

# NATURAL AND SEMI-NATURAL VEGETATION IN JAPAN<sup>1)</sup>

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<sup>1)</sup> Contribution from JIBP-CT No. 34 supported by the special research project 'Studies on the dynamic status of the biosphere' sponsored by the Ministry of Education.

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## I. INTRODUCTION

Studies on the composition of the forests and other vegetation of Japan were initiated by J. Tanaka (1887) in the Meiji Era. According to his introduction his field survey started in 1879 and resulted into a classification of vegetation zones (forest zones), mainly of the lowland, based on physiognomy and dominant species. In later years some other major proposals of the vegetation zonation were made. Honda (1900) distinguished also altitudinal zones, based on his survey on dominance, and provided it with the first vegetation map. Nakano (1942—1943) stressed the physiognomy combined with species composition, sociology, and succession but did not produce a map. Kira (1949) described the forest zones of Japan stressing the climax concept and correlating ecology mostly with temperature; he added a map. Miyawaki (1967) wrote a large book (provided with a map) on the vegetation of Japan in which the climax concept played an important role, as it did in the study by Suzuki (1966a) who partly tried to integrate actual vegetation with climax types, paying great attention to the sociological aspect; he gave also a coloured map. Miyoshi (1903) introduced in Japan the study of plant communities and some years later (1907) the study of ecology, and these two disciplines have been pursued by the research schools of his pupils, Nakano at Tokyo University, Yoshii at Tohoku University, etc. A large number of papers have resulted in these two fields of vegetation study, mainly published in the Botanical Magazine, Tokyo (Botanical Society of Japan, 1887—), Japanese Journal of Botany (Japan Science Council, 1922—), Journal of Japanese Botany (Tsumura Laboratory, 1926—), Acta Phytotaxonomica et Geobotanica (Kyoto University, 1932—), Ecological Review (Tohoku University, 1935—), Bulletin of the Japanese Society of Plant Ecology (Tokyo University, 1941—1943), Physiology and Ecology (Physiol. & Ecol. Publish. Ass., Kyoto, 1947—), Hikobia (Hiroshima University, 1950—), Bulletin of the Society of Plant Ecology (Tohoku University, 1951—1954), Hokuriku Journal of Botany or Journal of Geobotany (Kanazawa University, 1952—), Japanese Journal of Ecology (Ecological Society of Japan, 1954—), etc.

Besides the papers in these journals, science reports of universities have contributed to the development of ecological studies in Japan. A historic review of plant ecology in Japan and basic concepts, principles, and methodologies of ecology was given by Numata (1953, revised edition 1967) and a very brief bibliography of the literature concerned was published in 'Ecology' (Numata, 1958).

The purpose of this paper is to describe briefly the entire picture of Japanese vegetation

with reference to the more important recent studies. Such overall aspect has been strongly requested by many foreign botanists, ecologists, and geographers, and the first author keenly realized the desirability of a concise summary of Japanese vegetation when he gave a brief lecture at the Department of Geography, University of Kansas (Prof. A. W. Küchler) and the Department of Botany, University of Illinois (Prof. L. C. Bliss) during his stay in 1967. Moreover, the recommendation of Prof. Dr. C. G. G. J. van Steenis whom we met at the 11th Pacific Science Congress in Tokyo in 1966 has led to the completion of this paper. The first author, attending an IBP-CT Meeting at Monks Wood, England 1965, to discuss the check sheet for reserved areas, submitted (with Itow) a paper 'Outline of vegetation and natural environment of Japan'. From this working paper the present critical compilation has emanated.

## II. PLANT LIFE AND ITS ENVIRONMENT IN JAPAN

The *climate* of Japan is temperate in a wide sense, though it is arctic or subarctic in northern Japan and highlands, particularly in winter, and subtropical in southwestern Japan, particularly in summer. The four major islands of Japan proper, Hokkaido, Honshu, Shikoku, and Kyushu are located between 30° and 45° NL, the Ryukyu and Bonin Islands extending further south almost to the Tropic of Cancer. Thus, the Japanese realm is a long chain of islands ranging over *c.* 22° of latitude.

Even in Tokyo at 36° NL it is rather cold in winter, and hot like in the tropics in summer. In summer the lowlands in southwestern Japan are hotter than those in Taiwan, and in winter the Tohoku District at about 40° NL is colder than northern Europe at 60° NL (Ministry Agr. For., 1961).

The distinction of the four seasons is, in general, very clear, though the periods of spring and autumn are rather shorter in the northern part. Weather and climate are variable and differ locally. Japan as a whole is under the influence of a monsoon climate. The southeast monsoon wind in summer brings a large amount of rain on the Pacific side, and the northwest monsoon wind in winter brings a large amount of snow on the Japan Sea side and in Hokkaido (Nemoto *et al.*, 1959).

There are mainly two types of climate, the Pacific type and the Japan Sea type, because of the above-mentioned influences of monsoon and the backbone mountain ranges running through the four major islands. These climatic types appear clearly from the climate diagrams (Fig. 1).

The mountainous topography often begins from the sea coast. Lowland plains are very few and valleys are deeply dissected. Rivers are mostly short and swift and even the longest river in Japan, the Shinano River, is only 369 km. Of the Japanese land 77 % is between 0 and 700 m altitude, 18 % is between 700 and 1300 m, and 5 % is highlands over 1300 m. The inclination of slopes is rather steep, being over 30° in 24 % of the land, 30°–15° in 31 %, and less than 15° in 45 %. The geomorphology is very complicated.

As principal characteristics of the Japanese climate, the annual mean temperature is from 0° C (central Hokkaido) to 18° C (southern Kyushu), the annual precipitation is 600 mm at the minimum (northeastern Hokkaido) and about 4,000 mm at the maximum (Odaigahara in Kinki District in southern Honshu and Yaku Island south off Kyushu).

The average annual precipitation in Japan proper is 1,600 mm which is a high figure compared with other parts of the world at comparable latitudes and testimony of an oceanic climate.

The frostless period in the lowlands is from 125 days in northeastern Hokkaido to 275

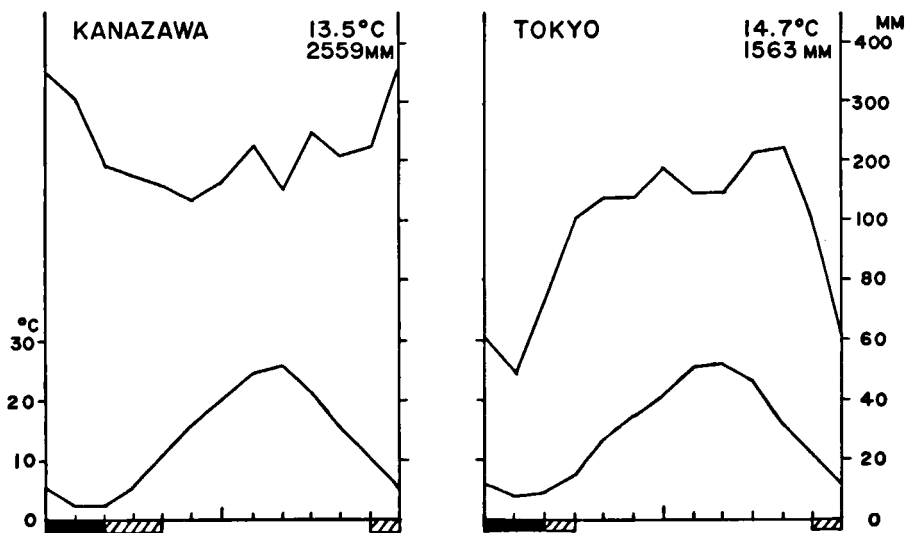


Fig. 1. Paired climate diagrams of the Japan Sea type (left) and the Pacific type (right), both lowland stations. The U-shaped curve of the precipitation distribution is characteristic to the Japan Sea type and the reversed U-shaped curve is that of the Pacific type. Scales for temperature and precipitation are on left and right hand respectively. The black bar indicates the months with mean minimum temperature below 0 °C, and the hatched bar indicates the months with the absolute minimum temperature below 0 °C. Mean annual temperature and annual precipitation are given in the right-top of the diagram.

days in southern Kyushu and 300 days in southern Kinki (central Honshu) and Shikoku.

A distinct dry season between the summer monsoon rain ('Bai-u', in June-July) and the typhoon season (in September-October) appears in the area from the lower reaches of the Yangtze to central Honshu.

Not only the amount of annual precipitation, but the seasonal distribution of rainfall in particular is important for plant life (Numata and Mitsudera, 1961). According to the record the maximum rainfall per 24 hrs. (Nemoto et al., 1959) was 200 mm in Hokkaido and 500 mm in southern Shikoku and Kyushu; there are occasionally exceptional figures, such as a record of over 1,100 mm per 24 hrs. in a local rain-storm at Isahaya-shi, Kyushu, on 25 July 1957.

The climate in Japan has been classified into several types based on the conditions mentioned above (Fukui, 1933; Sekiguchi, 1959). Such classifications become rather complicated by the topography which makes application to the various local situations difficult.

According to Köppen's climatic types, Hokkaido is Df and others are almost Cf in the lowland. According to Fukui's classification Japan is divided into three regions, viz. northern Japan (Hokkaido, except its southwestern Oshima Peninsula, having more than 4 months under 0° C monthly mean temperature), central Japan (under 20° C mean temperature and less than 3 months under 0° C in monthly mean temperature), and southern Japan (Ryukyu and Bonin Is., over 20° C in annual mean temperature), all figures derived from lowland records.

Regarding phenology, the average flowering date of for example *Prunus yedoensis* (a



spring-flowering plant) is 31 March in southern Kyushu, 10 May in the greater part of Hokkaido; the flowering date of (autumn-flowering) *Miscanthus sinensis* is early in July in Hokkaido, at the beginning of October in southern parts of Kinki, Shikoku, and Kyushu. This phenomenon is mainly due to the temperature differences and day-length effect between north and south.

The environment for plant life should be measured regarding its factors working during the vegetative season. Kira (1949) conceived a kind of accumulated temperature index, the *warmth index* (W), i.e.  $W = \sum (t - 5)$  for the lowland. W is an accumulated temperature of monthly mean temperature as the base temperature is, in general, equal to 5° C. The climatic classification of Japan by the warmth index is shown in Table 1.

Table 1. The climatic regions of Japan after Kira (1949)

Climatic region	Warmth index	Area	Latitude
Subarctic	15—(45—55)	N. E. Hokkaido	43—45°
Cool-temperate	(45—55)—85	S. W. Hokkaido and Tohoku	37—43°
Warm-temperate	85—180	Kanto-Kyushu	30—37°
Subtropical	180—240	Ryukyu Is. and Bonin Is.	24—30°

Kira also defined a *coldness index* (C) =  $\sum (5 - t)$  and mentioned that the *Castanea crenata* zone is an intermediate zone between the evergreen *Quercus* zone and that of the *Fagus crenata* zone, covering the zone over 85 in W and over 10—15 in C.

Reversely, Nakamura (1954) maintained that forests of *Pinus densiflora*, *Quercus serrata*, *Castanea crenata*, *Albizia julibrissin*, etc. are established at the sites of fire and should not be used as indicators of classifying forest zones.

Schmithüsen (1965, private comm.) classified Japanese climatic zones from the standpoint of a European geographer (Table 2).

Table 2. Another classification of Japanese climatic zones after Schmithüsen (1965, private comm.)

Climax	Climatic zone	
Evergreen needle-leaved forest	Temperate	Cold-temperate
<i>Fagion crenatae</i>		Cool-temperate
<i>Tsugion sieboldii</i>		Warm-temperate (Sub-mediterranean)
<i>Shiion sieboldii</i> <i>Sclerophyllous forest</i>	Subtropical	True-mediterranean

As secondary communities, such as pine forests, grasslands, etc. occupy considerable surfaces, their correspondence to climax and climate should also be considered (Table 3).

Table 3. Grassland vegetation zones in Japan (Numata 1961a, 1969)

Climate	Climax	Meadow	Pasture
Subarctic	Evergreen needle-leaved forest	Sasa -Miscanthus	Poa pratensis
Cool-temperate	Deciduous broad-leaved forest	Miscanthus	Zoysia japonica
Warm-temperate	Evergreen broad-leaved forest	Miscanthus -Pleioblastus	Pleioblastus -Zoysia

As stated before, precipitation is sufficient to allow the development of forest throughout Japan except in the alpine zone where the low temperature is the limiting factor. Thus, altitudinal and latitudinal zonation of vegetation in Japan are largely dependent upon temperature conditions.

Climatic climaxes are physiognomically recognized as evergreen broad-leaved forest in the warm-temperate zone, summergreen broad-leaved forest in the cool-temperate, evergreen needle-leaved forest in the subarctic and subalpine, and scrub communities in the alpine zone.

The first three of these climaxes are phytosociologically understood as the *Camellietea japonicae*, the *Fagetea crenatae* and the *Vaccinio-Piceetea japonica* respectively. The fourth, which is the *Pinus pumila*-dominated scrubland, also belongs phytosociologically to the *Vaccinio-Piceetea japonica*.

These climatic climaxes do not prevail in the whole area of each climatic zone, but minor natural communities are developed on edaphically, topographically, and micro-climatically delimited habitats.

The regional subdivisions of Japan here are made according to the range of each climatic climax, that is, the *Camellietea japonicae* region where the climatic climaxes belong to the *Camellietea japonicae* and minor natural communities are also developed according to habitat variations. In other words, the *Camellietea* region is physiognomically characterized by the evergreen broad-leaved forests and climatically by the warm-temperate climate. The *Fagetea crenatae* region is the summergreen broad-leaved forest region and is cool-temperate; the *Vaccinio-Piceetea japonica* region is the evergreen needle-leaved forest region and is the subarctic and subalpine zone.

Latitudinally, the Japanese territory does not extend to the arctic, but altitudinally to the alpine zone. Fig. 2 is the map that shows the ranges of the four regions mentioned above. A north-south cross section of the Japanese Archipelago is given on the left of Fig. 2.

The classification of vegetation regions stated above is usually based on the presence or absence of a special vegetation type. On the other hand, local characteristics are shown by the difference of growth and productivity of widely distributed vegetation all over the country, for example, the *Miscanthus sinensis* type of grassland. The physiological zero point of the perennial *Miscanthus sinensis* is 10° C daily mean temperature and the

end of its growing season is decided with the flowering date. The growing period is 60 days in northeastern Hokkaido, 100 days in Tohoku, 160 days in Kanto and Chugoku, 180—200 days in Kinki and Shikoku, and 240 days in southern Kyushu. The effective accumulative temperature (EAT) over 10° C is 1,500° C in Hokkaido and Tohoku, and 4,000° C in southern Kyushu. The effective accumulated insolation (EAI, Kcal/cm<sup>2</sup>/period) is 22 in Hokkaido and Tohoku, and 100 in southern Kyushu. Besides these, a kind of aridity index shows a drier climate in Hokkaido and a more humid one in southern Shikoku and Kyushu. The local productivity of *Miscanthus sinensis* grasslands correlates with EAT, EAI, aridity index, etc. (Numata and Mitsudera, 1969).

The soils of Japan were classified by Kanno (1953) into three main types under the concept of Swanson's soil associations; he showed the relationships between each soil association, precipitation, N-S quotient, annual mean temperature, etc. (Table 4).

Table 4. Soil associations of Japan (Kanno, 1953)

Soil association	Rain factor	N-S quotient	Annual mean temperature °C
Podzol ass.	150—250 <	600—1000 <	5 —8
Brown forest soil ass.	90—170 <	400—950 <	8 —14.4
Red soil ass.	70—150 <	350—700 <	14.5—18

A map of soil types, scale of 1:200,000, with explanation, has been compiled by the National Institute of Agricultural Sciences (Kamoshita, 1958). Table 5.

Table 5. Zonal soil types of Japan

Zonal soil types	Distribution
1. Podzol	northern Hokkaido
2. Rust-coloured forest soil (weakly podzolized)	northern sand-dune
3. Brown forest soil	central Honshu
4. Greyish brown forest soil	northern Honshu and Hokkaido
5. Red soil	southwestern Japan
6. Reddish brown soil	southwestern Japan

Among the soil types the numbers 1, 3, and 5 are the main types and others are transition-al. Azonal soil types are, in Japan, mostly belonging to mountain soils and colluvial soils. Intrazonal soils are classified into wet soil types (bog soil and half-bog soil in boggy areas, meadow soil in paddy areas), wet forest soil, and rock soil types (terra rossa, recent

volcanic ash soil, etc.). Muck soil is distributed in Hokkaido, Tohoku, and lowlands of Kanto. Volcanic ash soil, which is particularly important in relation to the grassland vegetation, is distributed in many areas in Hokkaido, Kanto, Kyushu, etc.

There are some areas severely eroded in forest-lands and grasslands. Such areas are found in Chugoku (western Honshu) and in the mountainous parts of western Shikoku, subjected to a predominantly bare or sheet erosion. They are caused mainly by the properties of the mother rocks and topographic features. In Japan, there is a great danger of severe accelerated erosion when the plant cover is removed or heavily degraded through the heavy rainfall and steep topography.

In Japan there are 23 National Parks and 28 quasi-National Parks. The former occupy about 5.3 % of the area of the total surface of Japan (36,978,000 ha) and the latter about 1.8 %. Among those, we have Special Protection Areas as strictly protected reserves. Besides these, principal vegetation types are reserved as Protected National Forests and National Natural Monuments.

### III. OUTLINE OF NATURAL AND SEMI-NATURAL VEGETATION

#### 1. Evergreen broad-leaved forest region. Table 6—I. Phot. 9, 10, 12, 14.

Natural forests in this region have several types of evergreen broad-leaved forests. Major tree species are *Machilus thunbergii*, *Castanopsis sieboldii*, and *C. cuspidata* in coastal areas, and *Quercus glauca*, *Q. gilva*, *Q. salicina*, *Q. myrsinaefolia*, and *Q. acuta* (evergreen oaks) in inland areas. In higher elevations, *Tsuga sieboldii* and *Abies firma* occur.

The natural vegetation including climax forests and other minor communities in this region (Fig. 2) has been largely deformed and destroyed since the rice cultivation was introduced to Japan about two thousand years ago.

The rice plant, *Oryza sativa*, is of humid-tropical origin, and its cultivation in Japan was largely restricted to this warm-temperate region before the Meiji Era, about 100 years ago. It is certain that human population around rice-fields at that time was denser than in other regions where rice was not or little planted.

A consequence of this denser population in the past is still reflected in the fact that twenty-nine out of thirty cities with a population over 300,000 are presently situated in this region. At present, rice- and upland fields prevail there, especially in lowland areas, and secondary forests of *Pinus densiflora*, *Quercus serrata*, and *Q. acutissima* and grasslands of *Miscanthus sinensis*, *Zoysia japonica*, *Pleioblastus chino*, and *P. distichus* var. *nezasa* substitute the original vegetation on foot-hills and lower mountains (Numata, 1961a).

Natural forests remain fragmentarily in sanctuaries around temples and shrines and on inaccessible steep slopes of gorges and mountains (Miyawaki and Itow, 1966).

#### 1.1 Natural Vegetation

##### 1.1.1. Natural forests of coastal areas

###### 1.1.1.1. *Quercus phillyraeoides* scrubs. Phot. 12.

Coastal slopes with shallow soils on the Pacific side support a scrub community that is dominated and characterized by *Quercus phillyraeoides*. The scrub is distributed from southern Kyushu, through Shikoku and the Inland Sea (Setonaikai) region, to the Izu Peninsula in central Honshu. *Q. phillyraeoides* is a sclerophyllous shrub and the community is physiognomically that of maquis.

Main components of the *Q. phillyraeoides* scrub are such evergreen trees and shrubs as *Q. phillyraeoides*, *Pinus thunbergii*, *Ligustrum japonicum*, *Rapanea neriifolia*, *Camellia japonica*,

*Eurya japonica*, *E. emarginata*, *Vaccinium bracteatum*, and herbs as *Farfugium japonicum*, *Paederia scandens*, *Cyrtomium fortunei*, etc.

