leaf area, and for relative growth rate of branch. For stem, tree-ring analysis was made. Area and dry weight of leaf were determined in the same way as for the ground vegetation. From April 1969 through the time of felling the sample trees, fallen leaf was collected with 16 traps, 50×50 cm, set randomly within the plot, to correct the value of production of leaf. After the works on aerial parts were made, roots of the ground vegetation in the subplots were recovered and measured. Later the roots of the tree layer were recovered and measured. Larger roots were pulled out by each sample tree and fine roots were recovered by soil block method.

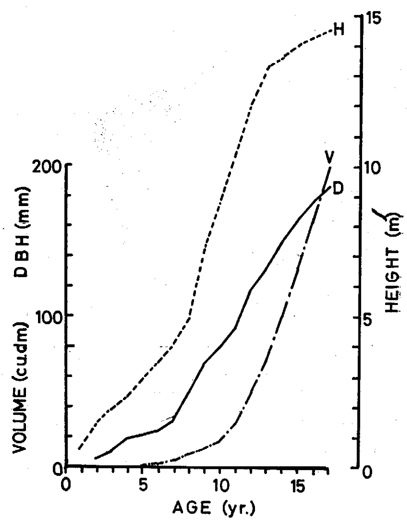

Fig. 1. Course of growth of average trees.
H: height, D: D. B. H., V: volume.

Works on the aerial parts were made in late October, works on roots of the ground vegetation were made in middle November, and the works on roots of the tree layer were made in middle December, 1969.

4. Growth of trees

Table 2. Constants of allometric equation: $Y=b \log D-a$, where D is D.B.H. in cm.

Y		b	a
Stem volume	cu. m	2.4754	3.8596
Stem volume increment	cu. m	2.4014	4.6485
Biomass	kg		
Stem		2.4401	1.3213
Branch		2.5739	2.1407
Leaf		1.7746	1.5568
Aboveground		2.4190	1.1766
Root		2.9522	2.4879
Whole tree		2.5106	1.2019
Leaf area	sq. m	1.8556	0.3642
Production	kg		
Stem		1.6232	1.1491
Branch		2.4401	2.4360
Aboveground		1.8556	1.1019

Table 3. Biomass and net production of the tree layer.

Method		G/g	Allometry
Stem volume	cu. m	174.447	179.660
Stem volume increment	cu. m	23.374	23.282
Biomass	kg		
Stem		54258	57729
Branch		12180	12652
Leaf		4301	4262
Aboveground		70739	72611*
Root		17135	16380
Whole tree		87874	90257**
Leaf area index		8.51	8.54
Net production	kg		
Stem		7092	6936
Branch		4152	4294
Leaf		5005	4966
Aboveground		16249	16194

*, ** Calculated with constants determined for aboveground or whole tree as shown in Table 2, not the sum of parts.

As there are very limited data on the growth of this species grown in stand, growth of trees with cross sectional area closest to the mean (D=20.0 cm) is given in Fig. 1, as mean of two trees: tree no. 4, D=19.6 cm, and tree no. 24, D=19.9 cm.

5. Biomass

Conversion of biomass of sample trees into per unit ground area basis was made by two methods (Satoo 1970a): the ratio of basal area to sum of cross sectional area at breast height of the sample trees (G/g) and the allometric method (aD^b). Constants of the allometric equations with diameter breast high as the independent variable are given in Table 2. Biomass per unit ground area is given in Table 3. The difference by the methods of conversion was very small. SAITO et al. (1970) reported leaf mass of two 9-year-old plantations of this species as 5.1 and 5.0 t/ha, which are not too much larger than the leaf mass of this stand. Leaf mass of 14 stands of *Larix leptolepis*, another deciduous conifer, averaged 3.8 t/ha, ranging from 2.8 to 5.3 t/ha (SATOO 1971). The leaf mass of stands of this species so far known is within the range of variation of leaf mass of *Larix leptolepis* forests. The relationship between leaf mass of stands and average life span of leaf among different species, which was reported previously (SATOO 1971), was still kept if the value for this species is added (Fig. 2), though the

