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Ecological Studies of Mixed Forests in Nopporo National Forest, Central Hokkaido, Japan

—Relationships Between the Distribution of Aged Forests and Environmental Factors—

Yukio Ishikawa, Masahiro Haruki and Koji Ito

Department of Biosystem Management, Division of Environmental Conservation, Graduate School of Environmental Science, Hokkaido University, Sapporo, 060, Japan

Abstract

A survey of forest vegetation and environmental factors was done in Nopporo National Forest. Thirteen forest communities which were determined by dominant species and three soil types were observed. None of these communities extended beyond 50 meters, and they were observed to be rapidly replacing each other. The distribution of these communities were not correlated with the topography and soil types. By using continuum analysis, 80 forest stands showed significant correlation to the soil water content ratio. On brown forest soil spread over almost all of the forest, forest stands were distributed with a good correlation to the depth from the soil surface to water impermeable C horizon. Impermeable C horizon subtly changed soil water gradient, and this caused the rapid replacement of communities and dominant species. Mosaic phenomenon of Mixed Forest Zone is observed in miniature in Nopporo National Forest.

Key Words: Nopporo National Forest, environmental factors, continuum analysis, soil water gradient, water impermeable C horizon, Mixed Forest Zone.

1. Introduction

Nopporo National Forest is located near the city of Sapporo, central Hokkaido, northern Japan. Despite frequent cuttings and wind damages, this forest was famed for its primitive state in the past but it is utilized as a recreational area and educational site at present. However, numerous mature individuals of *Abies sachalinensis*, the main component species of this forest, have died and the regeneration of the species is not coming along as smoothly as in recent years (Haruki and Ishikawa 1983). Thus, the point in this study is to create a new system for conservation with quantitative prediction of forest change.

The systems for conservation of forest communities were devised in Britain (Peterken 1981) and the United States (Kessell 1979, Potter et al. 1979). Quantitative predictions of forest changes have been carried out with the aid of computer simulation models [cf. Shugart and West (1980) and Shugart (1981)]. In Japan, quantitative predictions of forest change have been rarely put into practice. To construct such models it is necessary to clarify the major environmental factors which decide the distribution of forests in mature, because species characteristics change along with those factors (Hickman 1975). In Nopporo National Forest, Tatewaki and Igarashi (1973) described eighteen forest sociations by using dominant species in each synusia and discussed their habitat based on the belt transect method. However, they subjectively sampled stands where individual trees had large sizes. Furthermore, the analyses of environmental factors were not put into practice. In the present study, the authors investigated the relationships between the distribution of aged forests and environmental factors as the first step of model construction in Nopporo National Forest, and based on this, the characteristics of Nopporo National Forest will be discussed.

The authors wish to acknowledge and express their sincere gratitude to the menbers of Sapporo Regional Forest Office for providing all the required facilities for the study.

2. Study area

Nopporo National Forest is located in the Nopporo Hills (43°25′N, 141°32′E), Hokkaido, northern Japan (Figure 1). This forest is 2,040 ha in area and is roughly rectangular in shape; the south to north length is about 6 km, and the east to west width is about 4 km. The elevation is about 100 m on the southern margin and 20 m on the northern boundary near the city of Ebetsu. The main ridge of the Nopporo Hills extends from north to south. The east and west sides of the hills slope gently and are cut by small valleys. Over most of the forest, parent material is the Konopporo formation composed of an alternation of clay, silt and sand (Akamatsu and Yamada 1980). By using ^{14}C method, they estimated the age of the formation to be at least 30,000 years. Above the formation, the ejecta of Shikotsu volcano spreads thinly. Soils of the forest are mostly composed of brown forest soil except for the valleys (Yamamoto 1973). In those valleys, there are immature soil, gley soil and peat soil. According to the records of Nishinopporo meteorological station located in the center of Nopporo National Forest, the mean annual precipitation and mean annual temperature from 1889 to 1975 are 1,179 mm and 7.9°C, respectively.

