CLIMATOLOGICAL AND VEGETATIONAL STUDIES ON THE FOREST LIMIT: A REVIEW FOR THE STUDY OF FOREST LIMIT IN JAPAN

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Abstract In this paper, the author attempts to review studies on the forest limit. Comparing notion of the forest limit in various studies, we can find some confusion in the terminology and definition of the word. A difficulty of defining the forest limit due to existence of the ecotone affects this confusion. The forest limit is controlled not only by the present climatic conditions but also by the historical processes. Various informations on the climatic changes involve in the forest limit. In Japanese mountain area, the forest limit had been decided by the lower limit of *Pinus pumila* zone. For some similarities between the subalpine forests and *Pinus pumila* thickets, however, we can conclude the Japanese forest limit is not equivalent to the boundary between alpine and subalpine belts.

Key words: forest limit, ecotone, *Pinus pumila*, climatic change

1. Introduction

Altitudinal zonation of vegetation was identified in the late 15th century (Marek, 1910, cited in Yokoyama, 1983), and climatic conditions which control it were pointed out already in the 16th century. But only in the present century were their intensive studies on this theme have been done.

The forest limit separates the landscape dramatically and many scientists have described its worldwide distribution. For instance, Hermes (1955) discussed the forest limit globally with reference to the snowline and Swan (1967) to the latitudinal and altitudinal changes.

Horizontal vegetation zones and polar forest limit have been correlated with some climatic indices, *e.g.*, temperature of the warmest month (Köppen, 1936), accumulated temperature (Kira, 1945; 1948, cited in Kira, 1971; Holdridge, 1947), potential evapotranspiration (Hare, 1950) and mean position of arctic front in summer (Bryson, 1966; Krebs and Barry, 1970; Larsen, 1971; Mitchell, 1973). Main interest of these studies was the polar forest limit (Yazawa, 1989). Some of them treated the altitudinal forest limits and regarded both forest limits as alike in appearance, but different in physical conditions such as annual and diurnal variation of air temperature (Troll, 1964), air pressure, wind speed, sunshine and so on (*e.g.*, Hann, 1903; Löve, 1970; Tranquillini, 1979; Barry, 1981). In this paper, the author attempts to review the literature on the forest limit in mountain area to research the physical conditions of the altitudinal forest limit.

2. What Is the Forest Limit? —— Its Terminology and Definition

There is a treeless alpine belt between neve and forest in high mountains. The forest limit is defined as the upper border line of the forest (*e.g.*, Ellenberg, 1963). Troll (1972, 1973) described that the climate-ecological conditions, the plant formations on both sides of the forest limits, and also the life forms of trees at the forest limits are so heterogeneous in different latitudes and climatic belts that it seems unsuitable to use the term alpine forest limit in a worldwide sense. Hämet-Ahti (1979) warned that the altitudinal forest limit is too often regarded as an equivalent line in the comparative vegetation studies of various mountains. They claim to rearrange the term, clarifying the definition.

How has the forest limit been recognized in the field? Imanishi (1935, cited in Imanishi, 1969) and Swan (1967) recognized it as the limit of continuous distribution of trees. Larsen (1974) defined the forest as an area of which the surface is occupied by trees at least 50 %. Takahashi (1965a, b) identified the forest limit by the appearance of dwarf or shrub-like trees.

The forest limit cannot be defined clearly because of existence of a transitional belt called "Kampfgürtel" (forest-tundra ecotone), where tree growth struggles against the severe environmental conditions (Troll, 1973). Following Hustich (1953), the transition from the closed forests to the treeless alpine meadows and dwarfed shrubs is distinguishable an economic limit of forests or a generative forest line, a biological limit of forests or the vegetative limit of closed forests, the tree line or the limit of single trees or tree groups, and finally the limit of species, where the same tree species can still grow in shrubby or stunted form. Wardle (1968) and Tranquillini (1979) recognized three elements, namely, the forest, the tree islands and the krummholz in the transitional belt.

Löve (1970) considered the forest-tundra ecotone to be equivalent to the subalpine belt, which has a mosaic of biota of which distribution depends on some climatic factors such as temperature, moisture, wind, and radiation. The width of the ecotone itself is determined by extent and exposure of slope.

