

北海道中部天然林の組成と構造(2)

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論 文

Composition and Structure of Natural Mixed Forests in Central Hokkaido (II) Effect of Disturbances on the Forest Vegetation Patterns along the Topographic Moisture Gradients

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ISHIZUKA, Moriyoshi and SUGAWARA, Setsuko: **Composition and structure of natural mixed forests in Central Hokkaido (II) Effect of disturbances on the forest vegetation patterns along the topographic moisture gradients** *J. Jpn. For. Soc.* **71**: 89~98, 1989 On the basis of a national forest inventory of central Hokkaido, the effect of disturbances on the forest vegetation patterns along the topographic moisture gradients (TMGs) were studied quantitatively. Stand volume class (SVC) was used as an index of the severity of stand disturbances which resulted from selective cutting and windthrow. Specific distributions could be classified into six types by the response to a disturbance and the TMG. This diversification of specific responses to disturbances apparently enable rapid vegetation recovery of various habitats along the TMGs. Nonmetric multidimensional scale plotting of species with cluster analysis applied separately to three SVCs gave the following results: 1) the positive coexistence of eight species was recognized in the developed stands of the montane zone, 2) the disturbance of forest made the distributional segregation of these species along the TMGs. This floristic diversification along the TMGs resulting from the disturbances is considered to be a retrogression of the ecological convergence of the climatic climax forest.

石塚森吉・菅原セツ子：北海道中部天然林の組成と構造（II）地形の乾湿傾度に伴う植生パターンに及ぼす攪乱の影響 日林誌 71：89~98, 1989 北海道中部における国有林の資源現況調査をもとに、地形の乾湿傾度に伴う植生パターンに及ぼす攪乱の影響を解析した。ここでの攪乱とはおもに風害と有用材の選択的伐採が複合されたものであり、その影響度の指標として三つの林分材積クラスを設定した。乾湿傾度に伴う樹種の分布は攪乱の程度にもなって変化しており、そのパターンにはおよそ6型が認められた。攪乱に対する樹種の反応の多様性は、乾湿傾度に沿ったいろいろな立地における攪乱後の植生回復を容易にしていると考えられた。クラスター分析と併用した非計量多次元尺度構成法を林分材積クラスごとに適用した結果は、1) 山地帯の発達した森林では、8樹種（極相的針広混交林の構成要素）の高い共存性が認められるが、2) 攪乱後の森林では、樹種の分布が乾湿傾度に沿って分離化していることを示していた。攪乱による乾湿傾度に伴う種組成の分離化は、北海道中部における気候的極相林の生態的収れん（ある気候下でさまざまな立地の植生の種組成・構造が遷移に伴い均一化すること）の退行を示していると考えられた。

I. Introduction

Disturbance of vegetation often generates vegetation patterns along environmental gradients different from the original ones (4, 39). This implies that to fully understand the distribution of species along environmental gradients, one must consider disturbance effects. Recently, disturbance has been recognized as a gradient factor as well as the environmental gradients which determine the vegetation composition and structure (5, 18).

In the preceding study (12, 13), we evaluated the severity of disturbances, which resulted from complex of windthrow and selective cutting, on the forest stands of central Hokkaido, and conducted a quantitative analysis of the vegetation response to disturbances along the elevational gradient. They showed that the distributional mode of the specific dominance along the elevational gradient changes in response to the

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severity of the disturbances, and that intensive disturbance results in a distinct change in the elevational zonation and makes it difficult for the climax species to recover, especially in the subalpine zone.