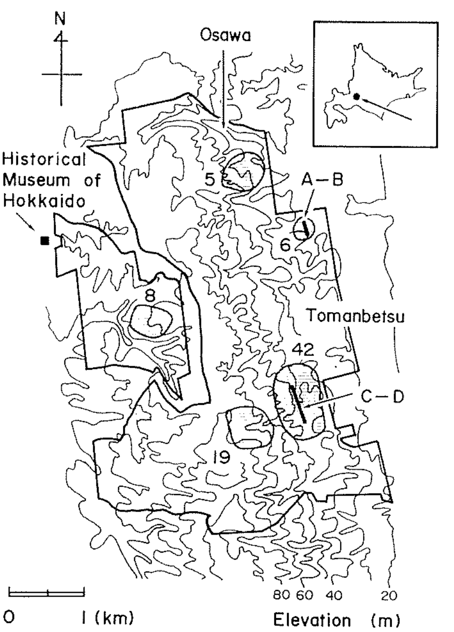

Figure 1. Location of survey areas in Nopporo National Forest. Figures represent the number of stands in each survey area. A–B and C–D show the location of two belt-quadrats.

Floral lists of the forest were constructed by Kudo (1928), Tatewaki and Matsue (1934), and Tatewaki and Igarashi (1973). Vegetation of the forest was described by Tatewaki and Igarashi (1973). Based on the classification system of Uppsala school, they described five coniferous sociations and thirteen deciduous broadleaved sociations. All five coniferous sociations are distributed on the ridges and the slopes of the hills. Almost all of coniferous trees that compose those sociations are *Abies sachalinensis*. *Picea jezoensis*, *P. glehnii* and *Taxus cuspidata* are rarely observed. Deciduous broadleaved species such as *Acer mono*, *Tilia japonica*, and *Quercus mongolica* var. *grosseserrata*, are mixed with *A. sachalinensis*. Swamp forests dominated by *Alnus japonica*, *Fraxinus mandshurica* var. *japonica* and *Salix subfragilis*, are distributed on the bottoms of the valleys. Eight deciduous broadleaved sociations belong to these swamp forests. There are five remaining deciduous broadleaved sociations on the ridges and the slopes of the hills. These five sociations consist of *Acer mono*, *Tilia japonica*, *Ulmus davidiana* var. *japonica*, *Acer mono* var. *mayrii* and *Quercus mongolica* var. *grosseserrata*.

3. Methods

In the summers of 1984 and 1985, 80 stands were selected on slopes, valleys and valley bottoms to search for the relationships between the distribution of forest stands and environmental factors (Figure 1). Tatewaki and Igarashi (1973) described eight dominant tree species in natural and seminatural forest communities in Nopporo National Forest. The authors selected 80 stands expecting to sample ten stands per one dominant species. Because the Nopporo Hills are gently sloping hills, and because ridges and slopes of the hills could hardly be distinguished, the ridges were classified together with slopes in the present paper. To exclude the effects of natural and artificial disturbances, these stands were selected where no stumps, no fallen trees and no large standing dead trees were seen. The size of these 80 stands ranged from 10 × 10 sq. m to 15 × 15 sq. m according to the highest tree of each stand. In each stand, the species of all living trees higher than 2 m were identified and their height and DBH (diameter at breast height : 1.3 m) were measured. Among the above 80 stands, 33 stands were selected at 10 m intervals as belt-quadrats (Tatewaki et al. 1966) to observe the relationships between the distribution of

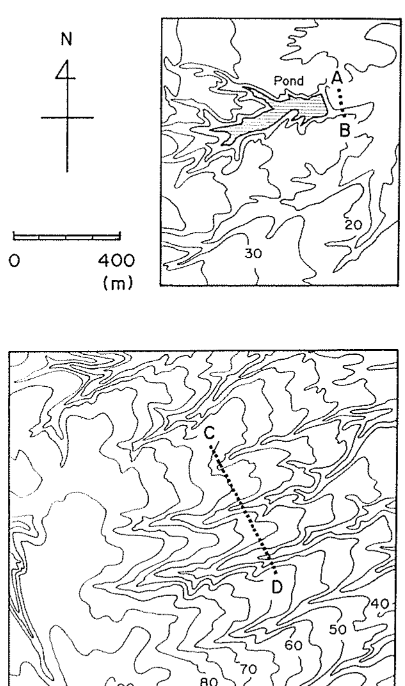

Figure 2. Location of two belt-quadrats for the observation of the relationships between the distribution of forest stands and topography or soil types. Solid squares show stands that have sizes of 10×10 sq. meter. These stands were set up at 10 meter intervals. Figures represent elevation above the sea level.

forest stands, and topography and soil types (Figure 2). These 33 stands were located on the eastern slope of the Nopporo Hills, where the topographical characteristics of the hills were typically observed.