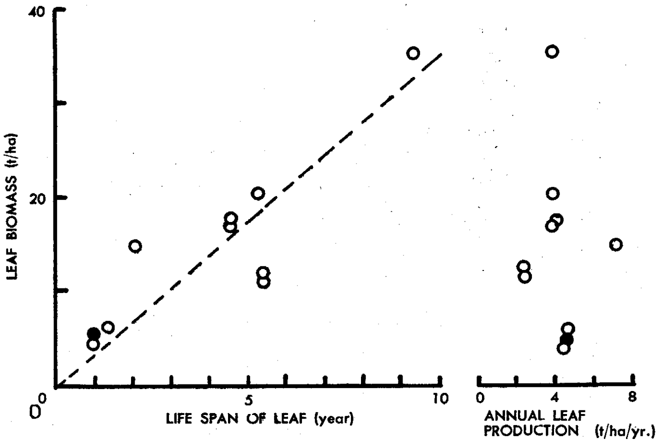

Fig. 2. The relationships between leaf mass per unit ground area and average life span and annual production of leaf of different tree species of conifers.
Filled circle: *Metasequoia glyptostroboides*.
Open circles: other species (SATOO 1971).
Broken line: regression for other species (SATOO 1971).

slope of the regression line might change slightly. Leaf area index was 8.5. This is much larger than the value for a stand of *Larix leptolepis* (SATOO 1970b) which was 4.2 with leaf dry weight of 3.6 t/ha. This difference in leaf area index is mainly due to the larger specific leaf area, or leaf area per unit dry weight, of this species. Biomass of the ground vegetation is given in Table 4. Leaf area index was 1. Leaf area index of all layers of this stand was 9.5 which is rather large compared with other stands of deciduous trees which was within a range between 6 and 8 (SATOO 1970a). Leaf area index could be enhanced by the light coming through the space below crown canopy of the forest border, but this stand was surrounded by other small woodlands and a concrete fence. Only one side faced to a road but lower branches were well kept at the forest border, and a zone of shrubs developed between the border of stand and the road. So the influence of the light from the side could not be of so much importance.

Table 4. Biomass and net production of the ground vegetation (kg/ha).

	Biomass	Production
Leaf	406.5	310.1
New shoot	260.3	260.3
Old branch	565.0	355.9
Culm of *Pleioblastus*	46.5	23.3
Aboveground	1278.3	949.6
Root	990.6	—
Total	2268.9	—
Leaf area index	0.99	

Poor development of the ground vegetation also means minimum influence of the light from the side. Moreover, dry weight of leaves of this stand, 4.3 t/ha, is not an unreasonable value.

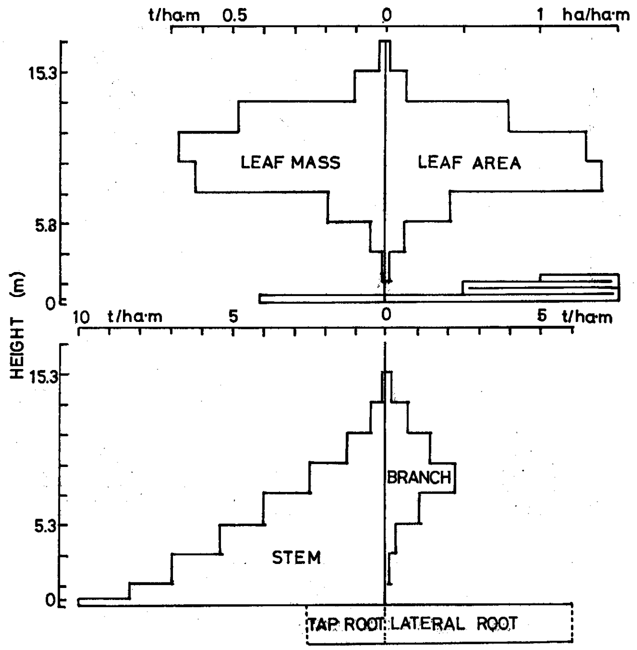

Fig. 3. Vertical distribution of biomass.

Vertical distribution of biomass is shown by Fig. 3. Leaf mass of the ground vegetation in the total leaf mass of the stand was not so large in dry weight but of considerable part in leaf area. This trend was already reported on woodlands of *Larix leptolepis* (SATOO 1970b) and *Cinnamomum camphora* (SATOO 1968a).

