Ecological and Physiological Studies on the Vegetation of Mt. Shimagare VI. Growth and Dry Matter Production of Young *Abies* Stand*

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Abstract

Growth and dry matter production, and consumption of dry matter by respiration and shedding of a young *Abies* stand about 15 years old were estimated in the subalpine zone (at altitude of 2,340 m) of Mt. Shimagare, Nagano Prefecture, Central Honshu. Seasonal changes of biomass of new organs were pursued by samplings at intervals of one or two months during the growing season of 1960. The dry weight of new leaves increased till the end of August, while that of new branches increased till the end of October. The total biomass of the stand at the end of the growing season was 3.3 kg d. w./m². Leaf biomass of 1.0 kg d. w./m² of this young stand was about a half of that in the mature subalpine *Abies* stand of the adjacent region.

Net production of the young stand, 0.74 kg/m² · yr, was about 65% of that of the mature. Both stands were nearly equal in production of leaves and branches, so the difference in the net production was mainly attributed to that in the production of stems and roots. About 70% of the net production of the young stand contributed to the increase of biomass, and the rest was lost by shedding of leaves.

Annual respiratory loss was estimated at 1.25 kg/m² by the measurements of seasonal change in respiratory activity of each organ. This amount was about 63% of the gross production, which was estimated to be 1.99 kg/m² · yr as the sum total of the net production and the respiration.

In the last decade the studies of productivity and turnover of matter in the forest ecosystem advanced very rapidly. Many of these works, especially those made by Japanese workers, were recently compiled by Kira and Shidei¹⁾.

The estimation of forest productivity has reached methodologically almost its completion, though some practical difficulties remain in estimating the growth and turnover of root systems, the loss by grazing of plant biomass, etc. A deep interest is now increasing in analytical studies of the economy of matter in plants throughout a year, or the processes of matter reproduction in plants²⁾. Such studies based on the growth analysis have mainly been performed in herbaceous plant communities either artificial³⁻⁵⁾ or natural⁶⁻¹²⁾. The huge biomass of the forest, however, prevents the strict application of the method developed in these studies to the forest communities.

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An object suitable for detailed studies on the forest is supplied by a dense stand of young subalpine *Abies* trees grown in the stripes of dead trees on Mt. Shimagare, Nagano Prefecture, of which peculiar structure was reported in a previous paper¹³⁾ of this series. In the series Kuroiwa^{14,15)} reported already the photosynthesis and the respiration of *Abies* trees and outlined the productivity of the stand. His attention, however, was rather given to the analysis of the competition between trees of different sizes grown in the same stand, and the results for the productivity of the stand seemed to be not fully satisfactory for the analysis of the production process based on the economy of matter accompanying the growth cycle of the plants.

The present paper deals with dry matter production, consumption of matter by respiration, and shedding in the young *Abies* stand about 15 years old grown in a stripe of dead trees (at altitude of about 2,340 m) on Mt. Shimagare. These results will be compared with those obtained for the mature *Abies* stand situated at 1.5 km from the present stand in the neighboring region¹⁶⁾. Seasonal change of productivity and economy of carbohydrates related to the growth of trees will be dealt with in the next paper.

Method

Vigorous regeneration of the young *Abies* trees made the stand relatively uniform in cover and density, but there were observed many clumps of various sizes and forms of young trees. Without reasonable sampling technique, therefore, it was difficult to obtain reliable values of the biomass as well as of its increment.

In early winter of 1959, when the growing season was over, a number of dense and closed colonies of trees about 80 cm high were marked with pieces of red cloth. At the center of each colony, a 50×50 cm quadrat was settled for measuring the plant biomass. The samplings were performed with adequate intervals during the growing season of 1960. Two quadrats were chosen at random at each sampling. For accurate estimation of the biomass and its annual increment, ten quadrats were sampled in December of 1960.

Plant materials from the quadrats were separated into several parts, i.e. needles and branches of current year, one year old, and two or more years old, stems, and roots. After being measured in fresh weight, each part was dried up at 90° to a constant weight to obtain its dry weight.

