

## SUBALPINE CONIFEROUS FORESTS OF CENTRAL HONSHU, JAPAN<sup>1</sup>

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**Abstract.** Mature subalpine forest communities were sampled at four locations in central Honshu, Japan—Mounts Fuji and Ontake and the Yatsugatake and Chichibu Mountains. Data were subjected to similarity-ordination and association analyses. There are three major groups of communities: *Tsuga diversifolia*/moss, *Abies* spp./herb, and conifer/*Sasa*. *Tsuga*/moss forest understories are depauperate in vascular plants or dominated by ericads such as *Rhododendron* and *Menziesia* and have very stony soils. *Abies*/herb forests have luxuriant understories in which herbs and ferns are conspicuous; they occur over a wide range of soil conditions. Conifer/*Sasa* forests have extremely dense layers of dwarf bamboo (*Sasa* spp.) 1–1.5 m in height and occur on deep, fine-textured volcanic-ash soils. Composition and structure of 11 community types and phases belonging to these groups are described. Successional trends appear to favor the more shade-tolerant *Abies mariesii* and *Abies veitchii* over *Tsuga diversifolia* and *Picea jezoensis* var. *hondoensis* although this varies with site. Japanese forests have many similarities with those in the eastern United States, but the dwarf bamboo communities are strictly an Asian phenomenon.

**Key words:** *Abies* spp.; Japan; *Picea jezoensis*; *Sasa* spp.; subalpine forests; succession; *Tsuga diversifolia*.

### INTRODUCTION

Coniferous forest commonly dominates subalpine regions in the northern temperate zone. True firs (*Abies* spp.) and spruces (*Picea* spp.) are the most ubiquitous dominants. In eastern Asia, including Japan, and in coastal western North America, hemlocks (*Tsuga* spp.) are also major components.

Subalpine forests are important in providing a protective cover for key watershed and recreational areas. They also represent substantial wood resources and, for that reason, are increasingly subject to logging. Unfortunately, environmental conditions are typically quite severe with short cool growing seasons and cold snowy winters. Regeneration of a new forest after cutting often proves difficult and success may require substantial silvicultural investments in man power and money. These facts coupled with a highly variable productive potential make separation of the landscape into ecologically uniform areas and development of basic ecological knowledge (e.g., of successional processes) of subalpine forests critical to sound land management planning. With proper stratification,

management potentials can be identified, reforestation problems foreseen, and appropriate silvicultural methods devised.

The subalpine forests found in central Honshu, Japan, are the subject of this paper. The purpose of the study is three-fold: (1) provide a synthesis of the communities and their characteristics using techniques and concepts comparable to those being used in western North America; (2) assist in stratifying the subalpine landscape in Japan; (3) provide American ecologists with a convenient summary of ecosystems that have counterparts in North America. Results of this Japanese study are based upon analyses of over 150 mature, virgin stands located in four major areas of subalpine forest—the Yatsugatake and Chichibu Mountains and Mounts Fuji and Ontake. Major community types are identified and described.

### STUDY AREAS

Two of the study sites are on major mountain massifs (Mounts Fuji and Ontake) and two are on mountain ranges (Yatsugatake and Chichibu Mountains) in central Honshu, Japan (Table 1). Each of these areas is isolated from other subalpine areas (Fig. 1).

All four locations extend to elevations above the

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FIG. 1. Location of the subalpine study areas on central Honshu, Japan.

limits of closed forest ( $\approx 2500$  m in these areas) thereby providing a full elevational span of subalpine forest. They differ markedly in topography as would be expected from differences in geologic age and mode of formation. The portions of the Yatsugatake and Chichibu Mountains sampled in this study are strongly dissected and slopes are typically steep and broken. Midslope benches and broad saddles and passes provide the major exceptions. Mounts Ontake and Fuji, on the other hand, are composite volcanoes with extensive, moderately steep slopes.

Aerially deposited volcanic ash is general over the landscape at Mount Ontake and occupies localized areas of gentle topography in the Yatsugatake Mountains. As will be seen, these deposits have profound consequences for soil and vegetation. At Mount Fuji, cinders and other scoriaceous deposits are typical rather than ash.

#### Climate

Cool, wet summers and cold, dry winters characterize the climate of these subalpine areas (Table 2). The climate is rather similar to that found in subalpine regions throughout much of Europe, eastern Asia, and the United States; it contrasts with subalpine climates in the Sierra Nevada, Cascade Ranges, and Olympic

Mountains of the United States which have strong summer-dry periods. Annual precipitation in the Japanese subalpine has two peaks—during June and July and again during the typhoon season of September and October. An annual snowpack of 1–2 m accumulates during the winter. Total snowfall and snowpack accumulations do vary substantially; however, of the four study areas, snowfall is greatest on Mount Ontake which stands at the boundary of the well-known heavy-snowfall region of the "Japan Sea," or northern side of Japan.

The typhoons are an extremely important environmental influence; they are the major agent of forest destruction and bring heavy summer rains. Wildfires are presently and historically negligible influences in these forests, but typhoons sweep the mountains every year. Essentially every location can expect a highly destructive typhoon (i.e., one that blows down essentially all of the overstory) during a period of one or two centuries. The oldest forests are no more than 250–300 yr old, and most are younger; at least some of them are believed to have originated following typhoons. Many forests which had received severe damage were encountered in various stages of regeneration.

#### Soils

Most soils encountered in subalpine study areas are podzolic to at least some degree. The five major groups are  $P_D$ ,  $P_{W(h)}$ ,  $P_{W(i)}$ ,  $dB_D$ , and  $B_D$  types according to the Japanese forest soil classification system (Forest Soils Division 1976).  $P_D$  soils are clearly podzolic with  $A_0$ – $A_1$ – $A_2$ – $B_1$ – $B_2$  horizon sequences; they are equivalent to the Spodosol of the new United States classification. Grades in the  $P_D$  series (I to III) reflect differences in degree of profile development (primarily the  $A_2$  horizon), with I strong and III weak. The "skeletal" soils referred to in this paper are basically  $P_D$  types with extremely high stone content.

TABLE 1. Location, geology, and number of sample stands for the major study areas.

| Locale                | Prefecture        | Latitude | Longitude | Geology   | Number of stands |
|-----------------------|-------------------|----------|-----------|---|------------------|
| Yatsugatake Mountains | Nagano            | 36°00'   | 138°23'   | Miocene andesite                                | 27*              |
| Chichibu Mountains    | Nagano<br>Saitama | 35°52'   | 138°38'   | Paleozoic sand<br>and shalestone<br>and granite | 23†              |
| Mount Fuji            | Yamanashi         | 35°22'   | 138°43'   | Pleistocene basaltic<br>andesite                | 32‡              |
| Mount Ontake          | Nagano<br>Gifu    | 35°53'   | 137°28'   | Miocene andesite                                | 75§              |

\* At two locations, 14 around Mount Nakayama and 13 at Mount Shimagara, between 2040 and 2500 m.

† At two locations, 9 around Jumongi Pass and 14 above Kawakami Village, between 1600 and 2570 m.

‡ All on the northeastern slopes of the mountain above Fujiyoshida, between 1660 and 2300 m.

§ At three locations, 23 in the Tanohara area on the east slope, 25 in the Nigorigo, and 27 in the Kurumijima areas on the west slopes of Mount Ontake, between 1680 and 2435 m.

TABLE 2. Mean temperature and precipitation at representative subalpine areas in central Honshu.

| Item          | Mount Fuji |      | Mount Kirigamine |      | Ozenuma |      | Mount Nantai-san‡ |     | Kamikochi |      | Kiso    |      |
|---------------|------------|------|------------------|------|---------|------|-------------------|-----|-----------|------|---------|------|
|               | °C*        | mm†  | °C               | mm   | °C      | mm   | °C                | mm  | °C        | mm   | °C      | mm   |
| Latitude      | 35°22'     |      | 36°06'           |      | 36°55'  |      | 36°46'            |     | 36°13'    |      | 35°56'  |      |
| Longitude     | 138°44'    |      | 138°12'          |      | 139°19' |      | 139°30'           |     | 137°37'   |      | 137°37' |      |
| Elevation (m) | 1640       |      | 1925             |      | 1665    |      | 2480              |     | 1495      |      | 980     |      |
| Month:        |            |      |                  |      |         |      |                   |     |           |      |         |      |
| January       | -6.5       | ...  | -3.8             | 23   | -9.5    | 180  | -14.3             | ... | -7.9      | 61   | -1.8    | 76   |
| February      | -6.3       | ...  | -4.4             | 232  | -9.1    | 126  | -14.3             | ... | -7.8      | 138  | -0.9    | 92   |
| March         | -2.4       | ...  | -1.4             | 87   | -5.5    | 120  | -10.3             | ... | -3.2      | 177  | 1.6     | 132  |
| April         | 5.3        | ...  | 5.6              | 130  | 1.4     | 86   | -3.4              | ... | 3.4       | 193  | 8.4     | 171  |
| May           | 7.7        | ...  | 12.6             | 136  | 6.8     | 93   | 2.2               | 115 | 9.1       | 186  | 13.9    | 156  |
| June          | 12.4       | ...  | 14.8             | 194  | 11.8    | 163  | 9.0               | 150 | 13.3      | 306  | 17.9    | 255  |
| July          | 17.0       | ...  | 19.7             | 240  | 17.2    | 210  | 11.9              | 336 | 17.4      | 298  | 20.7    | 252  |
| August        | 17.5       | ...  | 19.6             | 167  | 17.6    | 179  | 13.9              | 324 | 17.8      | 186  | 23.0    | 151  |
| September     | 13.9       | ...  | 15.6             | 176  | 13.0    | 196  | 8.9               | 184 | 13.7      | 251  | 19.2    | 239  |
| October       | 7.9        | ...  | 10.1             | 283  | 5.8     | 145  | 3.8               | 216 | 7.1       | 239  | 11.9    | 153  |
| November      | 3.3        | ...  | 3.5              | 88   | 0.1     | 80   | -2.8              | ... | 1.5       | 151  | 6.0     | 117  |
| December      | -3.4       | ...  | 1.2              | 99   | -6.0    | 130  | -12.8             | ... | -1.6      | 207  | 0.4     | 94   |
| Annual        | 5.5        | 2000 | 7.8              | 1855 | 3.6     | 1706 | -0.6              | ... | 5.2       | 2493 | 10.0    | 1888 |

\* Calculated from data at Shoji, Funatsu, and Mount Fuji using mean lapse rates of 0.54°C in summer and 0.62°C in winter per 100-m elevation. From Tadaki et al. 1967.

† No monthly precipitation values were available for Mount Fuji. Average values are 550 mm November–April and 1450 mm May–October.

‡ No precipitation data available for Mount Nantai-San from November through April; the annual total has consequently been omitted as well.

$P_{W(h)}$  soils are Humic Umbrepts with  $A_0$ – $A_1$ – $A_{2g}$ – $B_2$  horizon sequences; the  $A_1$  horizon is strongly developed while the  $A_{2g}$  (a gleyed horizon) is weakly developed. The  $P_{W(i)}$  type reflects even moister environments with  $A_0$ – $A_1$ – $A_{2g}$ – $B_{1g}$ – $B_2$  horizon sequences; grade I of this Aquic Spodosol has a strong  $A_{2g}$ .  $B_D$  soils present simple, slightly podzolized profiles in subalpine areas—an A horizon with some organic accumulation, a “color” B horizon and C; the United States equivalent is an Umbrept. The  $dB_D$  or dark brown forest soil has brownish black A horizons and dark brown B horizons. They lack evidence of podzolization or gleization; humus accumulation and detectable ferrous iron in the A horizon are characteristic.

In the areas studied, soils are frequently shallow and extremely stony; much of the vegetation, including trees, is rooted in the upper 10–20 cm of soil or on the soil surface beneath the layer of mosses. On many sites, the rooting medium consists of nothing more than jumbled boulders covered with moss and accumulated organic debris. These very stony soils and their opposite—i.e., the relatively deep, fine-textured soils developed in volcanic ash—have a strong influence on community composition. Stoniness is probably the single soil feature most closely correlated with community type.

#### Vegetation

The major vegetational patterns of Japan are outlined in English-language articles (see, e.g., Ohwi

1965, Numata 1972, 1974, Numata et al. 1972, Shidei and Kira 1977). Detailed knowledge of community types, environmental effects, successional processes, etc. in individual locales is accumulating due to extensive efforts of Japanese ecologists over the last several decades. Although community analyses are occasionally published in English (e.g., Oshima et al. 1958, Iwaki and Totsuka 1959, Kimura 1963), the most extensive works are in Japanese and usually in journals of limited availability in the Western world (e.g., Maeda and Shimazaki 1951, Tatewaki et al. 1963, Miyawaki et al. 1969, Ohsawa et al. 1971, Maeda et al. 1976). The following synopsis from the Japanese literature is designed to introduce the reader to the subalpine vegetation and provide perspective for the results of this study.

The subalpine forests in central Honshu are dominated by four coniferous species—*Tsuga diversifolia*, *Abies veitchii*, *Abies mariesii*, and *Picea jezoensis* var. *hondoensis* (nomenclature follows Ohwi 1965). Several other conifers may enter in locally: *Thuja standishii*, *Pinus koriensis*, *Larix leptolepis*, *Pinus parviflora*, and *Chamaecyparis obtusa* and *pisifera*. Several hardwoods are constant but usually minor associates such as *Sorbus comixta*, *Betula ermanii* (which may form a nearly pure band at the upper forest line), *Acer tschonoski*, and *Acer ukurunduense*.

The dominant *Abies* are not evenly distributed throughout the central Honshu subalpine. *Abies mariesii* has its center of distribution in northern Honshu, particularly in the area of the “Japan Sea” climate.

Most areas included in this study are on the Pacific Ocean side of Honshu where *Abies veitchii* is more abundant; Mount Ontake is considered to sit astride this climatic and floristic division. *Tsuga diversifolia* is rather uniformly distributed over the study areas.

Within a location, there is typically an elevational gradient in the abundance of *Tsuga* and *Abies* spp. *Tsuga diversifolia* is more abundant at lower elevations (e.g., 1600–2000 m), dominating most forests. *Abies veitchii* or *A. mariesii*, or more often both, dominate between the *Tsuga* forest and the forest line. This elevational gradient is sufficiently distinct that several ecologists have recognized it as two or even three zones or subzones—*Tsuga*, *Tsuga-Abies*, and *Abies* (e.g., Maeda and Shimazaki 1951, Ohsawa et al. 1971, Maeda et al. 1976).

Studies of stand structure suggest *Tsuga diversifolia* is often replaced successively by *Abies* spp. in the middle and upper portions of the subalpine zone (e.g., see Kimura 1963). This has led to substantial debate about what species to use in naming communities and associations. A logical selection is *Abies mariesii* which usually reproduces more successfully than *A. veitchii* where both are present. On the other hand, *Abies mariesii* is absent or sparsely represented in some of the subalpine areas of central Honshu. Nor do the various Japanese ecologists have identical views on the various climax concepts and their relative value. In any case, under normal stand conditions, the relative abundance of reproduction among the major dominants is *Abies mariesii* > *Abies veitchii* > *Tsuga diversifolia* > *Picea jezoensis* var. *hondoensis*.

Analyses and classifications by Japanese community ecologists typically use the Braun-Blanquet method. Three broad groups of communities are repeatedly reported: (1) depauperate *Tsuga diversifolia*—moss; (2) *Abies*—herbaceous; (3) conifer—dwarf bamboo. The broad groups occur on both the Japan Sea and Pacific Ocean sides of Honshu although floristic shifts occur. An example is the sequence of *Sasa kurilensis*, *Sasa paniculata*, and *Sasa nipponica* as dwarf bamboo dominants progressing down the snow accumulation gradient from the Japan Sea across Honshu (Shidei and Kira 1977). A similar spectrum of moss, herb, and dwarf bamboo types is also encountered in the cool temperate or boreal *Picea-Abies* hardwood forests of Hokkaido (Matsukawa 1955).