6. Net production aboveground

Annual net production as stem was determined by converting the volume growth of each layer with bulk density of samples into dry weight. Production as old branch was determined by multiplying the biomass of it with relative growth rate in cross sectional area of samples (Fig. 4) for every tree and every layer, separately for branch of the two size classes. Biomass of new shoots was used as annual production. Leaf mass of each tree was used as production of each tree and corrected with leaffall after converting it into per unit ground area basis. Correction for the loss of branch and other minor component of litter, which was not much, was not made. Conversion of values for sample trees into values per unit ground area was made in the same way as for biomass. Constants for the allometric equations with D.B.H. as independent variable are given in Table 2. Aboveground net annual production of the tree layer was estimated as 16.2 t/ha, as shown by Table 3. If the correction for leaffall was not made, the value was 15.5 t/ha, resulting an underestimation of about 4.3%. Loss of leaf during the growing season was very large in very young miniature stands of *Ulmus parvifolia* (TADAKI and SHIDEI 1960) and *Camptotheca cuminata* (KAWAHARA et al. 1968). SAITO et al. (1970) reported the aboveground net production as 17.1 t/ha which is not much different from the value presented here. These values are also not much different from the value for plantations of *Larix leptolepis*. The value for 4 stands of *L. leptolepis* averaged 15.0 t/ha (SATOO 1971).

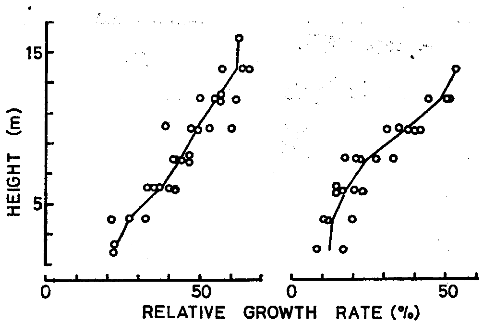

Fig. 4. Relative growth rate of branches in relation to the depth in crown canopy.
Left: branches smaller than 1 cm in diameter.
Right: branches larger than 1 cm in diameter.
The lines connect mean value for each layer, each circle represents mean of 10 samples of each tree in each layer.

Produced matter was distributed into stem at about 43%, into branch at about 26%, and into leaf at about 31%. Distribution ratio did not differ so much among sample trees and the trend observed among the trees of different size (SATOO 1966) was not recognized.

Aboveground net production of the ground vegetation is given in Table 4. Production of old woody parts was estimated with the relative growth rate in cross sectional area of samples for each species and subplot. Biomass of new shoot and leaf of deciduous plants was assumed as the current year production. Half of biomass of *Pleidoblastus chino* and leaf of evergreen shrubs and *Carex* was assumed as current year production. Aboveground net production by the ground vegetation is given in Table 4 as the mean of five subplots. Total annual aboveground net production of this stand including the ground vegetation was estimated as 17.2 t/ha, and the ground vegetation made about 5.5% of the total aboveground net production with 10.4% of the total leaf area of the stand.

7. Efficiency of leaf in net production

The relationships between annual aboveground net production and the amount of leaf per tree are given in Figs. 5a and b. Annual net production per tree (P kg) was dependent on dry weight (L kg) and area (F sq m) of leaf on them, and expressed as

$$P=0.182\,F,\ r=0.99^{**}$$

and

$$P=3.623\,L,\ r=0.99^{**}\ .$$

But annual net production per tree was independent from annual net production per unit leaf, or net assimilation rate, both in dry weight and area basis. This fact was already reported on stands of many tree species such as *Pinus densiflora* (SATOO 1968b), *Larix leptolepis* (SATOO 1971), and *Betula maximowicziana* (SATOO 1970a). The

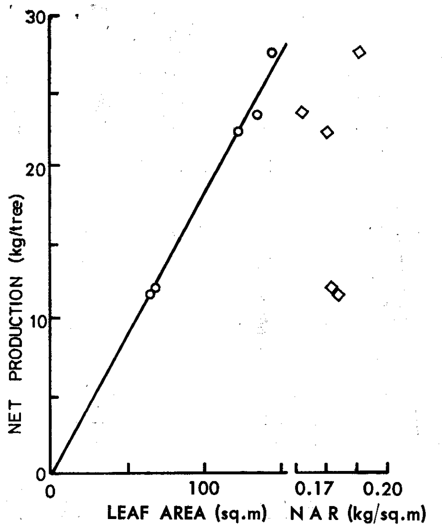

Fig. 5a. The relationships between net production per tree and leaf area and net assimilation rate.

