

A Tentative Study of Stratification Diagrams

by

Koji ITO

Graduate School of Environmental Science, Hokkaido University,
Sapporo, Japan

Introduction

Synusiae of a forest community may be visualized by means of a stratification diagram. Yoshioka (1960 & 1966) visualized influences of herbivorous animals and human impacts upon forest vegetation in Kinka Isle, Miyagi Prefecture, N. Honshu. He recognized two significant agents in the forest vegetation; one was deer browsing and the other was human impacts such as grazing, thinning of the forest etc. Deer browsing caused disappearance or diminishing of tree-, subtree-, shrub- and herb synusia respectively, and human impacts cumulative over a long time brought about fluctuation of cover degree of the forest and re-distribution of patterns of the stratification diagrams in the forest vegetation.

The author has given his special attention to the classification of synusia and regarded a forest as a unified entity which is an integration of separate synusiae. In a long-lived forest, the vertical synusiae match the passage of time, and the stratification diagram shown at a given time discloses a fragment of information on the process of establishment and development of the forest as well as the forest components.

In the present paper, the author makes an attempt to analyse, from the viewpoint of the stratification diagram, the Ishikari Virgin Forest, which was damaged and wiped out by the Fifteenth Typhoon in 1954 known as "Toyamaru Typhoon". The Ishikari Virgin Forest was undoubtedly a kind of "primaeval" forest in nature and apparently had never suffered from human impacts prior to 1954. In 1952 and 1953 this primaeval forest was investigated and the actual phytosociological records were published in 1955 by Tatewaki et al. (1955). The author applies these sociological records to the present stratification diagram analysis and makes an attempt to clarify the stratification structure of an undisturbed long-lived forest vegetation which is believed to be typical of the boreal coniferous forest in Japan.

I. The stratification diagram (or the S-diagram)

1. Synusiae

The S-diagram treated is composed of the following 4 synusiae (i) herb synusia which is less than 2 m in height; (ii) shrub synusia or the low layer which is from 2 to 8 m in height; (iii) subtree synusia or the middle layer which is

from 8 to 15 m in height; and (iv) tree synusia or the upper layer which is over 15m in height. In the present study, the herb synusia is generally omitted from the considerations.

2. The stratification diagram

The ordinate indicates the height of synusia and the maximum height of trees measured in a sociation in meters, and the abscissa shows the number of individual trees belonging to each synusia. The S-diagram is not a tree-height distribution diagram but a synusia distribution diagram.

3. Types of S-diagram (or Types)

A type of S-diagram is a category classified by numerical comparison among three synusiae, with the exception of the herb synusia, in a sociation. In the present study, seven types of S-diagram are as follows: (i) L-type in which the S-diagram has a configuration of capital "L", viz. shrub synusia >subtree synusia > tree synusia in the number of individual trees; (ii) rL-type in which the form of S-diagram appears as a reversed "L", viz. shrub synusia <subtree synusia < tree synusia; (iii) C-type in which the form of S-diagram has the appearance of capital "C", viz. shrub synusia >subtree synusia < tree synusia; (iv) D-type in which the form of S-diagram is similar to capital "D" in outline, viz. shrub synusia <subtree synusia > tree synusia; (v) I-type in which the form of S-diagram resembles capital "I", viz. shrub synusia = subtree synusia = tree synusia or shrub synusia \doteq subtree synusia \doteq tree synusia; (vi) i-type which is a variety of I-type, lacking tree synusia; and (vii) ri-type which lacks shrub synusia, or shrub synusia and subtree synusia.

4. Element types of S-diagram (or Element types)

A type of S-diagram of a sociation is not always identical with that of each component tree species, because the former is the sum of the latter. In the present study, the latter type of S-diagram is referred to as an element type of S-diagram and is distinguished from the former by adding an asterisk to the corresponding former type, that is, L: L*, rL: rL*, C: C* etc.

II. Outline of the Ishikari Virgin Forest

According to Matsukawa (1955), the Ishikari Virgin Forest covered an extensive area, approximately 44,000 ha in the headwaters of the Ishikari River, which is located at 142°55' E, 43°47' N in the central region of Hokkaido. The general character of this primaeval virgin forest was summarized by Tatewaki and Takahashi (1955); "The vertical distribution of the forests in the headwaters of the Ishikari River is very prominent. According to the altitude, the forest zone is shown by the dwarf siberian pine (*Pinus pumila*)-, the Erman's birch (*Betula ermanii*)-, the higher mixed (*Picea jezoensis*-*Abies sachalinensis*)-forests. The dwarf siberian pine forest occupies the highest altitude (over 1600 m. approximately), and the needle-leaved forest is developed in a lower altitude. Between these two types of forests there exists the Erman's birch forest which is often accompanied with the higher mixed forest. The zone of the needle-leaved forest was well developed and had mostly kept the primaeval aspect up to 1954 when the forest was almost entirely destroyed by typhoon. *Picea jezoensis* was dominant and *Abies sachalinensis* was usually associated with the former. *Picea*

