**Ecological and Physiological Studies on the
Vegetation of Mt. Shimagare VII.
Analysis of Production Processes of Young *Abies* Stand
Based on the Carbohydrate Economy***

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Abstract

The economy of carbohydrates was analysed in relation to the growth and the dry matter production of *Abies* stand about 15 years old in the subalpine zone of Mt. Shimagare, Nagano Prefecture, central Japan. Seasonal changes of sugar, starch and hemicellulose contents in needles, branches, stems and roots were pursued. Combining these results with those of seasonal growth and respiratory activity of each organ, balance sheets of matter economy of the community were constructed.

Three phases were recognized in the annual cycle of matter economy of the community. In the 1st phase, May and the early half of June, the plants did not show any growth, and about a half of the matter produced by photosynthesis was accumulated in the old organs and the rest was consumed by respiration. In the 2nd phase, from mid-June to late August, new organs grew rapidly depending partly on the conversion of carbohydrates reserved in the old organs. In the 3rd phase, from September to late November, most of the photosynthetic products were reserved for the use in the next year.

From these analyses, the role of the evergreen leaves in the habitat of severe winter was elucidated as follows; a) they play a role as the reserve organ of large capacity in winter, and b) they recover rapidly their photosynthetic activity in early growing season to accumulate reserves, in addition to those of the winter season, before buds break from dormancy. These reserves guarantee the subsequent rapid growth of new organs in early summer.

Recently, an emphasis has been laid upon the role of reserve materials in the study on the growth cycle of plants¹⁻⁵⁾. From the viewpoint of matter economy, the annual cycle of growth of plants can generally be divided into three phases⁶⁾. The first is the *phase of initial growth* in which the active plant body grows mainly at the expense of the reserve materials produced in the preceding year with the definite ratio of conversion^{3,7-9)}. The second is the *phase of expanding growth* in which the plants grow almost exponentially through the conversion of the photosynthetic products to the plant body. The usual procedures of growth analysis based upon the net assimilation rate, the leaf area ratio, etc., are applicable to this phase of growth. The third is the *phase of accumulation and withdrawal* of assimilates, in which the

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foliage system almost stops development. The major part of the photosynthetic products is accumulated in the reserve organs to provide for the growth in the following year^{4,5)}, and the considerable amount of materials is withdrawn from the shed organs at the end of the growing season¹⁰⁻¹²⁾.

The duration and the ecological significance of each phase are varied corresponding to the differences of the life form of plants and of their habitats. In the plants having small amount of reserve material, in which most of annual plants are included, the first phase is very short and the second one occupies the greater part of the growing season. Then it is reasonable that the second phase has been the focus of interest in the studies on the production processes of these plants^{7,13-15)}. In the perennial plants with large amount of reserve materials, the latter play a very important role in the rapid growth at the early growing season. In these plants so far studied, the reserve materials are rapidly refilled after being exhausted in high utilization for growth in the first phase, so the second phase is hardly recognized separately from the other two^{2-5,16,17)}. For the elucidation of the production processes of these plants, an analysis of the reserve material economy in the growth cycle seems to be indispensable.

Although there were many works concerning the matter economy of woody plants, many of those were rather fragmental or qualitative. Among the works, the intensive study of Gäumann¹⁷⁾ on the 105-year-old *Fagus silvatica* should be highly noticed. Apparently there have been no comparable studies on the growth and matter economy of evergreen trees.

The present paper deals with the economy of carbohydrate in relation to the growth and the dry matter production of young *Abies Veitchii* community grown in the upper subalpine region (2,340 m in altitude) of Mt. Shimagare, Nagano Prefecture, central Japan. This paper forms a sequel to the preceding paper¹⁸⁾ in which the biomass, annual growth and dry matter production of this community were reported. The role and the significance of evergreen leaves in the matter economy will also be discussed. The climate of the region was summarized in a previous report¹⁹⁾ of this series (monthly min. temp. -14.1° in Feb.; max. temp. 13.7° in Aug.; mean ann. temp. -0.3°).