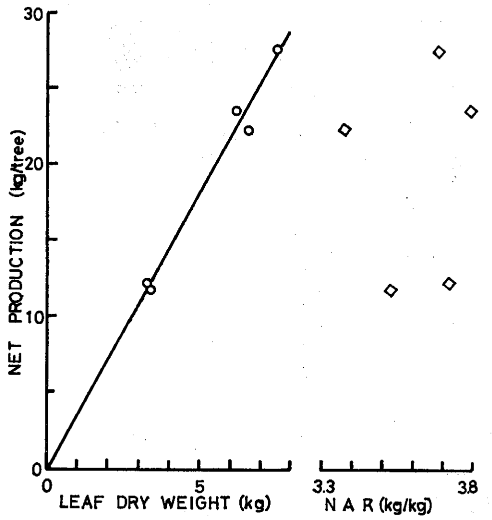

Fig. 5b. The relationships between net production per tree and leaf dry weight and net assimilation rate.

slope of the line in Figs. 5a and b means the efficiency of leaf in net production, or net assimilation rate. Net assimilation rate is also determined by dividing annual net production per tree or per unit ground area of stand by the amount of leaf per tree or per unit ground area of the stand, respectively. As shown by Table 5, value of net assimilation rate was not much different by the method of determination; 0.182 kg/sq. m. yr. or 3.62 kg/kg. yr. Correction of net assimilation rate for fallen leaf, which could only be applied for the calculation for per unit ground area basis, is also given in Table 5. Annual net assimilation rate of the ground vegetation, which is far smaller than the tree layer, is also shown in Table 5. Annual net assimilation rate for aerial parts of the tree layer of another stand of this species was calculated from the data presented by SAITO et al. (1970) as 3.35 kg/kg. yr., which is not much different from the value for this stand. Mean of net assimilation rate of 4 stands of *Larix leptolepis* was 3.45 kg/kg. yr., and a stand of *L. leptolepis* had net assimilation rate of 0.298 kg/sq. m. yr. (SATOO 1971). Annual net assimilation rate of *Metasequoia glyptostroboides* was not much different from that of *L. leptolepis*

Table 5. Net assimilation rate.

Method	kg/sq. m leaf	kg/kg leaf
Regression	0.1827	3.623
Mean of sample trees	0.1820	3.616
Stand	0.1828	3.615
Stand, incl. leaf fall	0.2046	4.046
Ground vegetation	0.0959	2.336

on unit leaf weight basis but far less than it on unit leaf area basis. This discrepancy is due to the difference in the specific leaf area between the two species. The relationship between net assimilation rate and leaf mass per unit ground area among different species (SATOO 1971) did not change by the addition of the value for this species, though the slope of the regression line might differ slightly (Fig. 6).

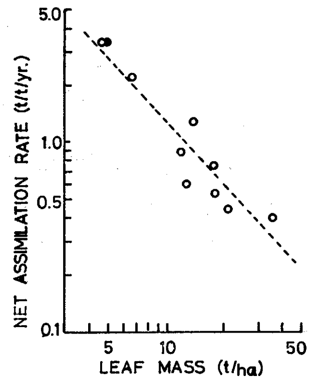

Fig. 6. The relationship between mean net assimilation rate of different species of conifers and their leaf mass per unit ground area.
Filled circle: *Metasequoia glyptostroboides*.
Open circles: other species (SATOO 1971).
Broken line: regression for other species (SATOO 1971).

8. Growth of branch

Since the leaves on lower branches are shaded by the upper crown, photosynthetic efficiency of them must be lower than those on upper branches. Indeed, relative growth rate of branches decreased with increasing depth in the crown canopy, both for larger and smaller branches (Fig. 4). However, as seen from Figs. 7a and b, annual increment of branch (Pb kg) of each layer was dependent on the amount of leaf, both in dry weight (L kg) and area (F sq. m.), and expressed as

$$Pb=0.934\,L,\ r=0.93^{**}$$

and

$$Pb=0.045\,F,\ r=0.99^{**},$$

but independent of the branch production per

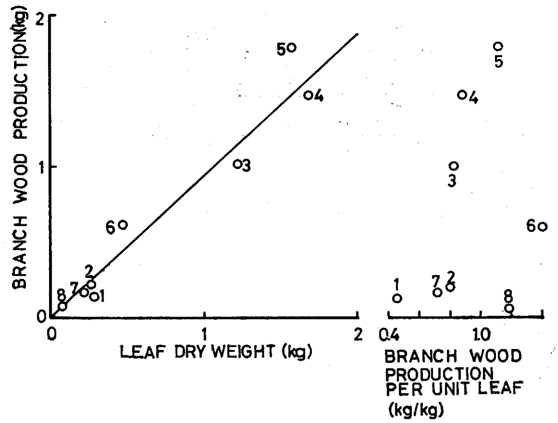

Fig. 7a. Branch wood production in relation to leaf dry weight and efficiency of leaves to produce branch wood of different layers in the crown canopy. The numbers attached to the circles represent the layer in the crown canopy, from top to bottom.