glehnii occurred often on the steep slopes or rocky places. The mixed broad-leaved trees such as *Acer mono* and *Quercus crispula* were rarely found in the western part of Daigakudaira. *Betula maximowicziana*, *Magnolia obovata*, *Acanthopanax sciadophylloides* and *Kalopanax pictus*, which grow very commonly in other mountain regions of Hokkaido, could hardly be found in the area under consideration. Along the Ishikari River in this needle-leaved forest, *Populus maximowiczii* and *Toisusu urbaniana* are codominant, whereas the willow forest consisting of *Salix sachalinensis*, *S. pet-susu* and *S. lackschewitziana* forms sometimes a narrow belt along the stream. *Alnus hirsuta* forms a pure forest in a rather small area. Sometimes such a mixed forest as *Populus maximowiczii*-*Picea jezoensis* forest is found on the river bed. The phytosociological and floristic composition of this needle-leaved forest zone seems to be very similar to the taiga type. The only distinctive characteristic of the physiognomy of the forest is the domination of *Sasa* on the forest floor."

The S-diagram analyses were attempted on 25 sociations belonging to the boreal coniferous forest of Hokkaido. The forest was composed mainly of *Picea jezoensis*, *P. glehnii* and *Abies sachalinensis* which formed their own pure stands, or mixtures of two or three species. The forest floors found were Moss type, Sedge type, Fern type, *Rhododendron* type and *Sasa* type according to Tatewaki and Takahashi (1955).

III. S-diagram Analysis of the boreal coniferous forest sociations of the Ishikari virgin forest

1. The frequency distribution of S-diagrams

The frequency distribution of S-diagrams of 25 sociations is shown in Table 1 and Figure 1. As seen in Table 1, C-type shows the highest frequency in 25 sociations and is followed by L-, rL-, D-, I-type and others in the descending order. It is interesting that the frequency distribution of the present sociations shows a similar tendency to that of Mt. Moiwa forest stands which have been preserved as a National Monument and kept free of human disturbance under

Table 1. The frequency distribution of S-diagrams based on 25 sociations of the Ishikari virgin forest (Tatewaki et al. 1955) and of 24 forest stands of Mt. Moiwa, Sapporo (Ito et al. 1969)

Types of S-diagram	Frequency of occurrence (%)	
	Ishikari	Mt. Moiwa
L	5 (20%)	7 (29.2%)
rL	5 (20%)	3 (12.5%)
C	10 (40%)	11 (45.8%)
D	2 (8%)	1 (4.2%)
I	1 (4%)	1 (4.2%)
i	0 (0%)	1 (4.2%)
L÷I	1 (4%)	0 (0.0%)
rL=I	1 (4%)	0 (0.0%)
Total	25(100%)	24(100.1%)