Phytosociologically, two associations have been reported: *Pittosporeto-Quercetum phillyraeoidetis* (Suzuki and Hattiy, 1951) and *Gleichenio-Quercetum phillyraeoidetis* (Imai, 1965). The former association is characterized by the presence of *Pittosporum tobira*, *Pyrrosia lingua*, *Rhaphiolepis umbellata* var. *integerrima*, and *Scutellaria indica* var. *japonica*; the latter by *Gleichenia dichotoma* and *Rhododendron tosaense*.

*Quercus phillyraeoides* and its scrub also occur on Yaku Island, which is situated south of the Kyushu mainland. Another type of coastal forests is reported from the northeastern coast of the island. It is composed of *Cinnamomum daphnoides*, *Eurya emarginata*, *Litsea japonica*, *Rhaphiolepis umbellata*, *Daphniphyllum teijsmannii*, *Camellia japonica*, *Euonymus japonicus*, *Psychotria serpens*, *Farfugium japonicum*, etc. (Okutomi, 1968). *C. cinnamomum daphnoides*, a sclerophyllous shrub, is distributed in a restricted area, ranging from the Danjo Islands at the north, through southernmost coasts of the Kyushu mainland, Tanegashima, Yaku Island, the Tokara Islands and Amani-oshima, to Iwotori-shima of the Ryukyu Islands at the south (Horikawa, 1961; Toyama et al., 1967). Probably, the *Cinnamomum daphnoides* scrub is ecologically equivalent to the *Quercus phillyraeoides* scrub.

*Quercus phillyraeoides* and *Cinnamomum daphnoides* are not distributed on coastal slopes in regions on the Japan Sea side of Kyushu and Honshu. The coastal slope vegetation of those areas is made up of most of the above-listed species except these two species, though details have not yet been studied.

#### 1.1.1.2. Forests of *Machilus thunbergii* and of *Castanopsis* (*Shiia*) *sieboldii*. Phot. 9.

Since gentle slopes of foot-hills and alluvial plains are almost completely changed into farmlands, paddy-fields, and urban areas, relict stands of natural forests are the key to the original communities that were there before man touched them. Based on data from such relict stands, mesic habitats with deep soils on alluvial plains originally supported the forests dominated by *Machilus thunbergii* (Suzuki, 1952, 1953; Numata and Asano, 1965). Although the floristic composition of the *M. thunbergii* forest shows somewhat regional variation, common components in Shikoku, for example, are such evergreen broad-leaved trees as *Castanopsis sieboldii*, *Camellia japonica*, *Elaeocarpus sylvestris*, *Ligustrum japonicum*, *Distylium racemosum*, *Symplocos lucida*, *Cinnamomum japonicum*, *Neolitsea sericea*, *Actinodaphne lancifolia*, *Daphniphyllum teijsmannii*, *Ilex integra*, *Myrica rubra*; evergreen shrubs as *Aucuba japonica*, *Gardenia jasminoides* f. *grandiflora*, *Maesa japonica*, *Euonymus japonicus*, *Rapanea neriifolia*, *Damnacanthus major*; deciduous shrubs as *Ficus erecta*, *Calli-carpa japonica* var. *luxurians*; herbs as *Alpinia intermedia*, *Arisaema ringens*, *Liriope platyphylla*, *Ophiopogon japonicus*; ferns as *Rumohra aristata*, *Dryopteris erythrosora*; and lianas as *Trachelospermum asiaticum*, *Piper kadsura*, *Hedera rhombea*, *Anodendron affine*, *Kadsura japonica*, *Ficus nipponica*, etc. (Yamanaka, 1962). Phytosociologically, four associations have been described: *Liriope*-, *Rumohra*-, *Polysticho*-, and *Polypodio-Machiletum*. (cf. Suzuki, 1966b).

*Castanopsis sieboldii* is almost always mixed with *Machilus thunbergii*, but it is a dominant species of forests in habitats with rather drier soils on foot-hill slopes and ridges. In rather inland portions, *Castanopsis cuspidata* also occurs (Numata and Asano, 1965). Relict stands are frequently found in forest reserves and national parks, as compared with those of *Machilus thunbergii*. Component species of the *C. sieboldii* forest are almost similar to those of the *M. thunbergii* forest, though their quantitative relations are not always alike. Phytosociologically, seven associations have been described: *Bladhio*-, *Rapaneo*- (Suzuki, 1952), *Symploco*- (Nomoto, 1953), *Ardisio*- (Hosokawa, 1958), *Lasianthero*-, *Arisaemo*-,

and *Symploco liukiensis*-*Castanopsis*etum (= *Shiitum*) (Miyawaki and Ohba, 1963). The first three associations were reported from Honshu, Shikoku, and the Kyushu mainland, the fourth from Yaku Island, and the last three from Amami-oshima and Tokunoshima.

As stated by Hara (1959), Amami-oshima and Tokunoshima belong to the Ryukyu Floristic Region, in which a number of tropical and subtropical species occur. Examples are *Wendlandia formosana*, *Cinnamomum doederleinii*, *Symplocos microcalyx*, *Randia canthioides*, *Eurya oshimensis*, *Illicium anisatum*, *Helwingia liukiensis*, *Ligustrum liukiensis*, *Callicarpa oshimensis*, *Osmanthus bracteatus*, *Smilax nervo-marginata*, *Turpinia ternata*, *Syzygium buxifolium*, *Lasianthus tashiroi*, *Psychotria rubra*, *P. serpens*, *Crataeva religiosa*, *Schefflera octophylla*, *Ardisia quinqueгона*, and *Rhododendron tashiroi*. Amami-oshima Island is the northern limit of the first eleven of the above-listed species. They are components of *Castanopsis sieboldii* forests of the island (Miyawaki and Ohba, 1963). The rest of those species are also found in natural forests on Yaku Island, some of which are distributed further north to the southernmost part of the Kyushu mainland.

### 1.1.2. Forests of inland areas

Inland areas of the evergreen broad-leaved forest region have also been exploited, and there presently prevail agricultural areas and secondary vegetation such as coppices and grasslands. Based on relict stands of natural forests, however, it is certain that the area originally supported forests of evergreen oaks, *Tsuga sieboldii* and *Abies firma*.

#### 1.1.2.1. Evergreen oak forests. Phot. 10.

Evergreen oaks mentioned here are *Quercus glauca*, *Q. gilva*, *Q. myrsinaefolia*, *Q. salicina*, and *Q. acuta*. These oaks are sometimes treated as species belonging to the genus *Cyclobalanopsis* from the morphology of their cupules.

Natural forests of *Quercus glauca* are distributed mostly in the area of the *Castanopsis sieboldii* forest, and are infrequently found in inland areas in western Japan (Yamanaka, 1966; Okutomi, 1967). The habitat is of limestone and andesite (Suzuki and Mori, 1957; Suzuki et al., 1964; Miyata and Shiomi, 1965; Yamanaka, 1966). The floristic composition of the *Q. glauca* forest is, as a whole, similar to that of the *Castanopsis sieboldii* forest. According to Yamanaka (1966), characteristic species are *Q. glauca*, *Xylosma japonica*, *Eriobotrya japonica*, *Trachycarpus fortunei*, *Citrus junos*, and *Nandina domestica*.

The *Quercus gilva* forest is frequently found on deep soils at gentle slopes of foot-hills. It is thought that pre-historic man settled first in the habitat of the *Q. gilva* forest (Suzuki, 1960; Miyawaki and Fujiwara, 1969), and therefore the relict stands are not abundant.

In the Kanto District of central Honshu, the *Quercus myrsinaefolia* forest is thought of as the original forest community that was developed on habitats with loamy soils (Yokoyama et al., 1967; Miyawaki, 1967; Miyawaki and Fujiwara, 1968a). Main components of the forest are such trees and shrubs as *Quercus myrsinaefolia*, *Camellia japonica*, *Eurya japonica*, *Aucuba japonica*, *Ardisia japonica*, *Fatsia japonica*, *Neolitsea sericea*; herbs as *Ophiopogon japonicus*, *Liriope platyphylla*; ferns as *Dryopteris erythrosora*, *D. uniformis*, etc. (Miyawaki, 1967). Natural stands of *Q. myrsinaefolia* are also found in an inland limestone area in western Honshu (Miyata and Shiomi, 1965).

The *Quercus salicina* forest is developed on steep slopes and ridges with shallow soils, at some places, with exposed blocks of the bedrock. Main components of the forest are *Cleyera japonica*, *Skimmia japonica*, *Pieris japonica*, *Illicium religiosum*, *Cephalotaxus harringtonia*, *Quercus acuta*, *Camellia japonica*, *Machilus thunbergii*, *Neolitsea sericea*, *N. aciculata*,

*Cinnamomum japonicum*, *Castanopsis cuspidata*, *Eurya japonica*, *Aucuba japonica*, *Trachelospermum asiaticum*, etc.

Phytosociologically, *Quercus salicina* forests are classified into four associations (Suganuma, 1965). The first association is *Osmantho-Cyclobalanopsidetum* (= *Osmantho-Quercetum*). It is characterized by the occurrence of *Osmanthus ilicifolius* and *Prunus jamasakura*, and is distributed on foot-hills and lower mountains on the Pacific side of central and western Honshu and in the Inland Sea District. The second is *Distylium-Cyclobalanopsidetum* that is characterized by *Distylium racemosum*, *Symplocos myrtacea*, *Ligustrum japonicum*, *Ilex integra*, and *Machilus japonica*. This association is found in Kyushu and in the southern half of Shikoku. The third is *Carici-Cyclobalanopsidetum*, characterized by *Carex reinii*, *Hydrangea scandens*, *Lindera sericea* var. *tenuis*, *Cephalotaxus harringtonia* var. *nana*, and *Struthiopteris nipponica* (Horikawa and Sasaki, 1959a). The fourth is *Aucubeto-Cyclobalanopsidetum* (Sasaki, 1958). These two associations are reported from western Honshu.

*Quercus acuta* is an evergreen oak that occurs frequently in inland forests. It predominates in the cloud zone of mountains in Kyushu (Suzuki and Sumata, 1964) and in western Honshu (Okutomi, 1967b). Main components of the *Quercus acuta* forest, for example, observed in eastern Kyushu (Suzuki and Sumata, 1964), are *Q. acuta*, *Skimmia japonica* (which are characteristic to the forest), *Distylium racemosum*, *Cinnamomum japonicum*, *Machilus thunbergii*, *M. japonicus*, *Quercus salicina*, *Ilex integra*, *Neolitsea sericea*, *N. aciculata*, *Actinodaphne lancifolia*, *A. longifolia*, *Castanopsis sieboldii*, *Camellia japonica*, *Cleyera japonica*, *Ligustrum japonicum*, *Aucuba japonica*, *Trachelospermum asiaticum*, *Marsdenia tomentosa*, etc.

#### 1.1.2.2. Forests of *Tsuga sieboldii* and of *Abies firma*. Phot. 4.

The *Tsuga sieboldii* forest is usually developed on mountain summits, ridges and steep slopes with shallow soils, at some places, with exposed blocks of the bedrock. Since the habitat of the forest is alike to that of the *Quercus salicina* forest, many of the components also are common to both. Phytosociologically, five associations have been described: *Carici-Rhododendro-*, *Symploco-*, *Illici-*, and *Pieridi-Tsugetum* (cf. Suzuki, 1952, 1966b; Yamanaka, 1961).

The *Abies firma* forest, on the other hand, is developed on gentle slopes with deeper soils, as compared with the *Tsuga* forest (Yamanaka, 1961). It is phytosociologically named *Illici-Abietum firmae* and is characterized by *Illicium religiosum*, *Schizophragma hydrangeoides*, *Ilex crenata*, *Parabenzoin praecox*, *Ilex macropoda*, *Schisandra repanda* (Suzuki, 1961).

Altitudinally, forests of *Tsuga sieboldii* and *Abies firma* are situated in the transition zone between the evergreen and the summergreen broad-leaved forest regions. Therefore, evergreen broad-leaved trees and shrubs occur in the lower portion of the *Tsuga*- and *Abies*-forest zone. Examples are *Pieris japonica*, *Ilex pedunculosa*, *Neolitsea aciculata*, *Quercus acuta*, *Q. salicina*, *Ligustrum japonicum*, *Symplocos myrtacea*, *Eurya japonica*, *Illicium religiosum*, *Cleyera japonica*, etc. On the other hand, deciduous trees and shrubs occur frequently in the forest, especially in higher elevations. Examples are *Ilex macropoda*, *Acanthopanax scidophylloides*, *Symplocos coreana*, *Magnolia salicifolia*, *Sorbus japonica*, *Cornus controversa*, *Viburnum furcatum*, *Lindera umbellata*, *Acer rufinerve*, *A. sieboldianum*, *Quercus mongolica* var. *grosseserrata*, *Carpinus japonica*, *C. laxifolia*, *Euonymus oxyphyllum*, etc.

Fig. 3. shows the distribution of natural forest communities in the Kanto District in relation to soil moisture and elevation.

#### 1.1.3. Volcanic vegetation. Phot. 25, 26.

Active and extinct volcanoes abound in the Japanese Archipelago. Plant communities on beds of lava, ashes, scoria and other ejecta differ from the above-mentioned natural

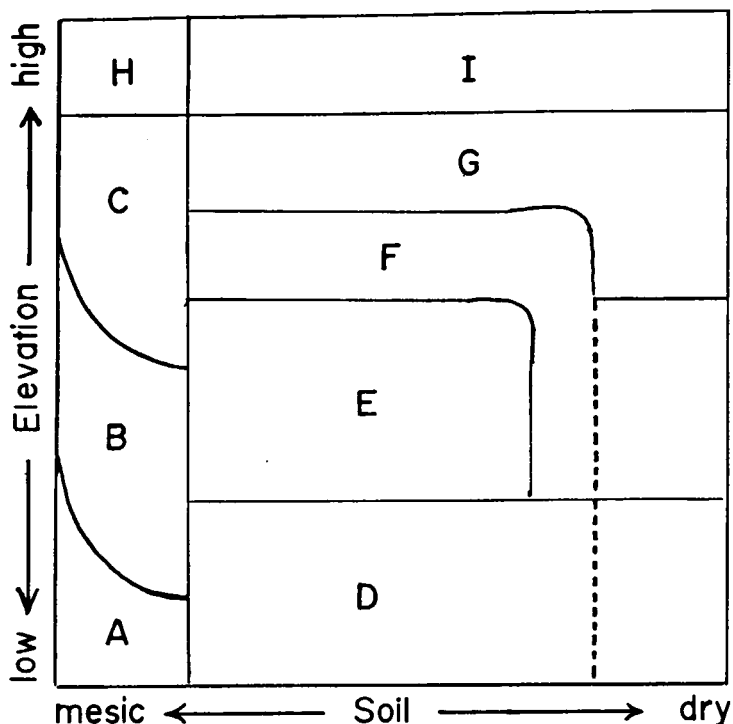


Fig. 3. Two-dimensional representation of the forest community-habitat relationships in the Kanto region, central Honshu. A. *Machilus thunbergii*-*Polystichum polyblepharum* Ass., B. *Zelkova serrata*-*Orixa japonica* Ass., C. *Zelkova serrata*-*Acer palmatum* Ass., D. *Castanopsis cuspidata* var. *sieboldii*-*Bladhia japonica* Ass., E. *Quercus myrsinaefolia* Ass., F. *Quercus salicina*-*Osmanthus ilicifolius* Ass., G. *Abies firma*-*Illicium religiosum* Ass., H. *Fraxinus spaethiana*-*Dryopteris polylepis* Ass., I. *Fagus crenata*-*Cornus kousa* Ass. The last two associations belong to the summergreen broad-leaved forest region (after Miyawaki, 1967).

communities. Mt. Mihara on Izu-oshima Island in central Japan and Sakurajima in southern Kyushu are representative of active volcanoes situated in the warm-temperate region. They are fields for observing the primary succession on volcanic habitats, since the year of eruptions and lava flows is recorded. Fig. 4 shows the series of the primary succession of plant communities, which was constructed from observations in various habitats on Izu-oahima (Tezuka, 1961). *Carex okuboi* and *Polygonum cuspidatum* var. *terminale* invade first the weathered lava flow, and are followed by evergreen and deciduous shrub and tree species. Last, evergreen broad-leaved forests dominated by *Castanopsis sieboldii* and *Machilus thunbergii* are developed. The structure of the communities are changed along the course of the succession from 'low' and 'sparse' at early stages to 'high' and 'dense' at later stages. Soils are also matured along the course from soils with a little amount of decomposed organic matters and nutrients and with thin A horizon, to mature soils with much amount of those and with thick A horizon (Tezuka, 1961).

There are also lava flows of different ages in Sakurajima, southern Kyushu. The primary succession observed there is shown in Fig. 5 (Tagawa, 1964). The two examples cited here are quite alike. In early stages of the succession, *Miscanthus sinensis* and *Polygonum cuspidatum*



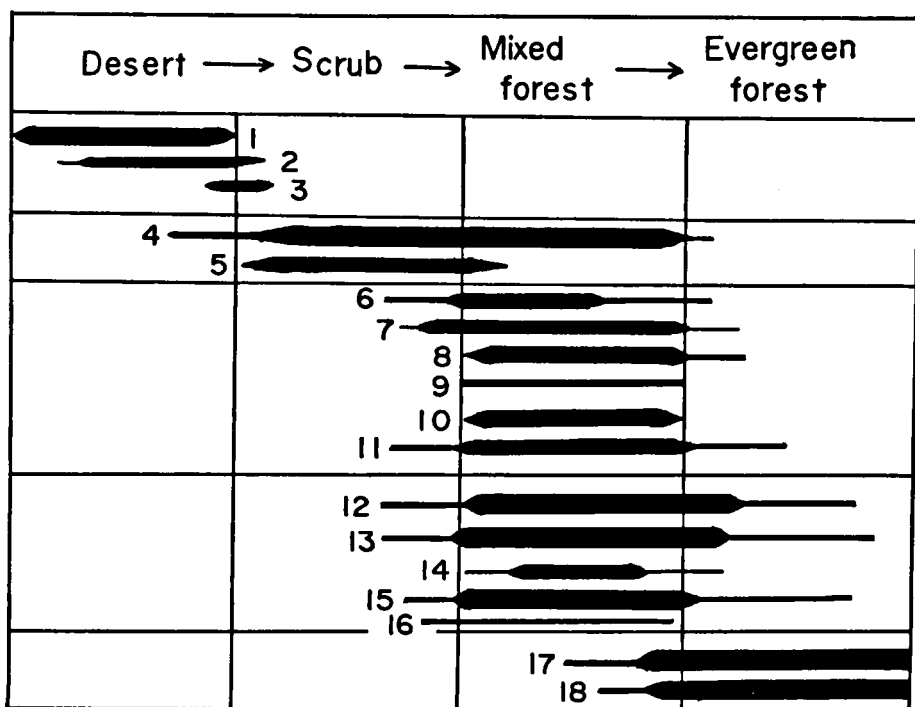


Fig. 4. Schematic illustration of the plant succession in volcanic habitats on Izu-Oshima, central Japan. 1. *Carex okuboi*, 2. *Polygonum cuspidatum* var. *terminale*, 3. *Miscanthus sinensis*, 4. *Alnus sieboldiana*, 5. *Weigela grandifolia*, 6. *Cornus controversa*, 7. *Prunus lannesiana* var. *speciosa*, 8. *Styrax japonica*, 9. *Fagaria ailantoides*, 10. *Stachyurus praecox* var. *matsuzakii*, 11. *Ligustrum pacificum*, 12. *Eurya japonica*, 13. *Neolitsea sericea*, 14. *Cinnamomum japonicum*, 15. *Camellia japonica*, 16. *Ilex crenata*, 17. *Castanopsis cuspidata* var. *sieboldii*, 18. *Machilus thunbergii* (after Tezuka, 1961).