Climatic factors controlling the krummholz include winter desiccation, some effects snow pack (*e.g.*, Wardle, 1968; Turner, 1968; LaMarche and Mooney, 1972; Tranquillini, 1976) and physical injury by collision of wind brown ice particles (Holtmeier, 1971).

Clausen (1965) suggested that the krummholz growth forms were genetic variants. Wardle (1974) distinguished environmentally dwarfed trees and genetically determined shrubs, which he called as "krummholz" and "scrub" respectively. Based on observations and field studies in the European high mountains and in the Rocky Mountains of

North America, Holtmeier (1981) proposed that the term "krummholz" should be applied to bush-like growth-forms of *Pinus mugo* prostrata, *Alnus viridis*, and some other species that were genetically determined, and timberline species (*e.g., Picea engelmannii, Abies lasiocarpa and Pinus flexilis*) deformed by local climatic conditions should be called "cripple-trees," "elfin wood," or "wind timber."

We should consider the "krummholz" defined by Wardle (1968) and Tranquillini (1979) to be equivalent to the "cripple-trees" called by Holtmeier (1981). It seems better not to subdivide the ecotone particularly, as the definition of what is meant by "tree" varies with different authors.

3. Effect of Recent Climatic Change on the Forest Limit

Ives and Hansen-Blistow (1983) remarked that the width of the kampfzone (ecotone) in the Colorado Rocky Mountains has fluctuated after change of climatic conditions. According to them, the treeline as species limit was established several thousand years ago, probably during a post-glacial warm period. Some later warm periods probably encouraged a rise of the altitude of the forest limit, but likely did not result in a significant increase in the altitude of the treeline itself. Colder periods would reduce the flagged trees in the mid-section of ecotone and deplete the forest limit but probably not significantly affect the altitude of the treeline. Thus, in favorable periods, the ecotone would be constricted in vertical extent, and during severe periods it would be extended. In the upper part of ecotone, the regeneration is supported only by layering (Marr, 1977), for example, the appearance of seedlings on Niwot Ridge is 120 meters below the upper limit of present-day treeline (Ives and Hansen-Blistow, 1983). This means that the climate during the time the treeline had been formed was warmer than now.

Similar results using tree-ring analysis and pollen analysis were reported in the Rocky Mountains and northern Canada (*e.g.*, Hansell *et al.*, 1971; Ritchie and Hare, 1971; Nichols, 1976). From the viewpoint of Ives and Hansen-Blistow, wood remnants above the present upper treeline in the Rocky Mountains may be regarded as the treeline during the past warm periods (LaMarche and Mooney, 1972; LaMarche, 1973). Black spruce in northern Canada reproduces mostly vegetatively by layering (Legere and Payette, 1981), and northernmost Canadian trees do not have current regenerative capacity (Elliott, 1979). These facts also suggest that the current treeline is historical, that is, a relic of a warm period. The example of Indian Peaks, U.S.A., by Hansen-Blistow and Ives (1985), suggests that evidence of response to climatic change through tree forms and propagation styles are found just in ecotone. After Brubaker (1986), the response of tree populations to climatic change through age structure is clearly observed at and near the treeline.

The recent researches of the forest limit have clarified the various responses of the forest limit to climatic change after the Little Ice Age, and especially to environmental change in the 20th century. Conspicuous tree establishment in subalpine meadows occurred from 1920–1950, the warmest interval in late 400 years, in the Rocky

Mountains (Franklin *et al.*, 1971; Heikkinen, 1984), the Swedish Scandes (Kullman, 1983), northern Canada (Scott *et al.*, 1987), and many other places in the Northern Hemisphere, when it is possible to correspond with climatic records. Kullman (1988) showed that in the late 20th century, the vigor and demography of subalpine *Picea abies* declined in the Swedish Scandes. He suggested that the basic cause of the decline is the reduction of summer temperature since the early 1960s.

Thus, We can find out various informations related the environmental changes in the forest limit and the tree limit.