#### Human influences

Most of the subalpine forests visited and all sample areas are believed to represent natural conditions with minimal human influence. Many Western ecologists have not appreciated the fact that extensive virgin forests still exist on the Japanese islands despite their long history of dense human occupation. Indeed, virgin temperate forests are rare but there has been very little human exploitation of the relatively inaccessible high mountain forests until recently, at least in central and

northern Honshu and on Hokkaido. Except in the lower subalpine in the Yatsugatake and Chichibu Mountains, suitable study sites were abundant.

Logging did begin in earnest with establishment of the Forestry Agency and National Forests following World War II and has converted large expanses of virgin subalpine forest to plantations of *Larix leptolepis*. The problem of regenerating and managing the subalpine forests is one of the reasons for this study.

#### METHODS

Field sampling utilized the reconnaissance technique described by Franklin et al. (1970), a method used successfully in the temperate and subalpine forests of western Oregon (Dyrness et al. 1974). Simply stated, this involves subjective sampling of stands along extended traverses of mountain slopes. This most frequently took the form of regularly spaced samples along elevational transects but with special care to insure adequate sampling of all landforms, slopes, aspects, and soil types. It also involved more frequent sampling where major changes in community structure and composition took place in small distances. Sampling was done without any preconceived notions about the community types.

The major criteria for selection of an individual stand were apparent uniformity in vegetation and environmental features, a mature condition, and lack of obvious human influences such as timber cutting. Maturity here does not imply successional stability or a climax condition but rather age sufficient to have allowed the dominant tree species to mature and the composition of the understory to stabilize. In most cases, stands were estimated as 150–250 yr since establishment of the largest trees, but in stands of the short-lived true firs, 100 yr were considered sufficient to meet the maturity criterion.

A circular plot  $\approx 25$  m in diameter was established on sites selected for study. Within this plot area the abundance and cover of tree overstory, tree reproduction, shrubs, herbs, and mosses were visually estimated by species. Abundance of tree species was ranked according to a nine-class system while abundance of shrubs, herbs, and mosses was rated using a six-class system. The understory abundance classification was intended to approximate the frequency rating each species would attain if 50 microplots were laid out in a  $25 \times 15$  m area within the stand (Daubenmire and Daubenmire 1968). Cover was estimated to the nearest percent up to 20% and by 5% increments after that. Total cover for each layer, ignoring overlap, was also estimated separately. Additional vegetation data collected included: (1) basal area tally by tree species using a wedge prism; (2) number of tree seedlings (stems >3 yr in age and <1 m in height) by species on from one to four (depending on seedling density) 1-m diameter circular plots systematically located around the plot center; (3) maximum height and

TABLE 3. Community types and phases recognized in the subalpine forest of central Honshu and the abbreviations and number of samples for each.

| Group      | Community type and phase  | Abbreviation   | Number of stands by locale |           |      |        |
|------------|---|--|----------------------------|-----------|------|--------|
|            |   |  | Yatsu-gatake               | Chi-chibu | Fuji | Ontake |
| Tsuga/Moss | <i>Tsuga diversifolia</i> / <i>Abies</i> spp./<br><i>Pleurozium schreberi</i>           | Tsdi/Absp/Plsh   |                            |           |      |        |
|            | Typical phase   | Tsdi/Absp/Plsh   | 5                          | 4         | 8    | 0      |
|            | <i>Menziesia pentandra</i> phase  | Mepe   | 4                          | 3         | 0    | 13     |
|            | <i>Rhododendron fauriae</i> phase   | Rhfa   | 0                          | 0         | 9    | 0      |
|            | <i>Vaccinium vitis-idaea</i> phase  | Vavi   | 0                          | 0         | 5    | 0      |
|            | <i>Tsuga diversifolia</i> / <i>Shortia ilicifolia</i>                                   | Tsdi/Shil  | 2                          | 1         | 0    | 4      |
|            | <i>Thuja standishii</i> / <i>Rhododendron degronianum</i>                               | Thst/Rhde  | 1                          | 3         | 0    | 7      |
| Abies/Herb | <i>Abies veitchii</i> / <i>Dryopteris austriaca</i>                                     | Abve/Drau  | 6                          | 4         | 10   | 7      |
|            | <i>Picea jezoensis hondoensis</i> / <i>Abies</i> spp./<br><i>Cacalia adenostyloides</i> | Pijeh/Absp/Caad  | 0                          | 0         | 0    | 16     |
|            | <i>Abies veitchii</i> / <i>Streptopus streptopoides japonicus</i>                       | Abve/Ststja  | 3                          | 2         | 0    | 0      |
|            | <i>Abies veitchii</i> / <i>Vaccinium axillare</i>                                       | Abve/Vaax  | 2                          | 5         | 0    | 0      |
|            | Conifer/ <i>Sasa</i>  | <i>Tsuga diversifolia</i> / <i>Abies</i> spp./<br><i>Sasa paniculata</i> | Tsdi/Absp/Sapa             | 3*        | 0    | 0      |

\* *Sasa* at Yatsugatake was *Sasa nipponica* not *S. paniculata*.

dbh. of one or more species. Approximately every 20 plots, a 25 × 15 m plot (Daubenmire and Daubenmire 1968) was measured in a stand to obtain more precise quantitative frequency and coverage estimates thereby "calibrating" the observers' ocular estimates; no systematic error was observed from these calibrations.

Environmental features described included landform, elevation, slope, aspect, and soil parent material. A soil pit was dug and described in each plot. Soil type was determined according to the Japanese system of forest soil classification. Stoniness of the soil varied widely and appeared strongly correlated with the plant community; consequently, stone content was recorded according to a five-class system:

- 1 = 0 to 5% stone content,
- 2 = 5 to 35%,
- 3 = 35 to 65%,
- 4 = 65 to 95%, and
- 5 = 95 to 100%.

In calculating average stone contents for types, the midpoints of each of the classes were used.

Data were analyzed with the help of program SIMORD, a Bray-Curtis ordination technique (Dick-Peddie and Moir 1970). Plots were selected for end points based upon ecological knowledge of the data, rather than by a computer program, and similarities between plots were computed as percentage similarities (Gauch 1973, Dyrness et al. 1974).

Analyses were run on the entire set of 164 stands or plots using different end point plots and character species. This gave unsatisfactory results due, in part,

to floristic differences between the four mutually isolated study areas. Subsequently, separate analyses were run on plots from each of the four major study locations, with much better results. One other problem encountered early in the analyses was use of *Sasa*-type communities as end point plots. These plots with a dense dwarf bamboo understory are very different from the remainder. A result was the occupancy of two-thirds of the ordination field by plots of this type with all the other plots being forced into a single quadrant. After this was discovered, *Sasa*-type plots were no longer used as end points in the ordinations. As will be seen, this did make it difficult to select end point plots for the second axis since only two other major "kinds" of communities were present.

## RESULTS

Division of the stands into three major groups and, within these, into some 11 community types and phases is possible from the similarity and associational analyses (Table 3). Variation is largely continuous between these types and phases. Nevertheless, distinct nodes exist which form the cores for type groupings. Continuity is emphasized when data from all of the stands are used in a single analysis and is much less evident when each of the four study areas is examined individually (Fig. 2).

The reader is reminded that data from only 164 stands and 4 localities are considered here. Samples of forests in the lower subalpine were particularly limited. Consequently, this classification is probably inadequate for the entire subalpine zone of Honshu. One

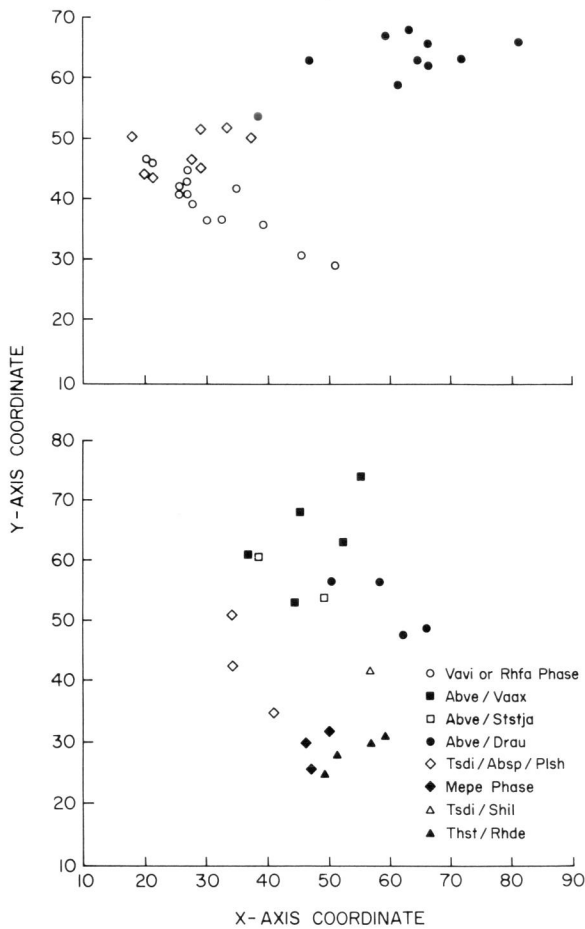


FIG. 2. Ordinations were most useful when individual study areas were analyzed separately as illustrated with the stands from Mount Fuji (top) and Chichibu Mountains (bottom).

author (Maeda), who has worked throughout this zone, recognizes *Rhododendron*, moss, herb (*Dryopteris-Cacalia* and *Cacalia*-moss phases), and *Sasa* community types with *Abies*, *Tsuga* and *Abies*, and *Tsuga* overstories as well as an *Abies/Vaccinium vitis-idaea* community type. Such a comprehensive classification was beyond the scope of this study.

The three major groups are the *Tsuga*/moss, *Abies*/herb, and conifer/*Sasa*. Each of these is extremely distinctive in understory and, to a lesser extent, overstory features. These differences also reflect contrasts in environmental (particularly edaphic) features. The *Tsuga*/moss group is characterized by an understory which is depauperate in vascular plants or strongly dominated by ericads. *Tsuga diversifolia* is the characteristic dominant although *Abies* spp. dominate the reproduction in most stands. The herbaceous understory in the *Abies*/herb group has high coverage and is rich in species. *Abies veitchii* and *Abies mariesii* typically dominate in both the overstory and the re-

production although *Picea jezoensis* var. *hondoensis* is also abundant in some types and *Tsuga diversifolia* is present in variable amounts. The conifer/*Sasa* group is the most distinctive with an understory totally dominated by species of dwarf bamboo, relatively open stands of variable composition, and sparse tree reproduction.

We will now examine the specific characteristics of each of the community types within these groups. The reader should recognize that the separations into communities and phases of communities are somewhat arbitrary. In fact, a case can be made for recognizing only three associations equivalent to the three major groups and phases within these. We have elected to recognize three groups, four community types within the *Tsuga*/moss and *Abies*/herb groups based on their relative distinctiveness, and phases within the very diverse *Tsuga diversifolia/Abies* spp./*Pleurozium schreberi* community types (Table 3).

*Tsuga diversifolia/Abies* spp./*Pleurozium*  
*Schreberi* community type

The TsdI/Absp/Plsh community is without question the most extensive type within the center of the subalpine zone in central Honshu. The typical phase of this community occupies moderately stony (20–45%) podzolic ( $P_1$ ) soils and moderate slopes. *Tsuga diversifolia* and *Abies veitchii* dominate the overstory. The understory contains little more than reproduction of *Abies* spp. and *Picea jezoensis hondoensis* and a carpet of moss (mainly *Pleurozium schreberi* and *Hylocomium splendens*) (Tables 4 and 5, Fig. 3). Other vascular plants scattered over the moss carpet are Orchidaceae (e.g., *Dactyloctenium aegyptium*, *Plantanthera ophryoides*, *Ephippianthus schmidtii*, *Goodyera repens*, and *Listera cordata*) and *Pyrola* spp., which belong to Furman and Trappe's (1971) group of achlorophyllous mycotrophic angiosperms, and a few individuals of the more ubiquitous, less demanding herbs (e.g., *Oxalis* and *Maianthemum*).

The *Menziesia pentandra* phase of the TsdI/Absp/Plsh community occupies substantially stonier soils (averaging 80–90% by volume); indeed, substrate is often simply boulder piles covered by moss and roots. The herb and in particular, shrub layers are substantially greater than in the typical phase (Fig. 4, Table 4). *Tsuga diversifolia* reproduction remains the most important shrub and *Vaccinium hirtum* is its most constant associate. At Mount Ontake *Viburnum furcatum*, *V. urceolatum procumbens*, *Euonymus macropeteris*, and *Oplopanax japonicus* are also constant shrubs (Table 4). The herb layer, while better developed than in the typical phase, is still relatively sparse (16 and 25% at Yatsugatake-Chichibu and Ontake, respectively) and composed mainly of widespread species tolerant of poorer site conditions—*Oxalis acetosella*, *Streptopus streptopoides* var. *japonicus*, *Cornus canadensis*, *Coptis quinquefolia*, and *Rumhora*



FIG. 3. Typical example of *Tsuga diversifolia*/*Abies* spp./*Pleurozium schreberi* community type in Yatsugatake Mountains; note depauperate understory (reference pole in this and other photographs is 1 m tall).

*mutica*. The moss carpet is well developed, and strongly dominated by *Pleurozium* and *Hylocomium* but with significant amounts of *Dicranum* spp., *Pogonatum grandifolium*, *Mnium speciosum*, *Lobaria*

spp., miscellaneous liverworts, and at Mount Ontake, *Sphagnum girgensohnii*.

At Mount Fuji the *Rhododendron fauriae* and *Vaccinium vitis-idaea* phases of the TsdI/Absp/Plsh com-



FIG. 4. The *Menziesia pentandra* phase of the TsdI/Absp/Plsh community type has a substantial shrub layer dominated by *Menziesia* and *Vaccinium hirtum*, Yatsugatake Mountains.