In order to clarify the major factors which determined the distribution of forest stands and species distribution, soil samples and analyses were carried out in the autumns of 1984 and 1985. Samplings were put into practice after two or three days of rainfalls for the sake of equalizing the effects of rainfall on soil moisture. At each of the 80 stands, a soil pit was excavated and a description of it was made in the field including the color, texture, thickness and concentration of roots in A_0, A, B, and C horizon. Soil types were decided according to Forest Soil Division (1976). Soil sapmles were taken from the 5–10 cm layer of A horizon, and 45–50 cm layer of C horizon for physicochemical analysis. Afterward, three physicochemical characteristics were measured in the laboratory as major environmental factors for vegetational pattern. 1) : Dry-wet gradient is a major environmental factor which decides vegetational pattern not only at macro distributional level (Whittaker 1975) but also at micro distributional level (Whittaker and Niering 1965, Saito 1971). Thus, soil water content ratio was measured. 2) : Because the availability of nutrients and the solubility of poisonous materials are strongly affected by soil pH (Aomine 1974), the measurement of soil pH was conducted. 3) : Soil humus performs as a repository of nutrients and its functions in soils are important factors of soil fertility (Kumada 1974). In the present study, these functions was approximated by the quantity of soil humus. Thus, the quantity of soil humus was measured by using ignition loss.

Dominant species were decided on the basis of SDR (Numata and Yoda 1957) to recognize forest communities. Although relative frequency was used to calculate SDR in the original paper of Numata and Yoda (1957), relative height was employed instead of it in the present study. Thus, SDR of a species was calculated by using relative height (RH), relative density (RD), and relative basal area (RBA).

$$SDR = (RH + RD + RBA)/3 \times 100$$

The value was calculated only with individuals larger than 10 m in height. Trees less than 10 m in height were excluded because it was not clear whether they could attain their mature size or not.

Morphological differences between *Acer mono* and *A. mono* var. *mayrii* were often so confusing in younger stage that it was difficult to distinguish these two species from each other. Thus, in the present study all individuals of *A. mono* var. *mayrii* was classified with *A. mono*.

4. Results

(1) *Relationships between community distribution, and topography and soil types*

Thirty three stands were classified into thirteen communities dominated by a certain species respectively. As shown in Figure 3, five stands of belt-quadrat A–B