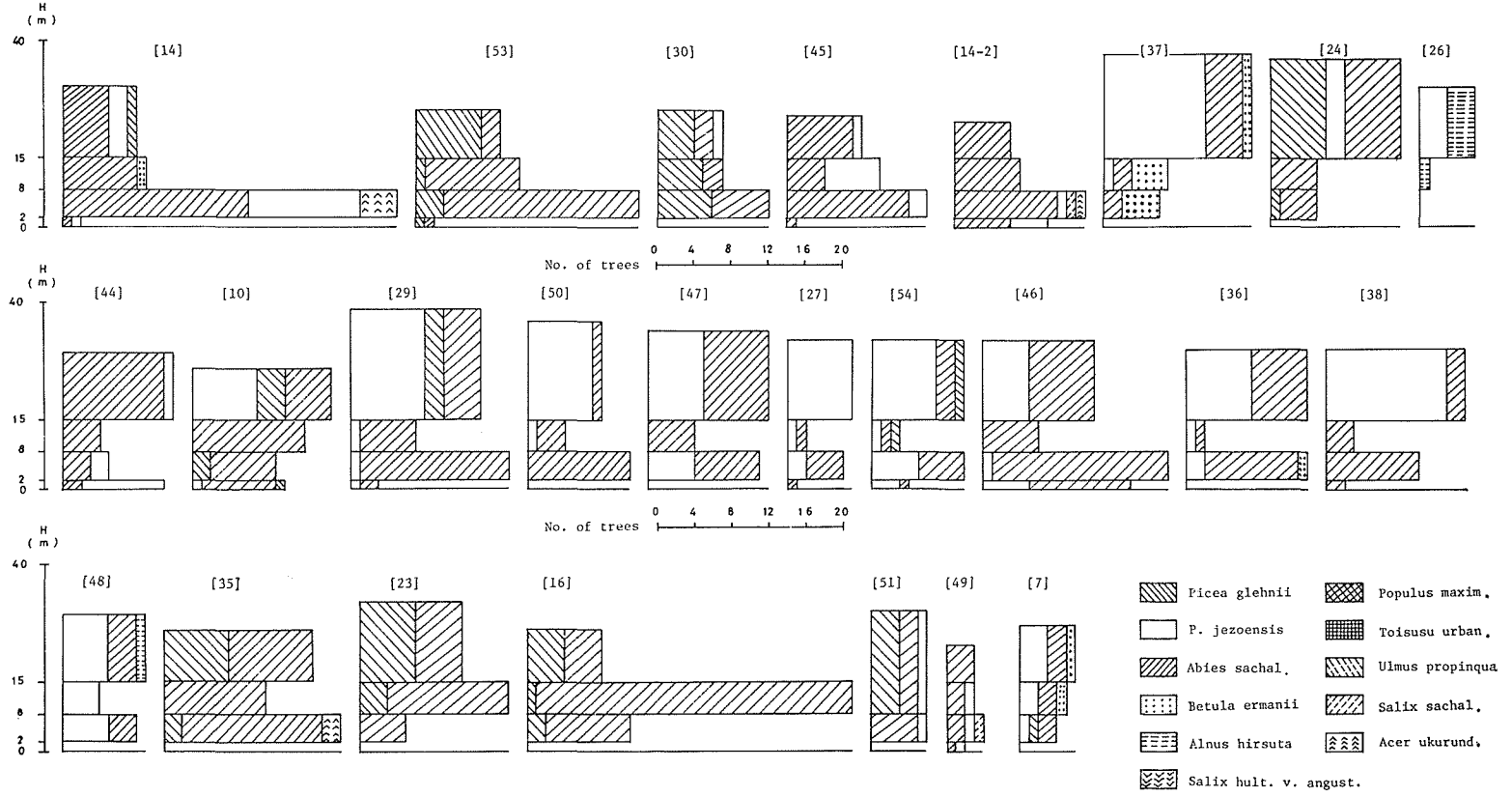


Fig. 1. Stratification diagrams of the Ishikari virgin forest sociations L-type: 14, 53, 30, 45 and 14-2; rL-type: 37, 24, 26, 44 and 10; C-type: 29, 50, 47, 27, 54, 46, 36, 38, 48 and 35; D-type: 23 and 16; I-type: 51, L≠I-type: 49, and rL≠I-type: 7. Number shows the belt-transsect (or Sociation) number. (see the explanation in the text)

Table 2. The occurrences of combination sets of the highest synusia tree species with the lower synusiae tree species based upon 25 sociations of the Ishikari virgin forest (Tatewaki et al. 1955)

Combination sets	Types of S-diagram							Total
	L	rL	C	D	I	L \div I	rL \div I	
<i>P</i> · <i>O</i>	0	1	0	0	0	0	0	1
<i>P</i> · <i>A</i>	0	1	4	0	0	0	0	5
<i>P</i> · <i>P</i> · <i>A</i>	0	0	1	0	0	0	0	1
<i>P</i> · <i>A</i> · <i>P</i> · <i>A</i>	0	0	2	0	0	0	1	3
<i>P</i> · <i>A</i> · <i>A</i>	0	0	3	0	0	0	0	3
<i>A</i> · <i>A</i>	2	0	0	0	0	1	0	3
<i>A</i> · <i>A</i> · <i>P</i>	1	1	0	0	0	0	0	2
<i>Pg</i> · <i>A</i>	0	0	0	0	1	0	0	1
<i>Pg</i> · <i>A</i> · <i>A</i>	1	2	0	2	0	0	0	5
<i>Pg</i> · <i>A</i> · <i>Pg</i> · <i>A</i>	1	0	0	0	0	0	0	1
Total	5	5	10	2	1	1	1	25

the control of the Prefectural Government since the 1870s.