*tum* (var. *terminale* on Izu-oshima) role in accumulating organic matters; then, *Alnus sieboldiana* (on Izu-oshima), *A. firma* (on Sakurajima), and some other deciduous shrubs and trees follow. Finally, the climatic climax forest co-dominated by *Machilus thunbergii* and *Castanopsis sieboldii* is developed.

#### 1.1.4. Coastal sand vegetation. Table 6-Ic. Phot. 23.

There is not such clear correspondence of coastal sand vegetation to the macroclimatic regions as that of inland vegetation. However, there are seaside vegetation types, northern and southern. The coastal zonation in the evergreen broad-leaved forest region is found as unstable, half-stable, and stable zones from sea-coast to inland. The unstable zone is represented by *Zoysia macrostachya*, *Calystegia soldanella*, *Carex kobomugi*, *C. pumila*, *Glehnia littoralis*, etc. The half-stable zone is represented by *Ischaemum antheophroides*, *Fimbristylis sericea*, *Vitex rotundifolia*, etc. The stable zone is covered by *Imperata cylindrica* var. *koenigii*, *Miscanthus sinensis* var. *condensatus*, *Pinus thunbergii*, *Machilus thunbergii*, etc. (Numata, 1949, 1961b; Numata and Nobuhara, 1952).

The zonation of coastal vegetation is caused by the fore-shore sea current and wind-

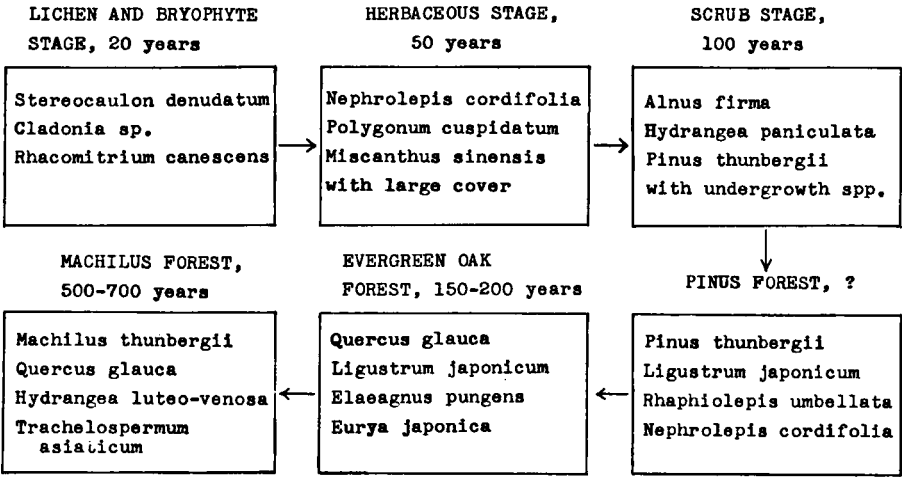


Fig. 5. A series of primary succession assumed from observations of communities on lava flows in Sakura-jima, southern Kyushu (after Tagawa, 1964, slightly modified).

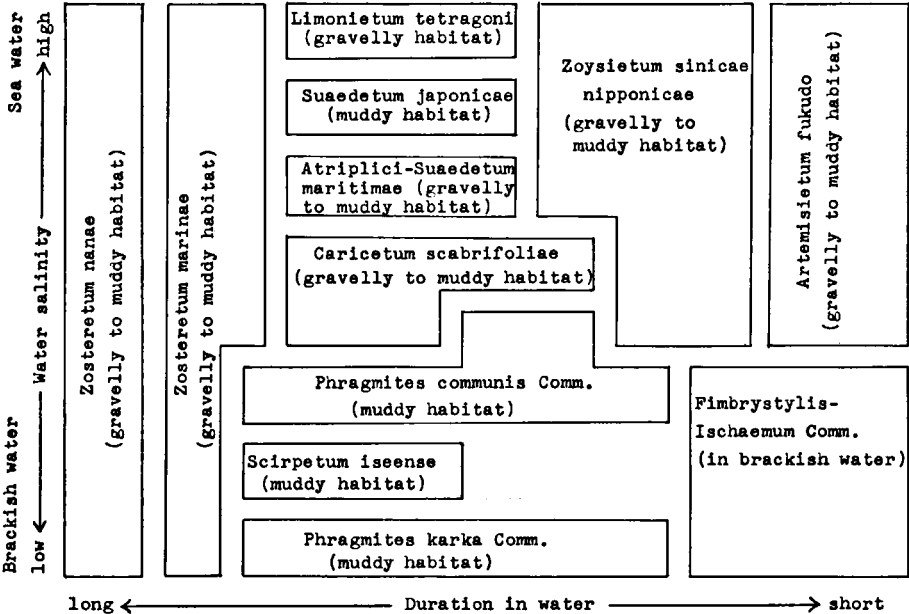


Fig. 6. Schematic illustration of relationships between salt marsh communities and their habitats in central and western Japan (after Miyawaki and Ohba, 1969).

borne salt (Numata, 1949; Kurauchi, 1964), by the invasion of saline water, and the sand-movement by wind and sea-waves (Nobuhara *et al.*, 1962, 1964), etc. The coastal zonation is expressed by the life-form spectra (Numata and Nobuhara, 1952; Nobuhara, 1965, 1967).

The coastal vegetation is divided into two types: open sea type and bay type (Numata, 1949; Mitsudera and Numata, 1964). The former is represented by *Calystegia soldanella*, *Zoysia macrostachya*, *Ischaemum antheophroides*, etc. and the latter by *Atriplex gmelinii*, *Calamagrostis epigeios*, etc. Phot. 23.

The leaves of trees of the coastal forest are classified into two groups: deposit type and entrance type (Kurauchi, 1956, 1964). The former is a leaf type in which salt deposits on their surface scarcely enters into the tissue, and the latter is a type in which salt soon enters into the leaves and damages are found. The coastal forest in central Japan mainly consists of the former species such as *Machilus thunbergii*, *Camellia japonica*, *Ilex integra*, *Cinnamomum japonicum*, etc.

#### 1.1.5. Salt marshes. Table 6-Id. Phot. 24.

Salt marsh communities are found at estuaries and lagoons where destruction by wave actions is weak. Many of such habitats have been destroyed by successive advances of reclamation on lands. Major plant in salt marshes in central and western Japan are *Zostera nana*, *Z. marina*, *Limonium tetragonum*, *Suaeda japonica*, *S. maritima*, *Atriplex gmelinii*, *Carex scabrifolia*, *Zoysia sinica* var. *nipponica*, *Artemisia fukudo*, *Phragmites communis*, *P. karka*, *Scirpus isensis*, *Aster tripolium*, *Kochia scoparia* f. *littorea*, *Cynodon dactylon*, *Triglochin maritimum*, and some others (Umezu, 1964; Miyawaki and Ohba, 1969). The halophytic characters of these salt marsh plants and strand dune plants were studied, especially as to the osmotic pressure, germination, and growth (Tsuda, 1961). Fig. 6 shows the distribution of salt marsh communities in relation to habitat conditions (Miyawaki and Ohba, 1969). Of these communities, the *Suaedetum japonicae* and the *Scirpetum isense* are restricted to northern Kyushu and Korea, and to the Ise Bay region of central Honshu, respectively; the *Zosteretum nanae*, the *Zosteretum marinae* and the *Phragmites communis* community are also common in salt marshes in northern Honshu and Hokkaido; and the rest are distributed only in central and western Honshu, Shikoku, and Kyushu.

For the mangrove vegetation is referred to section 1.1.8.

#### 1.1.6. Riverside vegetation

Riverside habitats are different from those of the above mentioned forest lands in soil and water conditions.

Generally speaking, the soils are made up of flood deposits and the ground water table is high. *Phragmites communis* is a very common and dominant species on silty and clayey deposits with a high water table along lower rivers. *Alnus japonica* is one of the common trees growing in riverside wet habitats and often in reed swamps. The undisturbed stand of this species is rare and the data, therefore, are insufficient, because the habitat has been exploited for paddy-fields.

*Salix gracilistyla* and *Phragmites japonica* are common on gravelly beaches along swift streams (Okutomi, in Miyawaki, 1967; Miyawaki and Okuda, 1969).

Phytosociological studies on riverside-, levee-, high water channel-, and flood plain plant communities have been made especially for dairy farming (Naohare, 1945, 1948, 1950, 1951, 1965). An example of riverside plant succession is shown from a bare ground to *Pinus densiflora* community through *Phragmites communis*-, *Salix*-, *Imperata cylindrica*-, *Pleioblastus chino*-communities, etc. (Kurita, 1943).

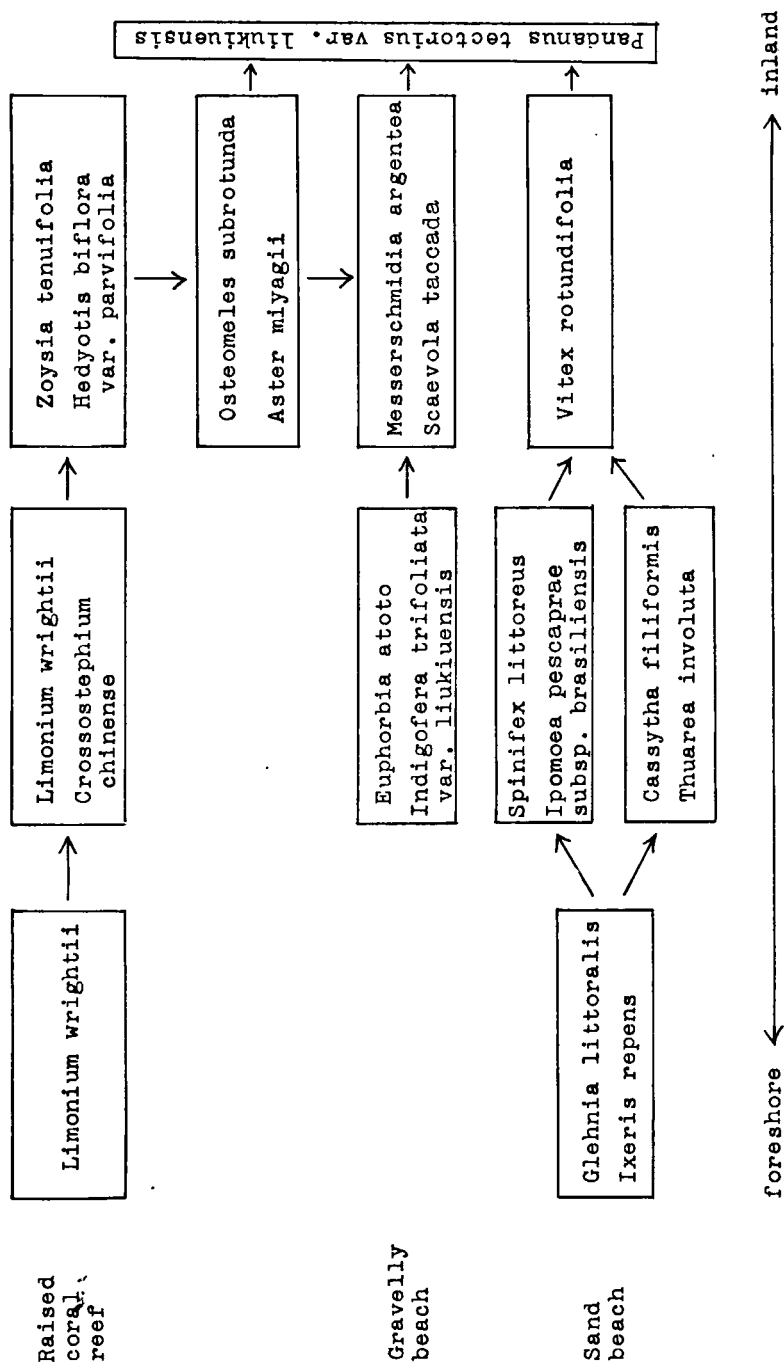


Fig. 7. Scheme showing the distribution of beach communities in the Ryukyu Islands (after Miyawaki, 1967, slightly modified).

### 1.1.7. Pond and lake vegetation

Aquatic plants are arranged in an order of emergent, floating-leaved, and submerged ones from shallow to deep waters on beaches of ponds and lakes (Nakano, 1911—16; Miki, 1957; Hogetsu, 1945). Prominent species of the emergent plant community are *Phragmites communis*, *Typha latifolia*, *T. angustata*, *Scripus tabernaemontani*, *S. triangulatus*, *Nuphar japonicum*, *Sparganium stoloniferum*; those of the floating-leaved community are *Nymphaea tetragona*, *Brasenia schreberi*, *Trapa japonica*, *Nymphoides indica*; and those of the submerged community are *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Najas minor*, *Potamogeton natans*, *P. crispus*, etc. Emergent plant communities are also found on beaches of the lower courses of rivers where the water flow is slow or almost nil. The most simple aquatic community is composed of one or two of such floating plants as *Lemna paucicostata*, *Spirodela polyrrhiza*, *Wolffia arrhiza*, *Azolla imbricata*, and *Salvinia natans* (Miyawaki, 1960).

### 1.1.8. Ryukyu Islands. Phot. 13, 14.

The Ryukyu Islands are located between Kyushu and Taiwan. The climate is sub-tropical. Mean annual temperature and annual precipitation at Naha, Okinawa Island, are 22.0° C and 2148 mm respectively. Floristically, the islands of Okinawa, Ishigaki, and Iriomote, together with Amami-oshima, Tokuno-shima, and the Tokara Islands, belong to the Ryukyu Floristic Region (Hara, 1959).

The natural forest has been considerably disturbed on Okinawa Island, but less so on Iriomote Island. Natural evergreen broad-leaved forests in Iriomote (Miyata and Odani, 1963) are composed of such trees as *Castanopsis sieboldii*, *Quercus miyagii*, *Distylium racemosum*, *Michelia compressa* var. *formosana*; shrubs as *Ardisia sieboldii*, *Psychotria rubra*, *Syzygium buxifolium*, *Lasianthus cyanocarpus*, *Daphniphyllum teijsmannii*, *Randia canthioides*; ferns as *Lindsaea chienii*, *Abacopteris triphylla*, *Rumohra aristata*, *Tectaria phaeocaulis*, *Diplazium virescens*, *Bolbitis koidzumii*, *Colysis pothifolia*; lianas as *Freycinetia formosana*, *Epipremnum mirabilis*, *Flagellaria indica*, *Smilax china* var. *kuru*, etc. Tree ferns in the forest are *Gymnosphaera podophylla*, *G. denticulata*, *Alsophila pustulosa*, and *Cyathea fauriei*; epiphytes are *Neottopteris australasica*, *Psilotum nudum*, and *Gastrochilus japonicus*. Details have not been studied as to the phytosociology and ecology of the natural forest, although the flora of the Archipelago is well investigated (Hatushima and Amano, 1958).

Mangrove forests at estuaries and lagoons are well developed in Iriomote. Phot. 13. There are six species: *Bruguiera conjugata*, *Kandelia candel*, *Rhizophora mucronata*, *Sonneratia alba*, *Lumnitzera racemosa*, and *Avicennia officinalis*. They are arranged from *Avicennia officinalis* and *Sonneratia alba* at the frontier, through *Rhizophora mucronata* and *Kandelia candel*, to *Bruguiera conjugata* at the inner portion, and further to the stand community of *Pandanus tectorius* var. *liukiuensis* and *Barringtonia racemosa* (Miyata and Odani, 1963). Of these mangrove species, *Bruguiera conjugata* and *Kandelia candel* are also distributed to Amami-oshima; the latter is further north to the islands of Yakushima and Tanegashima. A stunted stand of this species is found at Kiire in the southernmost Kyushu (Itow, in Miyawaki, 1967).

Strand communities on raised coral reefs and on sand beaches in the Ryukyus are different from those in Kyushu, Shikoku, and Honshu. The community distribution on those habitats are schematically shown in Fig. 7.

*Pinus luchuensis* is endemic to the Ryukyu Islands, ranging from Akuseki at the north, through Amami-oshima, Okinawa, to Iriomote. The forest of this pine is seen on some disturbed areas. Mowed and/or burnt habitats are dominated by *Miscanthus sinensis* and *Pleioblastus linearis*, or *Imperata cylindrica* var. *koenigii* (Yano, in Miyawaki, 1967).

### 1.1.9. Ogasawara (Bonin) and Volcano Islands. Phot. 15.

The Ogasawara Islands are situated about 1000 km south of Tokyo, between 26°30' and 27°40' N latitude in the Pacific, and composed of eight major islands and many islets. The Volcano Islands are situated further south between 24°15' and 24°50', about 200 km southwest of the Ogasawara Is. All the islands are of volcanic origin and the topography is generally steep. The climate is subtropical. Mean annual temperature and total annual precipitation on Chichi-jima are 22.6° C and 1613 mm respectively.

Floristically, the islands belong to the Ogasawara Floristic Region (Hara, 1959), and are outstanding in high endemism (Hattori, 1908; Nakai, 1930; Hosokawa, 1934; Tuyama, 1953). According to Tuyama (1968), eighty-five out of 128 ligneous species are endemic to the Ogasawara and the Volcano Islands. *Dendrocacalia* (Compositae) and *Boninia* (Rutaceae) are endemic genera.

The islands were inhabited since the first quarter of the 19th century. The population increased to about 8000 before the World War II and the vegetation was either destroyed or disturbed considerably. Most of the people left the islands to Honshu in 1944. Since then and at present, less than 200 persons inhabit only Chichi-jima Island. The vegetation has been less touched during this period. Recent survey made on the Islands of Chichi-, Haha-, and Ani-jima (Miyawaki, 1968a) offered an up-to-date information on the vegetation. The revegetation in disturbed habitats is only superficial. Large parts that were formerly destroyed or disturbed are covered by a dense growth of *Leucaena leucocephala*, an exotic shrub introduced from South America. Feral goat runs wild and African snail is abundant on some islands.

The undisturbed natural forest is restricted to inaccessible parts of the islands. It is composed of *Cinnamomum pseudopedunculatum*\*, *Ligustrum micranthum*\*, *Pittosporum boninense*\*, *Raphiolepis integerrima*, *Evodia kumagaiana*\*, *Distylium lepidotum*\*, *Boninia glabra*\*, *Hibiscus tiliaceus*, *Syzygium buxifolium*, *Rapanea maximowiczii*\*, *Schima mertensii*\*, *Hibiscus glaber*\*, *Ardisia sieboldii*, *Livistonia boninensis*\*, *Osmanthus insularis*, *Pouteria obovata*, *Calophyllum inophyllum*, *Hernandia sonora*, *Morus kagayamae*, *Machilus kobu*\*, *Sideroxylon ferrugineum*, *Pandanus boninensis*\*, *Freyinetia formosana* var. *boninensis*, *Trachelospermum foetidum*\*, etc. (The species indicated by an asterisk are endemic to the Ogasawara Floristic Region).

There are two kinds of natural communities on windy narrow ridges. One is composed of *Miscanthus boninensis*\*, *Trachelospermum foetidum*\*, *Carex hattoriana*, *Carex bongardii*, and some others. The community is developed on shallow soils on the ridge. Another is made up of *Osteomeles lanata*\* and *Fimbristylis diphylla* and is found only on the almost exposed welded tuff.

Plants on sand beaches are arranged from *Ipomoea pes-caprae* subsp. *brasiliensis* at the foreshore, through *Cynodon dactylon* and *Vitex rotundifolia*, to *Scaevola taccada*. The disturbed island slope is covered by *Leucaena leucocephala*, *Miscanthus boninensis*, *Cymbopogon angustispica*, etc.

## 1.2. Semi-natural Vegetation

As stated before, natural forests in the region have been extensively cut over and the lands now support various types of vegetation such as secondary forests, grasslands, weed communities, etc. In the present part, secondary forests and grasslands are treated.