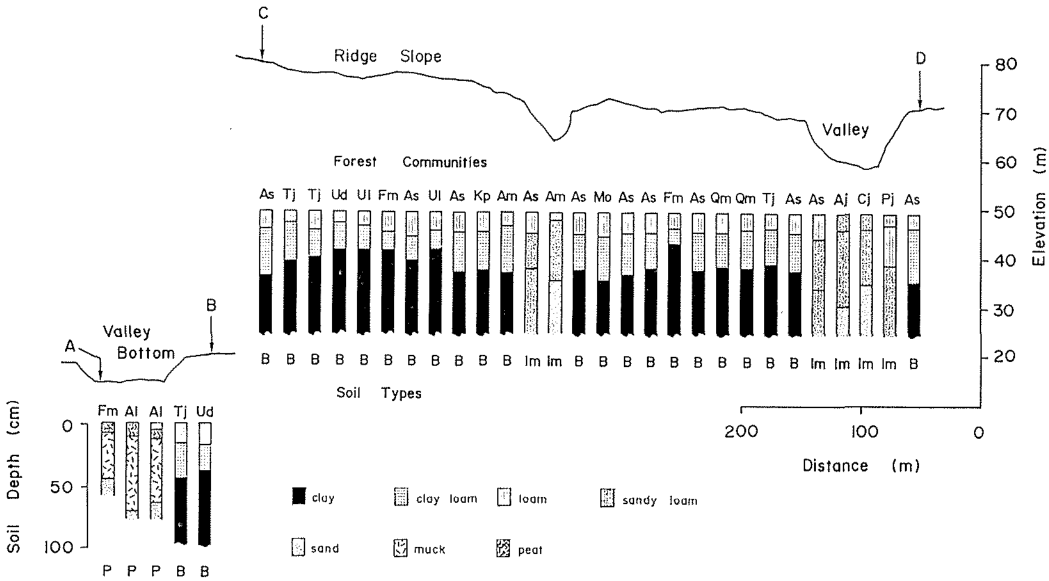

Figure 3. Topography, soil profiles, soil types, and communities of two belt-quadrats. Abbreviations above soil profiles show forest communities. Qm: *Quercus mongolica* var. *grosseserrata* community, As: *Abies sachalinensis* community, Tj: *Tilia japonica* community, Am: *Acer mono* community, Ul: *Ulmus laciniata* community, Cj: *Cercidiphyllum japonicum* community, Ud: *U. davidiana* var. *japonica* community, Fm: *Fraxinus mandshurica* var. *japonica* community, Al: *Alnus japonica* community, Aj: *Acer japonicum* community, Kp: *Kalopanax pictus* community, Mo: *Magnolia obovata* community, Pj: *Picea jezoensis* community. Abbreviations under soil profiles represent soil types observed. B: brown forest soil, P: peat soil, Im: immature soil.

were surveyed as a typical example of forest distribution on valley bottoms. Twenty eight stands of belt-quadrat C–D were selected on slopes across small valleys. These communities were named after the dominant species. *Abies sachalinensis* community consists of 11 stands; *Tilia japonica* community does 4 stands; *Fraxinus mandshurica* var. *japonica* community does 3 stands; *Quercus mongolica* var. *grosseserrata* community, *Acer mono* community, *Ulmus laciniata* community, *U. davidiana* var. *japonica* community, and *Alnus japonica* community does 2 stands respectively; *Acer japonicum* community, *Cercidiphyllum japonicum* community, *Kalopanax pictus* community, *Magnolia obovata* community, and *Picea jezoensis* community does 1 stand, respectively (Figure 3).

Figure 3 also shows the three soil types observed; brown forest soil on slopes, peat soil on valley bottoms, and immature soil on valley slopes. As reflected by topograpy, brown forest soil spread over almost all of the forest. The distributions of peat soil and immature soil were limited. *Alnus japonica* community and *Fraxinus mandshurica* var. *japonica* community were distributed on peat soil. Ishizuka (1974), Shinsho (1978), and Tsuneya and Ito (1983) reported in Hokkaido that *A. japonica* community was distributed in the same habitat as the present study. However, the community of *F. mandshurica* var. *japonica* was distributed not only on peat soil but also on brown forest soil in the present study. No characteristic communities were observed on immature soil. On brown forest soil, eleven communities were observed and none of these communities continued over more than three stands (ca. 50 meters). These eleven communities were rapidly replaced by each other. Therefore, these communities were arranged in a mosaic fashion and this mosaic pattern could not be explained by soil types or topograpy alone except for the *A. japonica* community on peat soil at valley bottoms.

(2) *Ordination*

To take the compositional and structural differences of 80 stands into account and to reveal the environmental factors which decided the distribution of forest stands, an ordination, continuum analysis (Brown and Curtis 1952), was done. Several terminologies of continuum analysis have been proposed after the original work of Brown and Curtis (1952), and this causes unnecessary confusion in later

Table 1. Mean SDR of species in 80 stands and species position indices

Species \ Stand types	Qm	As	Tj	Am	Ul	Cj	Ud	Fm	Al	Species position index
[Dominant species]										
Quercus mongolica var. *grosseserrata*	72	30	6	14	·	·	18	9	·	1
Abies sachalinensis	45	88	61	38	33	15	42	19	·	2
Tilia japonica	22	24	92	47	50	24	34	27	·	3
Acer mono	18	35	55	88	33	40	41	23	4	4
Ulmus laciniata	16	13	17	49	85	18	35	·	·	5
Cercidiphyllum japonicum	6	2	13	3	72	97	26	20	2	6
Ulmus davidiana var. *japonica*	4	16	14	30	66	20	89	33	7	7
Fraxinus mandshurica var. *japonica*	·	9	13	13	15	33	24	92	49	8
Alnus japonica	·	·	·	·	·	3	6	22	98	9
[Minor species]										
Fraxinus lanuginosa	31	33	25	21	26	11	21	11	·	3
Acer japonicum	13	17	7	5	·	8	·	2	·	2
Acanthopanax sciadophylloides	5	8	2	7	·	·	·	·	·	2
Ostrya japonica	19	7	10	18	·	9	·	·	·	2.5
Taxus cuspidata	1	2	8	4	6	·	2	·	·	3
Acer palmatum var. *matsumurae*	7	5	13	5	·	·	8	4	·	3
Kalopanax pictus	17	13	29	29	12	3	12	3	·	3.5
Sorbus commixta	20	16	6	6	16	4	11	2	·	3.5
Betula maximowicziana	·	·	9	8	·	·	·	·	·	3.5
Cornus controversa	13	4	12	15	·	·	7	4	2	4
Sorbus alnifolia	8	6	5	12	·	2	·	·	·	4
Prunus ssiori	6	10	6	15	·	24	13	·	4	6
Magnolia kobus var. *borealis*	15	17	11	5	15	7	29	7	9	7
Salix subfragilis	·	·	·	·	·	·	·	·	15	9.5