TABLE 4. Characteristics of the community types and phases belonging to the *Tsuga diversifolia*/moss community group and number of sample plots by location.\*†

| Characteristic                          | Community type and phase   |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
|---|--|----------------------------|---------|-----------------------------|-------|------------------------------|--|---|-------|------|-------|------|-------|------|-----|----|
|   | <i>Tsuga diversifolia</i> / <i>Abies</i> spp./ <i>Pleurozium schreberi</i> |                            |         |                             |       |                              | <i>Tsuga diversifolia</i> /<br><i>Shortia ilicifolia</i> | <i>Thuja standishii</i> /<br><i>Rhododendron degroenianum</i> |       |      |       |      |       |      |     |    |
|   | Typical  | <i>Menziesia pentandra</i> |         | <i>Rhododendron fauriae</i> |       | <i>Vaccinium vitis-idaea</i> |  |   |       |      |       |      |       |      |     |    |
| Location‡                               | Y and C  | F                          | Y and C | O                           | F     | F                            | Y and C  | Y, C, and O   |       |      |       |      |       |      |     |    |
| Number of plots                         | 9  | 8                          | 7       | 13                          | 9     | 5                            | 7  | 11  |       |      |       |      |       |      |     |    |
| Environmental features                  |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
| Elevation (m)                           | 2225   | 1930                       | 2120    | 2070                        | 1930  | 2230                         | 2185   | 1920  |       |      |       |      |       |      |     |    |
| Slope (%)                               | 24   | 19                         | 35      | 29                          | 28    | 35                           | 72   | 34  |       |      |       |      |       |      |     |    |
| Soil stoniness§                         | 2.7  | 2.1                        | 4.4     | 4.0                         | 4.1   | 4.0                          | 4.3  | 4.6   |       |      |       |      |       |      |     |    |
| General vegetative features             |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
| Basal area (m <sup>2</sup> /ha)         | 70.2   | 79.0                       | 65.3    | 66.0                        | 71.6  | 80.1                         | 64.4   | 79.1  |       |      |       |      |       |      |     |    |
| Conifer seedlings (1000/ha)             | 72   | 54                         | 124     | 143                         | 68    | 26                           | 88   | 53  |       |      |       |      |       |      |     |    |
| Maximum height (m)                      | 17.5   | 17.6                       | 18.0    | 19.7                        | 14.8  | 9.4                          | 8.0  | 16.7  |       |      |       |      |       |      |     |    |
| Maximum dbh. (cm)                       | 49   | 51                         | 49      | 44                          | 36    | 32                           | 26   | 47  |       |      |       |      |       |      |     |    |
| <i>Sasa</i> layer cover (%)             |  |                            | 2       |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
| Seedling layer cover (%)                | 49   | 15                         | 38      | 47                          | 44    | 38                           | 22   | 26  |       |      |       |      |       |      |     |    |
| Shrub layer cover (%)                   | 2  | 1                          | 16      | 32                          | 29    | 37                           | 49   | 54  |       |      |       |      |       |      |     |    |
| Herb layer cover (%)                    | 7  | 10                         | 16      | 23                          | 5     | 4                            | 37   | 8   |       |      |       |      |       |      |     |    |
| Moss layer cover (%)                    | 89   | 99                         | 95      | 93                          | 96    | 75                           | 86   | 79  |       |      |       |      |       |      |     |    |
| Constancy and coverage of plant species |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
|   | Cons.  | Cov.                       | Cons.   | Cov.                        | Cons. | Cov.                         | Cons.  | Cov.  | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. |     |    |
|   | ----- Percent -----  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
| Overstory trees                         |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
| <i>Tsuga diversifolia</i>               | 100  | 56                         | 88      | 64                          | 100   | 84                           | 100  | 65  | 100   | 78   | 80    | 40   | 100   | 74   | 100 | 65 |
| <i>Abies veitchii</i>                   | 100  | 23                         | 100     | 35                          | 86    | 4                            | 77   | 23  | 89    | 18   | 100   | 42   | 29    | 5    | 27  | 1  |
| <i>Abies mariesii</i>                   | 78   | 15                         | 12      | 2                           | 57    | 5                            | 85   | 16  | 22    | 10   | 40    | 1    | 43    | 6    | 45  | 5  |
| <i>Picea jezoensis hondoensis</i>       | 89   | 16                         | 25      | 2                           | 86    | 17                           | 100  | 34  |       |      |       |      | 57    | 4    | 18  | 3  |
| <i>Larix leptolepis</i>                 | 22   | tr                         | 38      | 22                          | 29    | 5                            |  |   | 44    | 18   | 100   | 50   |       |      | 9   | tr |
| <i>Pinus parviflora</i>                 |  |                            | 12      | 2                           | 14    | 4                            |  |   | 22    | 9    | 20    | 2    | 29    | 2    | 27  | 10 |
| <i>Pinus koriensis</i>                  |  |                            |         |                             |       |                              | 8  | 2   |       |      |       |      |       |      | 54  | 15 |
| <i>Thuja standishii</i>                 |  |                            |         |                             |       |                              |  |   |       |      |       |      | 14    | 3    | 91  | 46 |
| <i>Chamaecyparis obtusa</i>             |  |                            |         |                             |       |                              |  |   | 11    | tr   |       |      |       |      | 9   | 7  |
| <i>Betula ermanii</i>                   | 67   | 8                          | 25      | tr                          | 29    | 2                            | 8  | 3   | 11    | 1    | 80    | 18   | 57    | 12   | 9   | 2  |
| <i>Sorbus comixta</i>                   | 44   | 2                          | 25      | 2                           | 14    | tr                           | 8  | 1   | 55    | 5    | 40    | 16   | 71    | 12   | 18  | 2  |
| <i>Betula corylifolia</i>               | 22   | 4                          |         |                             | 14    | tr                           |  |   |       |      |       |      |       |      | 9   | 1  |
| <i>Acer ukurunduense</i>                |  |                            | 12      | 1                           |       |                              |  |   | 11    | 1    |       |      |       |      | 9   | 1  |
| <i>Acer tschonoski</i>                  |  |                            |         |                             |       |                              | 54   | 5   |       |      |       |      |       |      |     |    |
| <i>Alnus matsumurae</i>                 |  |                            |         |                             |       |                              | 38   | 8   |       |      |       |      |       |      | 9   | tr |
| <i>Prunus nipponica</i>                 |  |                            |         |                             |       |                              | 8  | 2   | 11    | 1    |       |      |       |      |     |    |
| <i>Betula maximowicziana</i>            |  |                            |         |                             |       |                              | 8  | 2   |       |      |       |      |       |      |     |    |
| <i>Alnus maximowiczii</i>               |  |                            |         |                             |       |                              |  |   |       |      | 20    | tr   | 14    | 1    |     |    |
| <i>Acer nipponicum</i>                  |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      | 9   | 1  |
| Reproduction trees                      |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      |     |    |
| <i>Tsuga diversifolia</i>               | 100  | 6                          | 100     | 3                           | 71    | 22                           | 100  | 7   | 89    | 8    | 80    | 5    | 100   | 15   | 91  | 8  |
| <i>Abies veitchii</i>                   | 100  | 14                         | 100     | 12                          | 100   | 7                            | 100  | 17  | 100   | 22   | 100   | 33   | 86    | 2    | 54  | 2  |
| <i>Abies mariesii</i>                   | 89   | 34                         | 12      | tr                          | 71    | 11                           | 92   | 27  | 33    | 11   | 40    | 3    | 71    | 5    | 73  | 9  |
| <i>Picea jezoensis hondoensis</i>       | 33   | 1                          | 12      | tr                          | 43    | 1                            | 100  | 3   |       |      |       |      | 57    | 1    | 18  | tr |
| <i>Pinus parviflora</i>                 | 11   | tr                         | 38      | tr                          | 14    | tr                           | 15   | tr  | 44    | tr   |       |      | 29    | tr   | 18  | 1  |
| <i>Thuja standishii</i>                 |  |                            |         |                             |       |                              | 15   | tr  |       |      |       |      | 14    | tr   | 64  | 3  |
| <i>Pinus koriensis</i>                  |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      | 45  | 1  |
| <i>Chamaecyparis obtusa</i>             |  |                            |         |                             |       |                              |  |   |       |      |       |      |       |      | 9   | 1  |
| <i>Sorbus comixta</i>                   | 78   | 1                          | 88      | 1                           | 100   | 2                            | 85   | 1   | 78    | 1    | 60    | 3    | 86    | 2    | 54  | 1  |
| <i>Acer ukurunduense</i>                | 11   | tr                         | 62      | 1                           | 43    | 1                            | 77   | 1   | 44    | 1    |       |      | 14    | tr   | 18  | tr |
| <i>Betula ermanii</i>                   | 33   | tr                         |         |                             | 29    | 2                            | 31   | 2   |       |      |       |      | 14    | tr   | 9   | tr |
| <i>Acer tschonoski</i>                  | 22   | tr                         |         |                             | 86    | 3                            | 69   | 1   | 11    | tr   |       |      | 71    | 1    | 45  | 1  |



TABLE 4. Continued

| Constancy and coverage<br>of plant species | Cons.   |    | Cov. |    | Cons. |    | Cov. |    | Cons. |    | Cov. |    | Cons. |    | Cov. |    |
|--|---------|----|------|----|-------|----|------|----|-------|----|------|----|-------|----|------|----|
|  | Percent |    |      |    |       |    |      |    |       |    |      |    |       |    |      |    |
| Shrubs                                     |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |    |
| <i>Vaccinium smallii</i>                   | 11      | tr | 32   | tr | 57    | 1  | 77   | 2  | 67    | 2  | 60   | 1  | 100   | 4  | 73   | 3  |
| <i>Menziesia pentandra</i>                 | 22      | tr | 12   | tr | 100   | 11 | 100  | 19 | 22    | 2  |      |    | 100   | 14 | 100  | 11 |
| <i>Rhododendron fauriae</i>                | 11      | tr | 25   | tr | 57    | 1  |      |    | 100   | 26 | 100  | 34 | 100   | 17 | 82   | 8  |
| <i>Ilex rugosa</i>                         | 11      | 1  |      |    | 29    | 2  | 46   | 2  |       |    |      |    | 43    | 1  | 45   | 2  |
| <i>Vaccinium hirtum</i>                    | 11      | 1  |      |    | 14    | tr | 8    | tr |       |    |      |    | 14    | 1  | 9    | tr |
| <i>Vaccinium axillare</i>                  | 11      | tr |      |    |       |    |      |    |       |    |      |    | 14    | 1  |      |    |
| <i>Oplopanax japonicus</i>                 | 22      | tr |      |    | 14    | tr | 54   | 1  |       |    |      |    | 14    | tr | 9    | tr |
| <i>Euonymus macropteris</i>                |         |    | 62   | 1  |       |    | 69   | 2  |       |    |      |    | 14    | tr | 64   | 2  |
| <i>Viburnum furcatum</i>                   |         |    | 25   | tr | 14    | tr | 85   | 4  | 56    | 1  |      |    | 43    | 5  | 9    | tr |
| <i>Vaccinium yabei</i>                     |         |    |      |    | 29    | 2  | 38   | 2  |       |    |      |    | 14    | 2  | 36   | 2  |
| <i>Viburnum urceolatum</i>                 |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |    |
| <i>procumbens</i>                          |         |    |      |    | 14    | 1  | 62   | 3  |       |    |      |    | 14    | 4  | 64   | 2  |
| <i>Enkianthus campanulatus</i>             |         |    |      |    |       |    | 38   | 3  |       |    |      |    | 54    | 7  | 18   | 1  |
| <i>Skimmia repens</i>                      |         |    |      |    |       |    | 15   | 1  |       |    |      |    |       |    |      |    |
| <i>Vaccinium vitis-idaea</i>               |         |    |      |    |       |    |      |    | 11    | tr | 100  | 8  | 57    | 2  | 9    | tr |
| <i>Leucothea grayana</i>                   |         |    |      |    |       |    |      |    |       |    | 40   | 1  |       |    |      |    |
| <i>Rhododendron degronianum</i>            |         |    |      |    |       |    |      |    |       |    |      |    | 29    | 5  | 73   | 18 |
| <i>Ilex macrapoda</i>                      |         |    |      |    |       |    |      |    |       |    |      |    | 14    | 1  | 64   | 6  |
| <i>Pieris japonica</i>                     |         |    |      |    |       |    |      |    |       |    |      |    |       |    | 9    | 5  |
| Herbs                                      |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |    |
| <i>Oxalis acetosella</i>                   | 100     | 2  |      |    | 71    | 1  | 100  | 2  |       |    |      |    | 43    | 1  | 27   | tr |
| <i>Coptis japonica dissecta</i>            | 78      | 1  |      |    | 57    | 1  | 8    | tr |       |    |      |    | 14    | tr | 9    | tr |
| <i>Maianthemum dilatatum</i>               | 78      | 1  | 88   | 8  |       |    | 46   | 2  | 78    | 2  | 60   | 1  | 56    | 1  |      |    |
| <i>Streptopus streptopoides</i>            |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |    |
| <i>japonicus</i>                           | 67      | 1  | 25   | tr | 100   | 1  | 62   | 1  | 33    | tr |      |    | 100   | 1  | 18   | tr |
| <i>Rumhora mutica</i>                      | 44      | 1  | 12   | tr | 86    | 2  | 100  | 4  | 11    | tr |      |    | 29    | 1  | 45   | 1  |
| <i>Cornus canadensis</i>                   | 33      | 1  |      |    | 86    | 3  | 100  | 5  | 11    | tr |      |    | 86    | 2  | 54   | 1  |
| <i>Coptis quinquefolia</i>                 | 33      | 1  |      |    | 29    | 2  | 62   | 3  |       |    |      |    | 43    | 1  |      |    |
| Orchidaceae†                               | 22      | tr | 50   | 1  | 14    | tr | 15   | tr | 78    | 1  | 100  | 1  | 43    | tr | 27   | tr |
| <i>Pyrola renifolia</i>                    | 22      | tr | 88   | 2  |       |    |      |    | 78    | 2  |      |    |       |    |      |    |
| <i>Pyrola secunda</i>                      |         |    | 75   | 1  |       |    |      |    | 78    | 1  | 80   | 1  |       |    |      |    |
| <i>Clintonia unduensis</i>                 |         |    | 25   | tr |       |    |      |    | 22    | tr | 40   | 1  | 14    | tr |      |    |
| <i>Pternopetalum tanakae</i>               |         |    | 25   | 1  |       |    |      |    | 11    | tr |      |    |       |    |      |    |
| <i>Phegopteris polypodioides</i>           |         |    | 25   | tr |       |    | 31   | 1  | 22    | tr |      |    |       |    |      |    |
| <i>Cacalia adenoslyoides</i>               |         |    | 25   | tr |       |    | 31   | 1  |       |    |      |    |       |    | 9    | tr |
| <i>Dryopteris austriaca</i>                |         |    | 25   | tr |       |    | 31   | 1  |       |    |      |    |       |    |      |    |
| <i>Coptis trifolia</i>                     |         |    |      |    | 43    | 1  | 8    | tr |       |    |      |    |       |    |      |    |
| <i>Chiogenes japonica</i>                  |         |    |      |    | 14    | 1  |      |    |       |    |      |    |       |    | 45   | 2  |
| <i>Shortia ilicifolia</i>                  |         |    |      |    |       |    | 23   | 1  |       |    |      |    | 100   | 19 | 18   | tr |
| <i>Pedicularis kieskeki</i>                |         |    |      |    |       |    | 31   | 6  |       |    |      |    | 71    | 8  |      |    |
| <i>Sasa paniculata</i>                     |         |    |      |    |       |    | 31   | 2  |       |    |      |    |       |    |      |    |
| <i>Plagiogyria matsumureana</i>            |         |    |      |    |       |    | 23   | 1  |       |    |      |    |       |    |      |    |
| <i>Calamagrostis hakonensis</i>            |         |    |      |    |       |    |      |    | 11    | tr | 20   | tr | 29    | 1  |      |    |
| Mosses and Lichens                         |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |    |
| <i>Pleurozium schreberi</i>                | 100     | 47 | 100  | 39 | 100   | 44 | 100  | 44 | 100   | 48 | 100  | 54 | 100   | 30 | 100  | 17 |
| <i>Hylocomium splendens</i>                | 100     | 49 | 100  | 68 | 100   | 46 | 100  | 40 | 100   | 54 | 80   | 25 | 100   | 31 | 91   | 50 |
| <i>Dicranum</i> spp.                       | 100     | 4  | 88   | 2  | 86    | 5  | 85   | 4  | 89    | 2  | 80   | 4  | 86    | 11 | 91   | 7  |
| <i>Pogonatum grandifolium</i>              | 44      | 2  | 88   | 2  | 71    | 3  | 85   | 4  | 44    | 1  | 40   | 1  | 71    | 6  | 26   | tr |
| <i>Cladonia</i> spp.                       | 44      | 1  | 12   | tr | 14    | tr | 15   | tr | 33    | tr | 40   | 1  | 57    | 1  | 27   | 1  |
| <i>Mnium speciosum</i>                     | 33      | 1  | 62   | 2  | 57    | 10 | 46   | 3  | 11    | tr |      |    | 29    | 2  | 45   | 3  |
| <i>Ptelium crista-castrensis</i>           | 33      | tr |      |    | 43    | 1  |      |    | 11    | tr | 40   | 1  | 14    | tr | 18   | 1  |
| <i>Peltigera</i> sp.                       | 33      | tr | 75   | 1  | 29    | tr | 8    | tr | 89    | 1  | 80   | 1  | 29    | tr | 54   | 1  |
| <i>Lobaria</i> sp.                         | 22      | 1  |      |    | 57    | 2  | 69   | 2  |       |    | 20   | 1  | 29    | 1  | 54   | 1  |
| <i>Pheterophyllum</i> sp.                  |         |    | 12   | tr |       |    |      |    | 67    | 2  | 60   | 7  | 57    | 5  | 9    | 1  |
| <i>Loeskeobryum cavifolium</i>             |         |    | 12   | tr | 14    | tr | 8    | tr | 22    | tr | 20   | tr |       |    | 45   | 5  |
| <i>Sphagnum girgensohnii</i>               |         |    |      |    | 57    | 2  | 62   | 2  | 11    | tr |      |    | 14    | 1  | 54   | 2  |
| <i>Bazzania</i> sp.                        |         |    |      |    |       |    |      |    |       |    |      |    | 14    | 2  |      |    |
| <i>Mnium punctatum</i>                     |         |    |      |    |       |    |      |    |       |    |      |    |       |    | 9    | 1  |
| Miscellaneous cryptogams                   | 11      | 1  | 25   | 1  | 14    | 2  | 54   | 4  | 44    | 2  | 20   | 1  | 57    | 8  | 45   | 4  |

\* All plant species with at least 1% average cover or 50% constancy in one of the associations or phases are included.