### 1.2.1. Secondary forests

#### 1.2.1.1. Coppices of *Castanopsis cuspidata* and *C. sieboldii*

Coppices of *Castanopsis* are found in forest lands that have been periodically logged at several decade intervals (Itow, 1968a; Yamanaka, 1968). Though data are still inadequate,

such a stand appears to be developed in warmer areas of the evergreen broad-leaved forest region, to which *Castanopsis* is well adapted. The floristic composition of the forest of this type is almost the same as that of the natural forest of the same species, except for the occurrence of such shade-intolerant trees as *Mallotus japonicus*, *Albizia julibrissin*, *Zanthoxylum ailanthoides*, etc. Physiognomically, the sprout-origin coppice is different from the natural one in its low stature and in an even-aged canopy.

Sprout-origin forests of *Pasania edulis* and of *Quercus glauca* are found, at least, in part of Kyushu, but the details are not yet known.

#### 1.2.1.2. *Pinus densiflora* forests. Phot. II.

Natural stands of *Pinus densiflora* are restricted to extreme habitats such as narrow ridges, steep slopes, and lava flows with little soils or exposed bedrocks, and as peripheries of fens and swamps. The growth in those habitats is usually sparse and stunted. On the other hand, secondary forests of this pine are very extensive not only in the evergreen broad-leaved forest region (except on islands south of Yakushima), but also in the summergreen broad-leaved forest region (except on Hokkaido). *P. densiflora* is now one of the most prominent conifers in inhabited regions of Japan, and its forests are developed on lands that originally supported *Castanopsis-Machilus* forests, evergreen oak forests, and *Abies firma* forests. (Pine forests both in the evergreen and the summergreen forest regions are treated together here.)

The pine forest has long been maintained by logging at 15–50 year intervals and by disturbance of the forest floor vegetation.

The floristic composition and the structure differ, more or less, with regions, localities, years after the latest logging, and intensity of disturbance on the forest floor. Based on an analysis of the data in Yoshioka (1958), which were gathered throughout Japan, species common in the forests are *Pinus densiflora*, *Quercus serrata*, *Castanea crenata*, *Clethra barbinervis*, *Vaccinium oldhamii*, and *Ilex crenata*, and herbs as *Miscanthus sinensis*, *Solidago virga-aurea* var. *asiatica*, and *Pteridium aquilinum*. The above-listed trees except the pine are deciduous and shade-intolerant and the last three herbs are components of the grassland vegetation. Regional differences in the composition are as follows. The forests in the summergreen broad-leaved forest region consist of many other deciduous trees: *Quercus mongolica* var. *grosseserrata*, *Sorbus alnifolia*, *Ilex macropoda*, *Magnolia obovata*, *Fraxinus lanuginosus*, which also occur in beech forests and which are not or rarely found in the *P. densiflora* forest of the evergreen broad-leaved forest region. On the other hand, the following tree species are largely restricted to the forests in the latter region: *Eurya japonica*, *Juniperus rigida*, *Vaccinium bracteatum*, *Quercus glauca*, *Q. salicina*, *Ligustrum japonicum*, *Ilex chinensis*, *Castanopsis sieboldii*, and *Camellia japonica*. These species, except for *Juniperus rigida*, are major components of the evergreen natural forest, as stated before. It is certain that the pine forest will be replaced by summergreen forests in the former region and evergreen ones in the latter, if kept free long enough from human interference.

The floor vegetation of the forest in the latter region is frequently dominated by either *Pleiblastus chino* (in central Honshu), *P. distichus* var. *nezasa* (in western Honshu, Shikoku, and Kyushu), *Gleichenia japonica*, or *Gleichenia dichotoma*. At some stands in the Inland Sea region, bare condition of the floor has resulted from repeated gathering of fallen leaves and clearing of the floor vegetation, associated with dry condition of the region. Such a forest has suffered of erosion and is so deteriorated that the habitat is not potentially capable any more to support the *Castanopsis* forest that originally was there.

The floristic characteristic of the pine forest is the occurrence of *Rhododendron* species. *Rh. kaempferi* is one of the most widely distributed species in the pine forests ranging

from northern Honshu to Kyushu. Besides this, *Rh. macrosepalum*, *Rh. weyrichii*, and *Rh. kiussianum* are characteristic of the pine forest of the eastern Inland Sea region, of the southern half of Kii Peninsula, Shikoku, and Kyushu, and of Mt. Kirishima in Kyushu, respectively (Suzuki, 1966b).

#### 1.2.1.3. Mixed forests of *Quercus serrata* and *Quercus acutissima* (deciduous oaks)

Forests of mixed *Quercus serrata* and *Q. acutissima* are developed on part of the lands that originally supported evergreen broad-leaved forests. The forest of the deciduous oaks has been maintained by logging at 15 to 25 year intervals, and is composed of such deciduous trees as *Prunus jamazakura*, *Castanea crenata*, *Clethra barbinervis*, *Styrax japonica*, *Carpinus tschonoskii*, etc. The floor vegetation of the forest is made up of *Miscanthus sinensis*, *Pleiblastus chino* (in central Honshu) or *P. distichus* var. *nezasa* (in western Honshu), *Aster scaber*, *Solidago virga-aurea* var. *asiatica*, *Potentilla freyniana*, *Ixeris dentata*, which are components of the *Miscanthus sinensis* grassland (Miyawaki and Fujiwara, 1968a; Miyawaki et al., 1968; Miyawaki, 1969). In addition, seedlings and saplings of evergreen broad-leaved trees are usually found on the forest floor, even though they are sparse. This means that the habitat of the deciduous oak forests is potential to support the forest of evergreen trees. Those found in the deciduous oak forest in the *Machilus-Castanopsis* forest region in central Honshu are *Aucuba japonica*, *Machilus thunbergii*, *Castanopsis cuspidata*, *C. sieboldii*, *Neolitsea sericea*, *Cinnamomum japonicum*, *Dendropanax trifidus*, while those in the *Quercus myrsinaefolia* (evergreen oak) forest region are *Quercus myrsinaefolia*, *Q. glauca*, *Eurya japonica*. If logging would ever be ceased, the deciduous oak forest will surely be replaced by the evergreen broad-leaved forest that is the climatic climax of the region (Miyawaki, 1967).

#### 1.2.1.4. Bamboo forests. Phot. 18.

There are many bamboo stands, cultivated or semi-natural, mainly dominated by three species of *Phyllostachys* (*Ph. bambusoides*, *Ph. pubescens*, and *Ph. nigra* var. *henonis*). Phot. 18. The semi-natural bamboo brakes belong to a seral stage which converges in the climaxes *Shiion sieboldii* and a part of *Fagion crenatae* (Numata, 1955; Ueda and Numata, 1961; Numata and Aoki, 1962; Numata, 1965a). This is judged by the dynamics of ground vegetation of the east Japan type or west Japan type. For example, the ground flora of the former is composed of *Carex lanceolata*, *Oplismenus undulatifolius*, *Pleiblastus chino*, *Wistaria brachybotrys*, *Viburnum erosum*, *Disporum sessile*, *Houttuynia cordata*, etc., and that of the latter *Nandina domestica*, *Aucuba japonica*, *Camellia japonica*, *Ophiopogon japonicus*, *Callicarpa japonica*, *Dryopteris lacera*, *Ligustrum japonicum*, *Torreya nucifera*, *Eurya japonica*, *Asplenium incisum*, *Polystichopsis pseudoaristata*, etc.

#### 1.2.2. Grasslands

Grasslands are described later together with those in the summergreen broad-leaved forest region.

### 2. Summergreen broad-leaved forest region. Table 6—II. Phot. 4, 9.

As shown in the vegetation map (Fig. 2), the summergreen broad-leaved forest region occupies the montane area in central and southern Japan, and montane to foothill and lowland areas in northern Honshu and Hokkaido. A large number of new varieties of rice plant adapted to particular areas or to other special conditions have been produced as a result of the breeding program. Especially, the rice acreage has expanded northwards thanks to new varieties adapted to cooler climates (Japan FAO Ass., 1958). As a result of



population increment in the region, natural habitats have become narrower, while man-made and man-influenced habitats wider. Nevertheless, the region under consideration was sparsely populated as a whole and the natural vegetation was less touched, at least before World War II, as compared with the evergreen broad-leaved forest region. Since then, however, the encroachment is advancing further to back countries and cutover forest lands are reforested uniformly with coniferous trees such as *Cryptomeria japonica*, *Chamaecyparis obtusa*, and *Larix leptolepis*.

## 2.1. Natural Vegetation

### 2.1.1. Beech forests. Phot. 2.

The beech forest is the climatic climax that occupies large parts of the region. Main components common in the forest in Japan are such deciduous trees as *Fagus crenata*, *Kalopanax septemlobus*, *Tilia japonica*, *Quercus mongolica* var. *grosseserrata*, *Magnolia obovata*, *Acanthopanax sciadophylloides*, *Fraxinus sieboldiana*, *Sorbus alnifolia*, *Acer mono*, *A. palmatum* var. *matsumurae*; deciduous shrubs as *Viburnum furcatum*, *Rhus trichocarpa*; and vines as *Schizophragma hydrangeoides*, *Rhus ambigua*, *Hydrangea petiolaris*, etc.

As has been stated before, the climate differs with regions on the Pacific side and on the Japan Sea side. Beech forests are also subdivided into two major types which occupy these two regions, respectively. Such a difference in the beech forest was firstly pointed out by Suzuki (1952). Later, Sasaki (1964) confirmed it and studied forests in detail throughout Japan.

The *Fagus crenata*-*Sasa kurilensis* forest is developed in regions on the Japan Sea side. It is characterized by *Sasa kurilensis*, *Acer japonicum*, *Hugeria japonica*, *Oxalis acetocella* var. *japonica*, *Mitchella undulata*, *Rumohra mutica*, *Plagyogyria matsumureana*, *Aucuba japonica* var. *borealis*, *Daphniphyllum macropodum* var. *humile*, *Cephalotaxus harringtonia* var. *nana*, *Skimmia japonica* var. *repens*.

Those species are absent, or very rare, in the *Fagus crenata*-*Sasamorpha purpurascens* forest that is developed in regions on the Pacific side. *Sasa kurilensis* and the last four of the above-listed species are evergreen shrubs. They have an ecological advantage in the photosynthetic activity soon after the accumulated snow melts away. *Fagus crenata*-*Sasamorpha purpurascens* forests (phot. 2) are characterized by *Sasamorpha purpurascens*, *Acer sieboldiana*, *A. shirasawanum*, *A. micranthum*, *Betula grossa*, *Symplocos coreana*, *Lindera umbellata*, *Stewartia pseudo-camellia*, *S. monadelphica*, *Fagus japonica*, *Parabenzoin trilobum*, *Sasa nipponica*, *Abies homolepis*, *Tsuga sieboldii*, and *Skimmia japonica* (Sasaki, 1964).

Phytosociologically, the two types of the beech forest were first regarded as the associations: *Saseto-* and *Sasamorpheto-Fagetum crenatae* (Suzuki, 1952, 1966b; Sasaki, 1964). But recent detailed studies revealed several associations which are distinctive from each other in their floristic composition and ecological relation to the habitat (Miyawaki et al., 1964, 1968, 1969). The *Corno-Fagetum crenatae* is found on mountain slopes with rather shallow soils and the *Miricacalio-Fagetum crenatae* is developed in the cloud zone with high air humidity in Mts. Tanzawa, Fuji, and Hakone, which are situated in regions on the Pacific side of central Honshu (Miyawaki et al., 1964, 1968, 1969). In the Okutadami region on the Japan Sea side, central Honshu, on the other hand, *Aucubo-* and *Hamamelo-Fagetum crenatae* have developed in low and high elevations of the beech forest zone respectively (Miyawaki et al., 1968). Based on these detailed studies, the major two types of the beech forest in Japan, which were regarded as associations, viz. *Saseto-* and *Sasamorpheto-Fagetum crenatae*, might be treated as alliances: *Saseto-* and *Sasamorpheto-Fagion crenatae*, which occupy the montane regions of the Japan Sea side and of the Pacific side respectively, and to which several associations belong (Miyawaki et al., 1964, 1967, 1968, 1969).

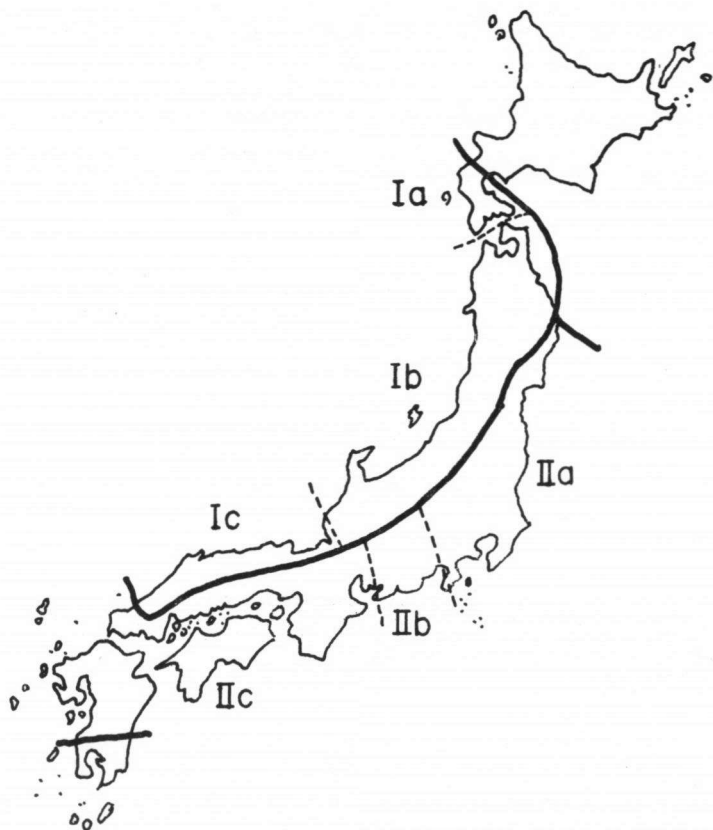


Fig. 8. Map of Japan showing the range of (I) the *Fagus crenata*-*Sasa kurilensis* forest and (II) the *Fagus crenata*-*Sasamorpha purpurascens* forest. Detailed explanation in text (after Sasaki in Miyawaki, 1967).

Geographical variation in the floristic composition of beech forest is shown in Fig. 8 (Sasaki, in Miyawaki, 1967). The Region I in Fig. 8 is the range of the *Fagus crenata*-*Sasa kurilensis* forest (*Saseto-Fagion crenatae*). Beech forests in Ia are characterized by *Sasa cernua*, *Hydrangea macrophylla* var. *megacarpa* and *Pachysandra terminalis*; those in Ib by *Hamamelis japonica* var. *obtusata*, *Rhododendron albrechtii*, and *Carex morrowii* var. *temnolepis*. Beech forests in Ic show a transitional composition between the Regions I and II, and are characterized by *Cryptomeria japonica* var. *radicans*, *Lindera umbellata*, *Symplocos coreana*, and *Rubus pectinellus*. The Region II in Fig. 8 is the range of the *F. crenata*-*Sasamorpha purpurascens* forest (*Sasamorpheto-Fagion crenatae*) on the Pacific side. Beech forests in IIa are the typical type of the beech forest on the Pacific side; those in IIb are characterized by *Abies homolepis*; and those in IIc by *Parabenzoin trilobum*, *Rhododendron metternichii*, and *Enkianthus cernuus* f. *rubens* (Sasaki, in Miyawaki, 1967).

*Fagus japonica* is a minor counterpart of *F. crenata*. It is distributed in montane regions only on the Pacific side. Forests of *F. japonica* are infrequently found in a limited scale (cf. Tohyama, 1965).

### 2.1.2. *Pterocarya rhoifolia* forests

Moist habitats in valley bottoms and on alluvial fans in the summergreen forest region support *Pterocarya rhoifolia* forests. Such habitats are surrounded by beech forests unless the area is disturbed, and soils are well drained and made up of boulders, gravels, and sands with decomposed organic matter (Saito, 1967). Common plants of the *Pterocarya rhoifolia* forest are *Ulmus laciniata*, *Cercidiphyllum japonicum*, *Phellodendron amurense*, *Pachysandra terminalis*, *Stellaria diversiflorum*, *Athyrium pycnosorus*, *Matteuccia struthiopteris* (which are characteristic to the *P. rhoifolia* forest), *Acer mono*, *Sorbus alnifolia*, *Ligustrum tschonoskii*, *Rhus ambigua*, *Schizophragma hydrangeoides*, *Hydrangea petiolaris*, *Asperula odorata*, *Galium japonicum*, *Laportea bulbifera*, *Dryopteris crassirhizoma*, etc. (which are common, more or less, to some of the summergreen forests in the region).

Phytosociologically, *P. rhoifolia* forests are subdivided into three associations. One is the *Polysticheto-Pterocaryetum* (Suzuki et al., 1956; Miyawaki et al., 1968). It is mostly distributed in regions on the Japan Sea side and characterized by *Aesculus turbinata*, *Laportea macrostachya*, *Viola vaginata*, *Polystichum retroso-paleaceum*, *P. tripterum*, *Dryopteris monticola*. The second association is *Dryopteridi-Fraxinetum commemoralis* (Suzuki, 1952), which is synonymous with *Chrysosplenio-Fraxinetum spaethianae* (Miyawaki et al., 1964). This is distributed in regions on the Pacific side and is characterized by *Fraxinus spaethiana*, *Acer carpinifolium*, *A. diabolicum*, *A. argutum*, *Scutellaria shikokiana*, *Chrysosplenium macrostemon*, *Cardamine anemonoides*, *Asarum caulescens* and *Dryopteris polylepis*. The third is *Polysticheto-Aesculetum turbinatae*, which was reported from western Honshu (Horikawa and Sasaki, 1959a). The species composition is similar to the first association.

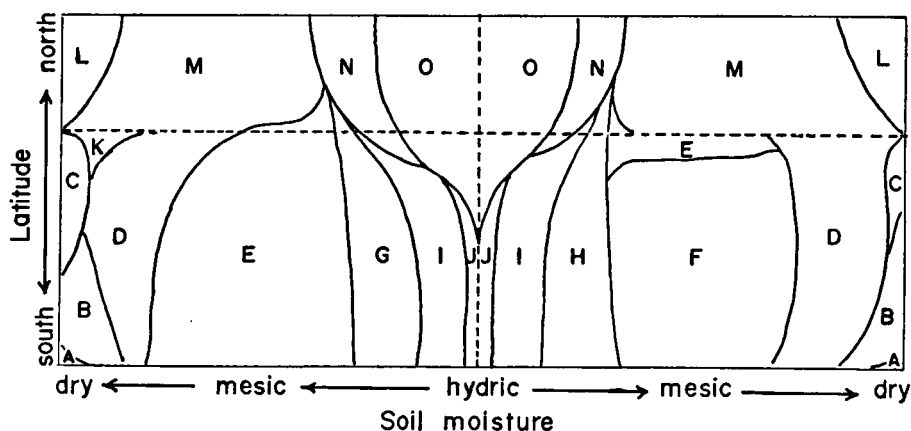


Fig. 9. Schematic summary of plant community distribution in relation to latitude and soil moisture gradient in the summergreen broad-leaved forest region of Japan. Forests on the Japan Sea side are given on left half; the Pacific side, right half; Hokkaido, above the broken line; and Honshu, Shikoku, and Kyushu, below. A. *Pinus densiflora* forest, B. *Abies firma*-*Tsuga sieboldii* forest, C. *Tsuga diversifolia* forest, D. *Quercus mongolica* var. *grosseserrata* forest, E. *Fagus crenata*-*Sasa kurilensis* forest, F. *Fagus crenata*-*Sasamorpha purpurascens* forest, G. *Pterocarya rhoifolia*-*Polystichum tripterum* forest, H. *Fraxinus spaethiana*-*Pterocarya rhoifolia*-*Dryopteris polylepis* forest, K. *Quercus mongolica* var. *undulatifolia* forest, I. *Salix-Alnus hirsuta* forest, J. *Phragmites communis* moorland (fen), L. *Picea glehnii* forest, M. *Quercus mongolica* var. *grosseserrata*-*Quercus dentata* forest, N. *Fraxinus mandshurica*-*Ulmus davidiana* forest, O. *Sphagnum* bog (after Miyawaki, 1967).