studies. Thus, in the present study, the authors followed the recent terminology of Goff and Cottam (1967). There were 13 dominant species in 80 stands; *Abies sachalinensis* dominated in 20 stands; *Acer mono* and *Fraxinus mandshurica* var. *japonica*, in 9 stands respectively; *Quercus mongolica* var. *grosseserrata* and *Ulmus davidiana* var. *japonica*, in 8 stands respectively; *Alnus japonica* and *Tilia japonica*, in 7 stands respectively; *Cercidiphyllum japonicum*, in 6 stands; *Ulmus laciniata*, in 2 stands; *Acer japonicum*, *Kalopanax pictus*, *Magnolia obovata*, and *Picea jezoensis*, in each 1 stand. Because 4 species (*Acer japonicum*, *Kalopanax pictus*, *Magnolia obovata*, and *Picea jezoensis*) out of those 13 species dominated only in 1 stand, they were not regarded as leading dominants. 80 stands were classified in 9 stand types by using leading dominants as shown in Table 1. At the head of the table, 9 stand types are arranged; *Quercus mongolica* var. *grosseserrata* stand type, *Abies sachalinensis* stand type, and so on. Figures show mean SDR of each species against each stand type. For example, *Acer mono* obtains maximum mean SDR in *A. mono* stand type and the values gradually decrease from its stand type to the both ends as shown in the fourth row of the table. The

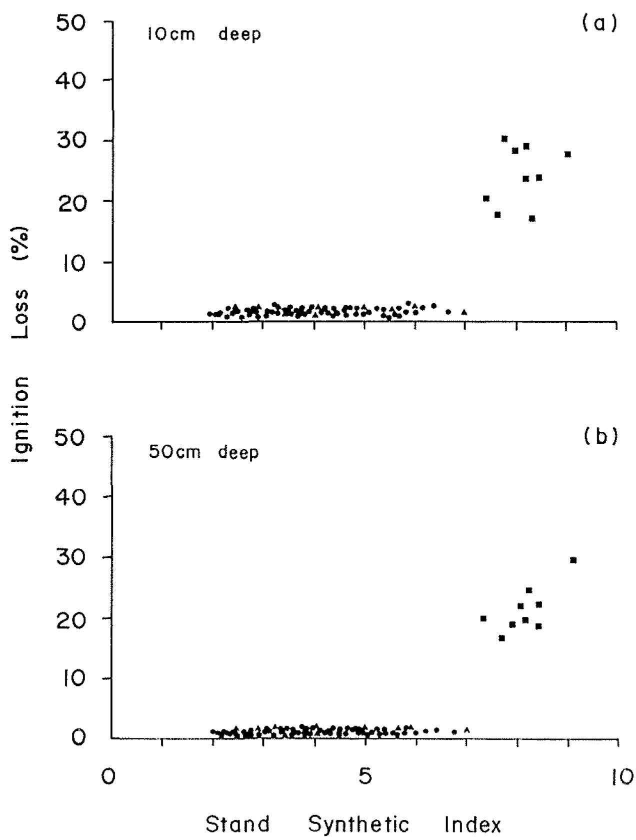

Figure 4. Correlations between soil ignition loss and stand synthetic index. Solid circles: brown forest soil; solid triangles: immature soil; solid squares: peat soil.

remaining leading dominants which are arranged in the first column of the table roughly show normal distribution. This result indicates that these leading dominants are distributed along an environmental gradient. Thus, in the present study, species position indices (Goff and Cottam 1967) of leading dominants along this gradient were given from 1 (*Quercus mongolica* var. *grosseserrata*) to 9 (*Alnus japonica*) in the order as shown in the right column of the table. Minor species which do not predominate but have high frequency or high dominance value were given index from 2 (*Fraxinus lanuginosa, Acer japonicum*, and *Acanthopanax sciadophylloides*) to 9.5 (*Salix subfragilis*).