† "tr" indicates trace occurrence, i.e., <0.5%; blanks indicate a species absence.

‡ Abbreviations for localities are: Y and C = Yatsugatake and Chichibu, F = Fuji, and O = Ontake.

§ According to five-class scheme where 1 = 0–5% stones, 2 = 5–35% stones, 3 = 35–65% stones, 4 = 65–95% stones, and 5 = 95–100% stones.

|| A group average of the maximum heights and diameters observed in individual plots.

¶ Group of ecologically related species including *Dactylostalix ringens*, *Plantanthera ophryoides*, *Ephippianthus schmidii*, *Goodyera repens*, and *Listera cordata*.

TABLE 5. Basal area (m<sup>2</sup>/ha) by species in each community type; based on wedge prism counts.\*

| Location‡                         | Community type and phase† |                  |           |      |         |         |             |           |               |      |      |      |         |          |           |
|-----------------------------------|---------------------------|------------------|-----------|------|---------|---------|-------------|-----------|---------------|------|------|------|---------|----------|-----------|
|                                   | Tsd/Absp/Sapa             | Pijeho/Absp/Caad | Abve/Drau |      |         |         | Abve/Ststja | Abve/Vaax | Tsd/Absp/Plsh |      |      |      |         | Tsd/Shil | Thst/Rhde |
|                                   |                           |                  | O         | F    | Y and C | Y and C |             |           | Typical       | Mepe | Rhfa | Vavi | Y and C |          |           |
| Tree species                      |                           |                  |           |      |         |         |             |           |               |      |      |      |         |          |           |
| Gymnosperms                       |                           |                  |           |      |         |         |             |           |               |      |      |      |         |          |           |
| <i>Tsuga diversifolia</i>         | 17.2                      | 12.5             | 4.5       | 19.4 | 13.8    | 8.8     |             | 43.0      | 32.0          | 52.8 | 26.0 | 43.1 | 23.8    | 50.1     | 33.0      |
| <i>Picea jezoensis hondoensis</i> | 15.0                      | 21.1             | 19.7      | 1.2  | 5.0     | 8.8     | 3.6         | 0.8       | 7.0           | 7.2  | 17.3 |      |         | 1.8      | 0.6       |
| <i>Abies veitchii</i>             | 5.4                       | 11.0             | 9.8       | 37.6 | 21.3    | 26.3    | 26.8        | 21.1      | 16.7          | tr§  | 11.1 | 7.6  | 18.8    | 2.7      | 0.6       |
| <i>Abies mariesii</i>             | 2.0                       | 15.3             | 4.5       |      | 3.8     | 12.5    | 18.8        | 1.6       | 8.3           | 1.8  | 5.8  | 6.9  | tr      | 1.8      | 1.7       |
| <i>Chamaecyparis obtusa</i>       | 1.8                       |                  |           |      |         |         |             |           |               |      |      | tr   |         |          | 2.8       |
| <i>Chamaecyparis pisifera</i>     | 0.2                       |                  | 0.9       |      |         |         |             |           |               |      |      |      |         |          |           |
| <i>Thuja standishii</i>           | 1.3                       |                  |           |      |         |         |             |           |               |      | 1.0  |      |         | 0.9      | 27.9      |
| <i>Pinus koriensis</i>            | 0.4                       |                  | tr        |      |         |         |             |           |               |      | tr   |      |         |          | 5.7       |
| <i>Pinus parviflora</i>           | tr                        | tr               |           |      | tr      |         |             | tr        |               | 1.8  |      | 4.2  | 1.2     | 0.9      | 4.6       |
| <i>Larix leptolepis</i>           | 0.7                       |                  |           |      |         |         |             | 11.7      | tr            | 1.8  |      | 9.7  | 33.8    |          | tr        |
| Angiosperms                       |                           |                  |           |      |         |         |             |           |               |      |      |      |         |          |           |
| <i>Betula ermanii</i>             | 4.0                       | 2.3              | 8.0       | 0.6  | 3.8     | 6.3     | 7.2         | tr        | 3.5           | tr   | 2.4  | tr   | tr      | 3.6      | 0.6       |
| <i>Sorbus comixta</i>             | 0.7                       | 2.0              | 1.8       | tr   | 0.6     | 1.2     | 0.9         | 0.8       | tr            | tr   | 1.9  | tr   | 2.5     | 2.7      | tr        |
| <i>Betula corylifolia</i>         | 0.4                       | tr               | tr        |      | tr      |         |             |           | 0.7           | tr   | tr   |      |         |          | 0.6       |
| <i>Betula carpinifolia</i>        | 0.2                       |                  |           |      |         |         |             |           |               |      |      |      |         |          |           |
| <i>Prunus spp.</i>                | 0.2                       | tr               |           | 3.1  |         |         |             | tr        |               |      | tr   | tr   |         |          |           |
| <i>Acer ukurunduense</i>          | tr                        | tr               | tr        | 1.9  | 2.5     |         |             | tr        |               |      | tr   | tr   |         |          | 0.6       |
| <i>Alnus matsumurae</i>           |                           |                  | 0.9       | 1.2  |         |         |             |           |               |      |      | tr   | tr      | tr       |           |
| <i>Tilia japonica</i>             |                           |                  |           | 0.6  |         |         |             | tr        |               |      |      |      |         |          |           |
| <i>Acer nipponica</i>             |                           |                  |           |      |         |         |             |           |               |      |      |      |         |          | 0.6       |
| Total all species                 | 49.5                      | 64.2             | 50.1      | 65.6 | 52.0    | 63.9    | 57.3        | 79.0      | 68.2          | 65.4 | 65.5 | 71.5 | 80.1    | 64.5     | 79.3      |

\* Only those species achieving an average basal area of at least 0.1 m<sup>2</sup>/ha in at least one community are included.

† Abbreviations are: Tsd/Absp/Sapa = *Tsuga diversifolia*/*Abies* species/*Sasa paniculata*; Pijeho/Absp/Caad = *Picea jezoensis hondoensis*/*Abies* spp./*Calcia adenostyloides*; Abve/Drau = *Abies veitchii*/*Dryopteris austriaca*; Abve/Ststja = *Abies veitchii*/*Streptopus streptopoides japonicus*; Abve/Vaax = *Abies veitchii*/*Vaccinium axillare*; Tsd/Absp/Plsh = *Tsuga diversifolia*/*Abies* species/*Pleurozium schreberi*; Typical, Mepe, Rhfa, and Vavi are phases of the Tsd/Absp/Plsh community type with Mepe = *Menziesia pentandra*, Rhfa = *Rhododendron fauriae*, and Vavi = *Vaccinium vitis-idaea*; Tsd/Shil = *Tsuga diversifolia*/*Shortia ilicifolia*; and Thst/Rhde = *Thuja standishii*/*Rhododendron degronianum* community type.

‡ Abbreviations are O = Mount Ontake, F = Mount Fuji, and Y and C = Yatsugatake and Chichibu Mountains.

§ "tr" refers to basal area <0.05 m<sup>2</sup>/ha. Blanks indicate a species was absent.



FIG. 5. Stand representative of the *Thuja standishii*/*Rhododendron degronianum* community type; the substrate consists entirely of large stone blocks covered by moss (Chichibu Mountains).

munity replace the *Menziesia* phase on extremely stony soils (Table 4). The *Rhododendron* phase differs from the *Menziesia* phase mainly in the abundance of *Rhododendron fauriae* and relative paucity of other species including *Menziesia pentandra* (Table 4). *Picea jezoensis* var. *hondoensis* is totally absent from the stands and *Abies mariesii* nearly so, while *Larix leptolepis* and *Sorbus comixta* are often conspicuous in the overstory. *Abies veitchii* is the most consistently successful reproducing tree in the absence of substantial *Abies mariesii*. Except for *Rhododendron* and mosses, the understory is extremely poor with small amounts of *Viburnum furcatum*, *Vaccinium smallii*, saprophytic Orchidaceae, *Pyrola renifolia* and *P. secunda*, and *Maianthemum dilatatum* being characteristic (Table 4). Major mosses are the ubiquitous *Hylocomium* and *Pleurozium* with *Dicranum* spp., *Pheterophyllum*, and *Peltigera* spp. as associates.

The *Vaccinium vitis-idaea* phase is simply a further variation on this same theme found near the upper forest line. On the exposed sites where it is found, basal areas are often high (80 m<sup>2</sup>/ha) but dominant trees are stunted (mean maximum height of 9.4 m). As is characteristic on approaching timberline, *Abies veitchii* exceeds *Tsuga diversifolia* in importance but *Larix leptolepis* is more important than either in the overstory; *Betula ermanii* is also conspicuous (Tables 4 and 5). *Abies veitchii*, however, clearly dominates the reproduction. The understory of the *Vaccinium* phase is extremely depauperate, consisting mainly of *Rhododendron fauriae* and *Vaccinium vitis-idaea* (Ta-

ble 4). *Pleurozium*, *Hylocomium*, *Dicranum* spp., and *Pheterophyllum* are the important mosses.

*Tsuga diversifolia*/*Shortia ilicifolia*  
community type

The *Tsuga diversifolia*/*Shortia ilicifolia* community type is characteristic of ridgetops exposed to strong storm winds. In the Yatsugatake and Chichibu Mountains it occurs along the north slopes of such ridgetops while at Mount Ontake stands are encountered along exposed south- and west-facing canyon margins or breaks. Soils are very stony, but exposure is the most important factor in forest stunting (average maximum height 8.0 m). *Tsuga diversifolia* and *Sorbus comixta* are the most important overstory trees, as are *Tsuga diversifolia*, both *Abies*, and *Sorbus* in the reproduction (Tables 4 and 5). The shrub layer is well developed with *Rhododendron fauriae*, *Menziesia pentandra*, and *Vaccinium smallii* and *V. vitis-idaea* most important. The herb layer is moderately well developed (average cover 37%) but three-fourths of this is made up by *Shortia ilicifolia* and *Pedicularis kieseki* (Table 4). Little distinguishes the dense moss layer which is dominated by *Hylocomium*, *Pleurozium*, *Dicranum* spp., miscellaneous liverworts, *Pogonatum grandifolium*, and *Pheterophyllum*.

*Thuja standishii*/*Rhododendron degronianum*  
community type

This final member of the *Tsuga*/moss group appears to be one of its most distinctive units (Table 4). This

TABLE 6. Characteristics of the community types belonging to the *Abies*/herb and conifer/*Sasa* community groups and number of sample plots by location.\*†

