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General Principles in Vegetational Zonation*

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Abstract Vegetation formations usually occur in zones, horizontally and altitudinally, not only on mountains but also in the vegetation zones from the coast inland. Even in the intertidal zone, there are different life zones consisting of algae and sedentary animals. The upper or northern limit of vegetation zones is set by extreme physical conditions such as low temperatures and others, while the lower or southern limit is caused by biological factors such as interspecific competition. There are active and dormant volcanoes and non-volcanoes in Japanese mountains. Immature vegetation is easily observed on volcanic mountains.

The *Fagus crenata* zone of Japan has its northern limit in southern Hokkaido and the southern limit in southern Kyushu. The *Fagus crenata* communities near the northern and southern borders are ecotonal, particularly in the undergrowth. In Hokkaido, there is vegetation transitional between the temperate East Asian region and subarctic Siberian taiga. On hills or low mountains there is a miniature version of the altitudinal zonation ("sun-zumari" phenomenon in Japanese).

Introduction

There are various problems in vegetational zonation on mountains in relationship to climate, soil, geomorphology, geographical situation, geological history, flora and life forms, etc. As an example, the altitudinal vegetation belts are described from the base to the top, such as tropical rain forest, subtropical monsoonal forest, warm-temperate evergreen broad-leaved forest, cool-temperate mixed forest, cold-temperate coniferous forest, subalpine scrub (the subalpine zone is a natural belt below the treeless zone, continuing to the closed forest : Löve, 1970 ; Numata, 1981), and alpine mat and cushion-plant vegetation. This is an example on humid high mountains in tropical Asia, such as on the humid Himalayas in Eastern Nepal, with variations and simplifications in different climates. Some aspects of vegetational zonation on mountains and the mechanism of vegetational zonation are discussed in this paper.

Mechanism of the establishment of vegetational zonation

Vegetational formations are usually stratified horizontally and altitudinally, mainly indicated by the dominants, physiognomy and landscape. Such physiognomic units are a basis for sampling and measuring vegetation. On the other hand, a vegetational continuum corresponds to an environmental gradient, for example from wet to dry, from hot to cold, or from lowland to highland. A vegetational continuum is, in fact, an overlapping of distributional patterns of various species, each corresponding to an optimum habitat as a combination of species with high fidelity. At the same time, a dominance-subordination relationship occurs among those spatially overlapped species, and some species are excluded from communities dominated by other species.

Cynodon dactylon is a dominant of the *Cynodon dactylon-Imperata cylindrica* pasture under 2500 m in altitude in eastern Nepal. It is excluded, however, from the *Festuca rubra-Carex nubigena* pasture above 2500 m and occurs sparsely on the mountain path up to 2700 m (Numata, 1965). It is no longer a dominant of highland pastures, but does occur as a subordinate species outside the pasture. Factors setting the upper limit of the *Cyndon dactylon-Imperata cylindrica* belt are usually physical, such as low temperatures.

The distribution areas of various tribes of Gramineae correspond to the mean monthly temperature in mid-winter, >10 °C or <10 °C (Hartley, 1950). The lower limit of each belt, however, is usually determined by biological factors, such

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as interspecific competition, and indirectly by physical factors, such as high temperatures. Therefore, the ecological optimum range of a species is, in general, narrower than the physiological optimum range (Knapp, 1954).

I studied the limiting factors of the distributions of temperate bamboo forests, particularly *Phyllostachys bambusoides*. The first limiting factor for the northernmost distribution in Japan was found to be the average of the lowest minimum temperatures being −10 °C in the coldest month (Numata, 1979). The main factor of the southernmost distribution, however, is not physical, such as high temperatures, but biological, i. e. interspecific competition with tropical bamboos and plants.