Based on above species position index, a stand synthetic index (SSI) which shows the position of a stand on a gradient was calculated with each stand.

$$\mathrm{SSI} = \sum (a_i \times R_i) / \sum a_i$$

where a_i is the SDR of species i and R_i is the species position index of species i in a particular stand.

Soil factors were examined in correlation with the stand synthetic index (Figures 4, 5, 6, and 7). Correlation coefficients are effective as the measure of relation

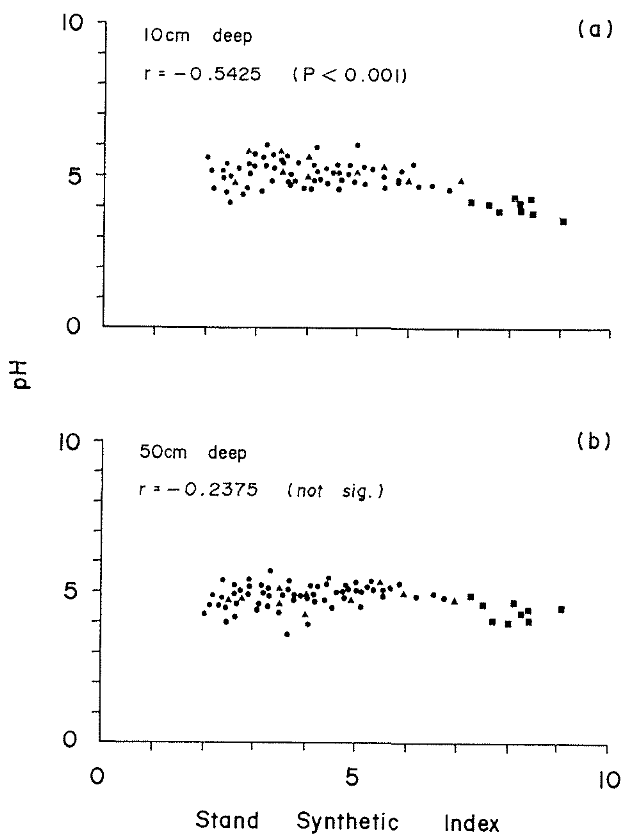

Figure 5. Correlations between soil pH and stand synthetic index. Symbols are the same as in Figure 4.

between two variables when they are related linearly (Hoel 1966). As for ignition loss, the calculation of correlation coefficient was not carried out, because neither ignition loss of A horizon nor that of C horizon had a linear correlation with the stand synthetic index. They actually reflected the difference of soil types (Figures 4 a, b). Soil pH of A horizon showed a significant negative correlation with the stand synthetic index (Figure 5 a). Soil pH is the determinant factor of the distribution of forests on particular parent materials (Eyre 1968, Whittaker 1975). For example, soils show conspicuous alkaline reaction on limestone. Mowbray and Oosting (1968) revealed that there was no remarkable causal relationship between soil pH and the distribution of forest stands in the mixed forests of the southern Appalachians, U. S. A. Because the parent material of Nopporo National Forest is not the same particular ones as Whittaker (1975) pointed out, soil pH was excluded from the prime factors determing stand distribution in the forest. Soil pH of C horizon showed no significant relationship with the stand synthetic index (Figure 5 b). Soil water content ratio of A horizon had a significant positive correlation with the stand synthetic index (Figure 6 a). Although the soil water content ratio used in the present study is sampled on a certain day in autumn;