Methods

The biomasses in dry weight of each organ and the whole plant in a unit ground surface of the young *Abies Veitchii* community were determined by samplings at intervals of one or two months during the growing season of 1960¹⁸⁾. Since a part of the plant material harvested in each sampling occasion was utilized for carbohydrate analyses, the samplings were performed restrictedly about the noon on fine days to avoid the possible effects of the daily fluctuations of carbohydrates to the annual cycle. Weighed fresh materials of needles, branches, stems and roots of *Abies Veitchii* trees were cut into small pieces and boiled with 80% ethanol for a few minutes immediately after sampling. In the laboratory, the preserved plant materials were dried in a vacuum and ground to fine powder. Sugars were extracted three times from the powder with boiling 80% ethanol under a reflux condenser for a total of 1.5 hours. The ethanol was evaporated under reduced pressure at 50° and the warm water soluble fraction was used for the determination of total sugar after clearing with lead acetate and inversion with HCl. Glucose was adopted for the standard sugar.

Residual plant powder was extracted with boiling water for 2 hours. The reducing power of the extract was determined after clearing and inversion. The results were expressed as glucose $\times 0.9$. This fraction is tentatively called starch.

After extracting starch, the residue was further extracted with 2% HCl under reflux condenser in a boiling waterbath for 5 hours. The reducing power of the extracts was determined after neutralization with NaOH. The results were expressed as glucose $\times 0.9$. This fraction is designated as hemicellulose.

Reducing power of the hydolyzates was determined after Schaffer and Somogyi²⁰. Chemical composition of the extracted carbohydrates was examined by paper chromatography. Pentosans in the hemicellulose fraction were determined gravimetrically by the furfural-phloroglucid method²¹. Crude fat was determined by extracting the dried materials with ethyl ether for 24 hours with Soxhlet apparatus.

Seasonal change in carbohydrate content

Sugar. Sugar fraction consisted mainly of sucrose and trace amount of glucose and fructose. In every old organ, sugar was maintained at high level in winter (Fig. 1). At the beginning of the growing season, the content was reduced rapidly toward the minimum level in June. It seemed to have a small peak in July followed by the second minimum in late August. Then it increased to the highest level of winter season. The annual minimum was observed for leaves in June and for branches in August. The annual maximum was observed in winter season and it reached about 20-25% of dry weight for leaves, 5-10% for branches, stems and roots, while the annual minimum was about 8% for leaves, 1-2% for branches, 1% for stems and roots. In general, sugar was contained in larger amount in the younger organs than in the older ones. The high content of sugar in winter was observed in various plants and often discussed in relation to the cold hardiness²²⁻²⁴.

Starch. Monosaccharides obtained as the starch fraction were glucose accompanied with small amount of pentoses. Seasonal change of starch content showed a marked contrast to that of sugar (Fig. 2). Starch was maintained at lower level in winter and increased at the beginning of the growing season when the sugar decreased. The highest starch content was attained in June: 6-7% for leaves, 5% for branches and 2-3% for stems and roots. Thereafter the content decreased till the end of August and was maintained at a minimum level of about 1% for all organs throughout the remaining seasons, except for roots which had the second peak in autumn as observed by several authors²⁵.

Hemicellulose. Hemicellulose showed much the same trend of change as starch (Fig. 3). The percentage for dry weight of hemicellulose was at the maximum 22-24% in leaves, 20-22% in branches, and 18-20% in stems and roots, and was at the minimum 5-6% in leaves, 14% in stems, and 11% in branches and roots. In the woody organs the minimum was remarkably high in comparison with the minima of sugar and starch.

The hemicellulose fraction might contain some amount of carbohydrates which were non-available as reserve materials¹⁷. To estimate the amount, the author determined the amount of pentosan in the hemicellulose fraction twice in the growing season, late in May and early in December. In every organ, the percentage for dry weight of pentosan was much the same in these determinations (Fig. 3), suggesting no seasonal fluctuation of the said substance. This means that the pentosan can not be regarded as the reserve material available for growth. The higher winter hemicellulose content in stems and roots than in leaves was brought about by the

Fig. 1. Seasonal change in sugar in percent of dry weight of each organ of *Abies Veitchii*. A and B represent the values in needles and branches, respectively, in which crosses show those in current-year organs, open circles, one-year-old organs and solid circles, two or more-year-old organs. Open circles in C represent the values of stems and solid circles, roots.

Fig. 2. Seasonal change in starch content in each organ of *Abies Veitchii*. Signs are the same as in Fig. 1.

Fig. 3. Seasonal change in hemicellulose content in each organ of *Abeis Veitchii*. Signs free of parentheses are the same as in Fig. 1. Open and solid circles in parentheses show the amount of pentosan contained in the corresponding hemicellulose fractions in percent of dry weight. The areas marked with vertical lines mean the pentosan fraction in hemicellulose which is assumed to be independent of the seasonal fluctuation.

high constant pentosan content in the formers.