2. Combinations of individual species in the highest synusia with those in the lower synusiae

The combination mentioned above is shown in Table 2. Here, the lower synusiae include subtree- and shrub-synusia. A combination set is shown as follows: if two letters are combined with a hyphen, the first letter means the dominant tree species and the second indicates the dominant in the lower synusiae, e. g. *P*·*A*; if two letters are combined with a dot, these indicate codominance, e. g. *P*·*A* means that *P* is codominant with *A* in a given synusia. For convenience sake, three coniferous species are abbreviated; *P* is *Picea jezoensis*, *Pg* is *Picea glehnii* and *A* is *Abies sachalinensis*, and *O* is none of the dominant.

In C-type, the combination set of *P*·*A* predominates while in L-type the combination sets of *A*·*A* and *Pg*·*A* are prevailing, and in rL-type, no preferential sets are found. It is noticeable, however, that *Abies sachalinensis* is nearly always dominant in the lower synusiae through these three types.

According to the data obtained by Tatewaki et al. (1955), both the max. height and the max. diameter of *Picea jezoensis* and *P. glehnii* in C- and rL-type are always superior to those of *Abies sachalinensis*. A similar tendency is found in L-type dominated by *A. sachalinensis*. Even though *A. sachalinensis* is more numerous in the highest synusia than *P. jezoensis* and *P. glehnii*, the former tree is smaller than the latter two. It is concluded from the facts mentioned that *P. jezoensis* or *P. glehnii* sociations with C- or rL-type are rich in big individuals in the highest synusia but these are few in the lower synusiae, while *A. sachalinensis* sociations with L-type are abundant in medium-sized individuals in the highest synusia and smaller ones in the lower synusiae. Although *Abies* saplings are usually predominant in the lower synusiae, *P. jezoensis* saplings are often as numerous as *Abies* saplings in the lower synusiae, too.

3. Analyses of rL- and L-type as the sum of each element type†

As seen in the preceding section, rL-type is usually characterized by *Picea jezoensis* in the highest synusia and by *Abies sachalinensis* in the lower synusiae.

Each rL-type is shown by the following sums of each element type:

$rL = rL^* + rL^*$, or $D^* + C^*$, or $rL^* + C^*$, or $ri^*(P. jezoensis) + rL^*$ (*Alnus hirsuta*). It will be expected that $rL = rL^* + L^*$, provided the total number of individual trees in the shrub synusia is smaller than that in the highest synusia.

Each L-type is shown by the following sums of each element type:

$L = L^* + L^*$, or $L^* + C^*$, or $L^* + i^*$.

In the above cases, if the max. number of individual trees of tree- and shrub-synusia in C-type and that of subtree-synusia in D-type is confined within a definite realm of numbers, the outlines of rL-shape and L-shape will be maintained, and also, if the number of individual trees of tree-synusia in rL-type and that of shrub-synusia in L-type is sufficiently large in each type, the original rL-shape and L-shape will be maintained, even if some increase in synusiae. In this regard, it should be noticed that rL-type is composed of combination sets of P-A or Pg-A which includes big individual trees of *P. jezoensis* or *P. glehnii*, and that L-type is composed of a combination set of A-A which is rich in medium-sized and smaller individuals of *A. sachalinensis*.

4. Analyses of C-type as the sum of each element type

Each C-type is shown by the following sums of each element type as far as *Picea* and *Abies* species are concerned:

$C = rL^* + C^*$, or $C^* + C^*$, or $i^* + L^*$.

Of the 10 C-types analysed, 6 examples are $C^* + C^*$ and 3 are $rL^* + C^*$. C-type will be maintained, if the subtree synusia is relatively low in number compared with the tree and shrub synusiae. While $rL^* + L^*$ will be expected if the shrub synusia is not extremely large in number, this sort of element type is not found in the present analyses. If shrub synusia is full of a large number of young saplings, $rL^* + L^*$ will lead inevitably to L-type, but this is not found, either.

There seem to be two ways of establishing C-type.

One is the case in which young shoots and saplings decrease in number in the course of the growth process through the interspecific and intraspecific competition, and finally a small number of saplings reaches the highest tree synusia containing more individual trees than the intermediate subtree synusia because of the addition of the older trees to the new comers. Successors will be supplied to the underfloor of forest or sociation, but the number of successors is not so large as that of L-type forest or sociation. Thus, C-type is characteristic of abundant numbers of individual trees in the tree- and shrub synusia and of less abundant numbers of those in the subtree synusia. This will be the case of the Ishikari virgin forest. The second case is that the subtree synusia is thinned by human impacts such as thinning, cutting grazing etc., or various kinds of natural damage that occurred in the past. As a result, the intermediate subtree synusia has relatively smaller numbers of individual trees than the tree- and shrub synu-

†In the present analyses, element types are those concerned with *Picea jezoensis*, *P. glehnii* and *Abies sachalinensis*.

siae, and a C-shape is formed.

