A Phytogeographical Account of *Hypnum cupressiforme* Hedw. in Japan*

by

Hisatsugu ANDO

Botanical Institute, Hiroshima University

Introduction

Hypnum cupressiforme Hedw. is a well-known cosmopolitan moss which is widely distributed in temperate to arctic-alpine or subantarctic regions of the Northern and the Southern Hemisphere. In the tropical area, this moss, as well as other species of the genus *Hypnum*, disappears, being replaced by members of a closely related genus, *Ectropothecium*.

This species is one of the most variable mosses and forms the *Hypnum cupressiforme* complex to which more than 60 varietal names have been applied. Such an extreme polymorphism of this moss has caused endless puzzlement and confusion to bryological students. As its great variability and world-wide distribution may suggest, this species seemingly has a wide adaptability, but actually its growth is strongly associated with certain climatic and man-made conditions. Furthermore, its variability and fertility are considerably different with geographical sections of the range. Examples of these facts are here illustrated by a situation of its Japanese population.

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I. Distribution pattern and ecology of *Hypnum cupressiforme* in Japan

1. Distribution pattern

The distribution of this species in Japan was once roughly discussed on the basis of the actual specimens which I had examined (Ando 1972). Since then, a considerable number of additional specimens have been obtained, and a pattern of its distribution has been better defined (Fig. 1). In the distribution map shown in Fig. 1, plotting was made following the grid system by Horikawa

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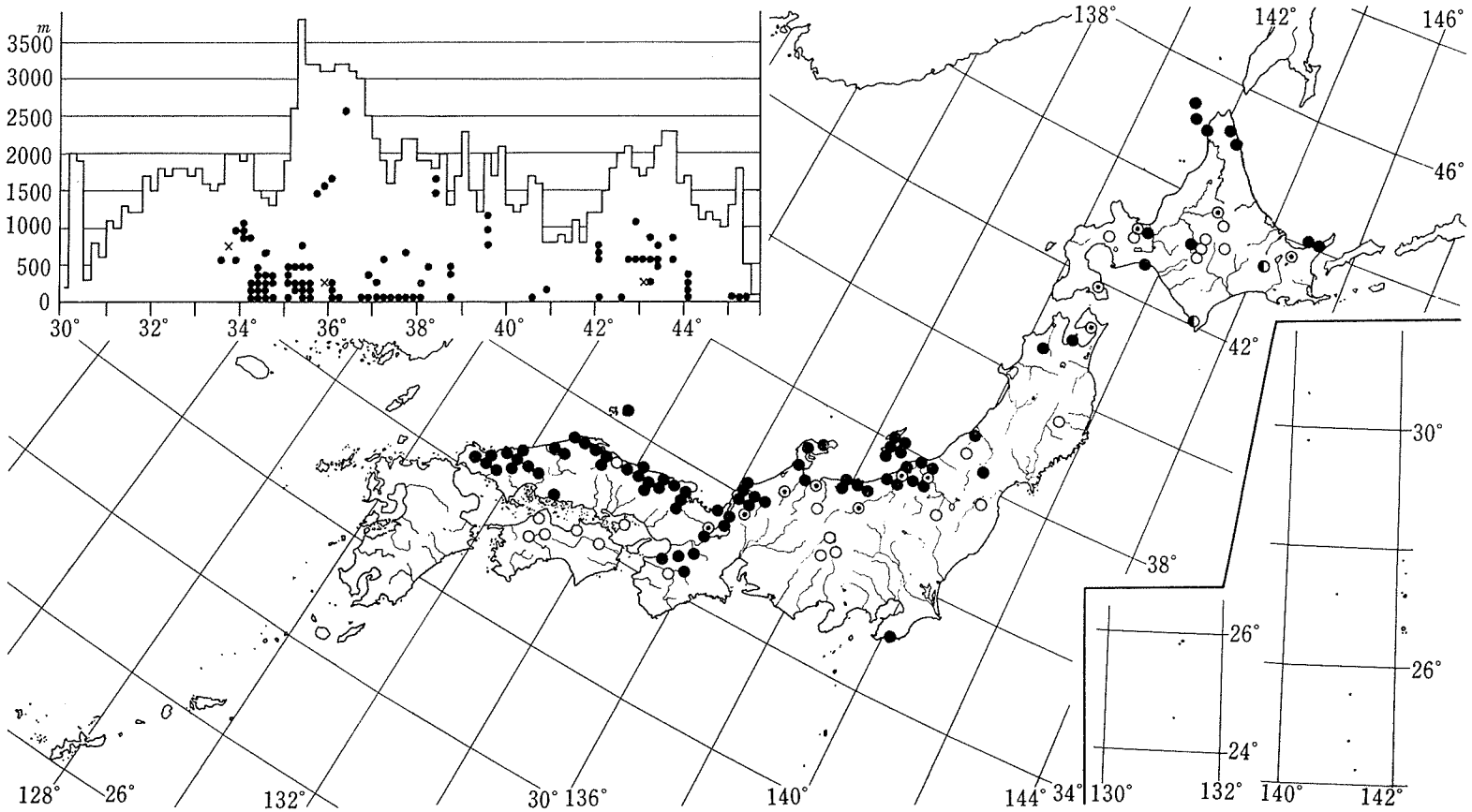