4. Forest Limit in Japan

Forest limit species

Japanese botanists define the forest limit as the demarcation between subalpine and alpine belts, defining the area that is widely dominated by *Pinus pumila* thickets as an alpine belt (*e.g.*, Nakano, 1944; Takahashi, 1962; Numata, 1972; Koizumi, 1984). The sharp boundary between *Pinus pumila* thickets and subalpine coniferous forests in Japan, is therefore regarded as the forest limit. Imanishi (1969) mainly described *Abies mariesii* and *Betula ermanii* as the species comprising the forest limit. Troll (1973) summarized that *Betula ermanii* characterized Japanese forest limit, making up a belt of 1,300-1,800 meters in Hokkaido and 2,400-2,600 meters in Central Honshu. On the gentle slope, however, *Pinus pumila* thickets are contiguous to coniferous forests without *Betula ermanii* of which stands combine strongly orographic gradient (Ohba, 1973). Therefore, we can consider that birch forests have only substituted for coniferous forests due to edaphic conditions.

On some of the mountains near the Sea of Japan in Northern Honshu, coniferous forests are absent, and deciduous scrub, *e.g., Quercus mongolica*, is directly contiguous to *Pinus pumila* thickets, which make up the "pseudo-alpine" zone (Shidei, 1956, cited in Shidei, 1973). On some of the mountains of Central Honshu, coniferous forests have been replaced by birch forests (Suzuki, 1970). As stated above, because Japanese upper forest limits are composed of various species, it is difficult to explain the forest limits by single controlling factor.

Many scientists attempted to explain the lack of conifers near the Sea of Japan in Honshu. The snowy environment in this region, combines with the strong northwesterly monsoon and its effects on vegetation are varied (Ishizuka, 1977). Many authors consider the effects of snow or wind to be the most important reason for the lack of conifers (*e.g.*, Shidei, 1973; Yoshino, 1973; Makita and Ogawa, 1978). Suzuki (1952) insisted that the phenomenon should be understood as a compound "monsoon effect" instead of an individual effect. Ishizuka (1978) emphasized the snow damage which had extensively affected the vegetational distributions, controlling the growth form of tree species.

Ishizuka (1978) suggested that the conifer and birch communities expanded during the last cool periods or at the beginning of the post-glacial age, on the basis of the pollen data at Mt. Gassan of Yamanaka *et al.* (1973). So he guessed that the snow depth in those periods should be less than in the present. Furthermore, he concluded that the distribution area of conifers declined due to warm and snowy environments during the early post-glacial age. Finally, conifers had varnished from the mountains near the Sea of Japan. Ishizuka's explanation introduced the geologic history viewpoint lent credence to the following ideas.

Kaji (1982) examined the relationship between the altitudes of mountain tops and the extent of conifers over the Japanese Islands. He concluded that the upward movement of vegetation zones in the warm period, in other words it's "pushing out effect," must have occurred. As a result, on the mountains not high enough to allow conifers to remain at individual latitudes, *Abies mariesii* has eventually vanished. Later, Ohmori and Yanagimachi (1991) confirmed this "effect," examining statistically the thermal conditions of subalpine tree species. Ono (1983) added that the lack of conifers relates not just to the height of mountain tops but also to the topography, in other words it's "*oitsume* (cornering) effect." Morita and Aizawa (1986) claimed that *Abies mariesii* forests had been absent until 3,000 years ago, when "pseudo-alpine" zone already consisted of deciduous shrub, according to the results of pollen analyses in northern Honshu. Sugita (1987, 1990) considered that *Abies mariesii* forests expanded in humid and snowy condition during the post glacial period, and whether *Abies mariesii* forests were indigenous or not depended on the extent of gentle slopes on each mountain.

Japanese mountains are remarkable for their low summit and heavy snow cover. As a result, the actual forest limit altitude is lower than the altitude calculated using a thermal index (Schwarz, 1983). In this sense, the upper forest limit may be temporary in Japan (Imanishi, 1969).

