Analysis of Production Processes of an Undergrowth of Subalpine *Abies* Forest, *Pteridophyllum racemosum* Population 1 Growth, Carbohydrate Economy and Net Production*

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Abstract

Annual growth cycle and seasonal changes of carbohydrate reserves in various organs were studied with populations of *Pteridophyllum racemosum*, an evergreen perennial herb of Papaveraceae, grown as an undergrowth of the subalpine *Abies* forest (2,250 m in altitude) of northern Yatsugatake Mountains, central Japan. The plants unfolded late in May, soon after snow melting. The growth of new organs in dry weight was inclined to leaves and flower stalks in early growing season and to roots in late summer and autumn. The annual growth of new organs of the population reached 51.5 g d. w./m².

Seasonal changes of sugar, starch and hemicellulose contents in leaves, roots and rhizomes were pursued. Carbohydrate reserves in the old organs decreased in the early growing season till the end of June, corresponding to the period of rapid development of new leaves and flower stalks. The old leaves as well as roots and rhizomes exported considerable amount of reserves in this period showing that they played in winter a role as the reserve organ. Reserves were filled again in overwintering old organs till the end of the growing season.

By combining monthly dry weight increments in new organs and the consumption or accumulation of reserves in old organs, monthly and annual net production of the population were calculated. The latter was 40.5 g/m²·yr which corresponded to 3.6% of the annual net production of the canopy *Abies* trees. During the initial two and a half months of the growing season, till the end of July, the plant produced 72% of the annual net production.

The subalpine region of central Japan is covered mainly with evergreen coniferous forest of *Abies Veitchii*, *A. Mariesii*, *Tsuga diversifolia*, etc. In the forest, the development of undergrowth is remarkably suppressed by a perpetual gloom and a short growing season, and the ground surface is covered mainly with the dark green carpet of mosses.

Among higher plants grown on the forest floor, herbaceous perennials are most abundant. They generally have rhizomes or stolons and reproduce vegetatively. The rhizomes or stolons and root systems are also utilized as storage organ of reserves which provide for the rapid development of shoots soon after snow melting¹⁻⁵⁾. For elucidation of production processes of these plants, an analysis of the economy

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of reserve materials in the growth cycle seems to be indispensable as has been noticed.^{6,7)}

The present paper deals with the economy of reserve carbohydrate and net production of *Pteridophyllum racemosum* population grown in the subalpine coniferous forest of northern Yatsugatake Mountains. *P. racemosum*, a monogenic endemic species of Papaveraceae, is an evergreen rosette plant with fern-like compound leaves (Plate 1). It grows abundantly on the *Abies* forest floor but scarcely in the *Tsuga* forest of the same region. Nakano⁸⁾ nominated the *Abies* forest in this region as *Abies Veitchii*—*Pteridophyllum racemosum*—Sociation.

Evergreenness of this plant is of special interest in relation to the matter economy, as the advantageous role of evergreen leaves in plant life under severe conditions has been pointed out by several authors.^{4,5,9)} The present author also showed recently that the evergreen leaves of subalpine coniferous trees play a role as the reserve organ of large capacity in winter.⁷⁾

In the *Abies* forest, most of the species of undergrowth distribute rather scatteringly making the application of the usual harvest method of growth analysis^{2,6,10)} almost impossible. *Pteridophyllum*, however, grows frequently forming almost pure and dense populations of 5-10 m in diameter making the application of this method easy.

Description of the habitat

The forest stand investigated was situated in elevation of about 2,250 m near Mugikusa Pass of northern Yatsugatake Mountains, Nagano Prefecture, central Japan. The temperature climate of this region was described in a previous paper.¹¹⁾ The annual mean, monthly minimum and monthly maximum air temperatures at the stand are assumed to be 0.2°, -13.5° and 14.0°, respectively. The first snow of winter season occurs usually in early November and forest floor is completely covered with snow by early December. The mean snow depth in the forest is 1.0-1.5 m and it remains usually till mid-May. The general description of the vegetation in this region is seen in the reports of Nakano⁸⁾ and Kimura.¹²⁾

The stand is a typical subalpine *Abies* forest with the tree density of about 2,000/ha. The forest canopy was composed of *Abies Veitchii*, *A. Mariesii* and *Betula Ermani* var. *communis*, of which basal area percentages were 48, 46 and 6%, respectively. A few slender trees of *Sorbus commixta* and *Acer Sieboldianum* were also mixed.