Fig. 1. Distribution of *Hypnum cupressiforme* in Japan. ● (areal distribution) at altitudes below 500 m; ○ above 500 m; ◐ below and above 500 m; ⊙ altitude unknown; × (vertical distribution) 0–500 m or 500–1000 m, accurate altitude unknown.

(1951, 1960). The unit square in the areal distribution map corresponds to the limits of a "topographic map of 1/50,000" issued by the Geographical Survey Institute of Japan, covering an area of 10 minutes in latitude and 15 minutes in longitude, which measures, in those on lat. 35° N, about S–N 18.5 km × W–E 22.82 km.

As clearly shown in the distribution map, *H. cupressiforme* is much more abundantly found on the Japan Sea side of Honshu, especially from Yamaguchi Prefecture northeastward to Niigata Prefecture, where it grows in lowlands usually below an altitude of 500 m, which belong to the zone of warm-temperate evergreen broad-leaved forests. It is noteworthy that a branch of the distributional range extends into the Kii Peninsula through Kyoto and Nara southward and upward to Mt. Koya (800–900 m alt.), Wakayama Prefecture.

In the Chugoku district (the western section of Honshu), this species is not found in the area along the Seto Inland Sea except in a few limited localities. Recently Shiomi (1977) found the species at an altitude of 160 m in Toyoda-cho, Yamaguchi Prefecture, located on about long. 131° E, which presently constitutes the westernmost limit of its distribution in Japan. According to Shiomi (in litt.), it grows there on rather sunny, dry rocks, stone walls and barks of maple trees in the precinct of an old Buddhist temple built on the slope of a mountain.

In Shikoku, the species occurs, beyond lowlands, disjunctively on mountains facing the Seto Inland Sea at altitudes above 500 m, ascending to around 1000 m.

In the inland part of central Honshu, the species is encountered very rarely at much higher altitudes, about 1500–2600 m, which correspond to the subalpine zone. It is almost absent there in montane deciduous forests dominated by *Fagus crenata.*

In the Tohoku district (the northeastern section of Honshu) and Hokkaido, it is dispersed, extending eastward to the Pacific side, from near the sea-level up to an altitude of about 1650 m, but occurs only locally. The very common occurrence in lowlands on the Japan Sea side from Yamaguchi to Niigata Prefecture is suddenly replaced by a much sparser distribution in coastal regions of the Tohoku district and Hokkaido, where, however, additional localities are expected to be found by further explorations.

The species has never been collected in Kyushu and the Pacific coast regions of both Shikoku and Honshu. However, one disjunct occurrence was exceptionally found on Mt. Kiyosumi, Chiba Prefecture, about 70 km southeast of Tokyo. The precise altitude of that locality is unknown, but it is apparently below 383 m.