A modified Boysen-Jensen's apparatus with a glass filter plate at the bottom of CO₂ absorber was adopted for the respiration measurement. Several trees of *Abies Veitchii* were carried to the laboratory at each sampling time, and respiratory activities were measured of twigs with needles of each age, stems, and roots, separately at room temperature.

The course of growth

The climate of the region was summarized in previous reports of this series (monthly min. temp. -14.1° in Feb., max. temp. 13.7° in Aug., mean ann. temp. -0.3°)^{13,15)}. In the mature forest the average snow depth in winter is 1.0-1.5 m. In the young stand studied, however, the depth reaches less than 50 cm because of the exposure to high wind, so the tops of the trees are exposed to the cold wind. The snow usually remains till the end of April. The monthly mean air temperature is

under the melting point till May, and the soil remains frozen until the middle of the month.

The herbaceous undergrowth of the mature stands and the deciduous trees mixed in the *Abies* forest unfold rapidly their leaves shortly after the snow melting. The *Abies* trees sprout their new needles late in June, when daily mean and minimum temperatures exceed 10° and 5° , respectively. The stems and branches elongate within one month and a half to reach their maximum length. As shown in Fig. 1, the dry weight increment of the current-year needles is almost completed by the end of August, while that of the current-year branches continues till the end of October. The dry weight increment of stems and older branches seems to have the same trend as that of current-year branches.

Fig. 1. Dry weight increment of current-year needle and branch of 15-year-old *Abies* stand. Each value is the mean of two quadrats except the values of December which were obtained based on the measurements in ten quadrats. Vertical lines attached show the standard deviation.

Biomass and net production

The biomass at the end of the growing season of the young *Abies* stand studied is shown in Table 1. The leaf biomass, 1.0 kg/m^2 , is about a half of that of the mature stand of this mountain region¹⁶⁾.

Needles of current-year, one-year-old, and two or more-year-old occupied respectively one third of the total leaf biomass, being distributed vertically as shown in a productive structure diagram¹⁷⁾ (Fig. 2). The vertical distribution of the needles of each age class is binomial as Saeki discussed the development of leaf system¹⁸⁾. Light intensity on the forest floor was 4-5% of the full light.

Annual dry weight increments in the stems and branches were estimated by the usual method for examining the annual rings at the end of the growing season in all stems harvested from four quadrats and in old branches chosen at random from the harvested trees. The obtained values of the volume increment were summed up for each sampled quadrat and converted into dry weight by multiplying the average dry weight—volume ratio. The annual increment was 107 g d. w./m^2 (c. v.*=

* Coefficient of variation among sample quadrats of $50 \times 50 \text{ cm}$.

Table 1. Variation of biomass during the growing season, increment and net production. Biomass at the end of the growing season and coefficient of variation (c.v.) were measured directly for ten sample quadrats of 50×50 cm. The signs ≥2, 1 and 0 indicate two or more-year-old, one-year-old, and current-year organs, respectively.

	growing season			increment (g/m ² ·year)	net production (g/m ² ·year)
	beginning* (g/m ²)	end (g/m ²)	c. v. (%)		
stems	872.....	979	22	107	107
roots	501.....	595	12	94	94
branches					
≥ 2	} 563.....	494	18	} 31	31
1		100	24		
0		0**..... 111***	13		
needles					
≥ 2	548.... { 378.....	394	6.7	-154	16
	{ 170...shed				
1	300.....	312	11	12	12
0	0**.... 366 {	318	6.7	318	366
	{ 48...shed				
whole stand	2,780	3,300	20	520	740

* Obtained indirectly from the examinations of annual increments and sheddings.
** Weight of buds are included in 1-year-old branches.
*** Include buds for the next year.

Fig. 2. Left: Productive structure of 15-year-old *Abies* stand after the fulldevelopment of current-year organs. The symbols 0, 1 and ≥2 are the same as in Table 1. Right: Vertical distribution of needles of each age class. Solid circles, current-year needles; open circles, one-year-old needles; and crosses, two or more-year-old needles.