| Association and phase                   |   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
|---|---|---------|---|------|---------|------|---|------|-------|------|-------|------|---|------|---|--|
| Characteristics                         | <i>Abies veitchii</i><br><i>Vaccinium axillare</i><br>(Abve/Vaax) |         | <i>Abies veitchii</i><br><i>Streptopus streptopoides</i><br><i>japonicus</i><br>(Abve/Ststja) |      | Y and C |      | <i>Abies veitchii</i><br><i>Dryopteris austriaca</i><br>(Abve/Drau) |      | F     |      | O     |      | <i>Picea jezoensis</i><br><i>hondoensis</i> /<br><i>Abies spp.</i> /<br><i>Cacalia adenostyloides</i><br>(Pijeho/<br>Absp/<br>Caad) |      | <i>Tsuga diversifolia</i><br><i>Abies spp.</i> /<br><i>Sasa paniculata</i><br>(Tsd/<br>Absp/<br>Sapa) |  |
|   | Y and C   | Y and C | Y and C   | F    | O       | O    | O   |      |       |      |       |      |   |      |   |  |
| Number of plots                         | 7   | 10      | 10  | 10   | 7       | 16   | 25  |      |       |      |       |      |   |      |   |  |
| Environmental features                  |   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
| Elevation (m)                           | 2490  | 2375    | 2135  | 1770 | 1905    | 2180 | 2080  |      |       |      |       |      |   |      |   |  |
| Slope (%)                               | 25  | 25      | 28  | 18   | 36      | 28   | 28  |      |       |      |       |      |   |      |   |  |
| Soil stoniness§                         | 3.4   | 2.2     | 2.2   | 1.6  | 3.6     | 2.6  | 1.6   |      |       |      |       |      |   |      |   |  |
| General vegetative features             |   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
| Basal area (m <sup>2</sup> /ha)         | 57.2  | 63.9    | 52.0  | 65.1 | 50.1    | 64.2 | 48.8  |      |       |      |       |      |   |      |   |  |
| Seedlings (1000/ha)                     | 177   | 202     | 46  | 19   | 43      | 56   | 3.4   |      |       |      |       |      |   |      |   |  |
| Maximum height (m)                      | 10.4  | 15.4    | 20.6  | 18.9 | 24.7    | 20.1 | 24.8  |      |       |      |       |      |   |      |   |  |
| Maximum dbh. (cm)                       | 27  | 48      | 55  | 55   | 61      | 49   | 71  |      |       |      |       |      |   |      |   |  |
| <i>Sasa</i> layer (%)                   | ...   | ...     | tr  | ...  | 1       | ...  | 93  |      |       |      |       |      |   |      |   |  |
| Seedling layer (%)                      | 37  | 53      | 34  | 14   | 25      | 39   | 10  |      |       |      |       |      |   |      |   |  |
| Shrub layer (%)                         | 29  | 8       | 8   | 16   | 33      | 24   | 8   |      |       |      |       |      |   |      |   |  |
| Herb layer (%)                          | 46  | 73      | 74  | 84   | 79      | 65   | 4   |      |       |      |       |      |   |      |   |  |
| Moss layer (%)                          | 84  | 76      | 72  | 69   | 76      | 91   | 10  |      |       |      |       |      |   |      |   |  |
| Constancy and coverage of plant species |   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
|   | Cons.   | Cov.    | Cons.   | Cov. | Cons.   | Cov. | Cons.   | Cov. | Cons. | Cov. | Cons. | Cov. | Cons.   | Cov. |   |  |
|   | Percent   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
| Overstorey trees                        |   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
| <i>Abies veitchii</i>                   | 100   | 44      | 100   | 40   | 100     | 44   | 80  | 56   | 100   | 40   | 100   | 31   | 60  | 16   |   |  |
| <i>Picea jezoensis hondoensis</i>       | 71  | 10      | 100   | 15   | 60      | 10   | 40  | 4    | 100   | 46   | 100   | 45   | 16  | 3    |   |  |
| <i>Abies mariesii</i>                   | 86  | 36      | 100   | 28   | 60      | 6    |   |      | 43    | 16   | 94    | 27   | 100   | 41   |   |  |
| <i>Tsuga diversifolia</i>               |   |         | 60  | 14   | 70      | 35   | 60  | 28   | 71    | 20   | 81    | 38   | 96  | 55   |   |  |
| <i>Chamaecyparis obtusa</i>             |   |         |   |      |         |      |   |      | 29    | 2    |       |      | 16  | 8    |   |  |
| <i>Chamaecyparis pisifera</i>           |   |         |   |      |         |      |   |      | 29    | 7    |       |      | 4   | 1    |   |  |
| <i>Thuja standishii</i>                 |   |         |   |      |         |      |   |      |       |      |       |      | 12  | 3    |   |  |
| <i>Pinus koriensis</i>                  |   |         |   |      |         |      |   |      |       |      |       |      | 20  | 1    |   |  |
| <i>Pinus parviflora</i>                 |   |         |   |      |         |      |   |      |       |      |       |      | 4   | 1    |   |  |
| <i>Larix leptolepis</i>                 |   |         |   |      |         |      |   |      |       |      |       |      | 4   | 2    |   |  |
| <i>Sorbus comixta</i>                   | 100   | 2       | 100   | 2    | 30      | 2    | 50  | 5    |       |      | 69    | 15   | 40  | 5    |   |  |
| <i>Acer ukurunduense</i>                | 14  | tr      |   |      | 30      | 8    | 50  | 11   | 86    | 31   | 50    | 5    |   |      |   |  |
| <i>Betula ermanii</i>                   |   |         | 20  | 1    | 50      | 15   | 30  | 2    | 14    | 6    | 62    | 11   | 80  | 21   |   |  |
| <i>Acer tschonoski</i>                  |   |         |   |      | 10      | 1    |   |      | 29    | 4    | 19    | 2    | 4   | tr   |   |  |
| <i>Prunus nipponica</i>                 |   |         |   |      |         |      | 40  | 10   | 14    | 4    | 16    | tr   | 16  | 3    |   |  |
| <i>Alnus matsumurae</i>                 |   |         |   |      |         |      | 40  | 6    |       |      |       |      |   |      |   |  |
| <i>Betula platyphylla</i>               |   |         |   |      |         |      | 20  | 2    |       |      |       |      |   |      |   |  |
| <i>Salix bakko</i>                      |   |         |   |      |         |      | 20  | 1    |       |      |       |      |   |      |   |  |
| <i>Cercidiphyllum magnificum</i>        |   |         |   |      |         |      |   |      |       |      |       |      | 16  | 3    |   |  |
| <i>Betula corylifolia</i>               |   |         |   |      |         |      |   |      |       |      |       |      | 8   | 2    |   |  |
| <i>Acanthopanax sciadophylloides</i>    |   |         |   |      |         |      |   |      |       |      |       |      | 8   | 1    |   |  |
| <i>Betula grossa</i>                    |   |         |   |      |         |      |   |      |       |      |       |      | 4   | 1    |   |  |
| Reproduction trees                      |   |         |   |      |         |      |   |      |       |      |       |      |   |      |   |  |
| <i>Abies veitchii</i>                   | 100   | 18      | 100   | 24   | 100     | 18   | 100   | 9    | 100   | 11   | 100   | 13   | 88  | 6    |   |  |
| <i>Picea jezoensis hondoensis</i>       | 71  | 1       | 40  | tr   | 60      | 3    | 50  | 1    | 100   | 4    | 100   | 2    | 80  | 1    |   |  |
| <i>Abies mariesii</i>                   | 100   | 22      | 100   | 36   | 70      | 9    |   |      | 57    | 8    | 100   | 23   | 20  | 1    |   |  |
| <i>Tsuga diversifolia</i>               |   |         | 40  | 2    | 60      | 12   | 80  | 5    | 86    | 5    | 88    | 4    | 84  | 2    |   |  |
| <i>Sorbus comixta</i>                   | 100   | 2       | 100   | 2    | 80      | 1    | 90  | 3    | 71    | 2    | 94    | 2    | 84  | 1    |   |  |
| <i>Acer ukurunduense</i>                | 14  | tr      |   |      | 60      | 2    | 90  | 2    | 86    | 7    | 81    | 1    | 8   | tr   |   |  |
| <i>Betula ermanii</i>                   |   |         | 20  | 1    | 20      | tr   | 20  | tr   | 29    | 2    | 12    | tr   | 52  | 1    |   |  |
| <i>Prunus nipponica</i>                 |   |         |   |      |         |      | 40  | 1    |       |      |       |      | 12  | tr   |   |  |
| <i>Acanthopanax sciadophylloides</i>    |   |         |   |      |         |      | 30  | tr   |       |      |       |      | 28  | 1    |   |  |
| <i>Tilia japonica</i>                   |   |         |   |      |         |      | 40  | 1    |       |      |       |      |   |      |   |  |
| <i>Acer shirasawanum</i>                |   |         |   |      |         |      | 10  | 1    |       |      |       |      |   |      |   |  |

TABLE 6. Continued.

| Constancy and coverage<br>of plant species | Cons.   |    | Cov. |    | Cons. |    | Cov. |    | Cons. |    | Cov. |    | Cons. |    | Cov. |  |
|--|---------|----|------|----|-------|----|------|----|-------|----|------|----|-------|----|------|--|
|  | Percent |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| Shrubs                                     |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>Vaccinium axillare</i>                  | 100     | 5  | 40   | 1  | 10    | tr |      |    |       |    | 6    | tr |       |    |      |  |
| <i>Menziesia pentandra</i>                 | 100     | 19 | 100  | 5  | 70    | 5  |      |    | 57    | 10 | 75   | 5  | 56    | 1  |      |  |
| <i>Vaccinium smallii</i>                   | 57      | 2  |      |    | 20    | tr | 20   | tr | 43    | 1  | 25   | 1  | 60    | 1  |      |  |
| <i>Vaccinium yabei</i>                     | 29      | 3  | 40   | 5  | 10    | tr |      |    | 14    | tr | 44   | 2  | 8     | tr |      |  |
| <i>Rhododendron fauriae</i>                | 29      | tr | 40   | 1  |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>Oplopanax japonicus</i>                 | 29      | tr | 40   | 1  | 60    | 1  |      |    | 80    | 3  | 81   | 1  | 24    | tr |      |  |
| <i>Rubus pseudojaponicus</i>               | 14      | tr |      |    | 10    | tr |      |    | 29    | 1  | 44   | tr |       |    |      |  |
| <i>Actinidia kolomixta</i>                 |         |    | 40   | 2  | 20    | 2  | 90   | 2  | 29    | 1  |      |    | 16    | tr |      |  |
| <i>Viburnum farcatum</i>                   |         |    |      |    | 20    | tr | 80   | 4  | 71    | 8  | 88   | 10 | 72    | 3  |      |  |
| <i>Viburnum urceolatum</i>                 |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>procumbens</i>                          |         |    |      |    | 10    | tr | 10   | tr |       |    |      |    | 48    | 1  |      |  |
| <i>Hydrangea petiolaris</i>                |         |    |      |    | 10    | tr | 40   | 3  |       |    |      |    |       |    |      |  |
| <i>Euonymus macropteris</i>                |         |    |      |    |       |    | 80   | 3  | 57    | 2  | 88   | 2  | 36    | tr |      |  |
| <i>Ligustrum tschonoski</i>                |         |    |      |    |       |    | 60   | 3  |       |    |      |    |       |    |      |  |
| <i>Ribes alpina</i>                        |         |    |      |    |       |    | 60   | 2  |       |    |      |    |       |    |      |  |
| <i>Rhus ambigua</i>                        |         |    |      |    |       |    | 40   | 1  |       |    |      |    |       |    |      |  |
| <i>Skimmia repens</i>                      |         |    |      |    |       |    | 10   | tr | 14    | tr | 44   | 1  | 12    | tr |      |  |
| <i>Sambucus sieboldiana</i>                |         |    |      |    |       |    | 10   | tr |       |    |      |    | 20    | 1  |      |  |
| <i>Lonicera tenuipes</i>                   |         |    |      |    |       |    | 10   | 1  |       |    |      |    |       |    |      |  |
| <i>Ilex rugosa</i>                         |         |    |      |    |       |    |      |    | 43    | 2  | 81   | 6  | 52    | 1  |      |  |
| <i>Clethera barbinervosa</i>               |         |    |      |    |       |    |      |    | 29    | 9  |      |    | 8     | 1  |      |  |
| <i>Rubus yabei</i>                         |         |    |      |    |       |    |      |    | 29    | 1  |      |    | 16    | tr |      |  |
| <i>Ribes japonica</i>                      |         |    |      |    |       |    |      |    | 14    | 2  |      |    |       |    |      |  |
| <i>Enkianthus campanulatus</i>             |         |    |      |    |       |    |      |    | 14    | tr | 12   | 1  | 16    | tr |      |  |
| Sasa                                       |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>Sasa paniculata</i>                     |         |    |      |    |       |    |      |    | 29    | 1  |      |    | 100   | 93 |      |  |
| <i>Sasa nipponica</i>                      |         |    |      |    | 10    | tr |      |    |       |    |      |    |       |    |      |  |
| Herbs                                      |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>Streptopus streptopoides</i>            |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>japonicus</i>                           | 100     | 20 | 100  | 5  | 100   | 3  | 20   | tr | 86    | 2  | 100  | 3  | 64    | 1  |      |  |
| <i>Cornus canadensis</i>                   | 100     | 3  | 80   | 4  | 90    | 2  | 20   | tr | 86    | 12 | 100  | 6  | 20    | tr |      |  |
| <i>Oxalis acetosella</i>                   | 100     | 3  | 100  | 3  | 100   | 6  |      |    | 100   | 3  | 94   | 3  | 88    | 1  |      |  |
| <i>Coptis quinquefolia</i>                 | 86      | 3  | 80   | 6  | 30    | 4  | 20   | tr | 71    | 4  | 94   | 9  | 12    | tr |      |  |
| <i>Maianthemum dilatatum</i>               | 71      | 4  | 60   | 1  | 70    | 4  | 100  | 26 | 14    | tr | 56   | 3  | 44    | tr |      |  |
| <i>Pedicularis kieseki</i>                 | 71      | 17 | 40   | 22 |       |    |      |    | 14    | 2  | 88   | 15 | 12    | tr |      |  |
| <i>Coptis japonica dissecta</i>            | 29      | 1  | 60   | 1  | 90    | 2  |      |    |       |    |      |    |       |    |      |  |
| <i>Veratrum sp.</i>                        | 29      | tr |      |    | 20    | 1  |      |    |       |    | 6    | tr |       |    |      |  |
| <i>Dryopteris austriaca</i>                | 29      | 2  | 40   | 2  | 100   | 32 | 100  | 25 | 100   | 26 | 68   | 2  | 36    | tr |      |  |
| <i>Viola spp.</i>                          | 14      | tr |      |    |       |    |      |    |       |    | 31   | 1  | 12    | tr |      |  |
| <i>Carex sachalinensis</i>                 | 14      | tr |      |    | 50    | 3  | 10   | tr |       |    |      |    |       |    |      |  |
| <i>Lycopodium serratum</i>                 | 14      | tr | 40   | tr | 20    | tr | 10   | tr | 57    | 2  | 94   | 2  | 12    | tr |      |  |
| <i>Pteridophyllum racemosum</i>            |         |    | 60   | 25 | 50    | 24 |      |    |       |    |      |    |       |    |      |  |
| <i>Rubus pedatus</i>                       |         |    | 40   | 4  | 40    | 2  |      |    |       |    |      |    |       |    |      |  |
| <i>Rumhosa mutica</i>                      |         |    | 40   | 1  | 50    | 3  | 10   | tr | 86    | 3  | 88   | 6  | 84    | 1  |      |  |
| <i>Phegopteris polypodioides</i>           | 14      | tr | 20   | 1  | 60    | 5  | 90   | 6  | 100   | 8  | 94   | 9  | 24    | tr |      |  |
| <i>Cacalia adenostyloides</i>              |         |    |      |    | 60    | 6  | 100  | 47 | 57    | 31 | 100  | 15 | 16    | tr |      |  |
| <i>Athyrium spp.</i>                       |         |    |      |    | 40    | 1  | 50   | 4  | 42    | 3  | 38   | 1  | 16    | tr |      |  |
| <i>Clintonia udensis</i>                   |         |    |      |    | 30    | 1  | 30   | tr | 14    | 1  | 6    | tr |       |    |      |  |
| <i>Athyrium yokoscense</i>                 |         |    |      |    | 30    | 1  | 10   | tr | 29    | 1  | 12   | tr | 12    | tr |      |  |
| <i>Trillium tschonoski</i>                 |         |    |      |    | 20    | tr | 60   | 1  | 29    | tr | 25   | tr | 4     | tr |      |  |
| <i>Osumunda asiatica</i>                   |         |    |      |    | 20    | tr | 40   | 1  | 14    | tr |      |    | 4     | tr |      |  |
| <i>Smilacina japonica</i>                  |         |    |      |    | 20    | tr |      |    | 57    | 2  | 62   | 3  | 40    | tr |      |  |
| <i>Salvia lutescens</i>                    |         |    |      |    | 10    | tr |      |    | 14    | 11 |      |    |       |    |      |  |
| <i>Pyrola secunda</i>                      |         |    |      |    | 10    | tr | 40   | tr | 43    | tr | 19   | tr | 4     | tr |      |  |
| <i>Pternopetalum tanakae</i>               |         |    |      |    |       |    | 100  | 8  | 29    | 1  |      |    | 4     | tr |      |  |
| <i>Circaea alpina</i>                      |         |    |      |    | 40    | 1  | 14   | tr | 6     | tr |      |    | 4     | tr |      |  |
| <i>Calamagrostis hakonensis</i>            |         |    |      |    | 40    | 1  | 14   | 1  | 25    | 1  |      |    | 4     | tr |      |  |
| <i>Tiarella polyphylla</i>                 |         |    |      |    |       |    | 20   | tr | 43    | 1  |      |    | 8     | tr |      |  |
| <i>Cimicifuga simplex</i>                  |         |    |      |    |       |    | 10   | 1  | 14    | 5  |      |    |       |    |      |  |
| <i>Shortia ilicifolia</i>                  |         |    |      |    |       |    |      |    | 14    | tr | 31   | 1  | 8     | tr |      |  |
| <i>Plagiogyria matsumureana</i>            |         |    |      |    |       |    |      |    | 14    | tr | 12   | 1  |       |    |      |  |
| <i>Blechnum nipponicum</i>                 |         |    |      |    |       |    |      |    | 14    | 1  |      |    | 8     | tr |      |  |
| <i>Rodgersia podophylla</i>                |         |    |      |    |       |    |      |    |       |    | 19   | 2  |       |    |      |  |
| Mosses                                     |         |    |      |    |       |    |      |    |       |    |      |    |       |    |      |  |
| <i>Pleurozium schreberi</i>                | 100     | 40 | 100  | 23 | 100   | 14 | 100  | 21 | 100   | 12 | 100  | 31 | 100   | 4  |      |  |
| <i>Hylocomium splendens</i>                | 100     | 13 | 100  | 22 | 60    | 5  | 90   | 30 | 86    | 20 | 100  | 16 | 92    | 4  |      |  |
| <i>Dicranum sp.</i>                        | 86      | 10 | 80   | 3  | 40    | 2  | 70   | 1  | 29    | 1  | 100  | 12 | 8     | 1  |      |  |

TABLE 6. Continued.