As mentioned already, if the number of trees of the shrub synusia is sufficiently large, L-type will be expected in even rL^*+L^* . In fact, such an L-type formation in the 25 sociations is not found. This may mean that the development of the subtree synusia and the shrub synusia by *P. jezoensis* and/or *A. sachalinensis* in the Ishikari virgin coniferous forest is suppressed by eco-physical influences of *P. jezoensis* dominating in the tree synusia upon the underfloor.

IV. Alteration of S-diagram of pioneer forests through successive phases

In the headwaters of the Ishikari river, pioneer forests establish on river-sides, sandy river-beds and flooded alluvial deltas. These forests are characterized by *Populus maximowiczii* and *Toisusu urbaniana*. In the two pioneer forests, *Populus* forests and *Toisusu* forests, alteration of S-diagrams accompanying the

Table 3. Correspondence of the max. height range of the two pioneer forests leading to prevailing S-diagrams, based on the data of Tatewaki et al. (1955)

Max. height range of the forests	Prevailing S-diagrams
2— 8 (m)	I
8—10	L
8—16	rL
15—20	L, L \div C, C
15—23	rL

height increment was investigated.

A basic series of alterations, namely from the young pioneer phase to the pre-mature phase, is I-L-rL in these pioneer forests. Three possible pathways leading to the destination of the mature phase are found: I-L-rL, I-L-rL-rL, and/or I-L-rL-C (including L \div C).

L-type is shown as the sum of numerous young shoots and a gradually diminishing amount of subtrees and mature trees which have survived from the struggle for existence. If an active seed invasion has not continued, L-type will be replaced by rL-type. In fact, there is a series of I-L-rL-rL as seen in Table 3. This type of series is found in *Populus maximowiczii* (*Pm*)-and *Toisusu urbaniana* (*T*)-sociation respectively. It is reasonable to assume that they can not have their own successors, young shoots and saplings on the shaded floor of their sociation stands, because they belong to the heliophytes. Thus, the final phase tends to appear as rL-type, its alternation series being I-L-rL-rL.

When such shade tolerant trees as *Alnus hirsuta* (*Ah*), *P. jezoensis*, *P. glehnii* and *Abies sachalinensis* have established their own seedlings on the floor of *Pm*-or *T*-sociations, the S-diagrams will be transformed. It is the case in which L-type predominates in some pioneer sociations of the max. height of 15 to 20 m. It should be considered, however, that the stability of habitat is important in this case. If the habitat is stable or undisturbed over a long period, the invading seedlings are *P*, *Pg*, *A* or *Ah* rather than *Pm*, *T*, or *Salix sacha-*

linensis (*Ss*), because the former seedlings are tolerant to shade, while if the habitat is unstable or periodically disturbed, the latter seedlings appear on the floor, particularly in the open, sunny floor patches under broken canopy. It is obvious that L-type sociations will change into rL-type sociations, if not disturbed thereafter. In the Ishikari pioneer forests, L-type sociations are established on stable sandy river deltas of the Ishikari river. If new seedlings occupy the stable floor of a given rL-type sociation, C-type sociation will be expected, because the medium-sized trees are relatively few in number. Thus, a mechanism of C-type formation seems to be biologically the same as that of L-type formation stated in the S-diagram analysis, i. e. by means of successive addition of seedlings to the shrub synusia, namely $C=rL^*$ (tree synusia) + L^* (shrub synusia).

All types of S-diagram of the mature *Populus maximowiczii* forests are *Pm*·*P*·*A*, *Pm*·*A*·*A* and *Pm*·*P*·*A*·*P*·*A*·*P*·*A*, and those of *Toisusu urbaniana* forests are *T*·*Ah*·*Ss*·*A* and *T*·*Ah*·*Ss*. It is quite interesting that conifers such as *P. jezoensis* and *A. sachalinensis* are found constantly under *Populus* crowns but not under *Toisusu* crowns, and that *Alnus hirsuta* and *Salix sachalinensis* combine with *T. urbaniana* in the forests under consideration.

Conclusion

The stratification analysis is useful in the understanding of the origin, regeneration and alteration of forest communities or sociations. In the present study, the stratification diagram analysis is composed mainly of three parts: the first is the S-diagram itself; the second is combination sets of the upper synusia and the lower synusiae; the third is alteration of S-diagrams according to aging.