"Soluble" carbohydrate. In the present study, the total amount of sugar, starch and hemicellulose is called tentatively "soluble" carbohydrate. The seasonal change of it in one-year-old needle is illustrated in Fig. 4, together with the changes of sugar, starch and hemicellulose. One can construct the same kind of figures for the other organs by combining the curves in Figs. 1, 2 and 3.

As shown in Fig. 4, the content of sugar decreased rapidly at the beginning of the growing season while those of starch and hemicellulose increased. A part of the increase in starch and hemicellulose may result from the conversion from sugar. The increase in the formers, however, highly exceeded the decrease in the latter, resulting in an increase of "soluble" carbohydrate. The annual maximum level of "soluble" carbohydrate was attained in mid-June when starch and hemicellulose were at their maxima. Then, "soluble" carbohydrate decreased with the decrease of starch and hemicellulose, and reached an annual minimum in late August. This

rapid decrease seems to indicate the high utilization of reserve materials in the development of the new organs. Starch and hemicellulose should be converted to sugar before they were translocated to the growing sprouts, because temporal

Fig. 4. Seasonal change in the contents of carbohydrates in one-year-old needles of *Abies Veitchii*. Open circles indicate, top to bottom, "soluble" carbohydrate, hemicellulose and starch. Solid circles, sugar. The "soluble" carbohydrate means the total of sugar, starch and hemicellulose.

Fig. 5. Seasonal change in "soluble" carbohydrate content in each organ of *Abies Veitchii*. A and B represent the values in needles and branches, respectively, in which crosses show those in current-year organs, open circles, one-year-old organs and solid circles, two or more-year-old organs. In C, open circles represent the values of stems and solid circles, roots.

increase of sugar content was observed in every old organ in July (cf. Fig. 1). The period from September to November was characterized by an accumulation of sugar, which brought about an increase of "soluble" carbohydrate, though the contents of starch and hemicellulose remained at lower levels.

Fig. 5 illustrates the seasonal changes of "soluble" carbohydrate percentage for dry weight of various organs. The ranges of annual changes were 37 or 40%-18% in leaves, 27%-14% in branches, 23%-17% in stems, 22%-14% in roots. Except for stems in which slight increase in the early growing season was observed, the winter levels lay near the average of the minimum and the maximum.

As already pointed out, the amount of "soluble" carbohydrate does not correspond to that of available reserve carbohydrate because it contains substances, e. g. pentosan, unavailable for the plant growth. We can not exactly account, for instance, how much reserve carbohydrate remains in late August when "soluble" carbohydrate was at its minimum. We can, however, estimate the amount of accumulation or consumption of reserve carbohydrate from the change of the amount of "soluble" carbohydrate.

Seasonal change in crude fat content

The rapid increase in "soluble" carbohydrate in May might be caused either by the conversion from reserve materials other than carbohydrate, or by an accumulation of photosynthetic products in the period. The seasonal change of crude fat was studied in each organ, since the fat seemed to be a material reserved much in winter and converted to carbohydrate in the early growing season¹⁷⁾.

As seen in Fig. 6, the range of the fluctuation of the crude fat content was far smaller than that of "soluble" carbohydrate and no high value was observed in winter. Moreover, fat increased during the early growing season to reach the annual maximum by late May or early June when the "soluble" carbohydrate was rapidly increasing. These facts denied the possibility of the conversion of fat to carbohydrate in the early growing season. The seasonal fluctuation of fat, however, suggested that there existed in general some mutual conversion between both substances, though the amount of conversion seems to be below the accuracy of the present study of carbohydrate economy.

Therefore, it should be concluded simply that the rapid increase of carbohydrate

Fig. 6. Seasonal change of crude fat content in each organ of *Abies Veitchii*. Signs are the same as in Fig. 5.

in the early growing season resulted directly from the accumulation of photosynthetic products in this period. This conclusion seems to be supported by the fact that the increase was most remarkable in leaves as seen in Fig. 5.

Carbohydrate economy in relation to the growth of the community

1. Accumulation and consumption of carbohydrate.

In order to examine the amount of accumulation and consumption of reserve carbohydrate by the whole community, the values on a dry weight basis should be converted into those on a unit ground surface basis. The biomass of each organ at the beginning and the end of the growing season was given in a previous paper¹⁸⁾, together with the seasonal growth curves of the leaves and branches of current year. The sprout began in late June and the growth in dry weight of the new leaves was completed by late August. The new branches attained about 60% of the annual increase in dry weight by late August and reached their maximum by late October. It was assumed that the trend of dry weight increase by the radial growth of old woody organs was the same as the increase of new branches. Amount of the old leaves shed mainly in the growing season was also given previously¹⁸⁾. As the seasonal fluctuation of the leaf fall was not estimated in the present stand, it was assumed tentatively that the shedding of the old leaves took place evenly throughout the growing season. Based on these facts and assumptions, seasonal change in dry weight of each organ in a unit land area was estimated.