2. Ecology

As already mentioned, *H. cupressiforme* is extremely multiform, but in Japan it is not so variable as demonstrated in Europe. Japanese plants of this species fall into two categories, recognized as var. *cupressiforme* and var. *filiforme* Brid. which are almost parallel in distribution, although each variety exhibits a further variation and occasionally shows a superficial resemblance to some other varieties. The var. *filiforme* sometimes appears in a transformed situation from var. *cup-*

ressiforme within the the same mat. It rarely intergrades into a form with homomallous leaves reminiscent of var. *resupinatum* (Tayl.) Schimp.

It is of interest that plants of the var. *filiforme* growing in elevated or northern regions become more silky, more strongly complanate and less fluffy. Japanese plants of this species are also characterized by a usually greenish color even in old herbarium specimens.

This species grows on various kinds of substrata, but more frequently occurs in Japan on tree-trunks and rocks or stone walls. Of the 246 specimens studied with a note of substratal nature, 108 (43.9%) were collected from tree-trunks or roots, 106 (43.1%) from rocks or stoneworks such as stone walls, stone lanterns and gravestones, 17 (6.9%) from decaying logs or stumps, and 15 (6.1%) from soils. As far as the Japanese specimens are concerned, they include only a few collections from limestone rocks. The var. *filiforme* usually grows on tree-trunks, and sometimes on vertical surfaces of rocks.

Especially interesting is the difference of its ecological preference between the populations of northeastern regions and of southwestern regions. In Hokkaido and northeastern Honshu (north of Lat. 38° N), it is widely but sparsely distributed both horizontally and vertically and principally grows in woodlands under natural or seminatural conditions, whereas in central and southwestern Honshu, it usually occurs in lowlands almost always confined to habitats under man-made conditions, such as the precinct of old Shinto shrine, Buddhist temples or castles, and the neighborhood of human habitation. The isolated localities in the Kii Peninsula and on low mountains of Shikoku are also in the grounds of old shrines or temples.

Hypnum cupressiforme is dioicous, and in Europe, it rather frequently bears sporophytes except in some varieties, as Watson (1955) even stated, "capsules are quite common," for British mosses. In Japan, however, fruiting specimens are quite rare or absent except in some restricted areas. Figure 2 shows the number of collections and fertility (frequency of fruiting specimens) represented by the size of circles in 25 prefectural sections of the Japanese range. Specimens with sporophytes are shown by the white portion of the circle. From this figure, it is clear that the fertility is highest in the Hokuriku district, namely, in Niigata (No. 7), Toyama (10) and Ishikawa (11) Prefectures, of which the latter two represent a value as high as 25%. In areas along the Japan Sea coast from Fukui (12) to Yamaguchi (21) Prefecture, the fertility fluctuates between 0 and 12.1%. In Hokkaido, the fertility is very low (1.5%) in spite of the largest number of collections. Specimens from southern localities (Prefectures Nos. 15–17, 22–25) are all sterile. Such a reduced fertility of this species in Japan is considered to be due to the quantitative unbalance of male and female plants, sometimes with the absence of male plants.

II. Discussion

Hypnum cupressiforme is very common and notoriously polymorphic in Europe, but in East Asia and North America, it is rather infrequent or local and less differentiated morphologically. In the territory of Japan, this species shows a pattern of typical Japan Sea side distribution, the center of which is in