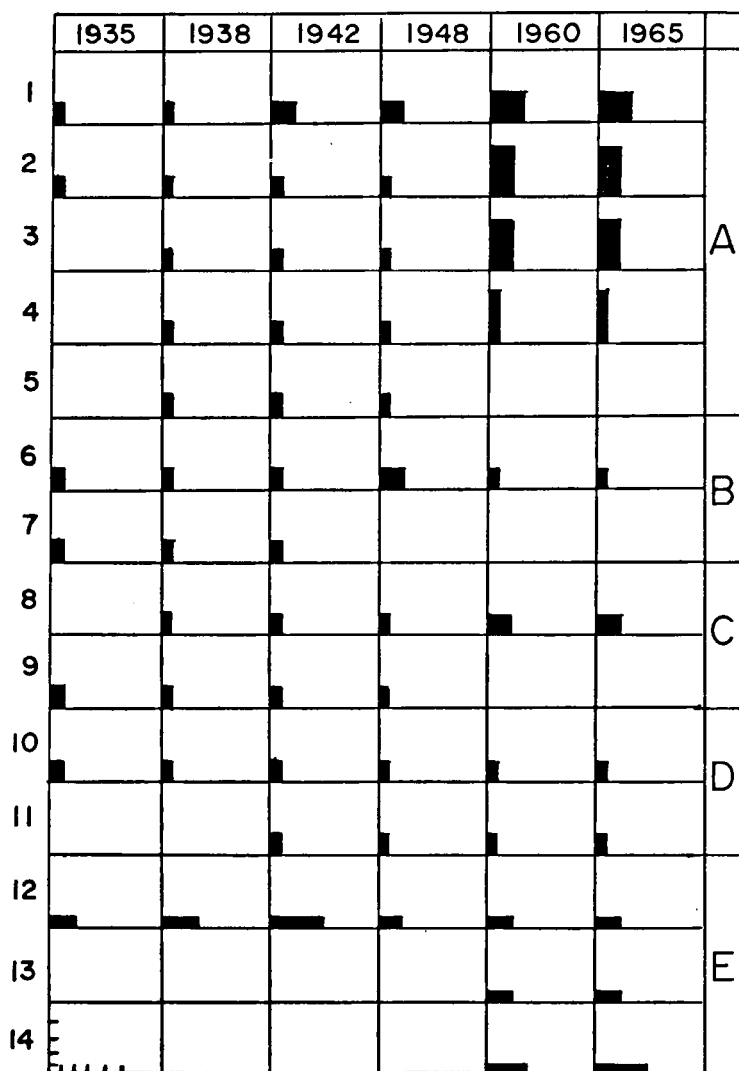


Fig. 10. Successive changes in coverage (abscissa) and height class (ordinate) of the important taxa composing the plant community on the central part of the Akaikawa pumice flow. A. (trees): 1. *Betula platyphylla* var. *japonica*, 2. *Populus maximowicziana*, 3. *Larix leptolepis*, 4. *Pinus densiflora*, 5. *Quercus mongolica* var. *grosseserrata*; B. (subtrees): 6. *Salix bakko*, 7. *Salix sachalinensis*; C. (shrubs): 8. *Salix integra*, 9. *Hydrangea paniculata*; D. (herbs): 10. *Polygonum sachalinensis*, 11. *Dryopteris rhizophragma*; E. (mosses and lichens): 12. *Polystichum commune*, 13. *Racomitrium canescens*, 14. *Stereocaulon vesvianum* (after Yoshioka, 1966).

### 2.1.3. *Ulmus davidiana*-*Fraxinus mandshurica* forests

Habitats with a high ground water table in lowlands of northern Honshu and Hokkaido support deciduous forests that are different from the above-mentioned ones. One is the *Alnus japonica* forest. It is developed on the periphery of fens and reed swamps and on flood deposits along the lower river courses. The ground water table of those habitats is as high as and in some places even higher than the ground level. If the water table is lower, *Alnus japonica* is mixed with *Fraxinus mandshurica* and further replaced by *Ulmus davidiana*. Based on our observations of relict stands, alluvial plains where cities and agricultural lands are now extensive originally supported the mixed forest of *Ulmus davidiana* and *Fraxinus mandshurica*. Main components of the forest are such deciduous trees and shrubs as *Ulmus laciniata*, *Pterocarya rhoifolia*, *Acer mono*, *Prunus maximowiczii*, *Syringa reticulata*, *Euonymus oxyphyllus*, *E. macropterus*, *Sambucus sieboldiana* var. *miquelii*; herbs as *Trillium kamschaticum*, *Fritillaria kamschaticensis*, *Meehania urticifolia*, *Scopolia japonica*, *Anemone flaccida*, *Urtica platyphylla*, *Impatiens noli-tangere*, *Cardamine leucantha*, *Filipendula kamschatica*, *Cacalia hastata* var. *orientalis*, *Veratrum grandiflorum*, *Maianthemum dilatatum*, *Carex dissitiflora*, *C. parviflora*, etc. (Miyawaki, 1967).

### 2.1.4. Volcanic vegetation. Phot. 4, 25, 26.

Several extinct and active volcanoes in the summergreen broad-leaved forest region are good fields for observing the primary succession on volcanic habitats. An example is Mt. Komagatake, which is situated in southernmost Hokkaido. An eruption took place on it in 1929 and the vegetation on the slopes was damaged, and, on some slopes, was completely covered by pumice and ash. After the eruption, the development and recovery of vegetation on a new pumice flow were studied by Yoshii and Yoshioka in 1933, 1935, 1938, 1942, and 1948, and by Yoshioka in 1960 and 1965. The details reported by Yoshioka (1966) are given in Fig. 10.

Vegetational development on lava can be observed on the andesitic lava bed dating from 1783 on the northeast slope of Mt. Asama, central Honshu. Phot. 26. The plant growth on the bed (1350 m in altitude) is still quite sparse and low. Species observed there are *Hydrangea paniculata*, *Salix vulpina*, *S. bakko*, *Betula platyphylla* var. *japonica*, *Polygonum cuspidatum*, *Alnus firma*, *Larix leptolepis*, *Pinus densiflora*, *Tripetaleia paniculata*, *Vaccinium uliginosum*, *Loiseleuria procumbens*, *Empetrum nigrum* var. *japonicum*, *Cassiope lycopodioides*, *Phyllodoce nipponica*, *P. aleutica*, etc. The first five of the above-listed species are common to the above-cited pumice flow on Mt. Komagatake. The last six species are alpine plants that usually grow in high elevations exceeding 2300 m in this area. Their occurrence in the cool-temperate zone is extraordinary and seems to result from the severe conditions on the lava flow that resembles conditions in the alpine zone.

On the habitats with loose scoria, sand, and ash are developed herbaceous communities. Such habitats in the montane, subalpine, and alpine areas on Mt. Fuji support three associations; viz. the *Carex stenantha*-*Stellaria nipponica* Ass., *Cirsium purpuratum*-*Campanula punctata* var. *hondoensis* Ass., and the *Angelica hakonensis*-*Miscanthus oligostachyus* Ass. The first and second associations are developed on rather unstable substrata, while the third occurs on stable habitats with dense growth of plants. Species commonly found in these associations are *Arabis serrata* var. *serrata*, *Artemisia pedunculosa*, *Astragalus adsurgens*, *Polygonum cuspidatum*, *Salix reinii*, *Carex doenitzii*, *Hedysarum vicioides*, *Larix leptolepis*, and *Polygonum weyrichii* var. *alpinum*. The last of these species grows alone on the most unstable habitats in high elevations (Miyawaki et al., 1967).

Plant communities around active solfataras differ from those just mentioned. Phot. 25. The habitat is characterized by gases of CO<sub>2</sub>, SO<sub>2</sub>, H<sub>2</sub>S, etc. and the soil is acidic. Obser-

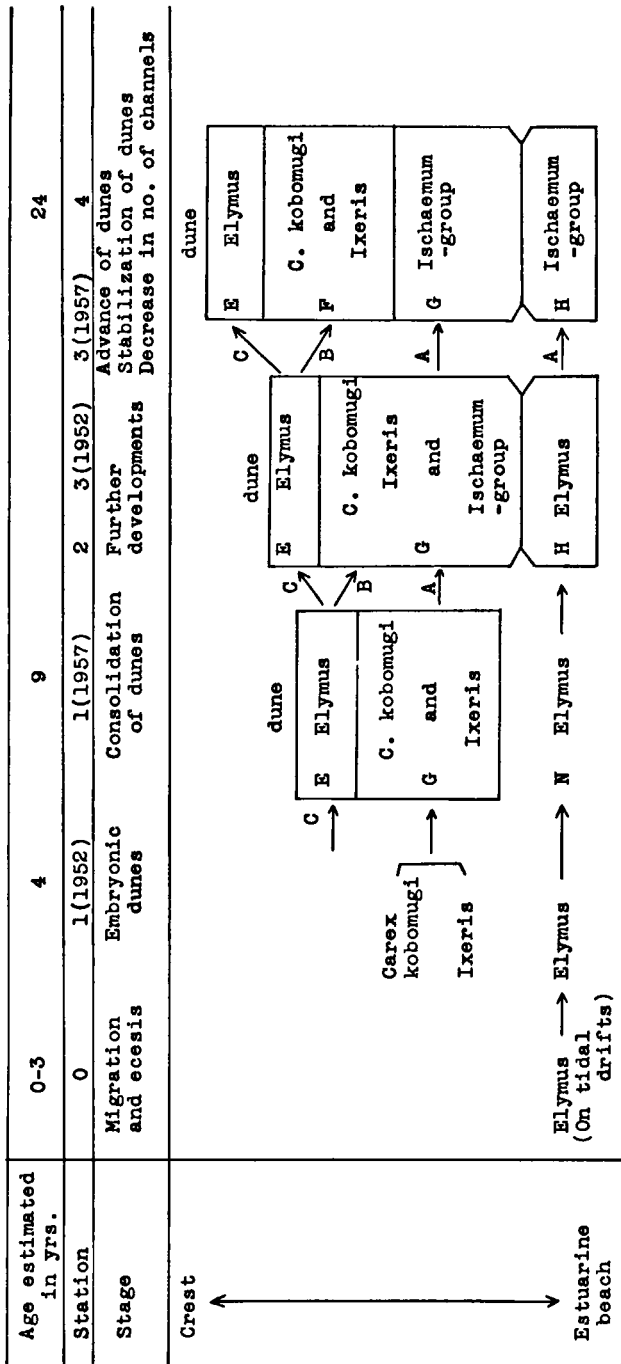


Fig. 11. The development of the topography-vegetation system on the sand bar. The plant names indicate the dominant species on the topographic units denoted by symbols. The capitals A, B, and C indicate the types of the successional trends, *Ischaemum*, *Calystegia*, *Lathyrus*, and *Linaria* are collectively called here as the *Ischaemum*-group (after Ishizuka, 1962).

vations made on Mts. Hakkoda and Osoreyama, northern Honshu (Yoahioka 1951; Yoshioka et al. 1965) indicate that surface soils near solfataras are extremely acidic ranging from 1.5 to 3.8 in pH value, on which no plants are found. Soils supporting plant growth also are acidic, from 2.0 to 4.5 in pH value. Plants growing on such habitats are acidophilic or acid-tolerant. Examples observed on Mt. Osoreyama are *Haplozia crenulata* var. *gracillima*, *Drepanocladus fluitans*, and *Carex angustisquama*. These three species are apparently acidophilic. In addition, the following species are observed there: *Deschampsia flexuosa*, *Juncus brachyspathus*, *Moliniopsis japonica*, *Miscanthus sinensis*, *Eubotryoides grayana* var. *grayana*, and *Ilex crenata* var. *paludosa*. Scrub communities in a distance from the solfataras are composed of *Ledum palustre* var. *diversipilosum*, *Ilex crenata* var. *paludosa*, *Vaccinium smallii*, *Rhododendron fauriei*, *Hydrangea paniculata*, *Ilex sugerokii* var. *brevipedunculata*, *Sasa paniculata*, *S. kurilensis*, *Eubotryoides grayana* var. *grayana*, *Sorbus commixta*, *Viburnum furcatum*, etc. Among the species listed above, *Deschampsia flexuosa*, *Ledum palustre* var. *diversipilosum*, *Rhododendron fauriei*, and *Ilex sugerokii* var. *brevipedunculata* are those whose distribution is usually restricted to the subalpine and alpine zones. Their occurrence around the solfataras results apparently from the severe conditions of the habitat. The same is true of the solfataras area on Mt. Hakkoda (Yoshioka, 1951).

#### 2.1.5. Coastal vegetation. Phot. 17.

##### 2.1.5.1. Sand dunes and sand bars. Phot. 23.

Plant communities on coastal sand dunes vary with habitats. Typical zonation of the dune communities is understood as ranging from (1) *Salsola komarovii* on nitrophytic habitats with decomposed tidal drifts, through (2) sparse communities on unstable slopes and crests with loose sand that consist of *Carex kobomugi*, *Elymus mollis*, *Ixeris repens*, *Glehnia littoralis*, *Calystegia soldanella*, *Linaria japonica*, and *Carex macrocephala*, to (3) the shrub community of *Rosa rugosa* and *Malus baccata* var. *mandshurica*, and further to (4) *Quercus dentata* forests on fixed dunes (Miyawaki, 1967).

On sand bars or spits extending outward into the open sea, various types of maritime and sub-maritime plant communities are found (Ishizuka, 1961, 1962). The interspecific associations or the disassociations of major species there are well correlated with similarity or dissimilarity among those topographic-distributional patterns of species.

Three groups can be recognized as positive associations, such as 1) *Suaeda maritima*, 2) *Elymus mollis* and *Carex pumila*, and 3) *Ixeris repens*, *Carex kobomugi*, *Carex macrocephala*, *Glehnia littoralis*, *Ischaemum antheophoroides*, *Calystegia soldanella*, *Lathyrus maritimus*, and *Linaria japonica*.

The interrelation between the vegetation and the dune topography on sand bars is regarded as a system of mutual interactions and development (Fig. 11).

##### 2.1.5.2. Salt marshes. Phot. 24.

Salt marshes in a natural condition remain abundantly on the eastern coasts of Hokkaido (Ito, 1963). Plants and communities of the salt marshes are distributed in relation to the salinity of water and soils, and to the intensity of wave actions. The arrangement of the communities observed in eastern Hokkaido are schematically shown in Fig. 12, in which the communities are named according to the phytosociological tradition (Miyawaki and Ohba, 1965). The plant distribution along the salinity gradient given on the top row of Fig. 12 is shown in Fig. 13, in which the sea weed communities are shown together.

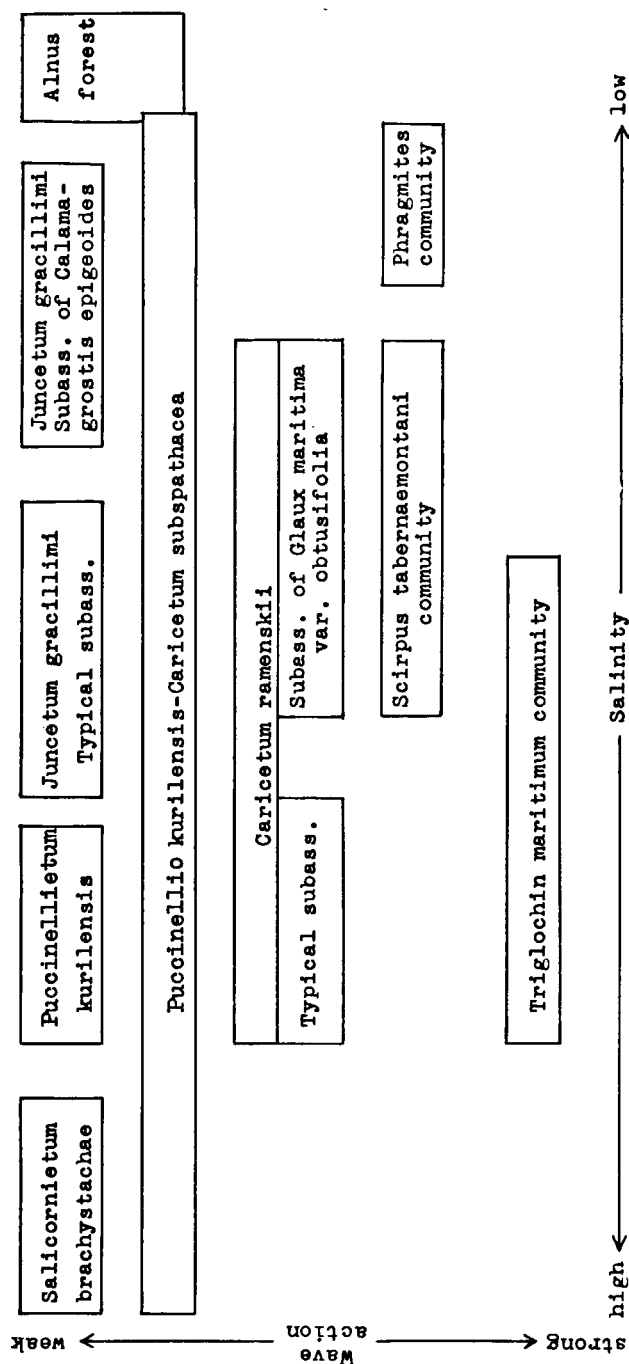


Fig. 12. Schematic illustration of salt marsh communities in relation to salinity and wave actions on the eastern coast of Hokkaido (after Miyawaki and Ohba, 1965, slightly modified).



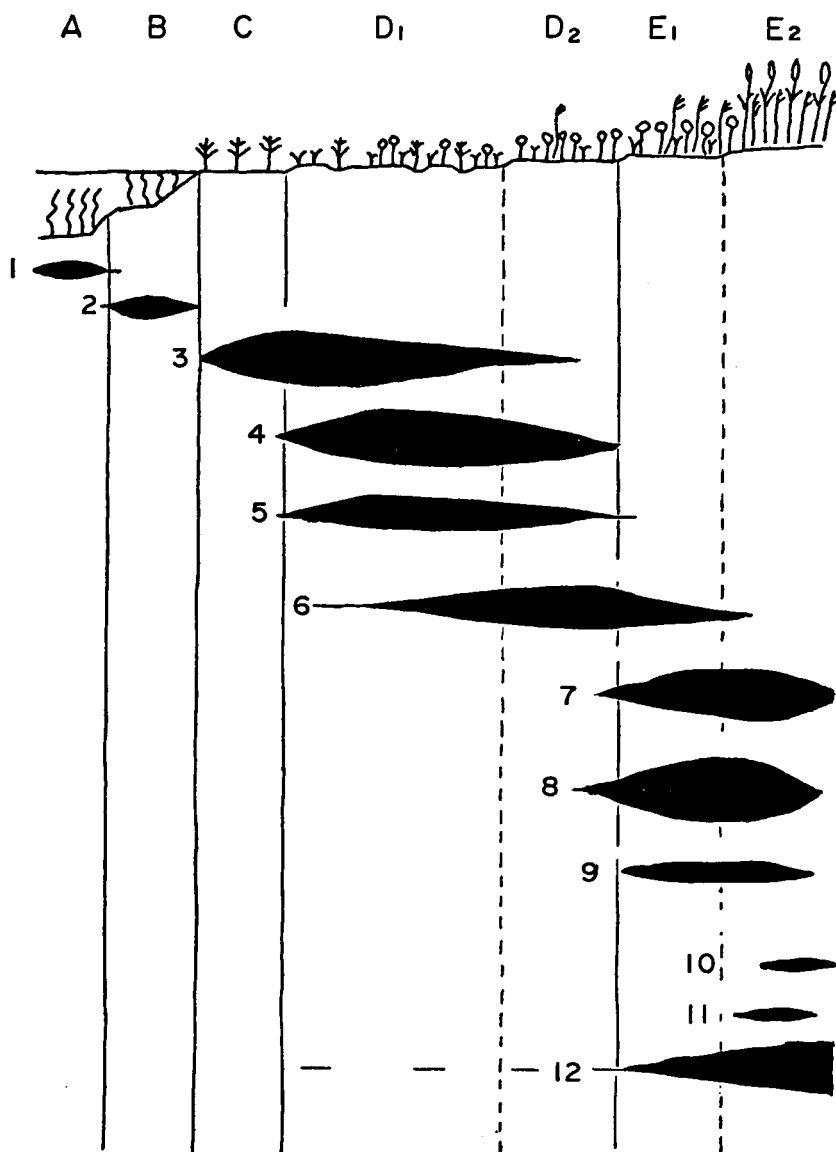


Fig. 13. Schematic illustration of plant-habitat relationships in salt marshes at the eastern coast of Hokkaido. Only dominant species are shown here. 1. *Zostera marina*, 2. *Zostera nana*, 3. *Salicornia brachystachya*, 4. *Puccinellia kurilensis*, 5. *Spergularia marina*, 6. *Glaux maritima* var. *obtusifolia*, 7. *Potentilla egedei* var. *grandis*, 8. *Juncus gracillimus*, 9. *Eleocharis kamschatica*, 10. *Calamagrostis epigeios*, 11. *Inula japonica*, 12. *Phragmites communis*. A. *Zostera marina* Ass., B. *Zostera nana* Ass., C. *Salicornietum*, D. *Puccinellietum* (1. typical subass., 2. subass. of *Glaux maritima* var. *obtusifolia*), E. *Juncetum* (1. typical subass., 2. subass. of *Calamagrostis epigeios*) (after Miyawaki and Ohba, 1965, slightly modified).