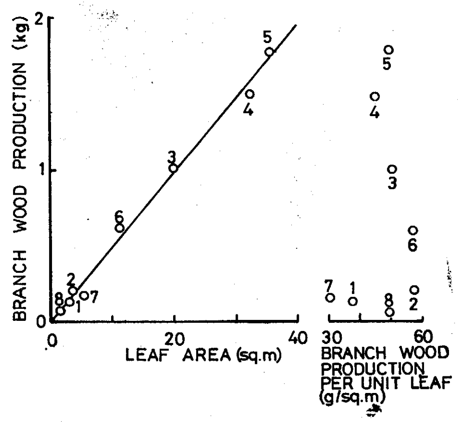

Fig. 7b. Branch wood production in relation to leaf area and efficiency of leaves to produce branch wood of different layers in the crown canopy. The numbers attached to the circles represent the layer in the crown canopy, from top to bottom.

unit leaf. Branch production per unit leaf was also independent from the depth of the layer in the crown (Fig.7). From these findings, it could be suggested that, from the surplus of matter produced by unit amount of leaf on a branch, a certain portion is used for the production of branch and the rest is transferred into stem to be used there or in roots. The decrease of relative growth rate with depth might be the result of the increase of branch relative to the amount of leaf and increase of the size of them. The production of branch per unit leaf does not have any direct relationship to photosynthetic efficiency of leaf on it.

9. Characteristics of leaf in relation to the depth in the crown canopy

It is generally known that leaf area per unit dry weight, or specific leaf area, increases with increase of depth in the crown canopy, or increasing shading. This trend was also recognized in this stand (Fig. 8). On this problem TADAKI (1970) discussed recently. Water content of leaf was also higher in the lower layer of the crown (Fig. 9).

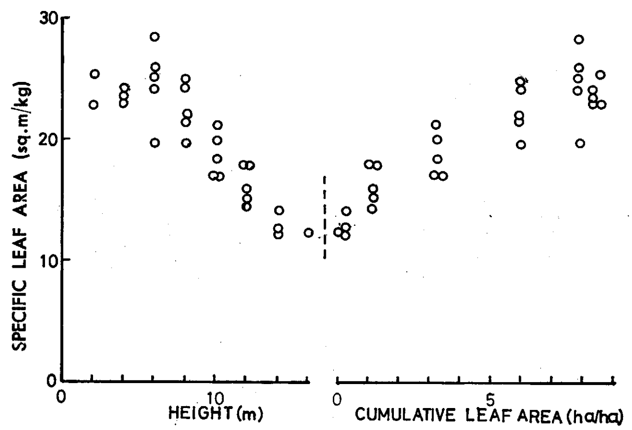

Fig. 8. Change of specific leaf area with depth in the crown canopy.

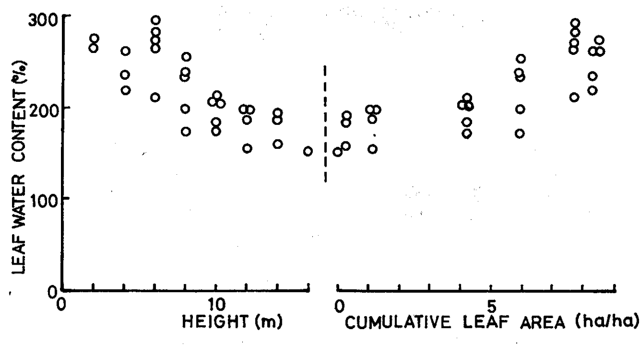

Fig. 9. Change of leaf water content with depth in the crown canopy.

References

KAWAHARA, T., et al. 1968. Movement of nutrients in a model stand of *Camptotheca acuminata* DENCE. J. Jap. For. Soc. **50**: 125–134.*

MURATA, Y., and HAYASHI, K. 1967. On a new, automatic device for leaf-area measurement. Proc. Crop. Sci. Soc. Jap. **36**: 463–467.