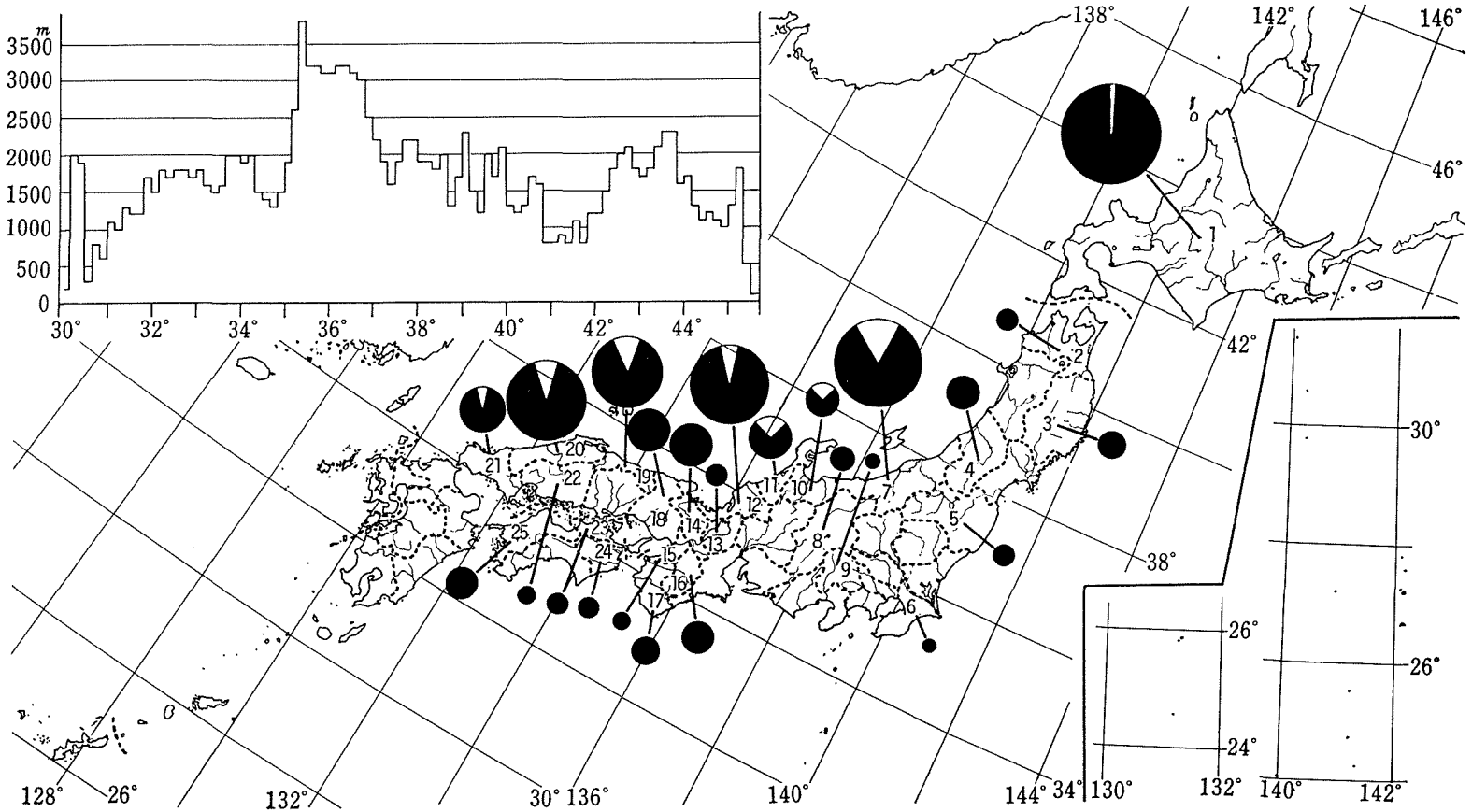

Fig. 2. Map showing the number of collections and fertility of *Hypnum cupressiforme* in 25 prefectural sections of the Japanese range. The number of collections is represented by the size of circle, of which the white portion shows specimens with sporophytes. 1:Hokkaido (number of specimens with sporophytes/total number of specimens=1/66), 2: Aomori (0/3), 3: Iwate (0/5), 4: Yamagata (0/8), 5: Fukushima (0/3), 6: Chiba (0/1), 7: Niigata (9/53), 8: Nagano (0/4). 9: Yamanashi (0/1), 10: Toyama (2/8), 11: Ishikawa (3/12), 12: Fukui (3/43), 13: Shiga (0/3), 14: Kyoto (0/12), 15: Osaka (0/2), 16: Nara (0/7), 17: Wakayama (0/5), 18: Hyogo (0/12), 19: Tottori (4/33), 20: Shimane (4/44), 21: Yamaguchi (1/14), 22: Hiroshima (0/2), 23: Kagawa (0/3), 24: Tokushima (0/3), 25: Ehime (0/7).

lowland areas of central to western Honshu facing the Japan Sea. Such a pattern of its distribution inclined to the Japan Sea side is apparently related to the peculiar climatic conditions of Japan.