### 2.1.6. Moorland vegetation. Phot. 22.

Moorlands under cool and cold climate are found abundantly in montane regions of central and northern Honshu and in Hokkaido, but infrequently at high elevations in southern Japan (Miyawaki 1968b). Of the moorlands in Japan, those in the Ozeegahara region and its vicinity (Mts. Tashiro, Aizukoma, and Hiragatake) have been studied in detail (Horikawa and H. Suzuki, 1954; T. Suzuki, 1954; Yoshioka, 1954; Miyawaki et al., 1967, 1968; Miyawaki and Fujiwara, 1968b). The present paper deals mainly with the moorland community in these areas.

Twenty-one species of *Sphagnum* have been reported from the Ozeegahara region (Horikawa and H. Suzuki, 1954). The high or raised moor in the areas is made up of a mosaic of hummocks and hollows. Hollow plants differ with the depth of water. Hollows with 5—30 cm deep water are characterized by the sparse growth of *Carex limosa* (the community is named *Caricetum limosae*, Miyawaki et al., 1967), while plants in shallow hollows with 0—5 cm deep water are represented by *Scheuchzeria palustris*, *Rhynchospora alba*, *Drosera anglica* (which in Honshu is found only in the Ozeegahara Basin but common in moorlands in Hokkaido), and *Lycopodium inundatum* (*Scheuchzerio-Rhynchosporietum albae*, Miyawaki et al., 1967). This community comprises constantly some other species such as *Carex middendorffii* and *Drosera rotundifolia*; *Sphagnum pulchrum* frequently grows in the water and *Carex omiana* in the waterless hollow (Miyawaki et al., 1967; Miyawaki and Fujiwara, 1968b).

The hummock communities are characterized by several species of *Sphagnum*. *Sph. papillosum* is characteristic to the 'young' hummock which fringes the hollow (*Sphagnetum pappilosi*, Miyawaki et al., 1967, 1968; Miyawaki and Fujiwara, 1968b). This community is distributed from low-elevation moorlands near the seacoast in Hokkaido (Miyawaki, 1968) through montane regions of Honshu to high elevations in Yakushima Island, southern Kyushu (Aragane, 1963). *Sphagnum magellanicum* and *Sph. compactum* are representatives of the intermediate hummock (*Sphagnetum magellanici* and *compacti*, Miyawaki and Fujiwara, 1968); *Sph. fuscum* is characteristic to the mature hummock (*Sphagnetum fusci*, Miyawaki et al., 1967). These four hummock communities comprise other common bog plants such as *Oxycoccus quadripetalus*, *Andromeda polifolia*, *Rhynchospora alba*, *Carex middendorffii*, *C. omiana*, *Moliniopsis japonica*, *Drosera rotundifolia*, *Tofieldia japonica*, *Eriophorum vaginatum*, etc. *Sphagnum ambryphyllum*, *Sph. rubellum*, and *Sph. pulchrum* are infrequently found in these communities. The hollow and hummock communities make up the complex mosaic of the high moor vegetation.

The *Moliniopsis japonica*-*Carex middendorffii* community is representative of the transition moor of Japan. It is named *Carici-Moliniopsietum japonicae* (Miyawaki et al., 1967, 1968). Physiognomically, this community is different from the above-stated high moor communities because of the dense growth of such tall prominent herbs as *Hemerocallis middendorffii*, *Solidago virga-aurea* var. *asiatica*, *Sanguisorba officinalis*, *Eriophorum vaginatum*, *Myrica gale* var. *tomentosa*, *Moliniopsis japonica*, and *Carex middendorffii*. *Heloniopsis orientalis*, *Drosera rotundifolia*, *Oxycoccus quadripetalus*, and *Pogonia japonica* are also found commonly in the transition moor. Some parts of the moorland of this type are dominated by one of following species: *Sphagnum capillaceum*, *Sph. ambryphyllum*, *Sasa oseana*, *Osmunda asiatica*, *Tofieldia japonica*, *Lysichiton camtschatcense*, and *Hosta albo-marginata* (Miyawaki et al., 1967; Miyawaki and Fujiwara, 1968b).

Bog pools in the moorland support an aquatic community. It is composed of *Comarum palustre*, *Menyanthes trifolia*, *Caltha palustris* var. *membranacea*, *Carex limosa*, *Lobelia sessilifolia*, *Equisetum limosum* f. *limosum*, and *E. limosum* f. *verticillata*. The community is named *Comareto-Menyanthetum* (Suzuki, 1954).

The high and transition moorland communities mentioned above are expected to be found in Hokkaido (Ito and Tohyama, 1968). *Ledum palustre* var. *diversipilosum* is restricted only to the latter (Miyawaki, 1968b).

Ecological studies of peat bogs (Yoshii and Yoshioka, 1940; Iwata, 1940, 1941; Suzuki, 1941; Jimbo, 1941, 1942, 1948; Nakamura, 1942, 1949; Ishizuka, 1949) clarified aquatic flora and vegetation, zonation and succession, pollen analysis of lake deposits and peat, microflora, and environmental conditions.

## 2.2. Semi-natural vegetation

### 2.2.1. Secondary forests. Table 7.

#### 2.2.1.1. *Pinus densiflora* forests. Phot. 11.

Secondary forests of *Pinus densiflora* are treated before under the evergreen broad-leaved forest region.

#### 2.2.1.2. *Quercus mongolica* var. *grosseserrata*-*Castanea crenata* forests

Secondary forests of mixed *Quercus serrata* and *Q. acutissima* are not developed in the summergreen broad-leaved forest region, while the *Quercus serrata* forests are found in lower montane areas in the region (Ishizuka, 1968). So far as we know, the latter is different from the former in lacking, at least, *Q. acutissima* and seedlings and saplings of evergreen tree and shrub species. However, many species are common to both.

The *Quercus mongolica* var. *grosseserrata*-*Castanea crenata* forest is representative of secondary forests in the region under consideration. They are, more or less, varied with localities and habitats. Components common to such forests in different localities are *Quercus mongolica* var. *grosseserrata*, *Castanea crenata*, *Rhus trichocarpa*, *Acer palmatum* var. *matsumurae*, *A. mono*, *Ilex macropoda*, *Clethra barbinervis*, *Styrax japonica*, *Viburnum furcatum*, *Sorbus alnifolia*, *S. japonica*, *Cornus kousa*, *Carpinus tschonoskii*, *C. japonica*, *Acanthopanax sciadophylloides*, etc.

#### 2.2.2. Grasslands. Phot. 19-21.

Grasslands of the warm- and cool-temperate and subarctic regions are treated here together. They are divided into two categories in terms of their origin. One is the natural grassland; another is the secondary one.

The natural grassland is developed in the alpine zone and on windy ridges on which the growth of trees is prevented and on volcanic habitats. Natural grasslands in northern Honshu and Hokkaido are dominated by *Sasa kurilensis*, *S. paniculata*, *S. nipponica*, or *S. nikkoensis* (Oshima, 1961). Those in central and western Japan are characteristic in accompanying species of *Rhododendron* or allied genera, and are restricted to high windy ridges. Ericaceous species are *Rhododendron tsusiophyllum* on Mts. Tanzawa and Hakone (extinct volcanoes) in central Honshu (Miyawaki et al., 1964; 1969), *Gaultheria adenothrix* in western Honshu (Horikawa and Sasaki, 1959), *Rhododendron tschonoskii* in Shikoku (Yamanaka, 1964), *Rh. kiusanum* on Mts. Kuzyu, Aso, and Unzen (active volcanoes) in Kyushu (Suzuki and Abe, 1959), and *Rh. metternichii* var. *yakushimanum* on Yaku-shima Island.

The secondary grassland is developed on deforested and disturbed areas, and is maintained by mowing, grazing, or burning. Dominance-types categorized by dominant (and sub-dominant) species are: *Sasa*-, *Miscanthus sinensis*-, *M. sinensis*-*Pleioblastus*-, *Zoysia japonica*-, *Z. japonica*-*Pleioblastus*-, *Pleioblastus*-, *Pteridium aquilinum*-, and *Poa pratensis*-types.

The *Sasa*-type secondary grassland is mainly distributed in northern Honshu and Hokkaido. Dominant species are *Sasa kurilensis*, *S. paniculata*, or *S. nipponica*. As is well

known, the Japanese Archipelago abounds in species of the genus *Sasa*. Most of these are associated with forest communities as their undergrowth in the cool-temperate, subalpine, and subarctic region. When timbers of the forest are logged down, there remains a dense growth of *Sasa* species which cover almost completely the logged forest land. Most of the *Sasa*-type grasslands except on windy ridges and on volcanic habitats result from such disturbance. The structure and function of *Sasa* communities are recently analysed from the standpoint of production ecology (Oshima, 1961, 1962).

The *Miscanthus sinensis* grassland (phot. 19) is maintained by yearly or every two-year mowing with frequent or infrequent burning. It is mainly distributed in the subarctic and warm- and cool-temperate regions from Hokkaido, through Honshu and Shikoku, to Kyushu (and further south to the Ryukyu Islands). The grassland is not natural but a seral community, as stated before. If kept long free from human interference, it is replaced by shrublands and successively by forests. Main components of the *Miscanthus sinensis* grassland are such grasses as *M. sinensis*, *Arundinella hirta*, *Spodiopogon sibiricus*; shrubs as *Lespedeza cyrtobotrya*, *L. bicolor*, *L. cuneata*, *Smilax china*, *Salix vulpina*; tall herbs as *Aster scaber*, *Solidago virga-aurea* var. *asiatica*, *Lysimachia clethroides*, *Cirsium japonicum*, *Patrinia scabiosaeifolia*, *Eupatorium lindleyanum*, *Platycodon grandiflorum*, *Pteridium aquilinum*, *Adenophora triphylla* var. *japonica*; and small herbs as *Carex lanceolata*, *Potentilla freyniana*, *Ixeris dentata*, *Disporum smilacinum*, *Viola grypoceras*, etc. (Yoshioka, 1955; Itow, 1963; Numata, 1966; Miyawaki and Fujiwara, 1968a; Miyawaki et al., 1968).

The *Zoysia japonica* grassland (phot. 20) is another type that is widely distributed in Japan. It is developed only in the continuously grazed habitat, and is distributed from southwestern Hokkaido at the north to Kyushu at the south. *Zoysia japonica* is a sod grass and forms extensive turfs by vegetative reproduction of rhizomes and stolons. Herbaceous plants found in the *Miscanthus sinensis* grassland also occur frequently or infrequently in the *Zoysia japonica* grassland in a reduced, stunted, and injured condition. In addition, common species of the grassland are such grazing- and trampling-tolerant perennials as *Haloragis micrantha*, *Polygala japonica*, *Carex nervata*, *Lotus corniculatus*, *Luzula capitata*, *Geranium nepalense* var. *thunbergii*, *Agrostis clavata*, *Hydrocotyle ramiflora*, *Plantago asiatica*, *Trifolium repens*; and annual plants as *Poa annua*, *Cerastium holosteoideis* var. *hallaisanense*, *Mazus miquelii*, *Kummerowia striata*, etc. (Yoshioka, 1955; Itow, 1963; Suganuma, 1966). Heavily trampled sites in the grassland support a weed community consisting of *Plantago asiatica*, *Poa annua*, *Trifolium repens*, and some other weeds (Iizumi, 1962; Itow, 1963). The community is similar to that on trampled trails (Numata, 1961a; Miyawaki, 1964). Phytosociologically, the *Zoysia japonica* grasslands were classified into four associations: *Violo*-, *Geranio*-, *Erigero*-, and *Arundinello-Zoysietum* (Suganuma, 1966). Our data from lowland grasslands in Kyushu suggest a new association which is developed on coastal grazed lands.

The *Pleiblastus*-type and its allied types (*Miscanthus sinensis*-*Pleiblastus*- and *Zoysia japonica*-*Pleiblastus*-types) are distributed in central Honshu (where *Pleiblastus chino* occurs), and in western Honshu and Kyushu (where *P. distichus* var. *nezasa* occurs). They are prevailing on volcanic ash soils in the Mts. Kuzyu, Aso, and Kirishima areas of central Kyushu (Itow, 1968b) and in the Mt. Sanbe area of western Honshu (Suganuma, 1966); and on non-volcanic soils in western and central Honshu (Okuda and Miyawaki, 1966; Miyawaki and Fujiwara, 1968b). Grasslands of these types are mostly, but not exclusively, distributed in the warm-temperate region. The floristic composition is similar to the *Miscanthus sinensis* grassland when it is yearly mowed, and to the *Zoysia japonica* grassland when grazed.

*Pteridium aquilinum* occurs as a component of *Miscanthus sinensis* grasslands, while it

frequently grows very densely within or contiguous to the *M. sinensis* and *Zoysia japonica* grasslands. The physiognomy is quite different from these, but the floristic composition is almost the same as that of the *Miscanthus sinensis* grassland when the bracken community is developed within or contiguous to it (Itow, 1963), and the same as that of the *Zoysia japonica* grassland when it is within or contiguous to the latter (Suganuma, 1966).

The *Poa pratensis* grassland is the sown and fertilized pasture. It is maintained by careful management, mostly in northern Japan (Numata, 1961a). *Poa pratensis* was introduced from Europe early in the 20th century and is now established as a good semi-natural pasture under proper intensity of grazing, especially in Hokkaido. The pasture is phytosociologically named *Phleum pratense*-*Poa pratensis* association (Miyawaki, 1962).

As stated before, secondary grasslands are developed on deforested and disturbed areas and maintained by mowing, grazing or burning. They are invaded by shrubs and trees, if kept long free from human interference. Succession of grasslands was first studied by Oseko (1937) and later by several authors (Yoshida, 1951; Sugawara and Iizumi, 1954, 1964; Iizumi *et al.*, 1957, 1961; Numata, 1961a; Itow, 1963). These studies are based on regional or local data. Stands of the grassland differ, more or less, from each other not only in the floristic composition but also in the successional status. The problem to be solved is the objective judgement of the dynamic status of each stand and of each grassland type in terms of vegetational succession. For example, there are a number of stands of the *Miscanthus sinensis* grassland, ranging from those in floristic composition close to the *Zoysia japonica* grassland to those close to the shrub community. To represent the ecological distance among grassland types and among stands under study, an index was proposed (Numata, 1961a). It is called the 'Degree of Succession' (hereafter abbreviated as DS), that is,

$$DS = [\Sigma(l \times d) / n] \times v,$$

where *l* is the life span of the component species, *d* is the dominance values as expressed by Summed Dominance Ratio (SDR, the summation percentage of the ratios of the coverage, height, frequency, density, etc.), *n* is the number of species occurring in the minimal area, and *v* is the total ground cover in percentages. The life span (*l*) of plant species is assumed as 1 for Therophytes, 10 for Geophytes, Hemicyptophytes, and Chamaephytes, 50 for Nanophanerophytes, and 100 for Micro-, Meso-, and Mega-phanerophytes. Values of the DS for each grassland type of Japan are distributed as shown in Fig. 14 (Numata, 1969a).

The DS index is applicable to grassland communities, beyond climatic zones, floristic provinces, and continents, since it is based on the life-form of plants, not on species. This was proved by applications to grasslands of Nepal Himalaya (Numata, 1965b) and southern Korea (Park, 1965).

### 3. Subalpine and subarctic coniferous forest region. Table 6—III. Phot. 7, 8.

Subarctic, subalpine, and alpine regions of Japan are less affected by man as compared with the other regions treated before. Large parts of this region have been designated as national parks in order to preserve the natural landscape.

#### 3.1. *Abies mariesii*-*A. veitchii* forests in Honshu

The subalpine region of Honshu and Shikoku supports coniferous forests dominated by *Abies mariesii* and/or *A. veitchii*. The coniferous forest is distributed from Mt. Hakkoda in northern Honshu, where *A. veitchii* is lacking, through the Japan Alps in central Honshu where *A. mariesii* and *A. veitchii* are usually mixed, to Mt. Ishizuchi where only *A. veitchii* var. *shikokiana* is found. Altitudinal lower limit of coniferous forests is gradually

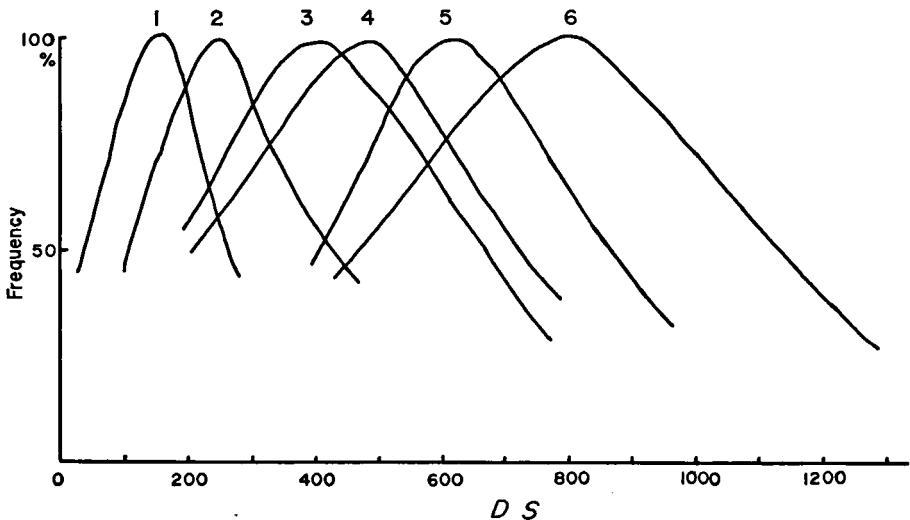


Fig. 14. Curves showing the frequency of each grassland type on the DS-index gradient. 1. *Erigeron canadensis* community (which is a pioneer community on abandoned fields, not treated in the present paper), 2. *Zoysia japonica*-, 3. *Pteridium aquilinum*-, 4. *Miscanthus sinensis*-, 5. *Pleiblastus distichus* var. *nezasa*- and *P. chino*-, and 6. *Sasa*-type grasslands (after Numata, 1969).

higher southwards, from 700 m above sea level in northern Honshu, through 1500 m at central Honshu, to 1900 m in Shikoku (cf. vegetation map).