| Constancy and coverage<br>of plant species | Cons. |      | Cov.  |      | Cons. |      | Cov.  |      | Cons. |      | Cov.  |      | Cons. |      | Cov.  |      |
|--|-------|------|-------|------|-------|------|-------|------|-------|------|-------|------|-------|------|-------|------|
|  | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. | Cons. | Cov. |
| <i>Pogonatum grandifolium</i>              | 100   | 10   | 100   | 20   | 90    | 28   | 40    | 1    | 86    | 18   | 100   | 28   | 24    | tr   |       |      |
| <i>Pleuroziopsis ruthenica</i>             | 57    | 6    | 40    | 3    | 80    | 24   | 80    | 8    | 86    | 12   | 68    | 2    | 4     | tr   |       |      |
| <i>Cladonia</i> sp.                        | 71    | 1    | 40    | tr   | 30    | 1    | 20    | tr   | 14    | tr   | 19    | tr   | 20    | tr   |       |      |
| <i>Lobaria pulmonaria</i>                  | 57    | 1    | 60    | 1    | 50    | 1    |       |      | 71    | 1    | 62    | 1    | 16    | tr   |       |      |
| <i>Ptelium crista-castrensis</i>           | 57    | 1    | 20    | tr   | 10    | tr   |       |      |       |      |       |      |       |      |       |      |
| <i>Rhytidiadelphus triquetrus</i>          | 57    | 8    |       |      |       |      |       |      |       |      |       |      |       |      |       |      |
| <i>Mnium speciosum</i>                     | 29    | 4    | 40    | 3    | 40    | 2    | 70    | 8    | 71    | 6    | 50    | 1    | 4     | tr   |       |      |
| <i>Peltigera</i> sp.                       | 29    | tr   | 12    | tr   | 60    | 1    | 50    | 1    | 29    | 1    | 12    | tr   |       |      |       |      |
| <i>Loeskeobryum cavifolium</i>             |       |      |       |      |       |      | 30    | 2    | 29    | tr   |       |      |       |      |       |      |
| <i>Polytrichum</i> sp.                     | 29    | tr   |       |      |       |      | 30    | 1    |       |      |       |      | 12    | tr   |       |      |
| <i>Sphagnum girgensohnii</i>               |       |      |       |      | 40    | 1    |       |      | 14    | 6    | 88    | 5    | 12    | tr   |       |      |
| <i>Pheterophyllum</i> sp.                  |       |      |       |      |       |      | 10    | 1    |       |      |       |      |       |      |       |      |
| <i>Mnium</i> sp.                           |       |      |       |      |       |      |       |      | 29    | 2    |       |      |       |      |       |      |
| Miscellaneous cryptogams                   | 14    | tr   | 40    | 6    | 40    | 2    | 40    | 2    | 71    | 7    | 62    | 5    | 80    | 3    |       |      |

\* All plant species with at least 1% average cover or 50% constancy in one of the associations or phases are included.

† “—” indicates absence; “tr” indicates trace occurrence, i.e., <0.5%.

‡ Abbreviations for locations are: Y = Yatsugatake, C = Chichibu, F = Fuji and O = Ontake.

§ According to five class scheme where 1 = 0 to 5% stones, 2 = 5–35% stones, 3 = 35–65% stones, 4 = 65–95% stones, and 5 = 95–100% stones.

|| A group average of the maximum heights and diameters observed in individual plots.

may partially be an artifact of the sampling, as will be discussed later. In any case, as recognized here the *Thuja standishii*/*Rhododendron degronianum* community type is distinctive in tree composition as well as having a well-developed and distinctive shrub layer (Fig. 5). It occurs on extremely stony podzolic soils (skeletal on 8 out of 11 sites) occupying a variety of landforms. Overstory dominants typically include *Thuja standishii* and either *Pinus parviflora* or *Pinus koriensis* along with the ubiquitous *Tsuga diversifolia* (Tables 4 and 5). In this community *Tsuga diversifolia* is the most abundant species in the reproduction although *Abies mariesii* (especially at Mount Ontake), *Abies veitchii*, and *Thuja standishii* may also be well represented (Table 4). The shrub layer is dominated by ericads: *Rhododendron degronianum*, *R. fauriae*, *Euonymus macropteris*, and *Viburnum ureolatum* var. *procumbens*. The sparse herb layer has few components of high constancy and none with high coverage; *Chiogenes japonica*, *Rumhora mutica*, and *Cornus canadensis* are most common (Table 4). The moss layer is rather strongly dominated by *Hylocomium splendens* with *Pleurozium schreberi*, *Dicranum* sp., *Mnium speciosum*, *Sphagnum girgensohnii*, *Loeskeobryum cavifolium*, *Lobaria* sp., and miscellaneous liverworts as the principal associates.

*Abies veitchii*/*Dryopteris austriaca*  
community type

The *Abies veitchii*/*Dryopteris austriaca* is the most widespread community type in the *Abies*/herb group. This rich community is found at all four locations generally occupying deeper, moist to wet soils of the Pw(h) or (especially at Mount Fuji) B<sub>D</sub> types. Soils are

generally much less stony than those under *Tsuga*/moss communities at the same locale; however, in many cases they are partially alluvial in origin and are rather gravelly in contrast with the fine-textured volcanic-ash soils associated with conifer/*Sasa* communities. Toe slopes and streamside terraces and benches are the most characteristic landforms this community occupies.

The outstanding features of this community type are the dominance of *Abies* in both the overstory and reproduction, and the rich, dense herb layer (Tables 5 and 6). *Abies veitchii* is the most important overstory tree followed by *Picea jezoensis hondoensis*, *Tsuga diversifolia*, and *Abies mariesii*. Because of the community's frequent occurrence in alluvial habitats and at the lower part of the subalpine zone, a rich array of hardwood associates is erratically represented (Tables 5 and 6) of which *Acer ukurunduense*, *Sorbus comixta*, *Betula ermanii*, and *Prunus nipponica* are most abundant. Reproduction is strongly dominated by *Abies veitchii* (Table 6). The shrub layer is poorly to moderately developed according to locale and is dominated by species such as *Viburnum furcatum*, *Euonymus macropteris*, *Ligustrum tschonoski*, *Oplopanax japonicus*, *Actinidia kolomikta*, *Ribes alpina*, and *Menziesia pentandra*. The herb layer is frequently very rich with *Dryopteris austriaca*, *Cacalia adenostyloides*, *Maianthemum dilatatum*, and *Phegopteris polypodioides* among the most constant dominants. *Dryopteris* and *Cacalia* are considered the characteristic herbs for this community type (Table 6). The moss layer is well developed (though lower in cover to that in the *Tsuga*/moss group). It is distinguished by *Pleuroziopsis ruthenica* and, except at Mount Fuji,

a high cover of *Pogonatum grandifolium* and greatly reduced cover of *Pleurozium schreberi* and *Hylocomium splendens* (though both are still important).

*Abies veitchii*/*Streptopus streptopoides japonicus* community type

On the mid- and upper slopes in the Yatsugatake and Chichibu Mountains, above the Abve/Drau type, is a more depauperate community with an herbaceous understory which we call the *Abies veitchii*/*Streptopus streptopoides japonicus* community type (Tables 5 and 6). Site conditions are drier and mosses more abundant than in the Abve/Drau type. *Abies veitchii*, *Abies mariesii*, and *Picea jezoensis hondoensis* dominate but substantial amounts of *Tsuga diversifolia* may also be present. *Sorbus comixta* is a constant hardwood associated sometimes with *Betula ermanii* (Table 5). *Abies mariesii* dominates the reproduction with *A. veitchii* a strong second. The only shrubs of consequence are *Menziesia pentandra* and, occasionally, *Vaccinium yabei* (Table 6). *Pteridophyllum racemosum* (at Yatsugatake) and *Pedicularis kieseki* (at Chichibu) are the dominant herbs (Fig. 6); but *Streptopus streptopoides japonicus*, *Oxalis acetosella*, *Coptis quinquefolia*, and *Cornus canadensis* are the most constant species with more than 1 or 2% average cover. *Cacalia*, *Dryopteris*, and *Pleuroziopsis ruthenica*, indicators of the Abve/Drau community, are either absent or present in very small amounts (Table 6). The major mosses are *Pogonatum grandifolium*, *Pleurozium schreberi*, and *Hylocomium splendens*.

*Abies veitchii*/*Vaccinium axillare* community type

On the high mountain summits and adjacent side slopes in the Yatsugatake and Chichibu Mountains is a closely related community, the *Abies veitchii*/*Vaccinium axillare* type. On these exposed habitats, trees are stunted as is the case with the Tsd/Sl and Tsd/Ab/Plsh (Vavi phase) community type discussed earlier; average maximum height of dominants is 10.4 m, generally 7–9 m on the summits and 12–15 m on the adjacent side slopes. *Abies veitchii*, *Abies mariesii*, *Picea jezoensis hondoensis*, and *Sorbus comixta* are the overstory dominants; *Tsuga diversifolia* is completely absent on the high (2400–2500 m) summits sampled (Table 5). *Abies mariesii* again dominates the reproduction with *Abies veitchii* a close second. The shrub and herb layers are moderately well developed but not very rich. Major shrubs are *Menziesia pentandra*, *Vaccinium axillare*, *V. smallii*, and *V. yabei*. Herbs of consequence are *Streptopus streptopoides japonicus* and *Pedicularis keiseki* with essentially the same constant associates found in the lower elevation Abve/Ststja community type. The moss layer differs from that found in the Abve/Ststja type in a clear dominance of *Pleurozium*, greater amounts of *Pleuroziopsis ruthenica*, and characteristic occur-

rences of small amounts of *Rhytidiadelphus triquetrus* and *Ptelium crista-castresis* (Table 6).

*Picea jezoensis hondoensis*/*Abies spp.*/*Cacalia adenostyloides* community type

On the western flanks of Mount Ontake the *Picea jezoensis hondoensis*/*Abies spp.*/*Cacalia adenostyloides* community type, one of the *Abies*/herb group, occupies the gentle mountain slopes above the Abve/Drau type. It differs consistently from the Abve/Drau type in the low amounts of *Dryopteris* and *Pleuroziopsis* as well as in the landform (midslopes) typically occupied. In many respects, it appears analogous to the Abve/Ststja type in the Yatsugatake and Chichibu Mountains but is much richer, especially in herbaceous species (Table 6). Major overstory trees, in order of importance, are *Picea jezoensis hondoensis*, *Abies veitchii*, *Abies mariesii*, *Tsuga diversifolia*, *Sorbus comixta*, *Betula ermanii*, and *Acer ukurunduense* (Tables 5 and 6). *Abies mariesii* is the dominant species in reproductive size classes, but substantial amounts of *Abies veitchii* are also present. A moderately well-developed shrub layer is characterized by *Viburnum furcatum*, *Menziesia pentandra*, *Ilex rugosa*, *Euonymus macropteris*, and *Oplopanax japonicum* (Table 6). Herb dominants are *Cacalia adenostyloides*, *Pedicularis keiseki*, *Coptis quinquefolia*, and *Cornus canadensis* (Table 6). *Dryopteris austriaca* and *Pleuroziopsis ruthenica* are often present but only in small quantities in contrast to the Abve/Drau community type. The moss layer is well developed with a strong codominance of *Pleurozium schreberi*, *Pogonatum grandifolium*, *Hylocomium splendens*, *Dicranum spp.*, and *Sphagnum girgensohnii*.

This community type occupies a broad range in soil types and stoniness and in elevation. Consequently, it exhibits a considerable gradient in composition from stands higher in shrub cover (especially *Menziesia*) and poorer in herb species at higher elevations and on stonier soils to shrub-poor and herb-rich stands at lower elevations and on finer textured soils. It was not possible to separate it into two phases by associational analysis because of the gradual nature of the changes. As is discussed below, there is also considerable question about the relationship of this community to the *Sasa* type, particularly where it occurs on deep volcanic-ash soils. It appears possible that the Pijeho/Ab/Plsh/Caad type could be replaced on at least some of these sites by *Sasa* communities.

*Tsuga diversifolia*/*Abies spp.*/*Sasa paniculata* community type

This extremely distinctive community type occupies the deep, fine-textured volcanic-ash soils (usually P<sub>w</sub>/h) or B<sub>p</sub> types) which cover nearly the entire landscape on the east slopes of Mount Ontake (Tanohara area) and similar soils in lower parts of the subalpine zone on the west slopes (Kurumijima and Nigorigo



FIG. 6. Understory in *Abies veitchii*/*Streptopus streptopoides japonicus* stand in Yatsugatake Mountains; *Pteridophyllum racemosum* and *Cacalia adenostyloides* dominate.

areas). This community type can occur anywhere within the elevational span of the subalpine zone provided soil conditions are suitable.

The outstanding feature of this community is the

total dominance (average cover 93%) by a dwarf bamboo, *Sasa paniculata* (Fig. 7) (Table 6). A variety of tree species find niches in the open, understocked stands. *Abies mariesii*, *Tsuga diversifolia*, *Abies veit-*



FIG. 7. The dwarf bamboo *Sasa paniculata* totally dominates the understory in the *Tsuga diversifolia*/*Abies* spp./*Sasa paniculata* community type; shrubs, herbs, mosses, and tree seedlings are severely constrained by *Sasa* competition.



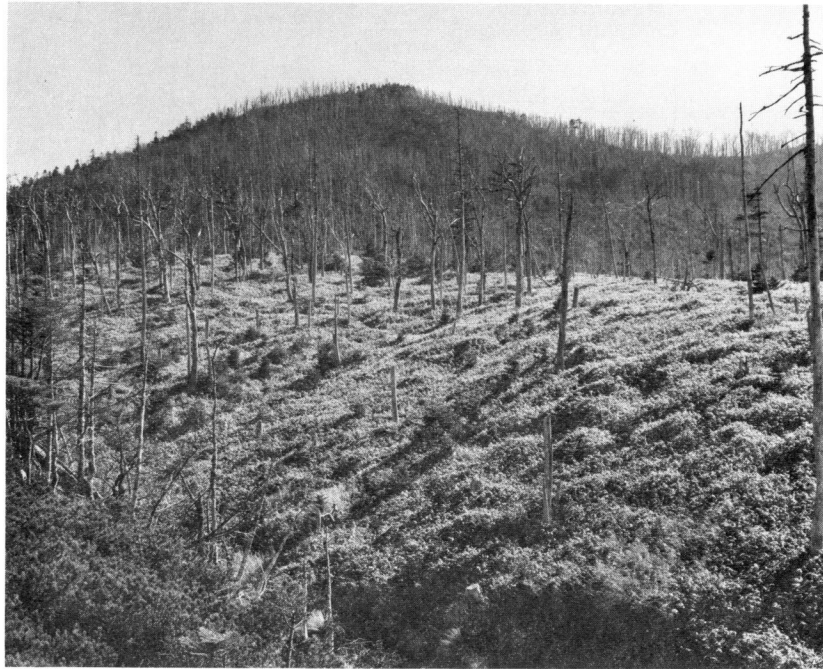


FIG. 8. Dense *Sasa nipponica* and few reproductive-size trees characterize this conifer/*Sasa* site which has been subject to timber cutting and windthrow; note the sharp line between *Sasa*- and moss-type communities in the background which reflects a change from volcanic-ash to lithosolic soils (Mount Shimagare, Yatsugatake Mountains).

*chii*, and *Betula ermanii* are most important (Tables 5 and 6). None of the tree species reproduces well under the intense competition of the *Sasa* (Table 6), and most seedlings and saplings are found on raised surfaces—down logs and around bases of individual and small groups of trees. The shrub, herb, and moss layers are all poorly developed consisting of erratic occurrences of a wide variety of species, none having substantial coverage, on raised surfaces and in small open pockets in the *Sasa*.

Communities identical in structure are found in the Yatsugatake (three stands sampled) and Chichibu Mountains and in Nikko-Oze National Park on sites with deep, fine-textured soils. The dwarf bamboo dominant in these areas is, however, typically *Sasa nipponica*. Also, as is expected with such a broadly distributed community type, there is an elevational gradient in tree species composition in a given locale. Such a gradient can be seen at Tanohara (east slope of Mount Ontake) where it was possible to sample a continuous forest of the *Sasa* type from 2260 to 1680 m.