The zonation of biotic communities and their successional sequences were observed in denuded quadrats in the rocky littoral zone (Okada and Numata, 1979). This is not zonation on mountains, but a common general principle for zonation as mentioned above, was recognized. According to the environmental gradient, different life zones are established temporally and spatially in the intertidal zone. Species in the upper belt were more pioneer-like than those in the lower belt. In general, pionner plants and animals in the upper belt of the intertidal zone are small in size, short in life span, and broad in distribution in the littoral zone. Grazers caused retrogressive succession, but some seres were stabilized as disclimaxes. The uppermost life zone is delimited by the environmental gradient caused by tidal action, such as drought for several hours per day ; the lower limit is caused mainly by interspecific competition.

On the sandy seashore in central Japan there is a characteristic zonation of coastal vegetation involving an unstable or frontal belt (*Zoysia macrostachya-Calystegia soldanella* community), a semi-stable or intermediate belt (*Ischaemum anthroides-Fimbristylis sericea* community), a stable or rear grass-shrub belt (*Imperata cylindrica-Vitex rotundifolia* community), and a stable or rear forest belt constituted by a *Pinus thunbergii-Pittosporum tobira* community (Numata, 1959). The factors regulating such a zonation are salt spray (Numata, 1949), flying sand (Mitsudera and Numata, 1964), etc. The sandy soil is changed in its physical and chemical properties by the plant cover, in particular the volume weight, porosity, and the amount of nitrogen and carbon. Changes in such soil properties regulate the development of vegetation (Aonuma, 1976). Even in the stable or rear forest belt, tree species with the leaves of salt depositing type, such as *Persea thunbergii, Ilex integra, Cinnamomum japonicum, Daphniphyllum teijsmanni, Camellia japonica, Dendropanax trifidus, Pinus thunbergii*, etc. are in the frontal part of the coastal forest, and those with the leaves of salt-invading type, such as *Clerodendron trichotomum, Celtis sinensis* var. *japonica, Mallotus japonicus, Ficus erecta, Zelkova serrata*, etc. are in the rear part (Kurauchi, 1956).

Salt-spray damage by typhoon was seen in the frontal parts of the coastal forest. The rocovery process of coastal forests damaged by typhoon in 1959 was observed later (Kurauchi, 1986). According to the results, the *Persea thunbergii* forest situated 60 m from the beach line had not recovered even 25 years after typhoon damage. These trees are still scrub-like. The *Persea thunbergii* forests 500 m behind the beach line had also suffered great salt spray damage 25 years ago. However, 16 years after the damage, they had almost recovered.

If we macroscopically observe the zonation of the forests from the coast inland in central Japan, there is the spatial sequence of *Pinus thunbergii* forest. *Persea thunbergii* forest, *Castanopsis cuspidata* var. *sideboldii* forest, and *Cyclobalanopsis myrsinaefolia* forest. In this region, *Pinus densiflora* forests are an inland pioneer forest, and *P. thunbergii* forest make up the coastal forest. However, in the northeastern part of Honshu, there is no *P. thunbergii*, and *P. densiflora* forests occur in coastal as well as inland forests. In Hokkaido, *Quercus mongolica* var. *grosseserrata, Q. dentata* and *Abies sachalinensis* sometimes form coastal as well as inland forests. The resistance to salt spray is one possible reason for the establishment of coastal forests. but not the only one. The possibility of changing the spatial sequence in the zonation of vegetation according to the geographic situation is another aspect.

Vegetation zones on volcanoes and extreme habitats

Mt. Fuji offers a good example for the identification of altitudinal vegetation belts. Hayata (1911) classified the altitudinal vegetation

of Mt. Fuji as follows: 1) prairie belt (his term was region) or basal belt, 2) deciduous broad-leaved tree belt, 3) evergreen conifer belt, 4) *Larix* belt, 5) *Salix-Alnus* belt, and 6) higher grass belt. Miyoshi's observation (1888) was similar though simpler. Honda (1928), the author of "The Forest Zones of Japan", criticized the Miyoshi-Hayata idea of the basal prairie belt, which had been maintained by burning. The prairie belt is now almost completely covered by pine (*Pinus densiflora*) forests. The *Larix* belt by Hayata is also an early stage of succession, because the zonation of Mt. Fuji, a dormant volcano at present is not mature. The subalpine scrub is composed of shrubby *Larix kaempferi, Abies veitchi* and *Tsuga diversifolia* (Ohsawa, 1984). The subalpine scrub on ordinary high mountains of Japan is composed of *Pinus pumila*, where ptarmigan is also found. According to Khomentovsky (1983), *Pinus pumila* seems to be derived evolutionarily from *P. parviflora*.