Pinus pumila thickets

When examining the upper forest limits in Japan, it is necessary to define the ecological niche of *Pinus pumila*. European ecologists consider that Japanese mountains are not high enough to support true high-alpine vegetation, except for Mount Fuji (*e.g.*, Hämet-Ahti *et al.*, 1974; Wardle, 1977; Franz, 1979). Hämet-Ahti *et al.* (1974) compared *Pinus pumila* thickets to the counterparts of the coniferous forests in middle and northern boreal Europe, and also of the physiognomically similar oro-boreal (subalpine) *Pinus mugo* stands of the European Alps. Although plants of *Pinus mugo* occur well above the forest limit, however, extensive *Pinus mugo* scrub appears to be as a subalpine alternative to forest, and for this reason *Pinus mugo* differs from *Pinus pumila* (Wardle, 1977; Okitsu, 1984; Ito, 1984).

Hämet-Ahti *et al.* (1974) pointed out that *Pinus pumila* thickets may be either local or regional vegetation. As local vegetation they may occur in almost any sub-zone from the temperate zone upward. As regional vegetation they may be found in the upper oro-boreal (subalpine) zone, especially in places where the snow cover is deep, but not too heavy. Japanese botanists have also said that *Pinus pumila* thickets locally occur out of the altitudinal zonation (*e.g.*, Imanishi, 1969; Numata, 1972), therefore, we must be careful to correlate their extent with climate (Makita, 1974). *Pinus pumila* stands advance selectively to the places controlled by edaphic condition, *e.g.*, block field (Suzuki and Shimizu, 1982; Yoshida, 1984; Shimizu and Suzuki, 1985). Their establishment depends on the degree of wind exposure and snow depth (Okitsu and Ito, 1984). Therefore, it may be considered that they dominate where tree species are disturbed in their growth (Imanishi, 1969), and that they develop to fill the treeless area formed by depression of the forest zones (Okitsu, 1984).

Mingling of forest species with *Pinus pumila* thickets as "elfin wood," productivity of *Pinus pumila* as high as that of forest species (Okitsu, 1984) and similarity of the forest floor vegetation between *Pinus pumila* thickets and coniferous forests (Ohba, 1967), show that *Pinus pumila* thickets should be combined with the subalpine coniferous forests and form together with them an upper class unit (Ohba, 1967). Occasionally, however, we can place the *Pinus pumila* thickets in an altitudinal vegetation sub-zone following the alpine zone because of their zonal extent (Ito, 1984).

The upper forest limits do not always agree with the boundary of the alpine and the subalpine zones. Therefore, we should treat the forest limit not as boundaries between alpine and subalpine zones but as boundaries of altitudinal changes of the growth form of tree species.

5. Conclusion: For a Study of the Forest Limit in Japan

The forest limits in Japanese mountains have been considered to correlate with the lower limit of the *Pinus pumila* zone, which corresponds to the boundary between alpine and subalpine zones. As there is the similarity of *Pinus pumila* thickets to subalpine coniferous forests in productivity and forest floor vegetation, and as there is the alpine relic feature of *Pinus pumila*, we can conclude that the lower limit of *Pinus pumila* zone is not a climatically defined boundary between alpine and subalpine zones. It is important to recognize the forest limit not as a line but as a zone including the ecotone. It means that the growth form variation of trees according to altitude is an important criterion. From this point of view, it is very important to research the distribution of *Pinus pumila* thickets. Dominance of shrub-like growth form above the forest limit, if genetical or environmental, is due to that physical conditions are not adaptable to tall-tree growth form there. Understanding the differences of physical conditions between shrub-like growth form and tall-tree growth form should be related to clarifying the controlling factors of the forest limit.

On the other hand, as the forest limits are found in various environments, we must examine them variously and extensively. For these examinations, firstly, it is important to estimate the potential altitudes of the forest limit, that is, the maximum altitude of the forest where all the other conditions are favorable and to evaluate the climatic environments at that altitude. Secondary, it is necessary to calculate the difference between the potential and actual altitudes of the forest limit, and to research controlling factors of the altitudinal difference.

This paper is dedicated to Professor Dr. Ikuo Maejima on the occasion of his retirement from Tokyo Metropolitan University.

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