In the present Ishikari virgin forest and also in the Moiwa natural forest, C-type of S-diagram is prevailing. This prevalence of C-type may suggest that the regeneration of this kind of forest has been brought about by catastrophes, and not by succession, nor by the successive establishment of seedlings in the underfloor.

At times prevalence of rL-type is of considerable interest. Under natural condition, rL-type is frequently found. High density, presence of strong competitors, extremely low light penetration, browsing, parasitism, allelopathy, specific reactions of substrate etc. may contribute to the completion of the discontinuity of synusiae in a given forest or sociation. Similar effects upon the natural forest have been observed under human impacts. Clearing, regular cutting of low shrubs and herbs, seed and fruit collection, picking of flowers, repealet trampling grazing etc. are major causes which may lead to rL-type.

The study of combination sets is also interesting with special regard to the regeneration of forest sociations. This is clearly shown in the analysis of *Picea glehnii* forest sociations.

According to the researches of Tatewaki (1944) and Tatewaki and Igarashi (1971), *Abies sachalinensis* is usually more abundant in *Picea glehnii* forest than *P. jezoensis*, but in a few cases *P. jezoensis* is found in the forest floor of *P. glehnii*, but usually fewer than *A. sachalinensis*. A belt-transect set at Osakuma-Rindo of the Experimental Forest of Hokkaido University shows that a replacement series of *P. jezoensis*, *P. glehnii* and *A. sachalinensis* occurs. *A. sachalinensis*

as well as *P. glehnii* is very abundant in a serpentine section of the belt-trnsect, but *P. jezoensis* saplings increase in a non-serpentine section of it, in which *P. jezoensis* and *A. sachalinensis* are prevailing, because of the disappearance of *P. glehnii*. In the case of sand-dunes at Shunkokutai (Tatewaki 1944, p. 112), *P. glehnii* forest is shown by a combination of *P. glehnii* and *A. sachalinensis*. In the coniferous forests of Mt. Yotei (Tatewaki, *ibid.* p. 125), *A. sachalinensis* is abundant and *P. glehnii* is extremely poor in number under the canopy of *P. jezoensis*-dominant forests, while *P. jezoensis* is absent from *P. glehnii*-*A. sachalinensis* forests of Makkarinupuri at the foot of Mt. Yotei.

An interesting numerical relation among *P. jezoensis*, *P. glehnii* and *A. sachalinensis* is found. In *P. glehnii*-dominant forests, the relation will be $Pg \cong A \rangle P$, but in *P. glehnii*-suppressed forests, it will be $P \cong A \rangle Pg$. It is a well known fact that *P. glehnii* is a specialized coniferous species and it usually establishes its own forests in a special habitat free from other competitive species. *A. sachalinensis* has a wider tolerance range than *P. jezoensis*. It combines with the two *Picea* species, but *P. jezoensis* hardly combines with *P. glehnii* or *vice versa*. From the facts mentioned above, it is reasonable to assume that combination sets of *P. jezoensis* and *A. sachalinensis*, *P. glehnii* and *A. sachalinensis*, and *A. sachalinensis* and *A. sachalinensis* are popular in the S-diagram analysis in the Ishikari virgin forest, while a combination set of *P. glehnii* and *P. jezoensis*, or *P. jezoensis* and *P. glehnii* is hardly found in it. An exceptional example is found on Mt. Kikin (Tatewaki 1944). An extensive *P. glehnii* forest was established owing to the forest fire. The most frequent combination set in it is that of *P. glehnii* and *P. jezoensis* rather than that of *P. glehnii* and *A. sachalinensis*. This may suggest that the present *P. glehnii* forest of Mt. Kikin is not the climatic climax forest, but *P. jezoensis* forest is the climax. In other words, *P. glehnii* forest is not a true climax vegetation of Mt. Kikin, but a kind of substitution forest.

Maeda et al. (1977) discussed the alteration from *P*-*Pg* forests to *A*-forests and an actual state of the climax in Hokkaido. They concluded that a cyclical change will be performed by these three conifers and none of them converge into the definite climax and final stable forest.

From the analytical results of S-diagrams, it is possible that the alternation between *Pg* and *A*, *P* and *A*, and rarely *Pg* and *P* may happen normally, and it proves that the cyclical change study as well as the S-diagram analysis will be valuable approach to explain these changes.