Confusion in the identification of vegetation zones of Mt. Fuji is closely related to differences on volcanoes versus non-volcanoes, geologically new versus old mountains. Mt. Fuji is a relatively new volcano. The old part of Mt. Fuji erupted 20,000 years ago, and the new part erupted in the Pleistocene epoch and up to 1707 (Tsuya, 1971). After the 1707 eruption, Mt. Fuji became dormant, but there has not been enough time for the formation of soil, or a diverse biota and vegetation. There are many dormant volcanoes in Japan, including Mt. Fuji, Mt. Tateyama, Mt. Norikura, Mt. Ontake, Mt. Miyanoura and Mt. Hakusan; Mt. Asama, Mt. Mihara, and Mt. Sakurajima are active. When compared to non-volcanic mountains, such as the Chichibu and Hida mountain ranges, there are various differences: 1) the mountain flora of new volcanoes is not mature, and the altitudinal vegetation zonation is not complete; and 2) under severe conditions, such as solfatara, alpine plants come down and vertical zonation is disturbed (cf. Lötschert, 1969).

Mt. Fuji is an example of the forest situation. It is the highest, but not a representative mountain in Japan, in regard to the zonation of its vegetation. On the lava flow in 864 A. D., 1126 years ago, *Chamaecyparis obtusa-Tsuga sieboldii* forest, including *Quercus mongolica* var. *grosseserrata, Fagus crenata, Picea polita, Abies homolepis*, etc., the so-called "Aokigahara Tree Sea" was established, and on the other lavaflows there are immature forests composed of *Chamaecyparis obtusa, Picea polita, Tsuga sieboldii* mixed with *Picea bicolor, Larix kaempferi, Pinus densiflora, Quercus mongolica* var. *grosseserrata, Q. serrata, Alnus hirsuta* var. *sibirica*, etc.

The *Abies veitchii* belt develops as the highest coniferous belt, but the *Fagus crenata* belt, the most common montane belt in Japan, does not develop well. The influence of pioneer tree species, such as *Pinus densiflora* and *Larix kaempferi* is strong in the interspecific relationship, and the altitudinal belts of climax forests are not completed. Examples of immature vegetation on volcanoes are easily observed after eruptions, as shown in a follow-up survey of environmental changes caused by the 1977-1978 eruptions of Mt. Usu, Hokkaido (Ito and Haruki, 1984).

Floristic relationships between altitudinal and horizontal vegetational zones

As a rule, in Japan the altitudinal vegetation belts correspond to the horizontal vegetation zones. For example, the cool-temperate *Fagus crenata* belt on the mountains of central and southwestern Honshu corresponds to the lowland climax forest of northeastern Honshu; the cold-temperate *Abies* belt on mountains of Honshu corresponds to the lowland *Abies-Picea* forest in Hokkaido. In these two examples, *Fagus crenata* is similarly distributed in southwestern mountains and northeastern lowlands. There are *Abies mariesii, A. veitchii, P. jezoensis* var. *hondoensis*, and *Chamaecyparis obtusa* on southwestern mountains. Northern lowland conifers in Hokkaido corresponding to those are *Abies sachalinensis, A. sachalinensis* var. *mayriana, P. jezoensis*, and *Thujopsis dolobrata*. The dominants of *Fagus* forests on mountains and lowlands are the same species, but the floristic composition differs depending on the geographical situation. In the southernmost natural *Fagus* forest, in Kyushu, the dominant tree layer is occupied by *Fagus crenata*, but the undergrowth involves many evergreen broad-leaved understorey trees and shrubs, such as *Illicium religiosum, Sapium japonicum, Camellia japonica, Symplocos myrtacea, Cyclobalanopsis salicina*, etc. (Sako, 1960). Therefore, the subordinate species of *Fagus* forests are different depend-

ing on whether they are northeastern lowland forests or southwestern montane forests.