5.8%) in the stems, where 12 g was the increment accompanying elongation, and 142 g d.w./m² (c.v.=6.8%) in the branches, where 111 g was the share of current-year branches (Table 1).

The dry weight increment of the older needles was estimated from the following data. The leaf dry matter index of the needles of *Abies Veitchii* was about 1.3 g d.w./100 cm², and it increased with a rate of about 0.05 g d.w./100 cm².yr¹⁴⁾. Accordingly, the annual increment on a dry weight basis is to be 0.04 g d.w./g d.w.. This amounts to 12 g d.w./m².yr for one-year-old needles and 16 g for more than two-year-old ones.

To the estimation of the amount of dry matter loss by shedding of needles, the life table method is applicable. The survivor curve of needles of *Abies Veitchii* is shown in Fig. 3, which has been obtained by a method presented by the senior author¹⁶⁾. About 15% of current-year needles was shed till the end of the growing season, and the amount attained 48 g d.w./m², provided that the shedding of the current-year needles occurred after reaching their maturity. The loss of one-year-old needles seemed to be negligible. The mortality rate of two- to four-year-old needles was equally about 31% per year. This rate was adopted for all of the two or more-year-old needles, since the biomass of the needles over four years old, which seemed to have higher mortality, was very small. The estimated annual loss of the older needles was 170 g d.w./m². This loss by shedding seemed to occur mainly in the growing season, because the survivor curve obtained at the end of the growing season indicated the same pattern as that obtained at the beginning of the season, but only with a time lag of one year.

The allometric relation in dry weight of the root to the whole plant was examined twice in a growing season, at the beginning and at the end. A common regression line of which gradient was about unity was applied to both examinations (Fig. 4). This means that the relative growth rate of roots is much the same as that of the whole plants. From this relation the annual increment of the roots was calculated as 94g d.w./m².

The results of these estimations are summarized in Table 1. The net production estimated was 740g/m².yr. Table 1 indicates obviously that the biomass increment in the growing season is no direct measure of net production. The former is only 70% of the latter.

Death of the suppressed small trees should occur in the growing season. The dead biomass, however, seemed to be so small that correction of the values in Table

Fig. 3. Survivor curves of *Abies Veitchii* needles in the 15-year-old stand. Solid circle, measured in late June; open circle, in early December.

Fig. 4. Allometry between dry weight of the root (W_r) and the whole plant (W) of 15-year-old *Abies Veitchii* trees. Individuals shown by solid circles were collected in late June, and open circles, in late October. The relation is given by $W_r = 0.214 W^{0.950}$.

1 was unnecessary. The annual mortality of young *Abies* trees in the dead tree stripe region was calculated to be about 7.5%¹⁹⁾ or about five trees/m²·yr for the present stand. In the early half of the growing season, three or four small trees less than 3 g in dry weight were found in every quadrat of a quarter sq. meter. Most of these small trees disappeared by December. Loss of biomass through the death of these small trees did not exceed 10 g d. w./m², i. e. about 0.3% of the total biomass of the stand. Death of the old branches of living trees in the period was also assumed to bring about only negligibly small loss of plant biomass.

It should be noticed that the productivity of this young *Abies* stand reached more than 65% of that of the mature stand of this region reported as 1.11 kg/m²·yr¹⁶⁾. The amounts of production of leaves and branches were surprisingly the same in both stands: the production of leaves in both stands was equally 0.39 kg/m²·yr, and that of branches, 0.14 kg/m²·yr in the young and 0.13 kg/m²·yr in the mature (cf. Table 3). Then, almost all of the differences in productivity between the two stands were attributed to those in the production of stems and roots. In the young stand the production of stems and roots was only 27% of the total net production, while in the mature, it reached 53%.

Respiration and gross production

The seasonal changes in respiratory activity of various organs at 20° are illustrated in Fig. 5. The activities measured at room temperatures at each sampling

were converted to those at 20° for comparison, with assumption that Q_{10} of the respiration was 2. The new shoots showed the maximum respiratory activity of 5 mg $\text{CO}_2/\text{g d.w.}\cdot\text{hr}$ late in June. The respiratory activities of current-year organs decreased with the lapse of time until December, as was reported by many workers^{3-6,9,11}. After thawing of the frozen soil, the respiratory activities of the older organs increased and reached their maximum in the early half of June when the buds were still in dormancy. This temporary high activity will be discussed in the next paper in relation to an active physiological state of plants at that time. Respiratory activities of the older organs remained nearly constant throughout the year except for the June maximum.