The topographic moisture gradient (TMG) is another major environmental factor affecting the occurrence and dominance of species (14, 26, 35), but vegetation response to disturbance along the TMG hardly has been discussed except for a few recent studies. ROMME and KNIGHT (21) reported that the composition of the subalpine forest in Wyoming (U. S. A) is determined by the frequency of fires and the rate of secondary succession after the fires along the TMG. HARMON *et al.* (5) indicated that disturbance gradients potentially influence and are influenced by the complex environmental gradients of WHITTAKER's original models (35). Our concern in this problem is that if the climatic climax forest occurs in a region by ecological convergence, how does it change after disturbance in relation to the TMG. Does divergence of vegetation along the TMG occur following disturbances? The objectives of this paper are to show how the species distribution and coexistence along the TMG change after forest disturbances in central Hokkaido and to assess the disturbance effect on the vegetation pattern along major environmental gradients under the disturbance regime of this area.

II. Data and Methods

The area of this study is shown in Fig. 1. The forest resources census data of 1976-79, provided by the Hokkaido Regional Forestry Office, were used for the analysis. A detailed description of the data was given in the preceding report (12). In this study, the data of 260 stands, at 100-1,000 m of elevation, on brown forest soils with six types (3) were adopted. The survey plot was 50 m × 20 m in size, and all trees larger than 5 cm in dbh (diameter at breast height) were measured. Soil types were determined indirectly by referring to 1/20,000 soil maps of the Forestry Agency.

1. Classification of stands into severity classes of disturbance

The disturbances prevailing on the stands analyzed were those of the complex disturbances of intensive selective cutting from 1942 (World War II) to 1953 and the windthrows of 1954 (31, 32), especially, the typhoon in September 1954 which brought great damage to the mountain forests of central Hokkaido (30). Although there are natural and artificial causes for disturbances, it is almost impossible to distinguish between them precisely by the stand structure because they overlap each other and are similar in effects on the structural changes of stands (20, 24). Both selective cutting and windthrow tend to remove the overstory and release the understory. If examined in detail, however, windthrow damages conifers in the

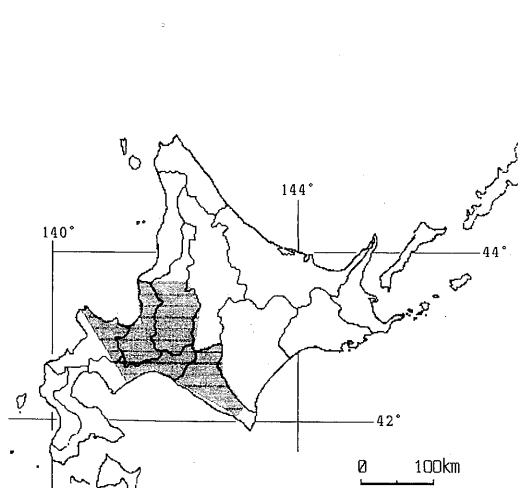


Fig. 1. Map of Hokkaido
The study area is shadowed.

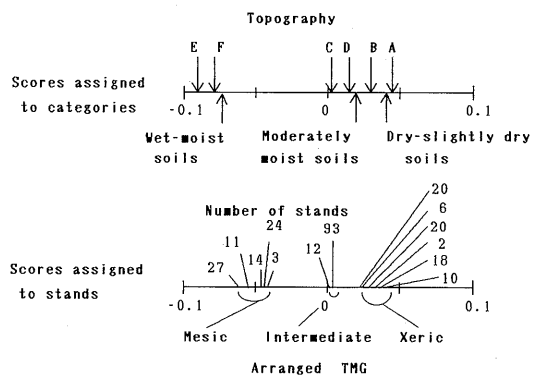


Fig. 2. The scores assigned to both the nine site-categories and 260 stands in the first dimension (maximum eigen value) by HAYASHI's pattern analysis

Maximum eigen value is .886. Explanations of symbols of topography are given in the text.

overstory more heavily than it does hardwoods. While the target trees of the selective cuttings were both conifers and hardwoods generally larger than 30-40 cm in dbh, some hardwood species, such as *Betula ermanii*, *Ulmus* spp., and *Alnus hirsuta* tended to be excluded from selective cuttings (12, 31). Another reason which makes it difficult to make a distinction between these two disturbances is that not only the wind-damaged trees but also some of the undamaged trees were taken from the wind-damaged stands by logging for commercial use and the prevention of outbreaks of harmful insects (30). Accordingly, it is considered to be impossible to analyze separately these two types of disturbances over a large area of the forests of central Hokkaido.