From the Kuromatsunai depression of southern Hokkaido to the Schmidt line of Sakhalin and the Miyabe line in the Kurile Islands (Fig. 1), there is a transitional vegetation between the temperate East Asian region and subarctic Siberian taiga (Tatewaki, 1958) which is called the cold-temperate district (Ito, 1980). In central and northern Sakhalin north of the Miyabe line, *Abies sachalinensis, Picea jezoensis, Betula platyphylla* var. *japonica, Acer mono*, etc. do not occur and the *Pinus pumila* scrub stretches to the seacoast. On the other hand, the climax of northern Sakhalin is *Larix kamtchatica* forest. In Honshu and Hokkaido, *Larix kaempferi* is a pioneer tree, mainly used for plantations. The same situation is seen in *Pseudotsuga menziesii* in western North America. *Pseudotsuga menziesii* is a pioneer or seral tree in some places of south-central Oregon and Washington, but is a climax tree on the drier eastern slopes of the central Oregon Cascade Range and in British Columbia (Franklin and Dyrness, 1973).

The *Dystilium racemosum* association, as the upper laurel-leaved forest belt, occurs in southern Kyushu, while the *Distylium lepidotum* association (Distylio-Pouterietum dubiae), as the lower laurel-leaved forest belt is found in the Bonin Islands. The *Distylium racemosum* belt appears between the lower belt of *Castanopsis cuspidata* var. *sieboldii* and *Persea thunbergii* and the higher belt of *Abies firma, Cyclobalanopsis acuta* and *Tsuga sieboldii*. This is an example from the warm-temperate (Kyushu) and sub-tropical (Bonin Is.) regions, and the other examples mentioned before are in the cool and cold temperate regions.

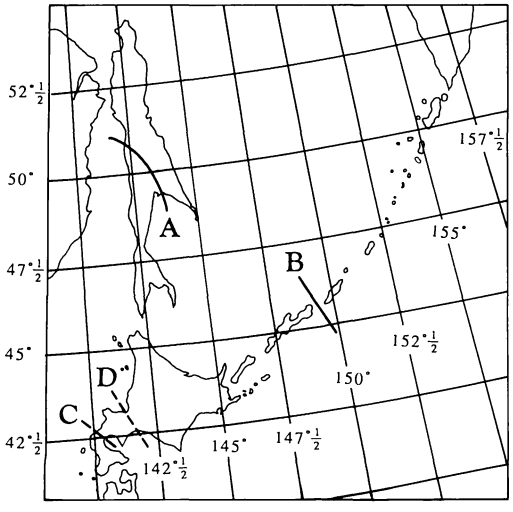

Fig. 1. Important biological demarcation lines. A, Schmidt's line; B, Miyabe's line; C, Kuromatsunai depression; D, Ishikari depression (Tatewaki, 1958).

The floristic differences, already mentioned, are based on climatic, edaphic, and geologic differences. In Japan which is a long chain of islands from north to south, the distribution of many species, climax and subordinate, are limited and closely related macroclimatically to temperature and then mesoclimatically to rain and snow, as on the southern slopes of the eastern Himalaya under the influence of monsoon rain and in the north Tibetan Plateau rain shadow. The southeastern slope of the Japan Alps, under the effect of monsoon rain, and the northwestern slope under monsoon snow are similar cases.