The loss of matter by respiration of the stand was calculated by the usual procedure with combining the mean temperature in the field and the respiratory activities and biomass of each organ. Conversion coefficient from the respired CO_2 to the dry matter loss was accounted as 0.53, as the carbon content of dry matter of this plant was 52%¹⁶. Fig. 6 represents the seasonal course of respiration of the young *Abies* stand under the field conditions. Respiration from December to April was neglected because of the low temperature and the freezing of soil, as assured by Pisek and Winkler²⁰ who studied the seasonal gas exchange of *Picea excelsa* at the forest limit of Austrian Alps where the temperature climate is similar to that in Mt. Shimagare.

The calculated respiration of the entire plant has a maximum of 9.8 g d.w./ $\text{m}^2\cdot\text{day}$ in August when the monthly air temperature reaches its maximum. A remarkable shoulder in June corresponds to the high respiratory activities of the older organs. Such spring shoulder of respiration curve was reported in bamboo grasses by Oshima^{7,8}. The annual respiratory loss in dry matter of this *Abies* stand was 1.25 kg/ m^2 , nearly six times of the loss by shedding, in the sum total

Fig. 5. Seasonal changes in respiratory activity of various organs of 15-year-old *Abies* trees at 20°. Solid circles represent from top to bottom, current-year branches with needles, one-year-old ones, two or more-year-old ones. Open circles, stems, and crosses, roots.

(Table 2), of which 74% was in the branches with needles.

It is practically often required to estimate the annual respiration of a forest stand without measuring the seasonal variation of respiratory activity in detail. Usually, on the basis of the data of respiratory activity measured at a certain time of the year, the annual respiration is calculated by combining the temperature coefficient of the respiratory activity with the monthly mean temperatures. Though the spring shoulder is inevitably neglected, the underestimation in annual respiration which might be caused by this simplification is less than 10% so far as the present stand is concerned.

The gross production of the stand was $1.99 \text{ kg/m}^2 \cdot \text{yr}$, and 63% of the assimilated matter being consumed by respiration. The gross and net production are nearly twice as large as those estimated by Kuroiwa¹⁶⁾ in a young *Abies* stand of similar age. This difference seemed to be reasonable because the present results have been obtained based on the biomass determined restrictedly at the center of the clumps. As to the average productivity of the whole young stand where trees were distributed somewhat unevenly, the results of Kuroiwa seems to be rather applicable. To assure reliable values of seasonal changes of biomass and reserve materials, which will be treated in the next report, we should repeat the measurement of biomass in quadrats

Fig. 6. Seasonal change of daily dry matter loss by respiration in 15-year-old *Abies* stand. Signs 0, 1 and ≥ 2 mean current-year branches with needles, one-year-old ones and two or more-year-old ones, respectively.

Table 2. Annual respiratory loss of the young *Abies* community. The numbers in parentheses are relative values to whole stand. The signs ≥ 2 , 1 and 0 are the same as in Table 1.

	Stems	Roots	Branches with needles			Whole stand
			≥ 2	1	0	
Annual respiration	206	120	373	266	301	1,250
(g. d. w./m²)	(16)	(10)	(30)	(20)	(24)	(100)

settled restrictedly in the closed clumps. Moreover, for the purpose of comparing the productive characteristics between the young stand and the closed mature stand, the values obtained at the clumps seem to be rather preferable to the average values for the whole uneven stand of young trees.