It is well known that the climate of Japan is divided into two major types: the Japan Sea type and the Pacific type. In summer, damp monsoon winds from the Pacific bring more plentiful rainfall in areas on the Pacific side, among which southern sections of the Kii Peninsula, of Shikoku and of Kyushu receive particularly high precipitation. In winter, on the other hand, dry cold winds (NW-monsoon) blowing from the Asiatic continent take up quantity of moisture while they pass over the Japan Sea and bring heavy snowfall and frequent showers to Japan Sea coast areas. During the same period, the Pacific areas on the leeward side are far less snowy and comparatively droughty under more sunny weather.

Such a striking contrast of the climate between the two sides has resulted in a differentiation of vegetation types, for example, the beech forest of Japan is divided into the alliance Saso-Fagion crenatae on the Japan Sea side and the alliance Sasamorpho-Fagion crenatae on the Pacific side, which are characterized by several species different between the two alliances (Sasaki 1970).

In relation to the vegetational differentiation, the Japanese flora includes a considerable number of species which are distributed confined to the Japan Sea side (Sugimoto 1954; Hara & Kanai 1959; Fukuoka 1966; Horikawa 1972, 1976). Representative examples of vascular plants showing the Japan Sea side distribution are *Ilex leucoclada* (Maxim.) Mak., *Epigaea asiatica* Maxim., *Weigela hortensis* (Sieb. et Zucc.) K. Koch, *Gaultheria adenothrix* (Miq.) Maxim., *Daphniphyllum macropodum* Miq. var. *humile* (Maxim.) Ros., *Ilex sugerokii* Maxim. var. *brevipedunculata* (Maxim.) S. Y. Hu, *Artemisia monophylla* Kitam., and *Sasa kurilensis* (Rupr.) Mak. et Shibata, of which the first three species have an extension of the range projecting southward into the Kii Peninsula and the fourth species, *Gaultheria adenothrix* is found also on mountains of Shikoku; these facts are homologous to the extended occurrence of *H. cupressiforme* in the same regions.

Among the bryophytes, only a few species are known as Japan Sea elements. They include *Orthoamblystegium longinerve* (Card.) Toy., *Brachythecium brotheri* Par., *Entodon scabridens* Lindb., *Cavicularia densa* Steph., etc., of which the latter two species of Musci grow jumping onto Shikoku, and the last species of Hepaticae, *Cavicularia densa* sometimes occurs disjunctively in Pacific areas.

The Japan Sea elements of both vascular plants and bryophytes cited above are, however, different from *H. cupressiforme* in that they are species distributed confined to Japan or Japan and its neighboring areas, and that they grow mainly in mountainous regions, usually in montane deciduous forests and are scarcely or never found in the neighborhood of human habitation at low altitudes.

Now I propose a question: what conditions have caused such an unusual distribution pattern of *H. cupressiforme* in Japan? To develop a discussion on this problem, a more detailed analysis of Japanese climate will be necessary.

H. Suzuki (1962, 1974) tried to classify the climatic regions of Japan on a combination of three bases: the difference of air mass prevalence, the regional