The soil surface was relatively smooth and covered completely with mosses and undergrowth of higher plants. Among the moss species, *Hylocomium splendens* and *Pleurizium Schreberi* were dominant. Among higher plants, besides *Pteridophyllum racemosum* and seedlings of canopy species, *Oxalis Acetosella*, *Ilex rugosa*, *Carex blepharicarpa*, *Maianthemum dilatatum* var. *nipponicum*, *Rumohra mutica* were usually present. The relative light intensity on the undergrowth was 6% in average.¹²⁾

Methods

Measurement of plant biomass was performed at intervals of one or two months during growing season of 1960. Biomass in a unit ground surface was measured by setting quadrats of a quarter sq. meter in the dense populations of *Pteridophyllum*

(Plate 1). Four quadrats were chosen at random at each sampling occasion. From each quadrat, plants were removed from soil by a hand scoop carefully. Since most of the rhizomes and roots of this plant were laid in the layers of litter debris and uppermost soil, the complete sampling of these organs was rather easy.

Plant materials sampled were separated into various organs such as flower stalks, leaves of current year, one-year-old and two-year-old, rhizomes, new roots and old roots. After being measured in fresh weight, each component thus sorted was oven-dried at 90° to a constant weight in the laboratory to obtain dry weight. Biomass data obtained from the four quadrats were summed up to get the figures per sq. meter.

A part of the each component was utilized for carbohydrate analysis. Weighed fresh plant materials were chopped separately, boiled in 80% ethanol for a few minutes and preserved in vials with stopper. The series of procedures used for carbohydrate extraction and analysis has been previously described.⁷⁾ The total amount of sugar, starch and hemicellulose was considered as "soluble" carbohydrate.

At the first and the last sampling occasions in mid-May and early December, the soil and litter layers were frozen hard. At the last sampling the plants were covered with snow of about 10 cm deep. The biomass determination could not be made at mid-May for underground organs and at early December for whole plant, and samples were limited only for chemical analyses.

The growth in biomass

Seasonal changes of leaf biomass of each age are shown in Fig. 1. At the beginning of the growing season, *Pteridophyllum* had two kinds of leaves; one-year-old and two-year-old. Most of the two-year-old leaves had already died out and even those still living had been lost their tips or many leaflets. They all died till the end of June. One-year-old leaves, on the contrary, seemed to be sound at the beginning of the growing season. With the progress of the season, they partly died and lost their leaflets, and were reduced to half in biomass at the end of the growing season.

The plant unfolded soon after the snow melting and new leaves and

Fig. 1. Seasonal changes in biomass of various organs in *Pteridophyllum* population. A represents the change in leaf biomass of each age, in which solid circles, new leaves; open circles, one-year-old leaves; and triangles, two-year-old leaves. Upper smooth curve shows the change in whole leaves. B represents the changes in non-photosynthetic organs in which open circles, flower stalks; solid circles, new roots; triangles, new rhizomes; and crosses, buds for the next year.

flower stalks were rapidly developed till the end of June. The biomass of new leaves at the full expansion was ca. 24 g d.w./m² and it increased to ca. 26 g d.w./m² by late August mainly because of the increase in leaf dry matter index of leaf lamina. Total leaf biomass of the population had the maximum of ca. 44 g d.w./m² in summer with the leaf area index of 0.99.

As seen in Fig. 1, biomass of flower stalks reached the maximum of ca. 8.5 g d.w./m² by late June. By this time, the length of the stalks reached 15–20 cm holding small white flowers as seen in Plate 1. Late in June, flowers fell leaving decaying stalks and seeds. Seedlings germinated in August could not develop beyond cotyledon-stage in this growing season.