To make the stands approximately homogeneous in the severity of disturbances, all of the stands were divided into the following stand-volume classes (SVCs) :

Class	Stand-volume	Number of stands
SVC-1	10-100 m ³ /ha	67
SVC-2	101-200 m ³ /ha	117
SVC-3	201-470 m ³ /ha	76

In the preceding paper (12), we found that these three SVCs represented the three levels of the severity of disturbances of the stands analyzed here. The number of large diameter stems (dbh > 30 cm) decrease in the order of SVCs-3, -2, and -1. Large diameter stems, which were removed extensively by selective cutting or windthrow, mostly disappeared in SVC-1. The proportion of number of the climax species in all dbh classes increased in the order of SVCs-1, -2, and -3. On the contrary, that of the pioneer or seral species, especially in the small dbh classes (5 cm < dbh = < 11 cm), increased in the order of SVCs-3, -2, and -1. These features of the compositions of SVCs indicate that SVC can be regarded as the index of the severity of disturbances. The details of the compositions of the three SVCs and the verification of SVC as an index of the severity of disturbances were given in the preceding paper (12).

2. Classification of stands into SVCs in terms of topographic moisture conditions

To plot the stands along the TMC we applied HAYASHI's pattern analysis (Quantification Method Type III) (6, 29) using topography and soil moisture conditions. Here, the topography was classified as follows :

- A: Peaks
- B: Ridges or upper part of concave slopes
- C: Rounded or flat summits
- D: Mid-slopes
- E: Deposit surfaces on the lower part of slope
- F: Eroded surfaces on the lower part of slope

According to the classification of forest soils in Japan (3), six soil types ; namely, BB, BC, BD_(d), BE, and BF were grouped, depending on moisture conditions, as follows :

Dry to slightly dry soils : BB, BC, and BD_(d).

Moderately moist soils : BD.

Wet-moist soils : BE and BF.

Then nine categories (six topographic types and three soil moisture conditions) and the 260 stands were plotted by HAYASHI's pattern analysis (6, 29). As shown in Fig. 2, the scores assigned to stands of the first dimension (maximum eigen value) indicate that the stands could be grouped into three classes according to the TMG. Each class consisted of the following topography and soil types :

TMG	Topography	Soil type
Xeric	A, B, C, D	BB, BC, BD _(d)
Intermediate	C, D	BD
Mesic	D, E, F	BE, BF

Mean elevations of stands of the nine classes (3 TMGs × 3 SVCs) were scattered around 450 m, and the differences in the distributional locations of the stands' elevations among them were not significant by the KRUSKAL-WALLIS test (29, 36) (Table 1).

3. Direct gradient analysis

Table 1. Mean elevation (m) of stands with deviations (s.d.) of nine SVC-site classes

Site		Stand volume class		
		SVC-1	SVC-2	SVC-3
Xeric	mean	486.7	402.1	481.4
	s. d.	167.7	143.3	241.3
Intermediate	mean	541.5	427.2	432.1
	s. d.	238.5	194.8	180.3
Mesic	mean	396.1	427.2	508.1
	s. d.	177.1	194.8	226.0

Notes: The differences in the locations of the elevational distributions in the nine SVC-site classes was not significant at the 5% level by the KRUSKAL-WALLIS Test.
 Test statics of KRUSKAL-WALLIS = 13.577
 Upper probability = 9.35 %