The successional dynamics of conifer/*Sasa* communities are not clearly understood. Given suitable habitat, one requirement being a deep fine-textured soil, the *Sasa* understory typically invades or expands to dominate the site following a major disturbance such as blowdown, logging, or, in Hokkaido, wildfire (Fig. 8). Once in possession of the site, the *Sasa* holds it for some 60, 70, or more yr, i.e., until it flowers and

dies providing the first opportunity for additional tree reproduction since the *Sasa* layer was established. Death, when it does occur, generally affects large areas as the "individuals" of the extensively developed clones die essentially simultaneously. Depending on speed and density of forest regeneration and the speed with which *Sasa* regenerates or reinvades following the dieback, the following stand may be *Sasa* dominated or essentially *Sasa* free. Because of the severe competition from *Sasa*, existing mature stands which we sampled typically have low densities of both mature trees and reproduction, compared with other forest communities in the subalpine zone (Table 6).

A dense overstory can reduce or essentially eliminate *Sasa* from stands or prevent its invasion. And, some suitable sites may have escaped *Sasa* invasion by chance. Consequently, some areas potentially occupied by *Sasa* type communities have other communities resembling structurally and floristically *Tsuga*/moss or *Abies*/herb community types. Recognition of sites of this type, which can potentially be occupied by *Sasa*, is a serious problem in land classification and forest management and appears to hinge largely on edaphic conditions. At Yatsugatake, several stands of this type were encountered which we refer to as "pseudo moss" communities. Floristically they would have to be grouped with the adjacent *Tsdi*/*Absp*/*Plsh* communities, but the deep, fine-textured soils indicate that ecological conditions—and potential response to disturbance—are different. At Mount Ontake, many

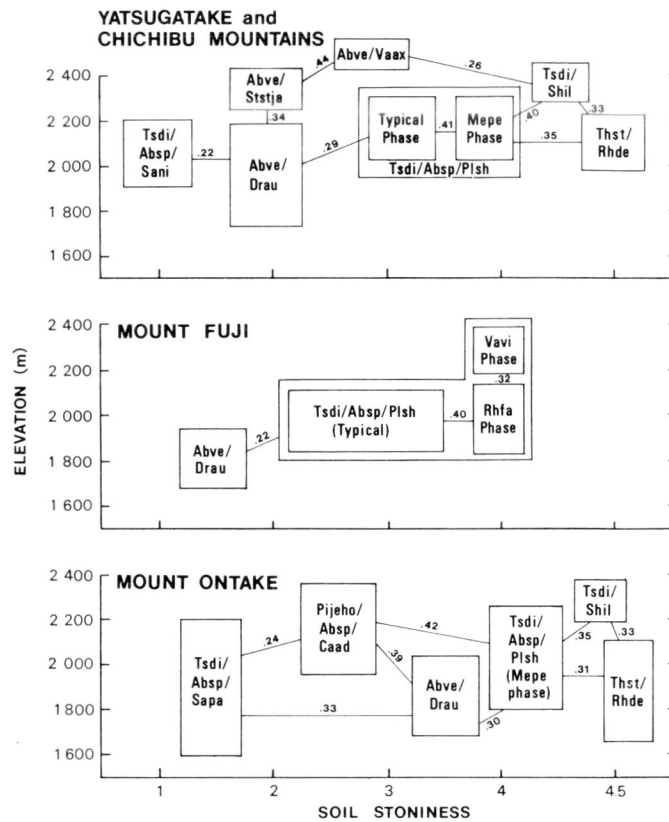


FIG. 9. Relationships among community types and between community types, elevation, and soil stoniness at the four study areas; small decimal numbers indicate similarities between types and phases. Abbreviations as in Table 3.

of the Pijeho/Absp/Caad stands may also represent potential sites of *Sasa* occupancy if disturbed in such a way as to allow *Sasa* invasion. Soils appear favorable for *Sasa*. At Tanohara on the east slope of Mount Ontake, *Sasa* already occupies essentially all suitable sites with islands of Tsdi/Absp/Plsh type on isolated pockets of stony soil. On the west slopes on Ontake, *Sasa* communities also occupy all suitable sites below 1900 m surrounding Abve/Drau and Tsdi/Absp/Plsh community types on small pockets of stony soils. *Sasa* communities are rare above 1900 m where the Pijeho/Absp/Caad community type dominates, but much of this area appears well suited to *Sasa* based upon soil conditions.

The timing and duration of *Sasa* cycles in relation to other stand constituents leads to interesting speculation regarding the climax or self-perpetuating community type on some of these sites. Theoretically, it seems that apparently stable communities of either *Abies*/herb or conifer/*Sasa* types are possible on some sites and that there would be times (e.g., of *Sasa* flowering and dieback or of a destructive typhoon) when switches from one community type to the other could occur. In fact, it seems more likely that *Sasa* would gradually expand the area it occupies because of an

aggressive response to natural or man-caused forest disturbances and persistence once it occupies a site.

#### DISCUSSION

The results of this study confirm and expand the previous outlines of Japanese subalpine forest communities. We will further discuss three aspects: relations among the communities including local variations in the patterns observed, distribution and successional status of tree species, and comparisons with subalpine conifer forests elsewhere, particularly in the United States.

#### *Relationships among communities and study areas*

The relationships among the community types and phases are illustrated in Fig. 9. As is apparent from Table 3, not all of the community types and phases are found in a single location and the most extensive types (e.g., Tsdi/Absp/Plsh) vary in structural, floristic, and environmental details from mountain to mountain.

The simplest pattern is at Mount Fuji where the *Tsuga*/moss community group is overwhelmingly dominant, varying only in phase with elevation, soil, and

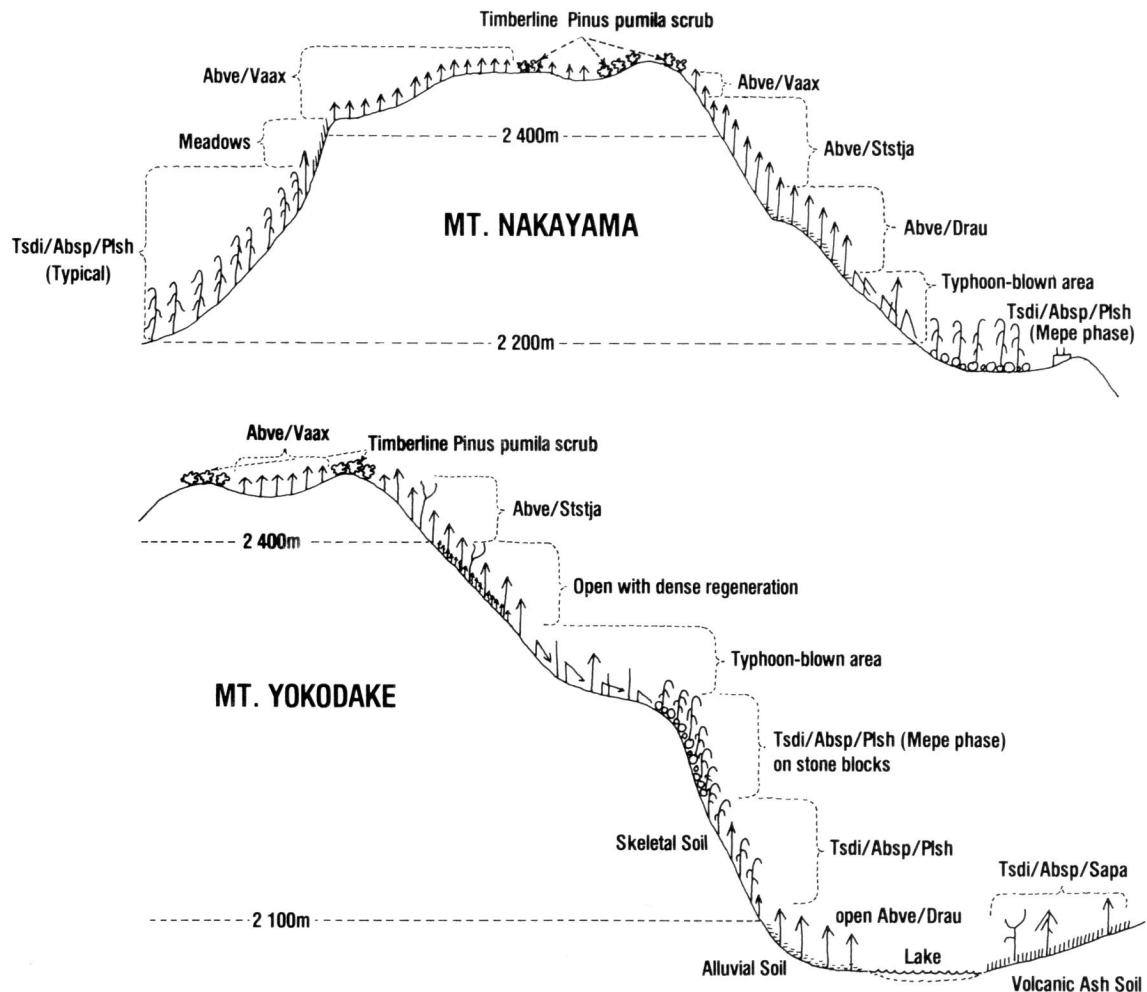


FIG. 10. Topographic relationships between community types at Mount Nakayama and Mount Yokodake in the Yatsugatake Mountains; both transects have a north-south orientation and extend 4 (upper) and 2 km, respectively. Abbreviations as in Table 3.

landform (Fig. 2). Soils occurring under the TsdI/Absp/Plsh (typical) community type, while not particularly stony, are typically gravelly, i.e., have large quantities of volcanic sand and cinders. In the lower part of the subalpine, the only herb-rich community (Abve/Drau) occurs, mainly on alluvial soils. Because of the position of Abve/Drau near the subalpine ecotone, many more typically temperate trees and shrubs are sprinkled erratically through the stands (Tables 5 and 6). Since Mount Fuji is an isolated and young mountain mass, some of the floristic contrasts to other mountain regions are to be expected. The reduced floristic diversity, however, may also be responsible for our separation of a *Rhododendron* phase of the TsdI/Absp/Plsh from the closely related Thst/Rhde type. This separation hinges largely upon the absence of *Thuja standishii* and *Rhododendron degronianum* from the Mount Fuji stands; in other respects they are very

similar. One of the authors (Maeda) feels that they are, in fact, best recognized as a single community type or phase of a broad TsdI/Absp/Plsh community type.

The stands in the Yatsugatake and Chichibu Mountains could consistently be placed together in the community classification because of their strong similarities. The only significant difference is the occurrence of *Pteridophyllum* and *Pedicularis* as ecologic (and mutually exclusive) analogues at Yatsugatake and Chichibu, respectively. The community variety and pattern of relationships in these mountain ranges is considerably more complex than at Mount Fuji (Fig. 9). The strongest community-environment correlations involve stoniness of soils, elevation (i.e., temperature), and exposure (Fig. 9). Certainly moisture regimes must also be involved. A moisture gradient is, however, extremely difficult to observe in this summer-wet climate except, perhaps, in the soil types

which progress from Pw(h) and B<sub>D</sub> types under the herb and *Sasa* communities to P<sub>D</sub> types on the stony soils under the moss types.

In any case, the community spectrum is quite well defined at Yatsugatake and Chichibu (Fig. 9). There is an edaphic gradient in the moss group (Tsdi/Absp/Plsh typical to Mepe to Thst/Rhde), an elevational gradient in the herb group (Abve/Drau to Abve/Ststja), two stunted forest community types on exposed mountain summits (Abve/Vaax) and lower ridgetops (Tsdi/Shil), and *Sasa* (*nipponica*, in this case) communities wherever deep ash soils occur. The paucity of species in Abve/Drau communities at Yatsugatake and Chichibu is almost certainly due to the fact that logging effectively eliminated sampling sites in the lower part of the subalpine. Topographic relationships between the communities are illustrated in Fig. 10.

Mount Ontake is rather distinctive in its complement of communities (Fig. 9). Again, it is an isolated massif, but much of its distinctiveness probably derives from its position on the floristic ecotone between the subalpine forests facing the Japan Sea and the Pacific Ocean and from more snowfall than at the other sites. The typical (and very depauperate) phase of the Tsdi/Absp/Plsh is absent, and the Mepe phase which is present is substantially richer in shrub and herb cover and in species than its analogue at Chichibu and Yatsugatake (Table 4). This may be due to more than simply the higher precipitation, e.g., possibly to the occurrence of many of these stands as isolated pockets within *Sasa* and rich herb-dominated communities. The Thst/Rhde community type was also somewhat richer at Ontake than at Yatsugatake and Chichibu, possibly for the same reason. The Abve/Drau type at Ontake shows an erratic pattern of species distribution (middle to low constancies in Table 6) and an affinity for stony soils which probably reflects its occurrence as small insular stands (surrounded by *Sasa* communities) on stony lower slopes and streamside benches and terraces. The relationship of the Pijeho/Absp/Caad and Tsdi/Absp/Sapa communities has already been discussed.

The average similarity index between all community types and phases is only 24; the highest value is 44. Similarity indices are highest, however, among the members of the two major groups—*Tsuga*/moss (including Thst/Rhde and Tsdi/Shil) (average index 28) and *Abies*/herb (including Abve/Vaax and Abve/Ststja types) (average index 25). The Mepe phase of the Tsdi/Absp/Plsh also shows a strong relationship to the *Abies*/herb group (average index 28). The stunted series of communities—Abve/Vaax, Tsdi/Shil, and Vavi phase of the Tsdi/Absp/Plsh—averages a similarity index of 24. The Abve/Vaax is absent at Fuji simply because an appropriate mountain summit is not present; it does occur on Ontake but was not sampled there. It is obviously closely related to the Tsdi/Shil type (indeed these intergrade in the Yatsugatake and

Chichibu Mountains) which occupies the exposed secondary ridgetops downslope. The Vavi phase of the Tsdi/Absp/Plsh is also closely related to the Tsdi/Shil type, differing mainly in being more depauperate as might be expected on youthful, isolated Mount Fuji.

#### *Distribution, growth, and successional status of tree species*

Several aspects of the distribution and successional status of the tree species are discussed in the earlier introduction to Japanese subalpine vegetation. The most ubiquitous conifers are clearly *Abies veitchii* and *Tsuga diversifolia* followed by *Abies mariesii* and *Picea jezoensis hondoensis* (Table 5). *Abies mariesii* is poorly represented on Mount Fuji and best represented in the wetter, Japan Sea climate of Mount Ontake. *Pinus parviflora* and *P. koriensis* never occurred on the same plot but seemed to favor similar habitats in this study—i.e., the extremely stony sites characterized by communities with a *Rhododendron*-dominated understory; in fact, this is probably the only favored habitat for *Pinus parviflora*.

In the data, *Larix leptolepis* appears by far most common in the communities at Mount Fuji, attaining its greatest eminence near timberline where it is well known as a major timberline species (Hayata 1929, Tatewaki et al. 1965). In fact, *Larix* has a unique (often bimodal) distribution pattern in the study areas occurring mainly on extremely stony soils high in the subalpine zone and on freshly deposited deeper soils low in the zone and at the ecotone between the temperate and subalpine zones (e.g., 1500–1700 m). The *Larix* stands of the Nikko Valley are an example of the latter distribution. Given this rather distinctive distribution and general absence from zonal soils in the central part of the subalpine zone, it is unfortunate that the species has been used so widely for reforestation of clear-cut areas to which it is often poorly adapted.