Pteridophyllum has a vertical rhizome of 3–6 cm long, which elongates upward about 3–4 mm in every year.¹²⁾ The biomass of new rhizomes reached ca. 2 g d.w./m² by August. New roots, most of which

were attached to new rhizomes and the rest lamified from one-year-old roots, began to develop in late July and reached 13 g d.w./m² in late October. Buds for the next year were also formed in summer with the dry weight of ca. 2 g/m². At the end of the growing season, well developed primordia of flower, flower stalk and leaf were recognized in the buds.

Fig. 2 shows the seasonal changes of biomass of underground organs. The biomass of roots and rhizomes should be changed seasonally according to the accumulation or consumption of reserve materials. The accuracy of direct determination of dry weight, however, was not enough to detect these changes. The smooth curves in Fig. 2 are the estimated seasonal changes in biomass of roots and rhizomes.

Fig. 2. Biomass of roots and rhizomes in *Pteridophyllum* population. Open circles represent whole roots, and solid circles, whole rhizomes. Smooth curves show the estimated seasonal changes in roots and rhizomes. The estimation procedure is given in the text.

rhizomes. The estimation procedure will be mentioned later.

Seasonal change in carbohydrate content

Figs. 3 and 4 illustrate the general trend of carbohydrate change in various organs of *Pteridophyllum*. Values for starch and hemicellulose in new leaves are not given for the first 2 sampling dates, since the sample size was insufficient for the analysis because of scanty growth.

Sugar. In every organ, sugar was maintained at the high level in winter. At the beginning of the growing season, the content was reduced toward the minimum level in summer. During July and August, sugar was almost constant at the minimum level of about 5% of dry weight in all organs except rhizomes which showed gradual decrease throughout these months. In autumn it increased rapidly to the highest level of winter season. The annual maximum reached at the end of

Fig. 3.

Fig. 3. Seasonal change in the contents of carbohydrates in rhizomes (A) and roots (B) of *Pteridophyllum*. Open circles indicate, top to bottom, "soluble" carbohydrate, hemicellulose and starch. Solid circles, sugar. "Soluble" carbohydrate means the total of sugar, starch and hemicellulose.

Fig. 4.

Fig. 4. Seasonal change in the contents of carbohydrates in one-year-old leaves (A) and new leaves (B) of *Pteridophyllum*. Signs are the same as in Fig. 3.

the growing season was 20% of dry weight in rhizomes and in roots and 17% in leaves.

Starch. Starch was maintained at lower level throughout the growing season in all organs. The level was about 2% of dry weight in rhizomes and 5% in roots and leaves.

Hemicellulose. Seasonal change of hemicellulose content showed a marked contrast to that of sugar. It was generally maintained at lower level in winter. At the beginning of the growing season, hemicellulose level seemed to increase temporally in old leaves and rhizomes. A part of this increase might result from the conversion from the sugar stored. Then it decreased rapidly to the minimum at the end of June. In roots, however, it showed rather inconspicuous changes. In rhizomes and roots, hemicellulose level increased during July reaching the annual maximum in August. In leaves, however, this increase was not remarkable. The summer level of hemicellulose was 26% of dry weight in rhizomes, 24% in roots and 11% in leaves. In autumn, hemicellulose decreased remarkably to reach the annual minimum in winter. The minimum was 9% of dry weight in rhizomes, 12% in roots, and 8% in leaves.

"Soluble" carbohydrate. In the early growing season, "soluble" carbohydrate decreased from the annual maximum level in winter to the annual minimum by late June. The minimum level was 23% of dry weight in rhizomes, 20% in roots and 18% in leaves. "Soluble" carbohydrate in rhizomes and roots increased during July to reach the summer maximum in August. Then it decreased in some extent

during autumn and increased again in early winter. In leaves, however, after diminution in early growing season, "soluble" carbohydrate maintained almost constant low level during summer. In autumn and early winter, it increased again to reach the high level in winter. The winter level was 32%, 34% and 28% of dry weight in rhizomes, roots and leaves, respectively.