The dry weight of each organ should be varied in parallel with the fluctuation of the reserve carbohydrate content. In the following calculation, however, this fluctuation in dry weight of each organ was not taken into account. This resulted doubtlessly in some underestimation in the seasonal change of reserve carbohydrate in the community.

Figs. 7 and 8 illustrate the seasonal change of "soluble" carbohydrate contained in each organ and the whole *Abies* community on a unit ground surface, respectively. General trend of the change was the same as observed in the contents on a dry weight basis. The fluctuation of reserve carbohydrate was most striking in leaves (Fig. 7). The increase in the early growing season was about 160 g/m² for the whole stand (Fig. 8), where 90 g was accumulated in leaves. The decrease of reserve carbohydrate in the old organs during July and August reached about 320 g/m², where 170 g was also attributed to the decrease in leaves. In autumn, reserve carbohydrate in the old organs increased again about 170 g/m² and recovered to much the same level as at the beginning of the growing season. In addition to this, the accumulation of "soluble" carbohydrate in the new organs brought the net annual increase of about 120 g/m² for the whole community.

2. Analysis of the production processes based on the matter economy.

As clearly seen in Fig. 8, the annual carbohydrate economy of this *Abies* community was constructed from three phases, indicated respectively by accumulation, consumption and re-accumulation of carbohydrate. The economy of matter in each phase was analysed quantitatively. The loss of matter by respiration in each organ was calculated from Fig. 6 of the preceding paper¹⁸⁾. The values of photosynthesis were given by the sum and/or the remainder of the other items.

First phase. This phase corresponded to the period of May and the early half of June. In this period the *Abies* trees did not change their appearance as if it was

Fig. 7. Seasonal change in the amount of "soluble" carbohydrate in each organ of *Abies Veitchii* in a unit ground surface. Signs are the same as in Fig. 5.

Fig. 8. Seasonal change in the amount of "soluble" carbohydrate in *Abies Veitchii* community. Solid circles represent the amount in the whole community, and open circle, in the old organs of the community.

still in the resting stage in winter, as they sprouted in late June¹⁸⁾. This period, however, was very important for the subsequent rapid growth of new shoots. Half of the reserve carbohydrate consumed in the second phase was produced in this phase by the photosynthesis of the wintered leaves. Accordingly, this phase must be peculiar to the evergreen plants. As reported previously¹⁸⁾, the respiratory activity of the old organs was increased in late May and June. This phenomenon should reflect the active physiological state of the plant. The shoulder of respiration curve in the early growing season (cf. Figs. 5 and 6 of the preceding paper¹⁸⁾) seems to correspond to the high content of reserve carbohydrate.

The balance sheet of matter in this phase (1½ months) was as follows.

Supplied by	photosynthesis	342 g d. w./m ²
Used for	respiration in old organs	182
	accumulation of reserves in	
	woody organs	70
	leaves	90
		160
		342

Second phase. This phase was the period from the middle of June to the end of August. The rapid elongation and increase in dry weight of new organs was observed after the start of growth in late June, partly depending on the conversion of reserve carbohydrate. Therefore, this phase should correspond to the *phase of initial growth* mentioned before, though the photosynthesis was carried out vigorously. The new leaves matured by the end of this phase, and the dry weight increase in the woody organs reached 60% of the annual increase.

The balance sheet of matter in this phase (2½ months) was as follows.

Supplied by	photosynthesis	930	
	break down of reserves in		
	woody organs	150	
	leaves	170	
		320	1,250 g d. w./m ²
Used for	respiration in		
	old organs	477	
	new organs	173	
		650	
	growth in		
	old organs		
	woody organs	139	
	leaves	28	
		167	
	new organs		
	woody organs	67	
	leaves	366	
		433	
		600	1,250

More than one fourth of the total matter supplied in this phase was reserved carbohydrate, about a half of which was produced in the first phase and the rest was stored in the preceding year. The efficiency of the conversion from the reserved carbohydrate to the active plant organs has been estimated at 0.5-0.6 on a dry weight basis^{3,7-9)}. Then, the reserves consumed from the old organs, 320 g/m², should make up 160-190 g/m² of new plant body, corresponding to 1/4-1/3 of the growth in this phase.