Provided that the gross production is almost proportional to the leaf biomass, the gross production in the mature *Abies* stand of this region can reach $4 \text{ kg/m}^2 \cdot \text{yr}$, as the leaf amount is twice as much as that of the young one¹⁶⁾. This may be assured by considering the respiratory loss and the net production of the matured stand. In the young stand the annual respiration of the branches with needles was estimated at $0.94 \text{ kg d. w./m}^2$ (Table 2), so in the mature stand the annual respiration of its needles and needle-bearing branchlets may be assumed to reach nearly 2 kg d. w./m^2 . As reported in a previous paper¹⁶⁾, the net production of the mature stand was $1.11 \text{ kg/m}^2 \cdot \text{yr}$. If we take further account of the respiration of stems, roots and large branches, it seems very probable that the annual gross production can reach 4 kg/m^2 in the mature *Abies* stand.

In Table 3 it is obvious that the ratio of net production to gross production is higher in the young stand than in the mature one. In the latter the huge biomass of leaves and woody organs respired 72% of the gross production. The ratios of total respiration to gross production estimated in several forest stands indicate that they are surprisingly equal in the climax forests, falling in the range of 70–80%, indifferent to the climatic conditions and the life forms of dominant trees, which are ranging from the tropical rain forest^{21,22)} through the warm temperate evergreen forest²³⁾ to the present subalpine coniferous forest.

Table 3 indicates also the characteristic difference between the young and the mature stands in the distribution of dry matter to each organ. As already mentioned, the production of leaves and branches is much the same in both stands, while the biomass of leaves in the young stand is about a half of that in the mature. This mainly results from the higher mortality of needles in the young stand. From Fig. 3 the half-life time of the needles in the young stand is estimated at about 3.4 years, while the corresponding value in the mature is about 5.2 years¹⁶⁾. The shorter life span of leaves in the former is to be considered as one of the disadvantageous characters to the dry matter production and growth of the stand²⁾, because the shorter the leaf longevity, the greater part of produced matter is required in the formation of new leaves for the maintenance of the present leaf biomass, and consequently the share for the biomass increment is reduced. The production of stems in the young stand is only one fourth of that in the mature. The ratio of production of leaves to the gross production in the young stand is twice as

Table 3. Comparison of dry matter production in the young and in the mature *Abies* forests. The values in parentheses are relative values to gross production.

	young stand	mature stand
gross production ($\text{kg/m}^2 \cdot \text{year}$)	1.99 (100)	4 (100)
net production ($\text{kg/m}^2 \cdot \text{year}$)	0.74 (37)	1.11 (28)
production of leaves	0.394 (20)	0.39 (10)
production of branches	0.142 (7)	0.13 (3)
production of stems	0.107 (5)	0.42 (11)
production of roots	0.094 (5)	0.17 (4)

large as that in the mature, while that of stems in the young stand is only a half of that in the mature.

Further studies on the change in the distribution of produced matter to the various organs as well as the change in the ratios of net production and dry matter increment to the gross production with forest aging will elucidate the general feature of the growth and development of the forest community.

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摘 要

木村 允*・本谷 勲**・宝月欣二*: 縞枯山の植生についての生態学的ならびに生理学的研究 VI. *Abies* 幼樹群落の生長と物質生産

縞枯山の縞枯部に成立する約 15 年生の *Abies* 幼樹林において、生長と物質生産量、呼吸および枯死による物質消失量を測定した。季節をおったサンプリングにより新成器官の生長経過をみると、芽の展開は 6 月末にはじまり、新葉の生長は 8 月末にはほぼ完了するが、新枝の生長は 10 月末までつづいた。

生育期間の終了後の生体量は 3.3 kg d. w./m^2 であり、この年の純生産量は 0.74 kg 、乾物増加量は 0.52 kg であった。この地方の成熟林で得られた結果と比較すると、純生産量はその 65% に達し、葉と枝の生産量は両群落ではほぼ等しい。両者の差は主として幹の生産量の差異による。ここに幼令林の特徴の一部がみられるようである。

各器官の呼吸速度の季節変化を測定することによって得られた群落の年間の呼吸量は、乾量に換算して 1.25 kg/m^2 であった。したがって年総生産量は 1.99 kg/m^2 であり、純生産量はその 37% に相当する。成熟林においてはこの割合は 30% 程度になると推定された。（*東京都立大学理学部生物学教室・**東京農工大学教養部生物学研究室）