In the Ishikari pioneer forest sociations, the basic process of S-diagram is shown by a series of I-L-rL according to aging, viz. from the pioneer phase to the premature phase of the cyclical change. Three possible pathways leading to the destination of the final mature phase are recognized; I-L-rL-L, I-L-rL-rL and/or I-L-rL-C (incl. $L \doteq C$). These branchings to the final phase are assumed to be dependent upon the biological conditions such as the propagation potentiality, vegetative growth capacity, competitive ability, light compensation points of individual plants, etc. as well as an environmental condition such as stability of the substratum as seen in the course of I-L-rL-L type series. It is, therefore, necessary to consider discrepancies of the S-diagram change in the two sociations

under consideration in relation to biological and environmental conditions.

As stated previously, the stratification diagram is a clue to understand the unified forest composed of separate synusiae. In this regard, the author has given his attention to the synusia classification stated by Du Rietz (1930) and Blyumental (1965), and made an attempt to classify the vegetation of Mt. Soranuma in the outskirts of Sapporo city with synusia method (Ito et al. in press). This synusia classification will be applied to an actual physiognomical or morphological unit of vegetation which occupies homogeneously a definite area. Tatewaki and his students (1956–1966) devoted themselves to record primaeval or virgin forest vegetations of Japan by the belt-transect method and had published numerous sociations based on the belt-transect recording system. These sociations are the most suitable materials for the aim of S-diagram analysis and synusia classification. The interpretation of S-diagrams, however, should be done with caution and not overestimated. First, three synusiae divisions are not significant mathematically but are reasonable biologically as far as they correspond to the life-form types, mega-, macro-, meso-, micro- and nano-phanerophytes, and reflect aging. Secondly, considerations are based upon a synusia. A type of S-diagram is imagined by a numerical comparison of the three synusiae of a given sociation.

This imagination should be always made through the combination of biological phenomena with the environmental factors. Thirdly, the present analysis is made on the boreal forest, of which species compositions are very simple, being composed of only 3 species. On such a forest as the temperate summergreens, it will be more complicated. The present study, therefore, is one step to the next, namely the temperate summergreens in which both the synusiae and the species composition are more complex.

Summary

- (1) The stratification diagram can be arranged seven types of stratification diagram or seven types of S-diagram which are classified by a numerical comparison among the three synusiae, i. e. tree-, subtree- and shrub synusia. In the present paper, they are called L-, reversed L- or rL-, C-, D-, I-, i- and reversed i- or ri-type of S-diagram respectively. Any type of S-diagram is considered to be the sum of types of S-diagram of every tree-, subtree- and shrub-species in a given sociation. The latter kind of type of S-diagram is called an element type of S-diagram and is indicated in such a manner as L^{*}-, rL^{*}-, C^{*}, D^{*}-, I^{*}-, i^{*}- and ri^{*}- type of S-diagram.
- (2) In the present paper, the author made an attempt to analyse, from the viewpoint of the stratification diagram, 25 sociations of the Ishikari virgin forest, which was composed mainly of the 3 conifers, *Picea jezoensis*, *P. glehnii*, and *Abies sachalinensis*, and was damaged and wiped out by the fifteenth Typhoon in 1954 known as "Toyamaru Typhoon". As a result, it is shown that C-type of S-diagram is the most frequency in it, and it is considered that the regeneration of this kind of forest has been brought about by catastrophes and not by succession, nor by successive establishment of seedlings on the underfloor in such an undisturbed condition as the Ishikari virgin