Table 2. Species names and symbols

Species names	Symbols
<i>Abies sachalinensis</i>	As
<i>Acer mono</i>	Am
<i>Alnus hirsuta</i>	Ah
<i>Betula ermanii</i>	Be
<i>B. maximowicziana</i>	Bm
<i>Cercidiphyllum japonica</i>	Cj
<i>Fraxinus lanuginosa</i>	Fl
<i>F. mandshurica</i> var. <i>japonica</i>	Fm
<i>Kalopanax pictus</i>	Kp
<i>Magnolia obovata</i>	Mo
<i>Ostrya japonica</i>	Oj
<i>Phellodendron amurense</i>	Pa
<i>Picea jezoensis</i>	Pj
<i>Quercus mongolica</i> var. <i>grosseserrata</i>	Qm
<i>Tilia japonica</i>	Tj
<i>Ulmus</i> spp.	Us

The 16 major species (Table 2) which dominate the volume of the vegetation of central Hokkaido (12) were analyzed. As an expression of species abundance, we adopted a relative importance value (RIV). The importance value (IV) used here is defined as the sum of the relative density (%) and the relative dominance (%) based on volume. It avoids the arbitrary evaluation of species importance by combining them into a measure which has a strong linear correlation with both of them (for relative density $r = .87-.98$; for relative dominance $r = .75-.95$). The RIVs of species in a stand are obtained by dividing the importance values of species by the sum of the importance values for all the species in the stand (14). Then specific mean values of RIVs were calculated for each class of stands.

The interaction of the elevational gradient and the TMG was examined. Stands of each TMG in each SVC were divided into the following three elevation classes (ECs): 100-399 m, 400-649 m, and 650-1,000 m. The elevational ranges of the ECs were established as described in the preceding paper (12). Then the mean RIVs of the 16 species were computed for each EC of each TMG in each SVC. KENDALL's coefficient of concordance (29, 36) on the specific mean RIVs along the TMG of the three ECs then were computed for each SVC (Table 3). KENDALL's coefficient of concordance is an expansion of SPEARMAN's rank correlation coefficient for multiple samples. With total agreement on the rank orders of RIVs along the TMGs of the three ECs, it takes the value of 1, whereas with complete disagreement it has the value of 0. As shown in Table 3, most of species fairly well agreed with the rank orders of RIVs along TMGs among the three ECs except for *Abies sachalinensis* in SVCs-2 and-3, and *Picea jezoensis* in SVC-1. For other species, we confirmed graphically that there were no important differences in the specific mean RIVs on TMGs among the three ECs. Accordingly, we conducted a direct gradient analysis along TMGs without dividing the ECs except for the above two species.

4. Ordination techniques for species

The following procedure for species ordination was adopted. First, MORISITA's $C\delta(p)$ (17) values for each pair of species were computed for each SVC based on the 260 stands. $C\delta(p)$ is an index of interspecific overlapping based on coverage. However, a RIV was adopted here for coverage. Then KRUSKAL's nonmetric multidimensional scaling (MDS) (15, 25) was applied to the $1 - C\delta(p)$ matrix of each SVC to assign the 16 species to the two dimensions. The initial configuration, to avoid the local minimal of stress in MDS computation, was given by eigen vectors of HAYASHI's Quantification Method Type IV (6, 29) applied to the $C\delta(p)$ matrices. Next, to provide a more precise representation of the relationships between species, group

Table 3. KENDALL'S coefficient of concordance on the distribution of mean relative importance values along the TMGs of the three ECs