A stand of the coniferous forest on Mt. Tashiro (Miyawaki et al., 1967), for example, is composed of such trees and shrubs as *Abies mariesii*, *A. veitchii*, *Picea jezoensis* var. *hondoensis*, *Acer ukurunduense*, *Sorbus commixta*, *Betula ermanii*, *B. coryfolia*, *Acer tschonoskii*, *Cornus canadensis*; and herbs as *Coptis trifolia*, *Plagiogyria stenoptera*, *Carex dolichostachya*, *Olopanax japonicus*, *Oxalis acetosella*, *Lycopodium serratum* var. *thunbergii*, *Pteridophyllum racemosum* (Papaveraceae, an endemic genus), *Tripterospermum japonicum*, *Smilacina yesoensis*, *Cacalia adenostyloides*, *Dryopteris austriaca*, *Trillium smallii*, *Smilacina hondoensis*, *Clintonia udensis*, *Pyrola alpina*, *Diphylleia grayi*, etc. The same is almost true of the forests in other regions in central Honshu (cf. Masamune, 1961; Suzuki, 1964).

### 3.2. Mixed forests of *Thuja standishii* and *Tsuga diversifolia*

The mixed forest of *Thuja standishii* and *Tsuga diversifolia* is another type of the coniferous forests in the subalpine region of Honshu. It is developed on ridges with shallow soils on which blocks of the bedrock are infrequently exposed on the ground surface. The forest is different from the *Abies mariesii*-*A. veitchii* forest in its floristic composition. For example, the *Thuja standishii*-*Tsuga diversifolia* forest which is contiguous to the above-cited stand is lacking the last thirteen of the above-listed species and comprises additional species such as *Pinus parvifolia*, *Ilex sugerokii* var. *brevipedunculata*, *Ilex rugosa*, *Rumohra mutica*, *Rhododendron metternichii* var. *pentamerum*, and *Viburnum urceolatum* var. *procumbens*. The forest is also developed on narrow ridges in the beech forest area (Miyawaki et al., 1967, 1968).

The above-mentioned arrangement in the *Abies*- and the *Thuja*-forests is usually found in the subalpine region of Honshu (Suzuki, 1964; Suzuki et al., 1963; Miyawaki et al., 1968).

### 3.3. *Larix leptolepis* forests. Phot. 5.

The natural distribution of *Larix leptolepis* is restricted mostly to montane and subalpine regions in central Honshu, although the reforestation of this conifer has been made widely in the summergreen broad-leaved forest region. The natural forests are fragmentarily or extensively developed on talus and volcanic habitats whose soils are less capable in holding water. *L. leptolepis* is a pioneer tree of these habitats. The floor vegetation of the forest is varied in types and in floristic composition from site to site. According to Tatewaki et al., (1965), the floor types categorized by constant and dominant species are *Sasa*-, *Fern*-, *Lonicera*-, *Malus sieboldii*-, *Azalea*-, *Rhododendron*-, *Grass*-, *Heath*-, *Moss*-, *Sapling of conifers*-, and *Herb*-types. Prevalent types among these are *Sasa*- and *Azalea*-types in the forests below 1900 m, and *Rhododendron*- and *Herb*-types in higher elevations. Major components of the *Larix leptolepis*-*Sasa paniculata* forest on Mt. Asama (1720 m), for example, are *Quercus mongolica* var. *grosseserrata*, *Rubus palmatus* var. *coptophyllus*, *Celastrus orbiculatus*, *Festuca parvigluma*, *Artemisia montana*, *Astilbe thunbergii* var. *congesta*, *Aquilegia buergeriana*, *Sanguisorba officinalis*; those of a high-elevation stand in the Nikko area (2320 m) are *Prunus ermanii*, *Maianthemum dilatatum*, *Polygonum cuspidatum*, *Solidago decurrens*, *Trientalis europea* var. *europea*; and those of the *Larix leptolepis*-*Vaccinium vitis-idaea* forest are *Salix reinii*, *Betula maximowiczii*, and *Pyrola incarnata*.

*Larix leptolepis* also grows naturally in moist and wet habitats like stream-side deposits, fens, and marshes. The herb layer of such a stand at Nikko, for example, is made up of such moorland plants as *Oxycoccus quadripetalus*, *Andromeda polifolia*, *Moliniopsis japonica*, *Osmunda asiatica*, *Eriophorum vaginatum*, *Sphagnum* sp. and *Malus sieboldii* (Tatewaki et al. 1966).

### 3.4. Thickets of *Quercus mongolica* var. *undulatifolia* (Nanoquercetum)

Mountains in the western half of northern Honshu are outstanding in lacking coniferous forests in the subalpine zone; thickets dominated by *Quercus mongolica* var. *undulatifolia* are developed. This is apparently because the mountains are subject to a severe northwesterly winter monsoon and to heavy snowfall which attains usually several metres. Mts. Chokai, Zawo, Iide, Aizu-Komagatake, and Shibutsu and the Okutadami area support such a thicket, more or less, in their subalpine habitat. The community is very dense and about 2 m tall. It is contiguous to beech forests at its lower limit and to alpine communities at the upper limit in very snowy areas; and the community and the coniferous forest make up a mosaic pattern in mountains where wind and snowfall are not so severe. Main components of the *Quercus mongolica* var. *undulatifolia* thicket, for example, in the Okutadami area, are *Hamamelis japonica* var. *obtusata*, *Sorbus commixta*, *Viburnum furcatum*, *Menziesia multiflora*, *Sasa kurilensis*, *Maianthemum dilatatum*, *Vaccinium smallii*, *Streptopus streptopoides* var. *japonicus*, *Plagiogyria stenoptera*, *Paris tetraphylla*, *Clintonia udensis*, *Tilingia holopetala*, etc. (Miyawaki et al., 1968). Fig. 15 shows the ecological relation of the thicket with other communities observed in the Okutadami area, central Honshu.

### 3.5. *Betula ermani* thickets. Phot. 7.

*Betula ermani* and *Alnus maximowiczii* are deciduous shrubs found in the subalpine and alpine regions. Mixed or pure stands of these species are developed on habitats with

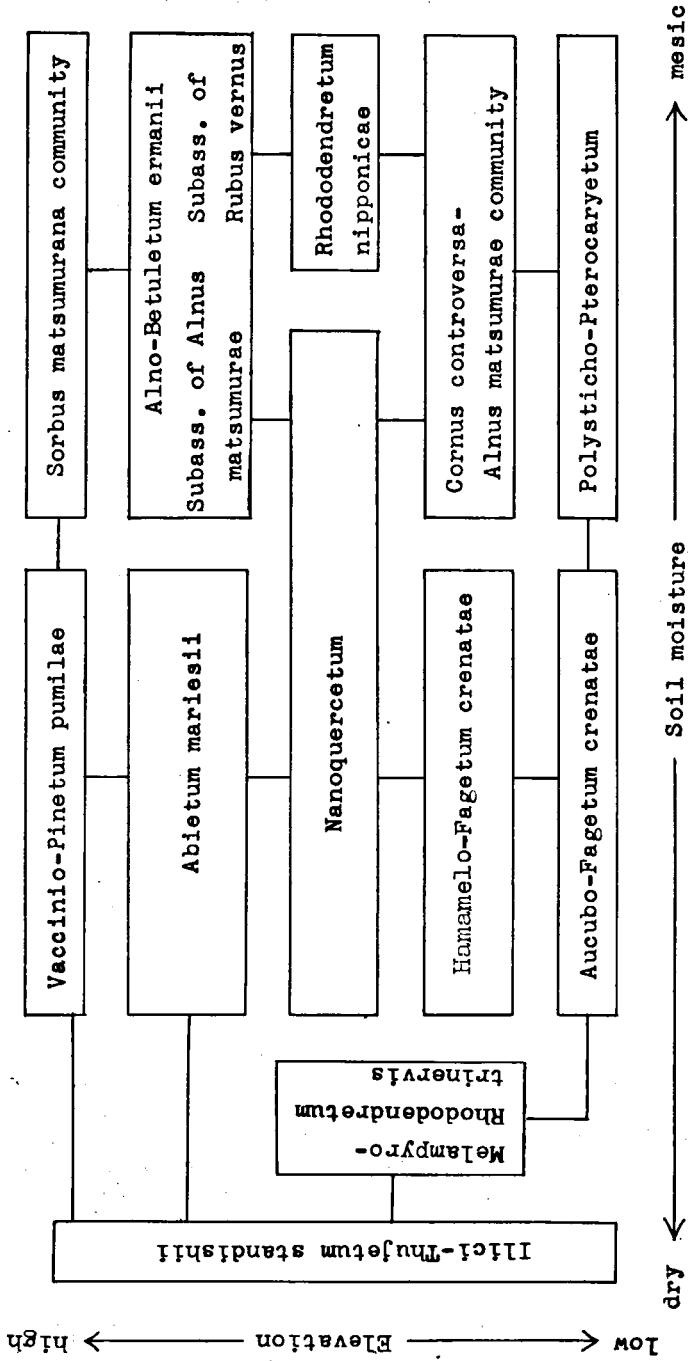


Fig. 15. Schematic illustration of vegetation-habitat relationships in the montane, subalpine, and alpine zones of the Okutadami region, central Honshu (after Miyawaki et al., 1968).



boulders and shallow soils along snow avalanche tracks and ravines (Masamune, 1961; Itow et al., 1964; Suzuki, 1964) and on subalpine volcanic habitats (Tohyama, 1966; Miyawaki et al., 1967). In many examples observed in the transition zone between the subalpine and alpine zones, the *A. maximowiczii* thicket is found in the mesic bottom of ravines and snow avalanche tracks; the *B. ermanii* thicket on the slope; and *Pinus pumila*, a shrub representative of the alpine region, is on the ridge. Species common to the *A. maximowiczii* and the *B. ermanii* thickets are such shrubs as *Sorbus matsumurana*, *S. tschonoskii*, *Acer ukurunduense*, *Rubus vernus*, *Weigela middendorffiana* (only in northern Honshu and Hokkaido); and herbs as *Glyceria alnasteretum*, *Streptopus amplexifolius* var. *papillatus*, *Trautvetteria japonica*, *Polystichum microchlamys*, *Athyrium melanolepis*, *Dryopteris austriaca*, etc. (Ohba, in Miyawaki, 1967).

### 3.6. *Picea jezoensis*-*Abies sachalinensis* forests in Hokkaido. Phot. 1.

Prevailing coniferous forests in Hokkaido are dominated by *Picea jezoensis* and *Abies sachalinensis*, accompanied by *Picea glehnii* or not. Based on the dominance type of the floor vegetation, the forests can be divided into several types. Prevalent types of the floor, for example, in part of central Hokkaido (Tatewaki et al., 1955), are *Sasa paniculata*-, *Carex sachalinensis*-, *Dryopteris amurensis*-types, etc. Floristic composition of these forest types, however, is quite alike, unless quantitative relations of the components are considered. Plants commonly found in the *Picea jezoensis*-*Abies sachalinensis* forest are such trees as *Betula ermanii*, *Sorbus commixta*, shrubs as *Ribes sachalinense*, *Euonymus macropterus*, *Vaccinium smallii*, *V. praestans*, *Acer ukurunduense*, *Ribes horridum*, and herbs as *Cornus canadensis*, *Oxalis acetosella*, *Tiarella polyphylla*, *Maianthemum bifolium*, *Streptopus streptopoides*, *Circaea alpina*, *Trillium tschonoskii*, *Dryopteris austriaca*, *Polypodium vulgare*, *Rumohra mutica*, *Lycopodium serratum* var. *thunbergii*, *Gymnocarpium robertianum*, etc.

### 3.7. *Picea glehnii* forests

*Picea glehnii* is distributed in Hokkaido and in southernmost Sakhalin and southern Kuriles. Its forests are developed both on dry habitats with shallow soils like volcanic ejecta, rocky or gravelly ridges and slopes, and serpentine areas, and in wet habitats like fens, sedge swamps, and marshes (Tatewaki, 1944).

Early stages of *P. glehnii* forests on serpentine habitats are sparse in physiognomy and associated with *Pinus pumila*, *Juniperus communis* var. *montana*, *Berberis amurensis*, *Crepis gymnopus* (the last two of these species are characteristic to the area), and later stages are associated with dense undergrowth of *Sasa kurilensis*. The forest on rocky and gravelly slopes are usually mixed with *Picea jezoensis* and *Abies sachalinensis*. The floor vegetation is dominated by either *Rhododendron fauriei*, *Menziesia pentandra*, *Carex sachalinensis*, or mosses.

Wetland forests of *Picea glehnii* are various in their composition. Based on the dominants of the floor, the forests are classified into six types: *Carex middendorffii*, *Moliniopsis japonica*, *Phragmites communis*, *Ledum palustre* var. *diversipilosum*, *Menziesia pentandra*, *Lysichiton camtschatcense*, *Osmunda asiatica*, and *Sphagnum* spp. (Tatewaki 1944).

### 3.8. Tall herb communities. Phot. 16.

Along snow avalanche tracks and in similar habitats, a community of tall herbs is developed in the montane, subalpine, and alpine regions. The community is distinctive from others in its physiognomy and floristic composition. Several examples are given below. Phot. 8. A community observed on Mt. Hakkoda (Yoshioka, 1948) is composed of

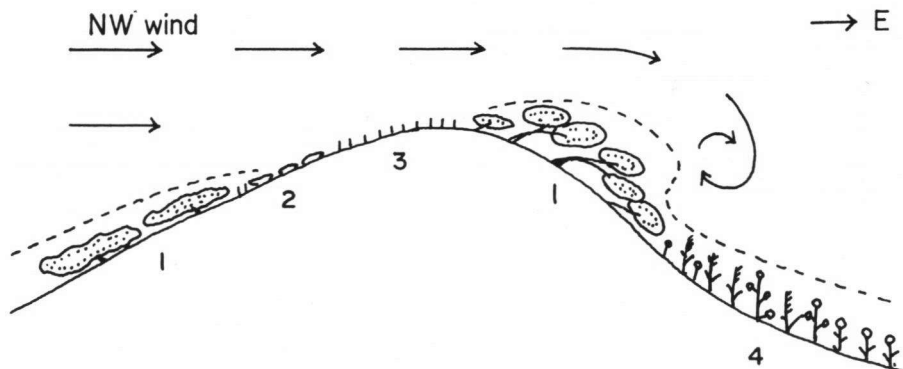


Fig. 16. Schematic illustration of community distribution on an alpine ridge. 1. *Pinus pumila* community; 2 and 3. wind-blown heathland, 2. *Arctio-Loiseleurietum*, 3. *Kobresia bellardii* community; 4. snow-patch community. Broken line indicates the snow accumulation in winter (after Ohba in Miyawaki, 1967, slightly modified).

*Angelica pubescens* var. *matsumurae*, *Aconitum gigas* var. *hondoense*, *Hydrangea macrophylla* var. *macrophylla*, *Rodgersia podophylla*, *Filipendula kamtschatica*, *Aralia cordata*, *Trautvetteria japonica*, *Petasites japonicus* var. *giganteus*, *Plectranthus trichocarpus*, *Athyrium pycnosorum*, etc. Dominant species of the community on Hokkaido (Tatewaki 1942) are *Angelica ursina*, *Artemisia montana*, *Cirsium kamtschaticum*, *Cacalia hastata* var. *orientalis*, *Senecio cannabifolius*, *Petasites japonicus* var. *giganteus*. Major components of the similar community in the subalpine and alpine regions of central Honshu (Suzuki and Nakano, 1965) are *Aconitum senanense*, *Cirsium babanum* var. *otayae*, *Rumex arifolius*, *Polystichum microchlamys*, *Veratrum stamineum*, *Saussurea nikkoensis* var. *sessiliflora*, *Artemisia monophylla*, *Angelica edulis*, *Carex multifolia*, *Galium kamtschaticum* var. *acutifolium*, etc.

Based on these examples and other observations, it is summarized that the characteristic components of the tall herb community are species belonging to *Angelica*, *Saussurea*, *Cirsium*, and *Aconitum* (Ohba, in Miyawaki, 1967; Miyawaki et al., 1968). Phot. 8. Ecological characteristics of altherbosa are analysed tracing precisely their developmental process, dry matter production, and absorption and accumulation of nutrient elements (Midorikawa, 1959).

#### 4. Alpine region. Phot. 5.

##### 4.1. Thickets of *Pinus pumila*. Phot. 3.

*Pinus pumila* is a prominent shrub in the alpine region of Japan. It is distributed from the alpine region of central Honshu at the south, to Hokkaido, and further north to the Kuriles, Sakhalin, Kamchatka, and Siberia. *P. pumila* thickets in Japan occur in high elevations exceeding the timber line and consist of *Pinus pumila*, *Vaccinium vitis-idaea*, *V. axillare*, *Empetrum nigrum* var. *japonicum*, *Gaultheria miqueliana*, *Cornus canadensis*, *Rhododendron aureum*, *Rubus pedatus*, *Coptis trifolia*, *Trientalis europea*, *Shortia soldanelloides*, *Sorbus sambucifolia*, *Tripetaleia bracteata*, etc. There are some floristic variations from habitat to habitat and from locality to locality.

The thickets are exclusively restricted to habitats that are sheltered by accumulated snow in winter and that are exposed early to sunlight in late spring or early summer. Fig. 16.

Phytosociologically, four associations have been reported from the alpine region of Honshu and Hokkaido. They are *Vaccinio*- (from central Honshu) (Suzuki, 1964; Suzuki and Umezu, 1965), *Sorbeto*-, *Rubeto*-, and *Ledeto*-*Pinetum* (from Hokkaido) (Kobayashi, 1967).

The main associations of the alpine thickets in Hokkaido are as follows according to Tatewaki (1963): *Pinus pumila*-*Rhododendron aureum*-*Empetrum nigrum* var. *japonica* ass., *P. pumila*-*Arctous alpina* var. *japonica*-*Vaccinium uliginosum* ass., *P. pumila*-*Ledum palustre* ass., *P. pumila*-*Sorbus matsumurana* ass., *P. pumila*-*Sasa kurilensis* ass., and *P. pumila*-non plant cover ass.

#### 4.2. Snow-patch vegetation. Phot. 6.

The snowfall blown by north-westerly winds in winter is accumulated on leeward slopes of ridges and in depressions. Accumulated snow is usually more than 5 m thick. The snow melts away, or remains unmelted as snow-patches in summer. Slopes below the snow-patch are mesic to wet, and those above the patch are dry. The plant community of the upper slopes, which is named *Anaphalio-Phyllodocetum aleutica* (Ohba, in Miyawaki, 1967), is made up of *Phyllodoce aleutica*, *Lycopodium sitchense* var. *nikoense*, *Shortia soldanelloides* f. *alpina*, *Geum pentapetalum*, *Arnica unalascensis* var. *tschonoskyi*, *Anaphalis alpicola*, *Deschampsia flexuosa*, etc. (Ishizuka, 1950; Masamune, 1961; Itow *et al.*, 1964; Ohba, in Miyawaki, 1967). Phot. 6.

On the other hand, mesic gentle slopes and flat places below the snow-patch support a different community composed of *Moliniopsis japonica*, *Fauria crista-galli*, *Carex blepharicarpa*, *Shortia soldanelloides* f. *alpina*, *Tofieldia japonica*, *Coptis trifolia*, *Tilingia ajanensis*, etc. *Plantago hakusanensis* and *Primula cuneifolia* var. *hakusanensis* (in central Honshu) or *P. nipponica* (in northern Honshu) are characteristic to the community that is developed on further wet habitats below the patch in the alpine region on the Japan Sea side (Yamazaki and Nagai, 1961; Ohba, in Miyawaki, 1967).

Flat ridges and gentle slopes in the subalpine and alpine regions of the Japan Sea side are outstanding in lacking forest communities, or in limited development of these, as stated before. The herbaceous community developed on such areas is also dominated by *Moliniopsis japonica*, *Fauria crista-galli* and/or *Carex blepharicarpa*. Other components are almost similar to the above-listed species, though with some locality-to-locality variations (Miyawaki *et al.*, 1967, 1968; Shimizu, 1967).