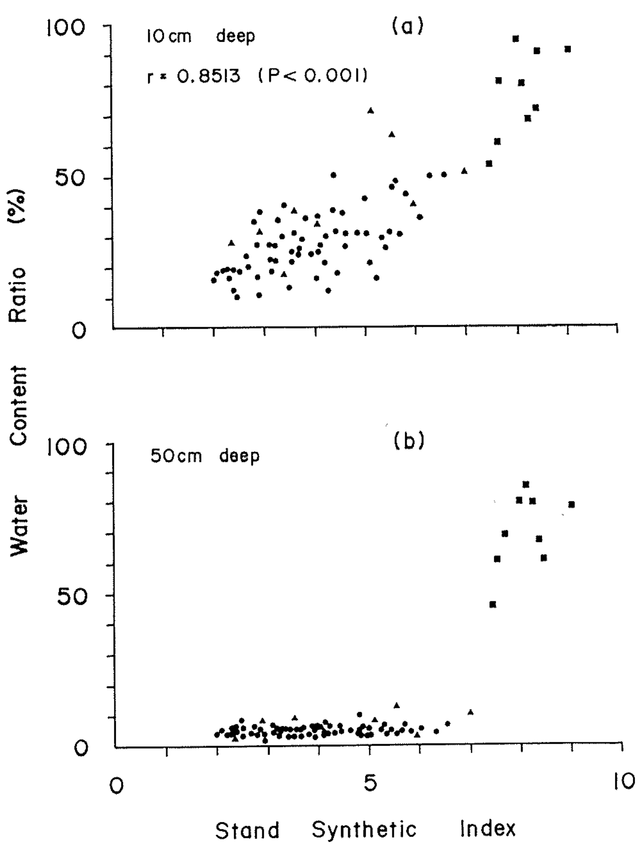

Figure 6. Correlations between soil water content ratio and stand synthetic index. Symbols are the same as in Figure 4.

this result suggests that the distribution of aged forest stands in Nopporo National Forest is primarily decided by soil water content and the dominant species are arranged along soil water gradient.

Yamamoto (1973) pointed out that the C horizon of the brown forest soil constructed by the Konopporo formation had a high water impermeability. Because the soil water content was assumed to be affected by this impermeable C horizon, the correlation between the thickness of A and B horizon, that is, the depth from soil surface to C horizon, and the stand synthetic index was examined. The depth from soil surface to C horizon did not show a significant correlation with the stand synthetic index when three soil types were examined together (Figure 7). However, as far as the brown forest soil was concerned, as shown in solid circles in Figure 7, a significant negative correlation between the depth from soil surface to C horizon and the stand synthetic index was observed ($r=-0.6342$. $P<0.001$). The results of the ordination could be summarized as follows: Stands where C horison is shallower and drainage seemed to be relatively bad have high stand synthetic index. These stands are distributed at the heads of valleys and consist of *Fraxinus mandshurica* var. *japonica* and *Ulmus davidiana* var. *japonica*. In contrast, stands where C horizon is deeper and drainage are seemed to be relatively well show low stand synthetic index. These stands are distributed in the midst of two valleys and consist of *Quercus mongolica* var. *grosseserrata* and *Abies sachalinensis*.

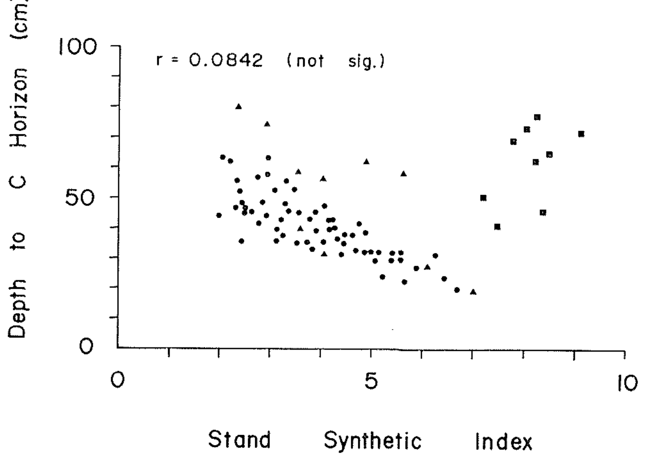

Figure 7. Correlation between the depth to water impermeable C horizon and stand synthetic index. Symbols are the same as in Figure 4.