Species	SVC-1	SVC-2	SVC-3
<i>Abies sachalinensis</i>	.78	.11	.11
<i>Acer mono</i>	.78	.78	.55
<i>Alnus hirsuta</i>	.78	.78	.55
<i>Betula ermanii</i>	.50	.55	.78
<i>B. maximowicziana</i>	1.00	.55	.78
<i>Cercidiphyllum japonica</i>	1.00	1.00	.67
<i>Fraxinus lanuginosa</i>	1.00	.75	.75
<i>F. mandshurica</i>			
var. <i>japonica</i>	1.00	.55	.78
<i>Kalopanax pictus</i>	.78	.50	.75
<i>Magnolia obovata</i>	.78	.75	.75
<i>Ostrya japonica</i>	1.00	1.00	1.00
<i>Phellodendron amurense</i>	.67	.44	1.00
<i>Picea jezoensis</i>	.11	.78	.78
<i>Quercus mongolica</i>			
var. <i>grosseserrata</i>	.78	1.00	.78
<i>Tilia japonica</i>	.75	.75	.78
<i>Ulmus</i> spp.	.78	.78	.55

mesic sites, especially in the developed stands (SVC-3). In the disturbed stands (SVC-1), however, it had little larger RIVs on xeric sites than on mesic sites at elevations less than 650 m.

3) *Quercus mongolica* var. *grosseserrata*, *Acer mono*, and *Tilia japonica*: RIVs of these species were relatively constant along TMGs and among all SVCs. *A. mono*, however, had little larger RIVs on both xeric and mesic sites in the disturbed stands (SVCs-1 and 2).

4) *Betula ermanii*, *Ostrya japonica*, *Magnolia obovata*, and *Fraxinus lanuginosa*: These species had increased RIVs on relatively xeric sites throughout all SVCs. Also *B. maximowicziana* had the largest RIVs on xeric sites except in developed stands (SVC-3).

5) *Cercidiphyllum japonica*, *Alnus hirsuta*, *Fraxinus mandshurica* var. *japonica*, and *Phellodendron amurense*: These species had increased RIVs on mesic sites especially in disturbed stands, except for *F. mandshurica* var. *japonica*. Also *Kalopanax pictus* had an intermediate tendency between these species and those species listed under 3) above.

6) *Ulmus* spp. and *B. maximowicziana*: These species have different dominating habitats along TMGs among SVCs. *U.* spp. (*U. davidiana* var. *japonica* and *U. lauciniata*) had the largest RIVs on mesic sites, and large values on xeric sites in intensely disturbed stands. *B. maximowicziana* had the largest RIVs on xeric sites in disturbed stands and on mesic sites in developed stands.

2. Coexistence patterns of species in relation to disturbances

The nonmetric MDS assignments of the 16 major species to the clusters, revealed by the cluster analysis (Fig. 6), are shown for each SVC in Fig. 5. The results of the direct gradient analyses of the elevational gradient in the preceding paper (12, 13) and of the TMGs in the present study support the fact that these 2-dimensional spaces consist of the altitudinal gradient and the TMG. In the ordination for the developed stands, all species, except for *F. mandshurica* var. *japonica* tended to gather around the center of the scales making large clusters. On the contrary, species were scattered widely, especially along the TMGs, in the ordination for the intensively disturbed stands (SVC-1). In other words, the floristic differentiations along the TMGs were distinct in the intensively disturbed stands. The ordination for SVC-2 showed an intermediate aspect between SVC-1 and SVC-2.

average clustering (29) was applied to the $C\delta(p)$ matrix.

III. Results

1. Changes in the specific distribution along the TMG by disturbance

Changes in the RIVs of the 16 species along the TMG are shown for each SVC in Fig. 3 without dividing the ECs. Figure 4 presents the differences of distribution among three ECs for *A. sachalinensis* (SVCs-2 and 3) and *P. jezoensis* (SVC-1) which have small coefficient of concordance values. The species responses to the disturbances in relation to the moisture conditions of the sites are summarized as follows:

1) *A. sachalinensis*: This species was rather constant in RIVs along TMGs in the less-disturbed stands (SVCs-2 and 3), but its RIVs greatly decreased on mesic sites in intensively disturbed stands (SVC-1). As is obvious in Fig. 4, the differences in rank order of RIVs along TMGs among ECs were insignificant.