It should be noticed here that the amount of "soluble" carbohydrate is by no means equivalent to that of carbohydrate reserves available for plants. As pointed out previously,⁷⁾ we can only estimate the amount of utilized or accumulated reserves from the changes in the amount of "soluble" carbohydrate.

Accumulation and consumption of carbohydrate

In order to examine the amounts of accumulation and consumption of reserve carbohydrate in the whole population, the values on a dry weight basis should be converted into those on a unit ground surface. The amount of "soluble" carbohydrate in leaves in a unit ground surface was estimated from the seasonal change of the content (Fig. 4) and that of leaf biomass (Fig. 1).

As reliable seasonal changes of biomass of rhizomes and roots were not detected directly as already mentioned, seasonal changes in "soluble" carbohydrate in these organs in a unit ground surface were estimated by following procedures. Biomasses of rhizomes and roots at the end of June, when the contents of "soluble" carbohydrate were in minimum, were taken as the basis of the estimation. Provided that the seasonal change in biomass of rhizomes or roots is brought about only by the accumulation or the consumption of carbohydrate reserves, the amount of "soluble" carbohydrate in these organs at any time could be obtained by the following equation:

$$x_t = Ay_t / (1 - y_t)$$

where x_t is the amount of "soluble" carbohydrate (g/m^2), and y_t is the "soluble" carbohydrate content on a dry weight basis (g/g). A is the non- "soluble" carbohydrate fraction of dry matter (g/m^2) at the end of June. For rhizomes, A was 12.3 g/m^2 , as the biomass in late June was 16.0 g/m^2 and "soluble" carbohydrate content was 23.3%, and for roots, it was 34.6 g/m^2 , as the biomass was 43.3 g/m^2 and the content was 20.0%.

Biomass in dry weight of rhizomes or roots at any time was obtained by adding A and x_t .

The seasonal changes of rhizomes and roots thus obtained are illustrated in Fig. 2 by smooth curves. Figs. 5 and 6 illustrate the seasonal changes of "soluble" carbohydrate contained in each organ and in the *Pteridophyllum* population on a unit ground surface, respectively. The "soluble" carbohydrate contents in the old and the new roots, which were not determined separately, were assumed to be equal for convenience.

General trend of the change thus obtained was much the same as those on a dry weight basis. "Soluble" carbohydrate decreased in the early growing season till the end of June. The decrease was about 2.5 g/m^2 in rhizomes, 8 g/m^2 in roots and 5.5 g/m^2 in old leaves. The total decrease in this period amounted to 16 g/m^2 . This period corresponded to the period of rapid development of new leaves and flower stalks. A part of the carbohydrate decreased in old organs must be translocated to the new organs. It should be noticed that about 35% of carbohydrate

Fig. 5.

Fig. 5. Seasonal change in the amount of "soluble" carbohydrate in each organ of *Pteridophyllum* in a unit ground surface. A represents the changes in leaves in which solid circles, new leaves; open circles, one-year-old leaves; and triangles, two-year-old leaves. B represents the changes in roots and rhizomes in which open circles, whole roots; solid circles, old roots; and triangles, whole rhizomes.

Fig. 6.

Fig. 6. Seasonal change in the amount of "soluble" carbohydrate in *Pteridophyllum* population. Solid circles represent the amount in the whole population; and open circles, the amount in the old organs.

decreased in this period was the diminution in leaves. The evergreen leaves of *Pteridophyllum* must play in winter a role of the reserve organs as evergreen coniferous leaves do.⁷⁾

During July, "soluble" carbohydrate was rapidly accumulated in roots and rhizomes. In old leaves, however, such summer re-accumulation was not observed.

In autumn, "soluble" carbohydrate in roots and rhizomes decreased again. This period corresponded to the period of new root and bud formation. Then, carbohydrate in all organs increased to the level of winter. During whole growing season, "soluble" carbohydrate in the old organs decreased to two-thirds of the amount at the initiation. The decrease was, however, completely compensated by the "soluble" carbohydrate accumulated in the new organs (Fig. 6).