5. Discussion

On the basis of the above ordination, the dominant species can be arranged in the following order, from dry to wet habitats; *Quercus mongolica* var. *grosseserrata* — *Abies sachalinensis* — *Tilia japonica* — *Acer mono* — *Ulmus laciniata* — *Cercidiphyllum japonicum* — *U. davidiana* var. *japonica* — *Fraxinus mandshurica* var. *japonica* — *Alnus japonica*. Tatewaki (1961) stated that the habitat of some forest communities along the contours of topography in a lower mixed forest near Lake Shikotsu was follows: communities dominated by *Q. mongolica* var. *grosseserrata*, *Q. dentata*, *Tilia japonica*, and *Acer mono* were distributed on mountain slopes; the community dominated by *U. davidiana* var. *japonica*, on small valleys; the community dominated by *Populus maximowiczii*, on alluvial plains; and the community dominated by *Alnus japonica*, on valley bottoms. Watanabe and Ishigaki (1961) also reported the distribution of dominant species and topography in the southern limit part of Mixed Forest Zone, in Hokkaido. They observed *Quercus mongolica* var. *grosseserrata* and *Abies sachalinensis* on ridges, *Tilia japonica* and *Acer mono* on steep slopes, *Fraxinus mandshurica* var. *japonica* on the lower part of slopes and valley bottoms. Considering the fact that topography gradient from ridges to valley bottoms is approximately equivalent to the soil water gradient, the results of the present study would be in agreement with those of the former studies. However, in Nopporo National Forest, the soil water gradient is strongly affected by impermeable C horizon on slopes.

Tatewaki (1958) proposed the Mixed Forest Zone which contained almost of all the lower parts of Hokkaido except for Oshima peninsula. The zone is an ecotone between temperate zone and subarctic zone and is characterized as in the following four patterns. 1): The needle-leaved or the deciduous broad-leaved forests that belong to the subarctic forests are not found in the whole area. 2): Mosaic arrangements of the needle forests belonging to the subarctic zone and those of the deciduous forests belonging to the temperate zone are found. 3): In the mixed forests, the mosaic mixture of the trees belonging to the subarctic and temperate element are seen. 4): Both in Eastern Asia and Northern Europe, the mixed forests have common genera of the ligneous flora. The second character mentioned above can be seen within a very narrow area in Nopporo National Forest. In the present study, it was showed that this mosaic arrangement does not arise from such climatic factors as Tatewaki (1958) mentioned, but results from edaphic factors, namely, the existence of water impermeable C horizon and subtle unevenness of topography in the forest. This peculiarity of the substratum affects soil water gradient, and causes the rapid replacement of the subarctic needle tree (*Abies sachalinensis*) and the temperate deciduous broadleaved trees (*Quercus mongolica* var. *grosseserrata*, *Tilia japonica*, *Acer mono*, *Ulmus laciniata*, *Cercidiphyllum japonicum*, *U. davidiana* var. *japonica*, *Fraxinus mandshurica* var. *japonica*, and *Alnus japonica*) within some ten meters as shown in Figure 3. Therefore, Nopporo National Forest is a unique miniature of the forests belonging to the Mixed Forest Zone in Hokkaido.

The regeneration process of *Abies sachalinensis* and the forest types of the species were different between ridges and heads of valleys in Nopporo National Forest (Ishihara 1933). His study revealed that this phenomenon had a close relation to L/W ratio (the ratio of soil air content and soil water content). Because the soil water gradient obtained in the present study should correlate to L/W ratio, species characteristics of all species and interspecific relationships should change along the gradient. Thus, without these informations, it is impossible to predict the change of a forest which has such environmental gradients. The authors presently intend to create a computer simulation model of the change of Nopporo National Forest which takes these informations into account. The changes of species characteristics and regeneration processes along soil water gradient will be further reported.

6. Summary

Eighty stands were surveyed in Nopporo National Forest to reveal the environmental factors that decide the distribution of aged forests. Thirteen forest communities which were recognized by the dominant species rapidly replaced by each other within some ten meters. The distribution of these communities could not be explained by topography or three soil types observed. However, by using continuum analysis (Brown and Curtis 1952), the distribution of 80 forest stands showed a good correlation with soil water content ratio of A horizon. Thus, dominant species could be arranged along the soil water gradient as follows from dry to wet habitats ; *Quercus mongolica* var. *grosseserrata*, *Abies sachalinensis*, *Tilia japonica*, *Acer mono*, *Ulmus laciniata*, *Cercidiphyllum japonicum*, *U. davidiana* var. *japonica*, *Fraxinus mandshurica* var. *japonica*, and *Alnus japonica*. This order agrees with former studies. Furthermore, it was found that forest stands were distributed with a significant correlation to the depth from soil surface to water impermeable C horizon on brown forest soil. Thus, it was concluded that the impermeability of C horizon affected the soil water gradient and caused the distinct mosaic arrangement of dominant species. This peculiarity of substratum renders Nopporo National Forest a miniature of forest belonging to Mixed Forest Zone (Tatewaki 1958).

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