- forest.
- (3) In all types of S-diagram, a combination of individual species in the highest synusia with those in the lower synusiae was investigated. In the Ishikari virgin coniferous forest, a combination set of *P. jezoensis* (highest synusia)-*A. sachalinensis* (lower synusiae) is dominant in C-type, while that of *A. sachalinensis* and *Picea glehnii*-*A. sachalinensis* is prevailing in L-type and no preferential sets are found in rL-type. From these facts and phytosociological data obtained by Tatewaki et al. (1955), it may be shown that *P. jezoensis*-or *P. glehnii* sociations with C- or rL-type are abundant in big individual trees in the highest synusia but contain few in the lower synusiae. while *A. sachalinensis* sociations with L-type contain abundant medium-sized individuals in the highest synusia and smaller ones in the lower synusiae, Also, it is shown that *A. sachalinensis* is usually the major species not only in *P. jezoensis* sociations but also in *P. glehnii* sociations which will be established on special substrata, i. e. on serpentine soils, or on marshy or boggy places etc.
 - (4) On three types of S-diagram, it was attempted to analyse them into elemental types of S-diagram. The following sums of elemental types of three conifers are recognized: $L=L^*+L^*$, or L^*+C^* , or L^*+i^* ; $rL=rL^*+rL^*$, or D^*+C^* , or rL^*+C^* , or $ri^*(P. jezoensis) + rL^*(Alnus hirsuta)$; and $C=rL^*+C^*$, or C^*+C^* , or i^*+L^* . Among them, the most frequent kinds of sum in each case of the three types are $L=L^*+L^*$, $rL=rL^*+rL^*$ and $C=C^*+C^*$. Some consideration is given to these three kinds of sum in relation to the establishment of the virgin coniferous sociations.
 - (5) On the pioneer forests found in the Ishikari virgin forest area which are composed mainly of *Populus maximowiczii* and *Toisusu urbaniana*, the alteration process of S-diagrams was traced. A series of S-diagrams is recognizable according to aging, being shown by the max. height range of the forests. This series of S-diagram is I-L-rL-L or -rL from the pioneer phase to the mature phase (but not the climax). In the present case, a pathway to L- or rL-type in the mature phase is proved to be related to the stability of substratum. Where stable, the pathway leads to L-type and to the development of a forest floor occupied by *Picea*, *Abies* and *Alnus* species which are tolerant to heavy shade.
 - (6) The stratification diagram is a clue to understand the unified forest composed of separate synusiae. The interpretation of S-diagrams, however, should be done with caution and not overestimated. First, three synusiae divisions are not significant mathematically but are reasonable biologically as far as they correspond to the life-form types, mega-, macro-, meso-, micro-, and nano-phanerophytes, and reflect aging. Secondly, considerations are based upon a synusia. A type of S-diagram is imagined by a numerical comparison of the three synusiae of a sociation. This imagination should be always made through the combination of biological phenomena with the environmental factors. Thirdly, the present analysis is made on the boreal forest, of which species compositions are very simple, being composed of only three species. On such a forest as the temperate summergreens, it will be more compli-

cated. The present study, therefore, is one step to the next one, namely, the temperate summergreens in which both the synusiae and the species composition are more complex.

Literature cited

- BLYUMENTAL I. Kh. 1965. On monographic studies of high-mountain formations, (Sukachev, V. N. ed.) "Studies on the flora and vegetation of high-mountain areas" 1-8. Akademiya Nauk SSSR. Jerusalem.
- Du RIETZ, E. 1930. Classification and nomenclature of vegetation units. in Sv. Bot. Tidskr. 24(4): 489-503.
- ITO, K., Chiba, S., Ichijyo, S., Nitta, N., and Yoshizaki, T. 1975. Forest vegetation of Mt. Moiwa (I). in Seibutsu-Kyozai No. 10. 58-77., (II). *ibid.* 78-104. (in Japanese)
- MAEDA, T., Miyakawa, K., Asanuma, S., Kaneda, Y. and Shinoda, S. 1977. Forest vegetation, (Sakaguchi, K. ed.) "A memoir of the scientific investigation of forests in the headwaters of the Ishikari River, Hokkaido, Japan" 82. (in Japanese)
- MATSUKAWA, K. 1955. Introduction, (Matsukawa, K. ed.) "A memoir of the scientific investigations of the primeval forests in the headwaters of the River Ishikari" 8-9. (in Japanese)
- TATEWAKI, M. 1944. Phytosociological studies of *Picea glehnii* forests. In Res. Bull. Coll. Exp. For. Coll. Agr. Hokkaido Univ. 13(2): 1-181. (in Japanese)
- . et al. 1956-1966. (Tatewaki, M. ed.) "The iconography of the vegetation of the natural forest in Japan" I-X. (in Japanese)
- . and Igarashi, T. 1971. Forest vegetation in the Teshio and the Nakagawa District Experiment Forests of Hokkaido University, Prov. Teshio, N. Hokkaido, Japan. in Res. Bull. Coll. Exp. For., Coll. Agr., Hokkaido Univ. 28(1): 1-192. (in Japanese)
- . and Takahashi, K. 1955. Plant communities, (Matsukawa, K. ed.) "A memoir of the scientific investigations of the primeval forests in the headwaters of the River Ishikari, Hokkaido, Japan" 16-21. (in Japanese)
- . Uchida, T., Ishikawa, T., Suzuki, H., Kusunoki, H., Katsui, Y. and Takahashi, K. 1955. Sample plots, *ibid.* 31-153. (in Japanese)
- YOSHIOKA, K. 1960. Effect of deer grazing and browsing upon the forest vegetation on Kinkasan Island. in Sci. Rep. Fac. Art. and Sci. Fukushima Univ. No. 9. 9-27.
- . 1966. Effect of herbivorous animals on forest vegetation. "Interaction in biological communities" 262-289. (in Japanese)