*Thuja standishii* appears strongly restricted to the wet stony habitats characterized by the Thst/Rhde community type (Table 5). The remaining species are typically temperate (*Chamaecyparis obtusa* and *C. pisifera*) and find their upper elevational limits in the lower part of the subalpine. One species not recorded on plots but which does occur on sites (in Nikko National Park) with deep, wet soils is *Thujopsis dolabrata*, which can form very dense, nearly pure stands in the lower subalpine zone; it is characteristic of the Japan Sea or northern Honshu climates.

The most ubiquitous hardwood associates are clearly *Sorbus comixta* and *Betula ermanii* (Table 5). Both find optima in the *Abies*/herb community types. *Betula ermanii* also seems to be favored by the open, poorly stocked stands associated with the *Sasa* community types. *Acer ukurunduense* and *A. tschonoski*, the next most important hardwoods, are generally small trees or exist as understory shrubs (shown as tree reproduction in Tables 4 and 5); they might better be con-

TABLE 7. Basal area of tree species by altitude, as a percent of the total in each elevational band, based on wedge prism tallies.

| Elevational band (m)                 | 1600<br>to<br>1799    | 1800<br>to<br>1999 | 2000<br>to<br>2199 | 2200<br>to<br>2399 | 2400<br>to<br>2599 | all  |
|--------------------------------------|-----------------------|--------------------|--------------------|--------------------|--------------------|------|
| Number of plots                      | 25                    | 40                 | 52                 | 33                 | 12                 | 162  |
| Mean basal area (m <sup>2</sup> /ha) | 57.8                  | 65.9               | 62.1               | 69.8               | 57.9               | 63.6 |
|                                      | Percent of basal area |                    |                    |                    |                    |      |
| Gymnosperms:                         |                       |                    |                    |                    |                    |      |
| <i>Tsuga diversifolia</i>            | 27.3                  | 46.1               | 39.9               | 41.8               | 0.9                | 37.5 |
| <i>Abies veitchii</i>                | 27.3                  | 14.0               | 12.8               | 19.6               | 46.8               | 18.9 |
| <i>Picea jezoensis hondoensis</i>    | 19.5                  | 10.2               | 14.3               | 17.4               | 8.1                | 14.3 |
| <i>Abies mariesii</i>                | 1.3                   | 6.4                | 14.3               | 9.0                | 32.4               | 10.5 |
| <i>Thuja standishii</i>              | 3.9                   | 9.5                | 2.9                | 0.8                | 0                  | 4.1  |
| <i>Larix leptolepis</i>              | 3.0                   | 1.9                | 4.8                | 6.0                | 0                  | 3.8  |
| <i>Pinus parviflora</i>              | 1.3                   | 1.2                | 1.7                | 0.3                | 0                  | 1.1  |
| <i>Pinus koriensis</i>               | 0.9                   | 2.6                | 0.4                | 0                  | 0                  | 0.9  |
| <i>Chamaecyparis obtusa</i>          | 2.2                   | 1.9                | 0                  | 0                  | 0                  | 0.8  |
| <i>Chamaecyparis pisifera</i>        | 1.3                   | 0                  | 0                  | 0                  | 0                  | 0.2  |
| Total                                | 88.0                  | 93.8               | 91.1               | 94.9               | 88.2               | 92.1 |
| Angiosperms:                         |                       |                    |                    |                    |                    |      |
| <i>Betula ermanii</i>                | 3.5                   | 4.3                | 4.8                | 3.3                | 9.9                | 4.5  |
| <i>Sorbus comixta</i>                | 0.9                   | 1.2                | 1.9                | 1.9                | 1.8                | 1.6  |
| <i>Betula corylifolia</i>            | 1.3                   | 0.7                | 1.0                | 0                  | 0                  | 0.7  |
| <i>Acer ukurunduense</i>             | 1.7                   | 0                  | 0.8                | 0                  | 0                  | 0.5  |
| <i>Prunus nipponica</i>              | 2.2                   | 0                  | 0                  | 0                  | 0                  | 0.3  |
| <i>Acer nipponica</i>                | 0.4                   | 0                  | 0                  | 0                  | 0                  | 0.1  |
| <i>Alnus matsumureana</i>            | 0.9                   | 0                  | 0.2                | 0                  | 0                  | 0.2  |
| <i>Betula carpinifolia</i>           | 0.4                   | 0                  | 0                  | 0                  | 0                  | 0.1  |
| <i>Prunus maximowiczii</i>           | 0.4                   | 0                  | 0                  | 0                  | 0                  | 0.1  |
| <i>Tilia japonica</i>                | 0.4                   | 0                  | 0                  | 0                  | 0                  | 0.1  |
| Total                                | 12.1                  | 6.2                | 8.7                | 5.2                | 11.7               | 8.2  |

sidered as shrub components. *Prunus nipponica*, *Alnus matsumureana*, and *Cercidiphyllum magnificum* are other subalpine hardwood associates. Most of the remaining hardwoods are primarily temperate species which occur erratically in the lower subalpine, especially on favorable sites such as those occupied by the Abve/Drau community type. Such species include *Tilia japonica*, *Salix bakko*, *Acanthopanax sciadophylloides*, *Acer nipponica*, and *A. shirwasanum*.

Relative basal areas confirm that the *Abies* are most important higher and *Tsuga diversifolia* lower in the subalpine zone (Table 7). The lowest elevation band (1600–1799 m) shows *Abies veitchii* and *Tsuga* of equal importance, but this reflects a weighing toward the *Abies*-rich Abve/Drau community type in the lowest elevation plots. The lack of *Larix* in the highest elevation band is considered an accident of sampling. Most hardwoods are obviously temperate zone species which extend only a short distance into the subalpine. The increased importance of *Betula ermanii* toward the forest line is obvious; this species often forms a narrow, nearly pure band at the ecotone with *Pinus pumila* scrub.

Biomass accumulations in these forests, as observed in basal area and maximum heights and diameters, appear typical of subalpine forest in eastern Asia and eastern North America (Tables 4, 5, and 6). Basal

areas are in the range (50–80 m<sup>2</sup>/ha) to be expected in subalpine coniferous forest. *Tsuga*/moss communities do consistently show substantially higher basal areas (65–80 m<sup>2</sup>/ha) than *Abies*/herb communities (50–65 m<sup>2</sup>/ha) and the poorly stocked *Sasa* stands have the lowest average values (49 m<sup>2</sup>/ha). In terms of maximum height (and almost certainly annual growth rate), the situation is reversed. Abve/Drau, Pijeho/Absp/Caad, and Tsd/Absp/Sapa communities have dominants averaging 19–25 m while they run 15–20 m in the mid-elevation *Tsuga*/moss types.

Figures on heights and diameters, basal area tallies, and coverage estimates for tree species are, of course, strongly influenced by differences in species longevity and growth habit. *Larix leptolepis*, *Pinus parviflora*, and *Pinus koriensis* are strongly emergent species whose canopies typically extend several meters (as much as 10 m was recorded) above the canopy of associated *Tsuga diversifolia* and *Thuja standishii*. Were it not for these species, the average maximum height in the stonier *Tsuga*/moss communities would be substantially less. The shorter statured *Tsuga diversifolia*, on the other hand, has a dense, sprawling canopy and is capable of attaining a substantial age (250-yr-old specimens were relatively common) and diameter. *Thuja standishii* is a somewhat smaller though long-lived tree. *Picea jezoensis hondoensis* is

another species which is frequently emergent above associated *Abies*.

*Abies veitchii* and *mariesii*, because of their relatively short life span, rarely attain dimensions comparable to those of *Tsuga*, *Picea*, and *Pinus* except where growth conditions are extremely favorable. Indeed, many *Abies* stands begin to disintegrate at 80–100 yr due to ordinary senescence and may go completely to pieces following a major typhoon. Disintegrating *Abies* stands can take some interesting forms such as patches and strips as described from Mount Shimagare (Oshima et al. 1958) and elsewhere in the Yatsugatake and Chichibu Mountains (Iwaki and Tot-suka 1959). All species are, of course, stunted on mountain summits and exposed ridgetops.

It is clear from seedling counts, as well as the abundance and coverage values for reproduction (Tables 4 and 6), that *Abies* spp. are major climax species throughout the bulk of the subalpine zone. The exception may be in the *Tsuga*-dominated forests in lower portions of the subalpine zone; *Tsuga* reproduction, not *Abies*, often dominates in these stands few of which were sampled in this study. Whether *Abies veitchii* or *mariesii* is the most important climax species is a difficult and, perhaps, irrelevant question. *Abies mariesii* is distributed erratically at Mount Fuji and is really within its main distributional range only at Mount Ontake. Two things are clear about the relation between the two *Abies*: (1) *Abies mariesii* reproduction is almost always more abundant than that of *Abies veitchii* where both species occur except in the Abvel/Drau community type; (2) *Abies veitchii* reproduction is consistently sufficiently abundant that it would rank as at least a minor if not major climax species.

Assignment of successional status to the other subalpine conifers is more difficult. This is partially due to variation in roles with habitat. The fact that several moderately shade-tolerant species have two to three times the life span of the *Abies* may be an even more important complicating factor. *Tsuga diversifolia*, *Picea jezoensis hondoensis*, and *Thuja standishii*, and possibly even the *Pinus* spp., may play a role similar to that of *Picea engelmannii* in the *Picea-Abies lasiocarpa* forests of the Rocky Mountains (Hanley et al. 1975). In effect, although *Abies* reproduction dominates in most stands, the longevity of species such as *Picea* and *Tsuga* allows them to maintain themselves on sites between disturbances or other events favorable for their reproduction.

We would hypothesize that *Tsuga diversifolia*, *Picea jezoensis hondoensis*, and *Thuja standishii* all play some climax role in Japanese subalpine forests. *Tsuga diversifolia* appears to be a major climax species in the lowest part of the zone and is also a reproductive dominant in the Thst/Rhde and TsdI/Shil community types and in the *Rhododendron* phase of the TsdI/Absp/Plsh community. *Tsuga* (elsewhere) and *Picea jezoensis hondoensis* are typically present in small

numbers as seedlings and saplings and with their long life spans can take advantage of periodic disturbances or stand openings to perpetuate themselves. *Thuja standishii* reproduction is sufficiently abundant in the Thst/Rhde community to justify its designation as a climax species.

*Larix leptolepis* and *Betula ermanii* appear to be seral species within the main body of the subalpine zone, although *Betula* forms a stable belt at the ecotone between subalpine forest and *Pinus pumila* scrub. *Sorbus comixta* is the major hardwood climax associate. We differ regarding the successional status of the *Pinus* spp.; two of us (Maeda and Matsui) favor minor climax status because of their moderate shade tolerance while one (Franklin) favors seral designation because of their limited reproduction in closed stands.

#### *Comparisons with other subalpine forests*

Broadly speaking, the subalpine forests of Japan are elements of the subalpine *Abies-Picea* formation characteristic of high mountain areas and high latitudes throughout the northern hemisphere. Closest affinities appear to be with subalpine forests of Taiwan, eastern North America, the Himalayan Mountains, and to a lesser extent, coastal western North America. Most of these areas have maritime climates.

Patterns of *Abies*- and *Tsuga*-dominated communities with moss, herb, dwarf bamboo, and *Rhododendron* understory types have been described in Taiwan and Nepal. On Taiwan there is apparently substantial altitudinal segregation of *Tsuga chinensis* and *Abies kawakanii*, with the former at lower and latter at higher elevations in the subalpine zone. Wang (1968) indicates that moss- and dwarf bamboo (*Pleioblastus niitakayamensis*)-dominated understories occur in stands of either tree species. One contrast is that *Tsuga* appears more capable of reproducing within stands than *Abies* in Taiwan suggesting seral status for *Abies* where mixtures occur. In Nepal (Yoda 1968, Stainton 1972) forests of *Abies spectabilis* and *Tsuga dumosa* provide subalpine analogues. Detailed community analyses are not available, but the generalized descriptions clearly indicate communities with depauperate (moss-type) and *Rhododendron*-type understories. Stainton (1972) also indicates that there are forests of *Abies spectabilis* with heavy understories of dwarf bamboo (*Arundinaria* in this case).

It is impossible to examine the subalpine forests of central Japan without quickly recalling descriptions of the Appalachian *Picea-Abies* forests of eastern North America (see, e.g., Oosting and Billings 1951 and Whittaker 1956). Many similarities exist: long-lived *Picea* associated with a more tolerant but shorter lived *Abies*, the trend toward pure *Abies* forests at higher elevations, *Betula* and *Sorbus* as major hardwood associates, and herbaceous, moss, and even *Rhododendron*-dominated understories. The similarities extend beyond physiognomy to the generic composition

of the forest dominants (e.g., *Picea*, *Abies*, *Menziesia*, *Vaccinium*, *Viburnum*, *Rhododendron*, *Maianthemum*, *Oxalis*, *Dryopteris*, *Streptopus*, *Coptis*, *Clintonia*, *Trillium*, *Cornus canadensis*, and *Hylocomium splendens*). The Japanese subalpine forests are, however, obviously much richer floristically than those found in the Appalachians. The list of constituent tree species, alone, makes the greater diversity quite apparent. The outstanding contrast is the total absence of subalpine *Tsuga* forests in eastern North America.

Wave-like patterns of mortality and regeneration in forests of short-lived *Abies* provide a further linkage between the Japanese and Appalachian subalpine. The phenomenon of dead-tree strips was first studied by Oshima et al. (1958) and Iwaki and Totsuka (1959) in central Honshu. Similar patterns in the northern Appalachians were studied in detail by Sprugel (1976). Sprugel (1976) suggests a 60-yr cycle for *Abies balsamea* forests and a slightly longer one for the Japanese *Abies* which "grow more slowly than balsam fir but live somewhat longer." Oshima et al. (1958) show ages of up to 86 and 97 yr for *Abies veitchii* and *A. mariesii*, respectively, in their study area. Tadaki et al. (1977) indicate that die off occurs between 100 and 130 yr in *Abies veitchii* near Mount Asahi.

Similarities between subalpine forests in Japan and those in the mountains of coastal western North America (Cascade, Coastal, and Sierra Nevada Ranges) are more limited than is the case with the Appalachian forests. The forests of the Cascade Range show the most similarities to those of Japan. Extensive subalpine forests dominated by a *Tsuga* species with *Abies* spp. as the potential climax are common to both areas (Franklin and Dyrness 1973). There are also compositional identities at the generic (essentially all the genera listed above) and, in a few cases, specific level (e.g., *Vaccinium ovalifolium*, *Cornus canadensis*, and *Streptopus streptopoides*). In all of these western North America areas subalpine trees grow to much larger sizes and, often, greater ages than do the Japanese subalpine tree species. Also, fire, not wind, is the major disruptive agent.

Similarities with the Rocky Mountain *Picea engelmannii*-*Abies lasiocarpa* forests are even more limited. The subalpine location and associations of a long-lived *Picea* with a shorter lived *Abies* is, of course, common to the two areas (Daubenmire and Daubenmire 1968). On the other hand, the continental nature of the Rocky Mountain forests results in strong floristic and environmental contrasts with the Asian subalpine forests (as well as those of eastern North America). As one example, there is the important seral role of a hard pine (*Pinus contorta*) in the Rocky Mountains, a phenomenon not encountered in any other subalpine zone discussed here, save only environmentally severe subalpine areas in northwestern North America and in the Sierra Nevada Range.

The *Sasa*-type communities appear to have no anal-

ogies anywhere in North America—for which North American foresters can be grateful! The subalpine forest with a dense understory of tall coarse grasses or dwarf bamboo appears to be an entirely Asian phenomenon. Such understory communities are also found in cool temperate forests of Japan (under *Fagus*, for example) where soils are suitable, and are very extensive on the largely ash-covered mountain slopes of Hokkaido under boreal mixed hardwood-conifer and conifer (*Abies sachalinensis*, *Picea jezoensis*, *Picea glehnii*) overstories.

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