Third phase. This phase was the period from September through the end of November when the reserve carbohydrate was accumulated again to the level in winter, and should correspond to the *phase of accumulation and withdrawal*.

The balance sheet of matter in the third phase (3 months) was as follows.

Offered by photosynthesis					721 g d. w./m ²	
Used for	{	respiration in	{ old organs	294	414	721
			{ new organs	120		
	{	growth in	{ old organs—woody organs	93	137	
			{ new organs—woody organs	44		
	{	accumulation of reserves in old organs	{ woody organs	110	170	
			{ leaves	60		

In Table 1, the items of the balance sheet of matter in each phase are given in daily rates. Daily photosynthesis (gross production) in the second phase, 12.1 g d. w./m², was the highest among three phases. This value fairly agreed with the value calculated from the photosynthetic activity of needles according to Saeki's equation²⁶⁾. In this calculation the light-photosynthesis curve of needles of young *Abies Veitchii* illustrated by Kuroiwa²⁷⁾, which was reexamined and confirmed by the present author, was adopted.

In the previous paper¹⁸⁾, the ratio of the annual respiration to the annual photosynthesis was estimated at 0.63. The ratio, however, varied considerably in each phase: 0.70 in the second phase, while about 0.55 in the first and the third. The high ratio in the second phase was explained with a supply of raw matter for respiration from the reserve carbohydrate, in addition to the photosynthetic products formed in this period. The ratio of respiration to the matter supplied was 0.53 in the second phase, too.

Daily net production was maintained almost constant throughout the three phases. It should be noticed that the growth of the old and the new organs was more than twice as large as the net production in the second phase.

Table 1. Daily rates of gross and net production, respiration, growth, and accumulation or consumption of reserve carbohydrate in each growth phase of the *Abies* community (g/m² · day). The ratios of respiration to gross production are also shown.

	gross production (Pg)	respiration (R)	net production (Pn)	growth in leaves	growth in woody organs	reserve carbo- hydrate	R/Pg
first phase	7.5	4.0	3.5	—	—	3.5	0.53
second phase	12.1	8.5	3.6	5.1	2.7	-4.2	0.70
third phase	7.9	4.5	3.3	—	1.5	1.9	0.57

The role of evergreen leaves in the matter economy

For the evergreen broad-leaved trees and conifers in warm temperate region, considerable photosynthetic activities in winter have been reported²⁸⁻³¹⁾. Measurements on the boreal conifers showed, however, that the photosynthetic apparatus lost most of its activity during winter months³²⁻³⁵⁾. No photosynthetic activities of conifers were often measured below 0°, or at least, below -5°³⁶⁾. In severe winter

the evergreen leaves can not contribute appreciably to photosynthetic gain.

Monsi³⁷⁾ pointed out an advantageous role of the perennial leaves in the matter economy: for the maintenance of the constant leaf biomass, the annual renewal of the perennial-leaved plant can be made by using small part of matter produced, and consequently a large share can be distributed for the biomass increment.

In the present study the important role of evergreen leaves was elucidated. The leaves played in winter a role as the reserve organ of large capacity which is situated nearest the new shoots. Moreover, the reserves for new shoots were increased by the photosynthesis of wintered leaves in the early growing season.

The conclusion reached here may be supported by the experimental evidence obtained by several workers^{28-30,34-43)}.

With *Picea excelsa* grown at the forest limit of Austrian Alps, Pisek and Winkler³⁴⁾ showed the rapid recovery of the photosynthetic activity of the old leaves before the new leaves begin to expand. Several measurements on the seasonal change of the photosynthetic activity of the coniferous^{35,36)} and evergreen broad-leaved trees²⁸⁻³⁰⁾, gave the same results. Guttenberg^{38,39)} and Prising⁴⁰⁾ showed that the rapid recovery of the photosynthetic activity in the early spring was followed by the rapid accumulation of starch in the old leaves of Mediterranean sclerophyllous trees.

Gäumann⁴¹⁾ found that hexosan, in which both starch and hemicellulose were included, in the sapwood of *Picea excelsa* and *Abies pectinata* increased in March to reach the maximum by April, followed by the rapid decrease during May and June to reach the annual minimum. The maximum occurred at the beginning of the growth of new shoot. He supposed that the increase of hexosan in spring should result from the recovery of photosynthetic activity of the wintered leaves.