2) *P. jezoensis*: This species dominated on

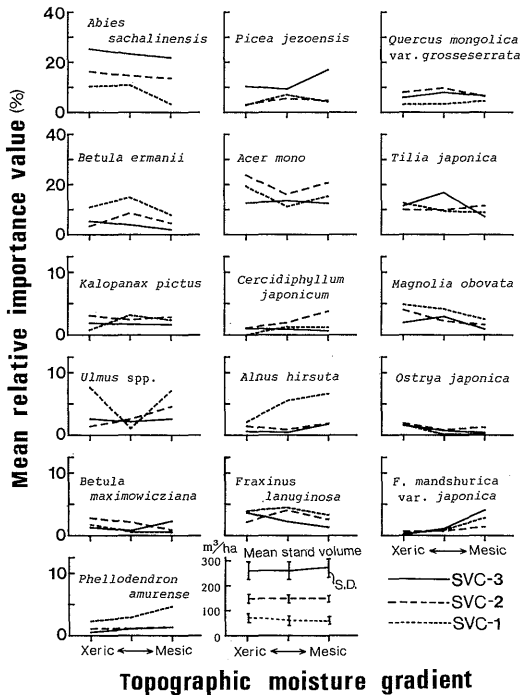


Fig. 3. Mean relative importance values (RIVs) of the 16 major species along the topographic moisture gradient (TMG) in the three SVCs

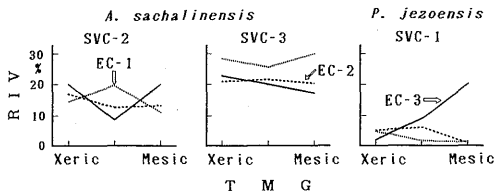


Fig. 4. Mean RIVs along the TMG in three ECs for *A. sachalinensis* (SVCs-2 and 3) and *P. jezoensis* (SVC-1)

EC-1: 100-399 m; EC-2: 400-649 m; EC-3: 650-1,000 m in elevation.

are established immediately after disturbances (38); therefore, an abundant number of their stems had small diameters in SVC-1 (12). Consequently, the increase of their RIVs in SVC-1 is regarded as the effect of both selective cutting and their development after disturbances as pioneers.

2. Species responses to disturbances along the TMG

In this study we recognized six types of species which are distinctly different in the pattern of response to disturbances and TMGs. Moreover, these species have strategy quite different from each other in survival systems such as in seed-dispersal patterns, seedling establishing processes, regeneration systems featuring sprouts or root suckers, and so forth (34, 38). Such diversification of the specific responses to disturbance apparently enable the rapid vegetation recovery on various habitats along the TMGs by regenerating patches by the various strategies (19). For example, *A. sachalinensis* dominates the various topographic

IV. Discussion

1. Effect of the disturbance complex of selective cutting and windthrow on specific RIVs after disturbance

The disturbances prevailing on the stands occurred 22-37 years before the survey was made. Especially, the serious disturbance by the typhoon in 1954 occurred 22-27 years before. According to the records of the secondary succession on the wind-damaged stands in central Hokkaido (7, 8, 23, 33), most of the small diameter stems (5 cm < dbh = < 11 cm) in SVC-1 were ingrowth from the advanced seedlings or the replacements established immediately after the disturbance and whose dbh had become larger than 5 cm. As shown in the preceding paper (12), the number of large diameter stems (dbh > 30 cm), except for some hardwood species, greatly decrease in SVC-1, so that the specific RIV in SVC-1 expresses more directly the abundance of small diameter stems developed after the disturbance as compared with those in SVCs-3 and -2.