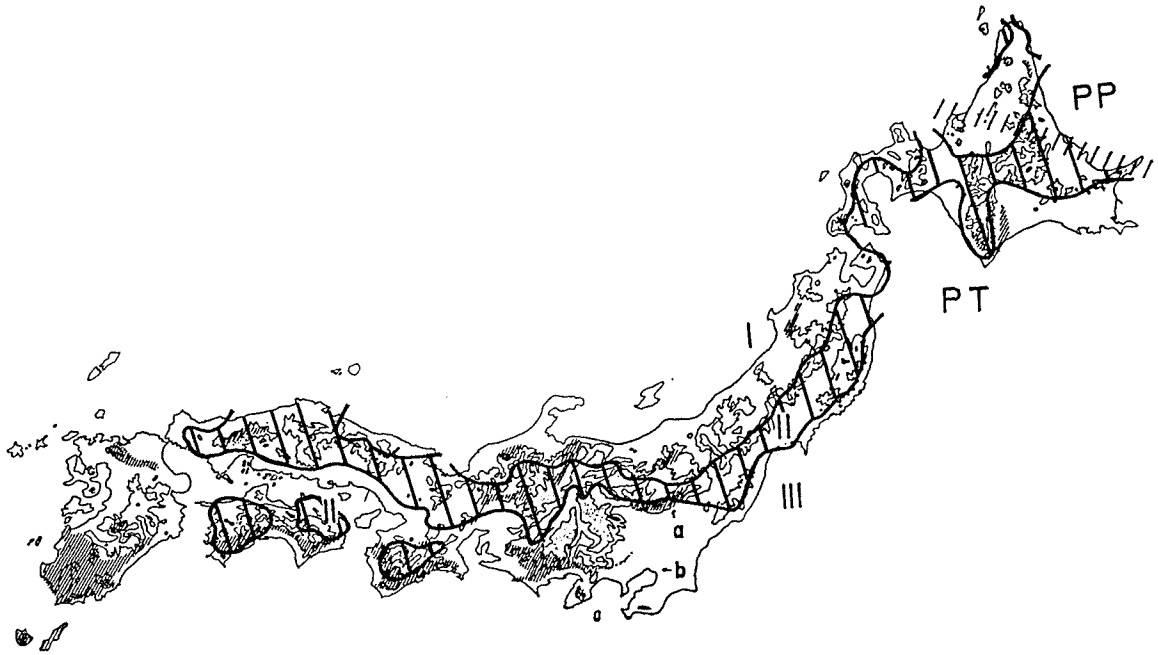

Fig. 3. Climatic regions of Japan (H. Suzuki 1962, 1974). I: Rear Japan (Climatic region of Japan Sea type); II: Semi-rear Japan (Climatic region of semi-Japan Sea type); III: Front Japan (Climatic region of Pacific type). For explanation of the other marks: PP, PT, a and b, see the text.

difference of winter precipitation and the frequency of heavy rainfall, using 365 daily precipitation charts (scale: 1/1, 500, 000) for a year (1955) obtained from about 2000 meteorological stations whose average distance is nearly 20 km. In this study by Suzuki, the second division based on the difference of winter precipitation has resulted in three climatic regions: I. Rear Japan with precipitation from the winter monsoon, II. Semi-rear Japan (transition from I to III), and III. Front Japan with no precipitation from the winter monsoon, which correspond to climatic regions of the Japan Sea type, the semi-Japan sea type and of the Pacific type respectively.

Figure 3 is Suzuki's map showing the climatic regions of Japan including the above-mentioned I, II and III, in which the area of PP is the arctic zone covered with polar air both in winter and in summer, and the area PT separated from the PP by a rough-hatched belt is the temperate zone where the polar air prevails in winter and the tropical air in summer; scattered fine-hatched areas (a) indicate regions with high frequency of heavy rains especially in the summer season and the other non-hatched areas (b) are those with low frequency of heavy rains. It must be noted that the climatic region of the semi-Japan Sea type (II: Semi-rear Japan) extends toward the east in both Hokkaido and the Tohoku district, and it is further shared disjunctively onto mountains in the Kii Peninsula and Shikoku. These separated parts of the II region are considered to have been influenced by the winter monsoon which penetrates through certain valleys crossing the Chugoku Mountains or the Shimonoseki Channel. In Kyushu, even its northern section is not referable to the climatic region of Japan Sea type.

We attempt to compare the distribution map of *H. cupressiforme* (Fig. 1) with the map showing the climatic regions of Japan (Fig. 3). Surprisingly interesting is an exhibition of the nearly parallel features between the distribution pattern of the *Hypnum* and the areal extension of the Rear and Semi-rear Japan, namely, of the areas of the Japan Sea and the semi-Japan Sea climate types.

For vascular plants of the Japan Sea elements, the more important factor to control the distribution has been considered to be the influence of snow cover. For example, S. Suzuki (1959, 1961) has determined that bamboo grasses belonging to the genus *Sasa* Sect. *Sasa* and Sect. *Macrochlamys* which are distributed on the Japan Sea side, are adapted to deep snow cover in their life form and occupy the area with snow depth more than 50 cm in mean annual maximum; on the other hand, species of *Sasa* Sect. *Crassinodi* are restricted to the Pacific side where the snow depth is below 50 cm.