According to Clark⁴²⁾, the new needles of *Abies balsamea* were in negative CO₂ balance in great quantity for about a month of early growth, and they attained the same level of photosynthetic activity as that of old needles by late summer after the shoots elongated completely. Several workers showed also the negative CO₂ balance of new shoots in early spring^{34,35)}. Thus the early growth of shoot must greatly depend on the reserves in old organs. Rutter⁴³⁾ found that in young *Pinus silvestris*, during the early period of shoot elongation, the increase in dry weight of new shoots was compensated by the remarkable decrease in weight of old needles. This suggests also the vigorous translocation of materials from the old needles to the new shoots.

There have been, however, few works concerning the quantitative role of the evergreen leaves in the growth and the matter economy of the whole plants throughout the growing season. As shown in the present study, the old leaves supplied 60% of the reserve materials translocated from the old organs to the developing shoots. It is generally believed that in the evergreen trees the reserve materials consumed in the early growing season is much smaller and the role of reserve materials in the annual growth cycle is less important than in the deciduous ones²⁵⁾. This conclusion was drawn from the observation on the seasonal change of reserve materials only in the woody organs of evergreen and deciduous trees, and failed to notice the evergreen leaves as the reserve organs of large capacity, as well as the additional accumulation of reserves in leaves by photosynthesis in the early growing season before the new shoots begin to grow.

For a 105-year-old *Fagus sylvatica* tree, Gäumann¹⁷⁾ showed that 26 kg of the reserve carbohydrate was consumed in the *phase of initial growth* while annual growth of the tree was 87 kg in dry weight. The ratio of the former to the latter

was 30%, corresponding with 43% in our *Abies* community. In herbaceous vegetations the reserve materials consumed in the *phase of initial growth* were, for instance, 450 g/m² in *Aconitum japonicum* community³⁾, 310 g/m² in *Miscanthus sacchariflorus* community⁵⁾, and 113 g/m² in *M. sinensis* community⁴⁾. The corresponding value of our young *Abies* community, 320 g/m², fell in the range of these estimations.

These considerations show clearly the important role of the reserve materials in the annual growth cycle of the evergreen coniferous trees, and also show the particular role of evergreen leaves in the matter economy.

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摘 要

木村 允*: 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 VII.

炭水化物経済にもとづく *Abies* 幼樹林の生産過程の解析

さきに現存量・生産量について報告した¹⁸⁾約 15 年生の *Abies* 幼樹林において、生長に伴う炭水化物経済のありさまを明らかにした。

炭水化物は、生材料から 80% 熱エタノールで糖を、残さから熱水ででんぷんを、さらに残さから 2% HCl でヘミセルロースを抽出し定量した。糖の含有量は各器官とも生育期間の開始とともに低下し、9 月以降ふたたび上昇して冬期は高いレベルを保つ。でんぷんおよびヘミセルロースは生育期間の初期に増加し、新芽の展開に際し減少し、以後秋冬を通じて低いレベルを保つ。以上を合計した“可溶性”炭水化物の季節変化は増加、減少、増加の 3 相をもつ。この 3 相について、光合成、呼吸、貯蔵炭水化物の蓄積と消費の諸項からなる物質収支表がつけられた。

第 1 相は 5 月および 6 月前半の期間で、新芽の展開は開始されず、光合成産物のほぼ半分が呼吸により消費され、他の半分が植物体中に蓄積される。この炭水化物蓄積は越冬葉の光合成能力の回復によりもたらされる。第 2 相は 6 月後半より 8 月末までの期間で、新芽の展開と貯蔵炭水化物の急激な消費がみられる。この消費量は第 1 相における蓄積量のほぼ 2 倍に達し、この期間中の新成植物体乾重量の 1/3-1/4 は貯蔵炭水化物よりの転換によると推察された。消費の 60% は越冬した旧葉でおこった。第 3 相は 9-11 月の期間で、貯蔵炭水化物の再蓄積が器官の生長を上まわる。このような解析を通じて、前報で報告したこの群落の年間生長量、年間純生産量等の実現過程が明らかにされた。

また、以上の結果にもとずき、寒冷な冬期をもつ環境下での常緑葉の生態学的意義が論議された。すなわち、このような環境下の常緑葉は、1) 冬期には新芽に最も近い位置にある容量の大きい貯蔵器官としての役割をはたし、2) 生育期間の初期に光合成能力を急速に回復し、貯蔵物質を大きく増加させる。この貯蔵物質が初夏の新芽の急激な生長を可能にさせると考えられた。(*東京都立大学理学部生物学教室)