Although selective cutting is similar to windthrow in the effect on the structural change of a stand, there are some differences between them in the effect on the specific RIV after a disturbance. The large decreases in the RIVs of *A. sachalinensis* and *P. jezoensis* in SVC-1 are thought to have been affected considerably by windthrow, because windthrows in 1954 more seriously damaged conifers than hardwoods (30), whereas selective cutting usually left the large trees of some hardwood species such as *B. ermanii*, *U. spp.*, *A. hirsuta* and *P. amurense* (12, 31). As a result, the number of stems of these four species with large diameters (dbh > 30 cm) were not very different among SVCs (12). Hence, selective cutting increased their RIVs. But these are pioneer or seral species which

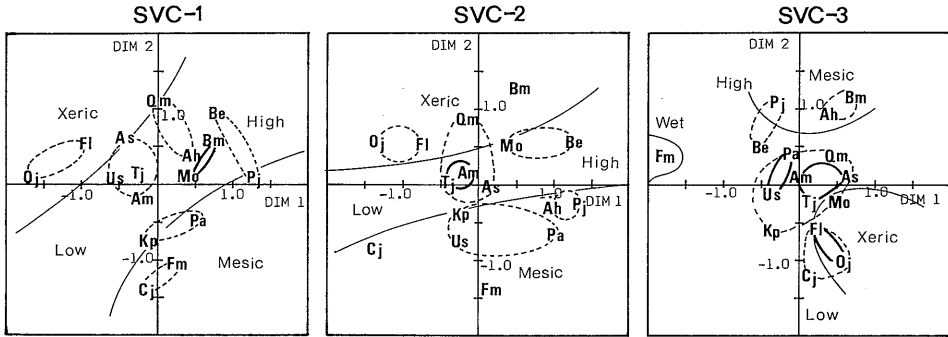


Fig. 5. Two-dimensional ordinations of the 16 species by non-metric MDS for the three SVCs

Lines connecting species show a cluster of species revealed by the group-average clustering. Clusters are divided by the mean $C\delta(p)$ values of .25 (-----) and .50 (—). Lines dividing species indicate the moisture conditions of the habitat based on the direct gradient analysis. “High” and “Low” indicate elevational gradients.

Stresses of ordination are .235 (SVC-1), .204 (SVC-2), and .168 (SVC-3).

Species names and symbols are given in Table 1.

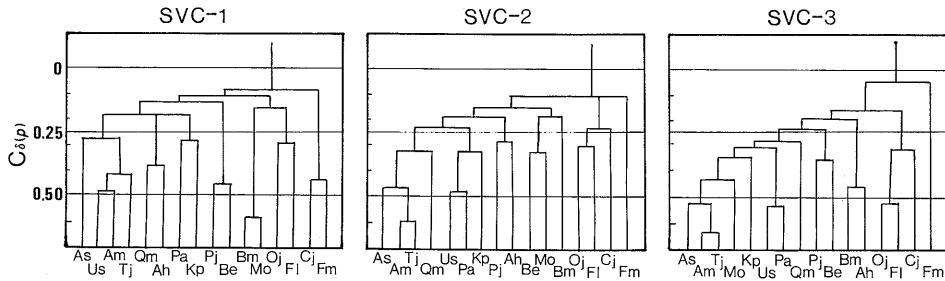


Fig. 6. Group-average clustering dendrogram of the 16 species based on the $C\delta(p)$ matrix

Species names and symbols are given in Table 1.

features in the climax state. After a disturbance however, its RIVs decrease greatly on mesic sites because it regenerates less successfully than on xeric sites for such reasons as interference by competing vegetation (37). On the contrary, some pioneer or seral species, such as *A. hirsuta*, *P. amurense*, and *C. japonica*, regenerate immediately after a disturbance on mesic site. Because they are fast-growing species in their early years, they can escape rapidly from the competing vegetation. *C. japonicum* makes it possible by sprouting, but *A. hirsuta* and *P. amurense* regeneration originates from seeds which are dispersed by wind and birds, respectively. Thus the vegetation recovers quickly by regenerating patches by various strategies.