The case of bryophytes, however, cannot be explained only by the snow factor, because some of the bryophyte species of Japan Sea element grow principally or exclusively on tree-trunks or vertical rock-faces where the condition of snow cover is less influential. The distribution at least of *H. cupressiforme* is not considered to be associated with the snow factor. The fact that this species occurs inclined to the Japan Sea side has more possibly been derived from some adaptation or a tolerance to the cloudy condition with more plentiful precipitation in winter, although this moss prefers rather sunny and dry places

as local habitat. It is here reminded that the same climatic condition prevails in Europe where *H. cupressiforme* is very common.

On the other hand, the great amount of rain in summer seems effective as a critical factor for limiting the distribution of this moss on the Pacific side. Furthermore, the warmer condition acts as an additional limiting factor. It is noteworthy that even on the Japan Sea side, the regions in and around the areas with high frequency of heavy rains (fine-hatched areas in the map of Fig. 3) are lacking or poor in this moss; they include Akita Prefecture, Toyama Prefecture, the southern part of Ishikawa Prefecture and the central part of Shimane Prefecture. Its preference of soil as substratum is much more weakened in Japan as compared with that in Europe, and this is also likely attributable to the more humid conditions of Japan.

The reduced occurrence or absence of this species in woodlands even on the Japan sea side is probably due to a defeat in competition with other species of the same genus that are ecologically better adapted to moist conditions, such as *Hypnum oldhamii, H. plumaeforme, H. tristoviride* and *H. fujiyamae.*

The more frequent occurrence of *H. cupressiforme* on tree-trunks and stone-works in the area under man-made conditions such as the precinct of shrines and temples is considered to be a result from its attribute more highly tolerable to such dusty and droughty environments.

In conlusion, puzzled problems concerning the uneven distribution pattern and ecology of *Hypnum cupressiforme* in Japan remain not fully interpreted, although some possible explanations were presented in this paper. The *Hypnum cupressiforme* complex is certainly a unique plant-being of great interest both taxonomical and ecological and is to be subjected to further researches on a world-wide scale.

Summary

1. *Hypnum cupressiforme* Hedw., a well-known cosmopolitan moss, is distributed in Japan principally on the Japan Sea side, but in Hokkaido and the north-eastern section of Honshu, it extends eastward to the Pacific side, and furthermore, branched or disjunct areas of the range appear in the Kii Peninsula and on low mountains in Shikoku. It has never been found in Kyusyu and Pacific coast regions of both Shikoku and Honshu (except one locality on Mt. Kiyosumi).
2. In Japan, this species is not so variable as in Europe, including only two varieties: var. *cupressiforme* and var. *filiforme* which are almost parallel in distribution. It grows much more frequently on tree-trunks or rocks than on soils or decaying logs. Especially interesting is that this species is, in north-eastern regions, widely but sparsely distributed, growing mainly in woodlands, while in southwestern regions, it usually occurs in lowlands principally confined to the precinct of old shrines, temples, castles, etc. and the neighborhood of human habitation.
3. Fertility (frequency of fruiting specimens) of this species is very low in Japan except in some restricted areas. The number of collections and fertility in 25 prefectural sections of the Japanese range were represented by the size of

circles and arranged on the map for comparison. The fertility is highest in the Hokuriku district, where it shows values of 17 to 25%.

4. It is obvious that the distribution of the species inclined to the Japan Sea side is related with the climatic condition of Japan that in summer, damp monsoon winds from the Pacific bring more plentiful rainfall on the Pacific side, whereas in winter, NW-monsoon winds from the Asiatic continent prevail in areas on the Japan Sea side with heavy snowfall and frequent showers. It seems that this species has some adaptation or a tolerance to the cloudy condition with more plentiful precipitation in winter; on the other hand, that it dislikes a condition with the great amount of rainfall in summer.
5. Its reduced presence or absence in woodlands and the more frequent occurrence in the area under man-made conditions are possibly attributable to a losing or winning competition with other species of the same genus, such as *H. oldhamii*, *Hypnum plumaeforme*, *H. tristoviride* and *H. fujiyamae*.

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