Monthly and annual net production

The net production for a given period can be estimated by summing up the growth in dry weight of new organs and the accumulation (+) or consumption (−) of the reserves in old organs. For the *Pteridophyllum* population, the monthly and annual net production were estimated as shown in Table 1. The data on growth of the new organs and those on reserve carbohydrates were given by reading of the smooth curves in Figs. 1 and 6, respectively.

Table 1. Monthly growth in dry weight of the new organs, monthly accumulation (+) or consumption (−) of reserve carbohydrate in the old organs, and monthly and annual net production (Pn) of *Pteridophyllum* population. Values are shown as g dry weight per square meter.

Month	Growth in					Total growth	Reserves in old organs	Pn
	leaves	flower stalks	rhizomes	roots	buds			
May (later half)	3.0	1.5	—	—	—	4.5	−5.0	−0.5
June	21.0	7.0	1.0	—	—	29.0	−11.0	18.0
July	1.0	—	1.0	0.5	—	2.5	+9.0	11.5
August	1.0	—	—	3.5	0.5	5.0	−2.5	2.5
September	—	—	—	6.0	1.0	7.0	−3.5	3.5
October	—	—	—	3.0	0.5	3.5	−1.0	2.5
November	—	—	—	—	—	—	+3.0	3.0
Annual total	26.0	8.5	2.0	13.0	2.0	51.5	−11.0	40.5

The method adopted here in the estimation of net production involves some simplification and is not generally applicable for every perennial plant. One of the simplification is to take no account of the withdrawal of materials from new organs during the senescence of some of them. In *Pteridophyllum*, almost all the new leaves survived and the flower stalks are the main new organ died in the current growing season. Although flower stalks even diminished their dry weight during July (Fig. 1), most of the dry matter lost is considered to be utilized for the formation of flowers and seeds and not to be withdrawn to the old organs. The respiration activity of flower stalks during this period, which will be reported in the other paper of this series, seems to justify this simplification. Nutrient elements such as nitrogen, however, seemed to be withdrawn during senescence as will be reported in the other paper. Another simplification is to assume no growth in old organs occurred. Although the increase in dry weight of old organs cannot be neglected for the perennial plants having lignified organs such as trees or some grasses, this simplification seemed reasonable for *Pteridophyllum* plant.

As seen in Table 1, the annual net production of the population was 40.5 g/m². As the annual net population of mature *Abies* forest in this region was 1.11 kg/m²,¹²⁾ the net production of well developed undergrowth population of *Pteridophyllum* was ca. 3.6% of that of canopy trees.

In the period of early growth till the end of June, new leaves and flower stalks developed fully to reach the dry weight of 32.5 g/m². A part of these new organs should be formed by the conversion of reserve carbohydrate. Provided that the efficiency of conversion from carbohydrate reserves to the plant organs was 0.5,^{2,10,13,14)} the reserves consumed in the old organs, 16 g/m², should make up new plant body of 8 g d.w./m², corresponding to 1/4 of the growth in this period. The highest monthly value of net production was observed in June. In July, as growth of new organs was remarkably reduced and the major part of the photosynthate might be accumulated, the old organs were rapidly refilled by reserves.

From August to October, roots grew rapidly depending partly on the reserve substance in old roots and rhizomes. The growth of new organs in this period was 15.5 g/m², while reserves consumed was 6.0 g/m², corresponding to 3.0 g/m² of the

plant body, or 1/5 of the growth. In November, plants ceased growth and reserves were accumulated in every old organ.

During the initial two and a half months of the growing season up to the end of July, the population produced 72% of the annual net production. Low productivity in late summer and autumn seems very curious since the leaves seemed to be sound during these period. This will be discussed in the other paper in relation to the analysis of matter economy of the plant including photosynthesis and respiration.

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Plate 1. A; *Pteridophyllum racemosum* with white flowers at the end of June.

B; Dense population of *Pteridophyllum racemosum*. The area of the quadrat is a quarter square meter. Wood sorrels seen in the quadrat are *Oxalis Acetosella*.