B. maximowicziana and *U. spp.* may select habitats in the developed stands different from those in disturbed stands. Previous reports concluded that the habitats of the former were “mainly in the valley” (26) or “on a mesic site” (16). Foresters, however, had noted that this species regenerates more frequently on ridges or southern slopes (28). The result of this study showed that it dominates on mesic sites in developed stands and on xeric sites in disturbed stands. Probably, it regenerates almost everywhere but more abundant-

ly on xeric sites. However, with maturity it is dominant on mesic sites. According to ISHIZUKA *et al.* (10, 11), seedlings of this species are abundant on disturbed sites with mineral soils exposed by logging but scanty on sites having less-disturbed soil conditions, although the growth rate of seedlings on the latter is 5-10 times greater than that on the former. This suggests that the dominating habitat of this species changes with development of the stands. SANADA and SHIOZAKI (22), however, reported that large trees of this species still remain on steep and relatively xeric slopes in the headwater of the Hidaka District, in the southern part of central Hokkaido. This may be due to the effect of past disturbances, such as the selective cutting along the valley especially during World War II (31).

3. Disturbance effects on vegetation patterns along environmental gradients in central Hokkaido

Nonmetric MDS ordination of species for the three SVCs indicates the underlying importance of disturbances to the patterns of species coexistence along environmental gradients. In the developed stands, the positive coexistence of eight species was recognized around the centers of ordination (Fig. 5) composed of *A. sachalinensis*, *Q. mandshurica* var. *grosseserrata*, *A. mono*, *T. japonica*, *K. picatus*, *M. obovata*, *U. spp.*, and *P. amurense*. These are the same main species which comprise TATEWAKI's "pan-mixed forest" (27) and the climatic climax forest which characterizes the montane zone of Hokkaido (34). After disturbance, however, distributional modes of these species are segregated along the TMG (Figs. 3 and 4), which means that the floristic differentiations along the TMGs become distinct in response to disturbances. This differentiation

in habitat selection of species following disturbances is considered to be evidence of retrogression of the ecological convergence in this climatic climax forest.

Ecological convergence is one of the ideas of the mono climax theory (2) meaning that vegetation occupying all site types within a given climatic region will continue to develop towards the same end point over periods of several centuries (14). According to KIMMINS (14), BOTKIN (1) challenged this idea by presenting evidence of major changes in climate and vegetation in North America over periods considerably shorter than that required for complete ecological convergence. However, the climatic climax forest described here is not a mono-species dominated forest but a mixed forest of several species, including mid-seral species, on different types of seres reflecting the micro-habitat (9). It is thought to be easy, not to converge toward a monospecies forest but to converge toward this mixed-species forest.

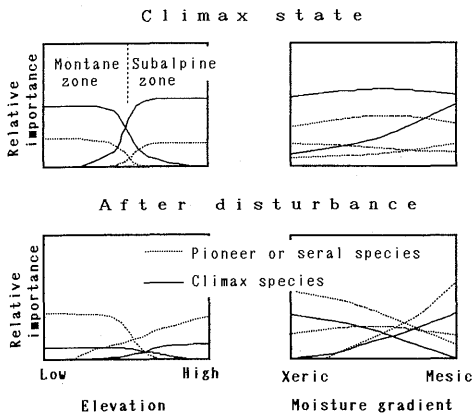


Fig. 7. Schematic representation of the disturbance effect on the vegetation pattern along environmental gradients

From the results of the preceding papers and the present study, the effects of the disturbances caused by windthrow and selective cutting on the patterns of forest vegetation in central Hokkaido are concluded to be a disorder of the elevational zonation and floristic diversification along the TMG. After disturbances of the climatic climax forest, the floristic differences along the elevational gradient (elevational zones) became obscure, whereas along the TMG it became distinct (Fig. 7). Thus the vegetation pattern along environmental gradients in central Hokkaido were altered by disturbances. This means that to fully understand the vegetation patterns along environmental gradients one must consider disturbance effect.

Acknowledgment

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* In Japanese with English summary

** Only in Japanese

*** Not referred to directly

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