SAITO, H., et al. 1970. Productivity of young stands of *Metasequoia glyptostroboides*. Bull. Kyoto Univ. For. **41**, 80–95.*

SASA, T., and SATOO, T. 1968. (Notes on estimation of litterfall.) Trans. 79th Mtg., Jap. For. Soc. 94–96.**

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

——— 1968a. Primary production and distribution of produced dry matter in a plantation of *Cinnamomum camphora*: Materials for the studies of growth in stands. 7. Bull. Tokyo Univ. For. **64**, 241–275.

——— 1968b. Primary production relations in woodlands of *Pinus densiflora*. In: Symposium on primary productivity and mineral cycling in natural ecosystems. (YOUNG, H. E., ed.) pp. 52–80. Univ. Maine Press, Orono.

——— 1970a. A synthesis of studies by the harvest method: Primary production relations in the temperate deciduous forests of Japan. In: Ecological Studies: Analysis and Synthesis Vol. 1. Analysis of temperate forest ecosystems (REICHLE, D. E., ed.) pp. 55–72. Springer, Heidelberg/New York.

——— 1970b. Primary production in a plantation of Japanese larch, *Larix leptolepis*: a summarized report of JPTF-66 Koiwai. J. Jap. For. Soc. **52**: 154–158.

——— 1971. Primary production relations of coniferous forests in Japan. In: Productivity of Forests Ecosystems, Proc. Brussels Symp. 1969. (DUVIGNEAND, P., ed.) pp. 191–205. UNESCO, Paris.

TADAKI, Y. 1970. Studies on the production structure of forest 17. Vertical change of specific leaf area in forest canopy. J. Jap. For. Soc. **52**: 263–268.

———, and SHIDEI, T. 1960. Studies on production structure of forests. 1. The seasonal variation of leaf amount and the dry matter production of deciduous sapling stand (*Ulmus parvifolia*). J. Jap. For. Soc. **42**: 427–434.*

* Japanese with English summary.

** Only in Japanese.

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わかいメタセコイア林の物質生産
—林分生長論資料 13—

佐藤大七郎

あらまし

東京ちかくにある樹木園にうえられた17年生のよく閉鎖したメタセコイア林について物質生産をしらべた。測定は根と林床植生についてもおこない，生育期間の落葉をしらべて生産量を補正した。乾重量で 4.3 t/ha，葉面積指数で 8.5 の葉をつけたこの林は，1年に 16.2 t/ha の乾物を

上木の地上部として生産した。落葉の補正をおこなわないとおよそ4% すくなめに生産量を推定したことになる。林床植生は，乾重量で 0.4 t，葉面積指数で 1.0 の葉をもって1年に 0.95 t/ha の乾物を地上部として生産した。この林の葉のオモサはカラマツ林の変動のハバのなかにあるが，葉面積指数は，比葉面積のチガイによって，はるかにおおきかった。林のなかのひとつひとつの木の生産量は葉の量に比例し，純同化率とは関係がなかった。葉の乾重量あたりの純同化率はカラマツ林とあまりかわらなかった。枝の生長率，葉の含水率，および比葉面積はクローネのなかでのフカサにともなって系統的に変化した。まえに報告した，ことなった樹種のあいだの単位面積の林のもつ葉の量と葉の平均寿命との関係および純同化量と単位面積の林のもつ葉の量の関係は，この樹種のアタイをくわえてもかわらなかった。

Appendix 1. Sample tree data.

Sample tree		4	12	16	23	24
D. B. H.	cm	19.6	16.8	24.8	14.8	19.8
Height	m	14.1	13.8	16.8	13.6	15.0
Stem volume	cu. m	0.21262	0.14460	0.39867	0.11463	0.22649
Stem increment	cu. m	0.03208	0.01379	0.04825	0.01680	0.02987
Biomass	kg					
Stem		65.514	43.688	128.474	37.458	67.068
Branch		16.282	11.213	24.327	6.433	18.336
Leaf		6.218	3.282	7.537	3.374	6.634
Root		21.956	13.165	40.194	9.041	23.400
Leaf area	sq. m	135.64	67.08	144.99	63.73	123.40
Production	kg					
Stem		12.725	4.783	10.732	6.017	10.344
Branch		4.622	4.145	9.427	2.471	5.432

Appendix 2. Stand table.

D. B. H.	N	D. B. H.	N
13	1	21	2
14	0	22	0
15	1	23	1
16	1	24	2
17	3	25	1
18	2	26	0
19	0	27	1
20	4		

Area: 251 sq. m.