The southernmost part of the Kii Peninsula (Wakayama Pref.) is warm and very humid (4000 mm rainfall per year), and the poly-dominant and multi-stratified structure of warm-temperate rain forest can be observed. The warm-temperate climax forest in Japan is usually mono-dominant, as by *Castanopsis cuspidata* var. *sieboldii*. Moreover, the altitudinal zonation of the Kii Peninsula is different from the normal zonation. *Rhododendron metternichii* var. *hondoensis* is usually found at several hundred m in alt. but grow there at 50 m elevation along rivers because of high humidity. *Quercus phylliraeoides* is characteristic of the coastal forest along the Seto Inland Sea, but it is also found on mountain ridge facing the sea, probably because of the influence of sea wind. The alpine plants descend along solfataras and on windward slopes of lowlands is well known. However, the phenomena of highland plants descending and lowland plants ascending in Kii are very curious (Numata, 1971).

The distribution of a five-needle pine, *Pinus parviflora*, accompanied by *Rhododendron keisukei*, on the Boso Peninsula, central Japan, is a similar phenomenon. This is a remnant vegetation distribution from the Ice Age, when *Fagus crenata* forest covered the Boso Peninsula. *Pinus parviflora* occurs even at 170 m in alt. in the warm-temperate zone there. The highest ridge in the Boso Peninsula is only 400 m in altitude which

belongs to the laurel-leaved forest zone. It is a geomorphological limitation of plant distribution. The warmth index (the accumulated monthly temperatures over 5 °C) of the highest altitude on the Boso Peninsula is 120 °C, which is out of the potential range of *Tsuga sieboldii* (40-110 °C) and *Pinus parviflora* (40-115 °C) (Numata, 1972).

If there were higher mountains in the Boso Peninsula, the ranges of the cool-temperate, upper warm-temperate and lower warm-temperate belts might be higher than 1000 m, 400-1000 m, and 0-400 m, respectively. However, these three belts actually occur above only 300 m, 150-300 m, and 0-150 m, respectively. This is a kind of compressed or miniature altitudinal zonation ("Sun-Zumari" phenomenon in Japanese—Fig. 2), related to the low altitude, in contrast to the "Massenerhöbung" or mountain mass-elevation