#### 4.3. Wind-blown heathlands

Alpine wind-blown heathlands are found on ridges with little snow accumulation which are subject to severe winds in winter. The compositional characteristics of heathland communities are the prevalence of such dwarf scrubs as *Arctous alpinus* var. *japonicus*, *Arcteria nana*, *Loiseleuria procumbens*, *Vaccinium uliginosum*, *V. vitis-idaea*, *Empetrum nigrum* var. *asiatica*, *Diapensia lapponica* var. *obovata*, etc. (Ohba, 1964; Suzuki, 1964; Suzuki and Umezu, 1965; Ohba, in Miyawaki, 1967). Herbaceous species are *Carex stenantha*, *Gentiana algida*, *Geum calthaefolium*, and *Deschampsia flexuosa*; common lichens are *Cetraria islandica* var. *orientalis*, *Thamnia vermicularis*, *Cladonia rangiferina*, *C. alpestris*, *Cetraria chrysantha*, etc. The first three species of the above-listed lichens and *Loiseleuria procumbens* are common to the European alpine flora (Suzuki, 1964). Phytosociologically, two associations of heathland communities have been reported: *Arcterio-Loiseleurietum* (Ohba, 1964; Suzuki, 1964; Suzuki and Umezu, 1965) and *Leontopodio-Arcterietum* (Shimizu, 1967).

The main associations of the alpine heath in Hokkaido are as follows according to Tatewaki (1963): *Empetrum nigrum* var. *japonicum*-*Rhododendron aureum* ass., *Vaccinium*

*uliginosa*-*Arctois alpinus* var. *japonicus* ass., *Diapensia lapponica* var. *obovata*-*Arctericia nana*-*Loiseleuria procumbens* ass., and *Phyllodoce caerulea*-*Phyllodoce aleutica* ass.

#### 4.4. Alpine desert vegetation

The alpine desert vegetation is developed on loose substrata with, more or less, movable sands and boulders on slopes, and is made up of sparse growth of plants. It is phytosociologically classified into 18 associations and 8 communities corresponding to associations (Ohba, 1969).

### IV. EPILOGUE

The purpose of the present paper was to outline the natural and semi-natural vegetation of Japan in relation to environmental conditions (Tables 6—7). Here we would like to refer to the changing trend of man-vegetation relationships and to the ecological and phytosociological approaches to the problems.

In Japan, like in other densely populated industrial countries, the original or natural vegetation is restricted to limited portions of the territory (Miyawaki and Itow, 1966). The evergreen broad-leaved forest region which occupies the lower region of the southern half of the Japanese Archipelago is of course most disturbed of all and at present only fragments of this climax forest are found. This destruction still goes on. As stated before, secondary forests and grasslands have long been maintained by human interference such as logging, mowing, burning, or grazing. Apparently, there was in the past an equilibrium between man and vegetation. In recent years, however, the population increment following the industrialization is outstandingly rapid in such big cities as Tokyo, Chiba, Yokohama, Nagoya, Osaka, and Fukuoka, and the consequence results, in part, in the thoughtless development of residential areas and traffic facilities in and around the cities. The balanced man-vegetation relationship is now upset by intrusion of big-machine-technology and pesticides in the suburban areas of secondary forests, grasslands, and farmlands; the environment of human life is deteriorated and becoming uniform in a depauperate state.

In the summergreen broad-leaved forest region, natural forests have been logged down over large surfaces. The logged forest lands are mostly reforested uniformly by coniferous trees such as *Cryptomeria japonica*, *Chamaecyparis obtusa*, or *Larix leptolepis* (Miyawaki and Itow, 1966).

The deforestation policy is also encroaching on parts of the primeval subalpine coniferous forest region; the deformation and destruction of natural habitat by tourism development invade further the alpine region, where the natural communities of *Pinus pumila*, dwarf shrubs, and herbs are developed under severe conditions. The restoration of these 'fragile' communities, once disturbed or destroyed, by their own revegetation potential can hardly be expected.

Under such circumstances, some of Japanese ecologists and phytosociologists have shown the scientific basis for the wise land use and for the revegetation planning of deteriorated or denuded areas in terms of their disciplines. Examples are those in the plannings of new town development and plant cover restoration made in the following areas in the vicinity of Tokyo: in Tsukuba (Yokoyama et al., 1967), Kohoku New Town area (Miyawaki et al., 1968), Minami-Tama New Town area (Miyawaki, 1969), Fujisawa (Miyawaki and Fujiwara, 1968a), and Chiba New Town area (Numata, 1969b). A revegetation program is also offered toward the development plan of tourist facilities and roads on the south and north slopes of Mt. Fuji (Miyawaki et al., 1967, 1969). In the Oze region,

studies are making steady progress regarding the ecological judgement and rehabilitation of the degraded moorland communities that result from trampling by hikers (Miyawaki and Fujiwara, 1968b).

Fundamental researches for the management and establishment of national parks and nature reserves have been made in a number of existing and proposed national parks and reserves. In some of those researches, a vegetation map is compiled, for example, in the following areas (arranged from north to south): central Hokkaido (Tatewaki *et al.*, 1955), the Mts. Tashiro and Aizu-koma region (Miyawaki *et al.*, 1967), Okutadami region (Miyawaki *et al.*, 1968), Mt. Tanzawa (Miyawaki *et al.*, 1964), Mt. Fuji (Miyawaki *et al.*, 1967), Mt. Hakusan (Masamune, 1961), Ise-Shima region (Miyawaki and Fujiwara, 1969), Minoo (Miyawaki, 1966c), Mt. Dogo (Horikawa and Sasaki, 1959b), Sandankyo and its vicinity (Horikawa and Sasaki, 1959a), Okunoshima Is. (Horikawa *et al.*, 1962), Danjo Is. (Toyama *et al.*, 1968), etc. (cf. Miyawaki, 1966a, b).

The mapping of actual vegetation in Japan in 1/200,000 is now being made on the basis of prefectural unit under the sponsorship of the Ministry of Education. The comparison of the map of existing with that of potential natural vegetation not only shows the vegetation-habitat relationships, but also offer the objective basis for the land use, the preservation of valuable endangered natural areas, and the restoration of deteriorated habitats and vegetation (Miyawaki, 1968d, e). A most important premiss in such vegetation studies is accurate observation, a wide view of Japanese vegetation as a whole and its relation to and integration with that of other parts of the world (Miyawaki, 1967).

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Phot. 1. Climax forest of *Abies sachalinensis* with a good regenerative structure in the Shiretoko Peninsula, northeastern Hokkaido. (Photo M. Numata)



Phot. 2. *Sasamorpha purpurascens*, a representative of the undergrowth species in the beech forest on the Pacific side of Honshu. Hakone, central Honshu. (Photo A. Miyawaki)



Phot. 3. A subalpine to alpine transition landscape. *Pinus pumila* (left) is on the ridge; *Betula ermani* on the slope (*Alnus maximowiczii* in the bottom of ravine, invisible). Elevation about 2500 m, Mt. Norikura, central Honshu. (Photo A. Miyawaki)



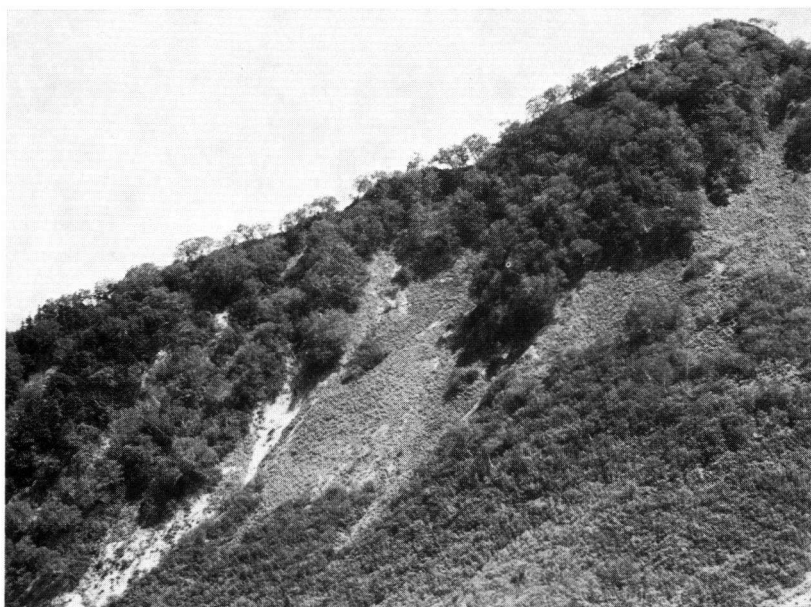
Phot. 4. A bird's-eye view of mixed pioneer forest of *Picea polita*, *Tsuga sieboldii*, *Chamaecyparis obtusa*, etc. growing on the lava bed that flowed in 865. Elevation about 900 m, Aokigahara at the north foot of Mt. Fuji, central Honshu. (Photo S. Itow)



Phot. 5. Shrubby growth of *Larix leptolepis*, *Tsuga diversifolia*, etc. at the tree line on Mt. Fuji, 2500 m alt. (Photo M. Numata)



Phot. 6. An alpine community of *Phyllodoce aleutica* and *Anemone narcissiflora*. Elevation about 2800 m, Mt. Tateyama, central Honshu. (Photo S. Itow)



Phot. 7. A subalpine landscape. *Betula ermani* grows on upper slope and *Alnus maximowiczii* on the middle slope (foreground) separated by grassland. Kurobe, central Honshu. (Photo S. Itow)



Phot. 8. Tall herb community of *Angelica pubescens* var. *matsumurae* and *Aconitum senanense*. Elevation about 2500 m, Mt. Norikura, central Honshu. (Photo A. Miyawaki)





Phot. 9. Interior of the *Castanopsis sieboldii* forest in coastal area. The floor community is composed of evergreen shrubs such as *Aucuba japonica*, *Fatsia japonica*, *Ligustrum japonicum*, etc. Kamakura, central Honshu. (Photo A. Miyawaki)

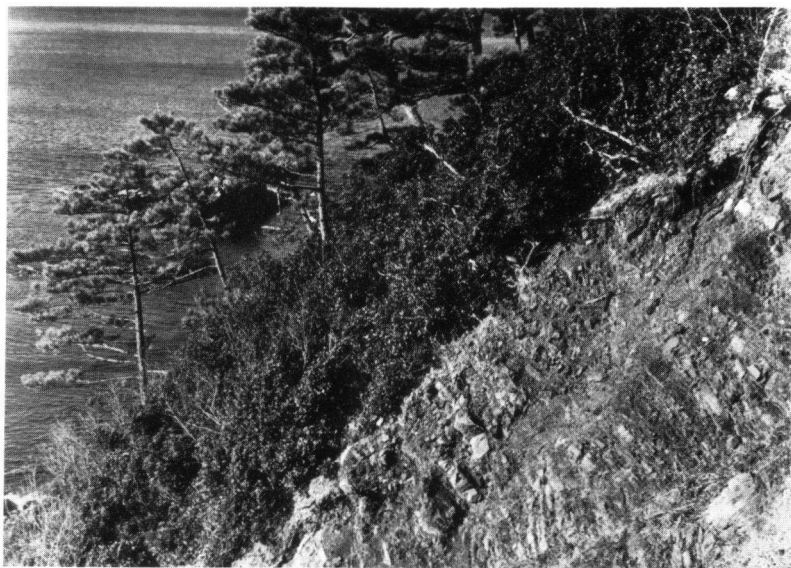


Phot. 10. A climax forest of *Cinnamomum camphora* at Fukuoka, Kyushu. (Photo M. Numata)

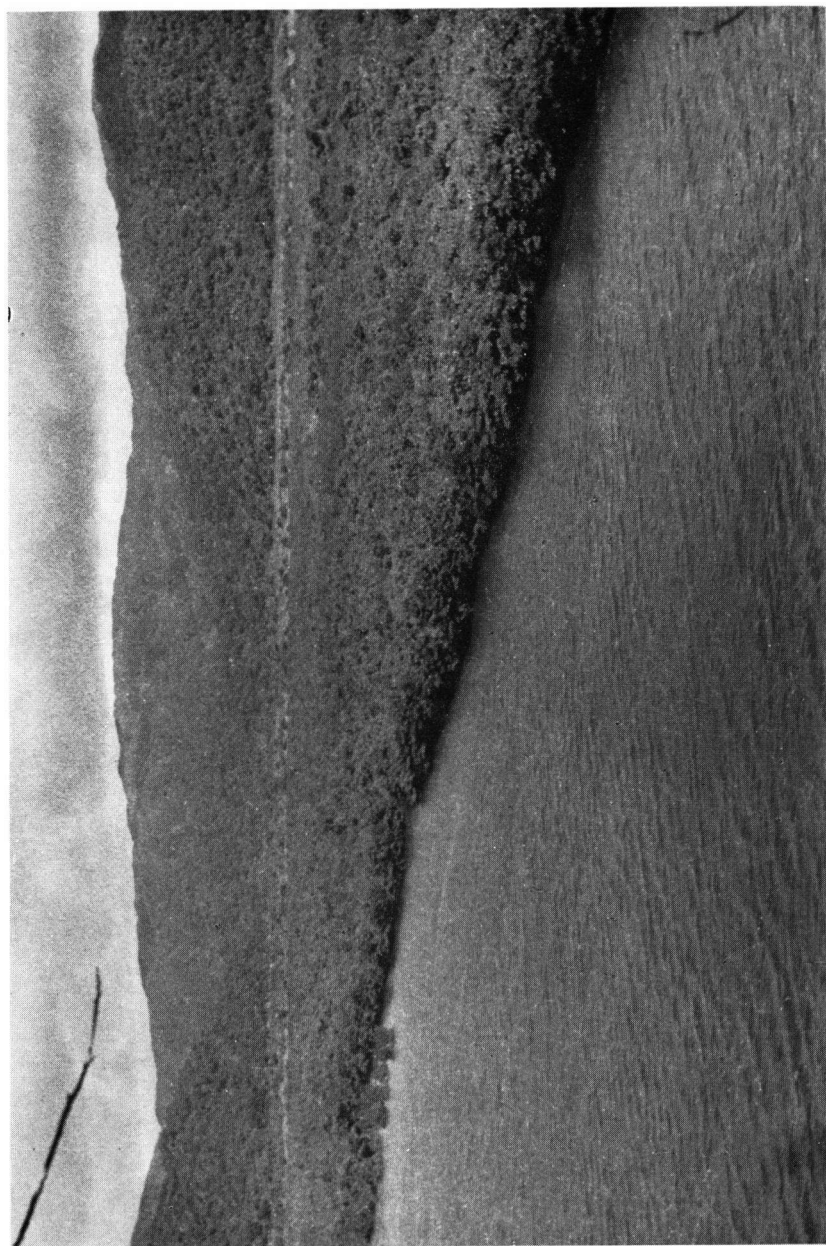




Phot. 11. A stand of *Pinus densiflora*, a representative of secondary forests. Tsukuba, central Honshu (Photo S. Itow)



Phot. 12. Coastal vegetation composed of *Quercus phillyraeoides*, *Pittosporum tobira*, *Pinus thunbergii*, etc. (*Pittosporeto-Quercetum phillyraeoidetis*). Kii Peninsula, central Honshu. (Photo A. Miyawaki)



Phot. 13. A mangrove landscape at the estuary of the Nakamagwa River in Iriomote Island. The mangrove forest consists of *Bruguiera conjugata*, *Kandelia candel*, *Rhizophora mucronata*, and *Lumnitzera racemosa*. Iriomote, Ryukyu. (Photo A. Miyawaki)



Phot. 14. A stand of *Livistona chinensis* var. *subglobosa* which is distributed from southernmost Kyushu and Shikoku southward. Aoshima Island, Kyushu. (Photo A. Miyawaki)



Phot. 15. Natural forest composed of *Livistona boninensis*, *Schima mertensii*, *Ardisia sieboldii*, *Hibiscus glabra*, *Raphiolepis integerrima*, etc. Mt. Yoake-yama, Chichi-jima, Bonin Is. (Photo A. Miyawaki)



Phot. 16. A moist grassland on peat covered by *Spodiopogon sibiricus*, *Iris setosa*, *Filipendula kamschatica*, etc. et Kerochi, Hokkaido. The upper part is a sown pasture. (Photo M. Numata)



Phot. 17. A sandy beach grassland dominated by *Elymus mollis*, facing the Sea of Okhotsk near the Lake Noto, Hokkaido. (Photo M. Numata)



Phot. 18. A natural bamboo brake of *Phyllostachys bambusoides* on a steep slope near Kyoto. (Photo M. Numata)



Phot. 19. General view of a high-grass type meadow dominated by *Miscanthus sinensis* widely distributed in Japan, at Kawatabi, northern Honshu. (Photo M. Numata)





Phot. 20. General view of a short-grass type pasture dominated by *Zoysia japonica* mostly distributed in the cool-temperate region. Hakkoda, N. Honshu. (Photo M. Numata)



Phot. 21. A dwarf-bamboo type pasture dominated by *Pleioblastus distichus* var. *nezasa* on Mt. Kuju, Kyushu. (Photo M. Numata)



Phot. 22. Moor community complex in the Ozegahara Basin. Major species are *Moliniopsis japonica*, *Drosera rotundifolia*, *Vaccinium oxycoccus*, *Andromeda polifolia*, *Sphagnum papillosum*. (Photo A. Miyawaki)

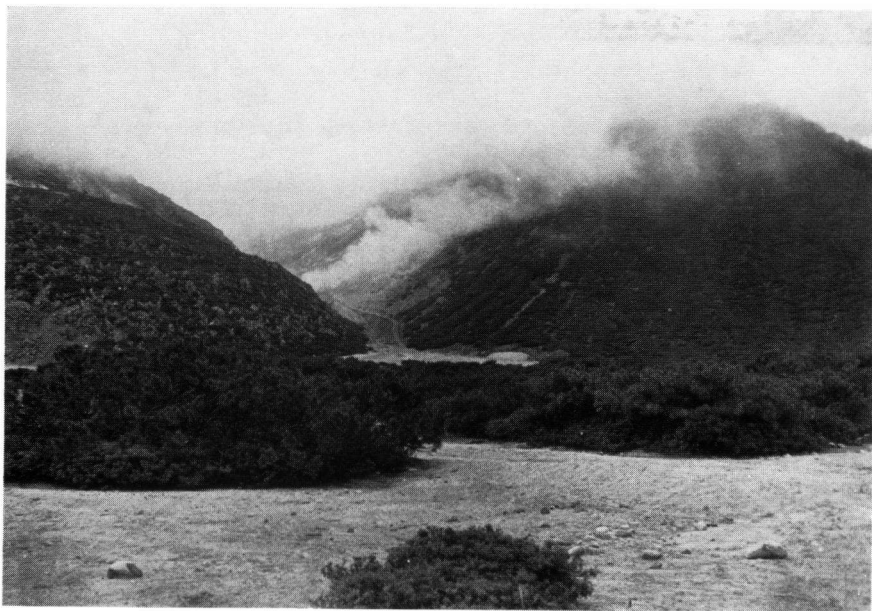


Phot. 23. A coastal sand-dune covered by *Ischaemum antheophroides*, *Carex kobomugi*, *Calystegia soldanella*, etc. at Kashimanada, central Japan. (Photo M. Numata)



Phot. 24. A halophytic vegetation of *Salicornia herbacea* along the shore of a lagoon, Aomori, eastern Hokkaido. (Photo M. Numata)





Phot. 25. A solfataric vegetation of *Pinus pumila*, *Ledum palustre* var. *yessoense*, *Miscanthus sinensis*, etc. at Iozan, Hokkaido. (Photo M. Numata)



Phot. 26. Sparse vegetation of *Pinus thunbergii*, *Pittosporum tobira*, etc. on the lava of Sakurajima, southern Kyushu. (Photo M. Numata)