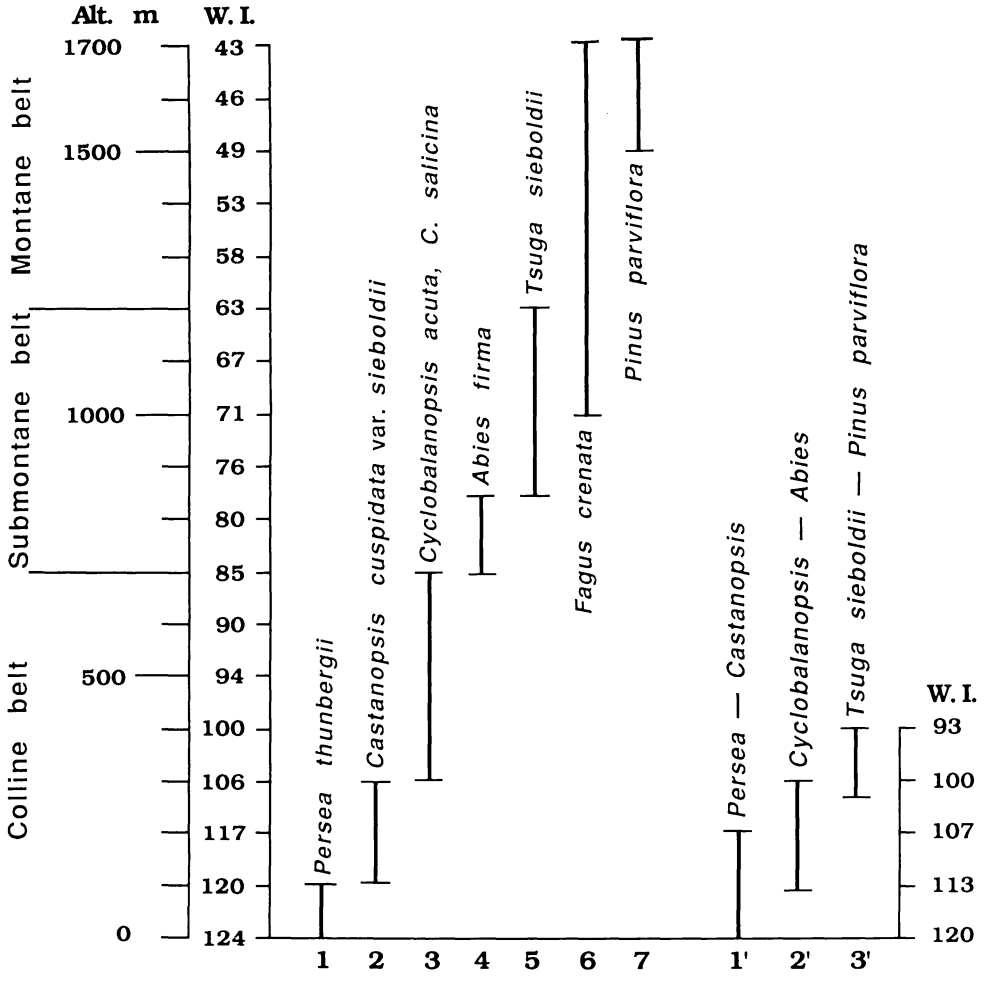

Fig. 2. Distribution of conifers and laurel trees by altitude with the warmth index in Oita Pref.: 1-7 on a non-volcanic mountain (Sumata, 1989). The warmth index (W. I.) is the accumulated monthly temperatures over 5 °C (Kira, 1949). W. I. of Boso is calculated based on the meteorological data of Katsuura City. The distribution of *Tsuga sieboldii* and *Pinus parviflora* actually continues to the upper part of laurel trees as the scale down (miniature) version ("sun-zumari" phenomenon in Japanese) in the Boso Peninsula (1'-3'). The distribution of conifers and laurel trees in Boso is quite different from the vertical distribution on higher mountains in Oita Pref. The width of vegetation belts of Oita vs. Boso is 0～300 m vs. 0～200 m in the *Persea-Castanopsis* belt (lower laurel forest belt), 300～850 m vs. 100～300 m in the *Cyclobalanopsis-Abies* belt (upper laurel forest belt), and 850～1700 m vs. 300～400 m in the *Tsuga sieboldii-Pinus parviflora* belt (lower montane + submontane belts).

effect (Brockmann-Jerosch, 1919 ; Backhuys, 1968). In our area in the Boso Peninsula, the main hills are Mt. Takago (315 m), Mt. Nokogiri (330 m), Mt. Kano (352 m) and Mt. Kiyosumi (370 m). In Fig. 2, the distributions of laurel trees and conifers in the Boso Penisula (Numata, 1972) and compared with those of the high mountains in Oita Pref. (Sumata, 1989).

Boysen-Jensen (1949) discussed the causes of plant distribution altitudinally and horizontally, based on positive net production, reproductive capacity, survival in the unfavorable season, and interspecific competition. In the differentiation of subalpine vegetation belts on Mt. Fuji, the basal area and biomass of dominant species of forest belts become less in the ecotones between them (Ohsawa, 1984).

The horizontal species distributions have been drawn based on existing data (Ohsawa, 1975). The northern limits of various climax species of the laurel-leaved forest are unified on a line, but those of seral species are not unified. Vegetational zone and belts are an aspect of vegetational continua, but for several reasons, the vegetational zonation is typologically recognized. I compared altitudinal vegetational zonations based on climax and seral (secondary forest and grassland) species in the Himalaya of Eastern Nepal (Numata, 1966). The zonation by seral species is only roughly classified by comparing climax species. This is similar to the previous case of the horizontal distribution of species on the northern limits.

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