A Recent Review of Vegetation Science in Japanese Geography

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Abstract: Vegetation science, the study of vegetation patterns and processes, is a relatively minor sub-field of geography in Japan. I summarize the major research on vegetation science by Japanese geographers with reference to similar studies conducted by plant ecologists, focusing on vegetation-environmental relationships. In a few decades, the studies on vegetation by Japanese geographers have generally adopted descriptive approaches that examined the spatial associations between vegetation patterns and environmental factors. However, these studies only demonstrated the covariation of environmental factors with vegetation patterns, whereas theoretical and empirical studies of the mechanistic aspects of the relationships between vegetation patterns and environmental factors were undertaken in plant ecology over a few decades. Thus, to better understand the relationships between vegetation and environment factors and enhance predictions of vegetation change in response to environmental change, I recommend that collaborative approaches to plant ecology, involving plant physiology, should be promoted in geographical studies of vegetation science in Japan.

Key words: geoecology, geographical comparative study, descriptive approach, vegetation science, vegetation-environmental relationship

Introduction

The geographic sub-field of vegetation science examines the spatial patterns and processes of plant species and communities, as well as the processes and relationships that affect their distributions. As one of the oldest themes of geographic inquiry, the study of vegetation engaged the founders of modern geography (e.g., Humboldt 1805), and has continued to develop into a modern science, with applications in environmental conservation and management (der Maarel 2006).

In Japan, plant ecologists have dominated the study on geographical patterns of vegetation. For example, phytosociologists completed vegetation maps of Japan in the 1980s (e.g., Miyawaki 1986). Kira (1948), a plant ecologist, proposed the climatic indices to explain the distribution of vegetation zones in Japan, and Ohsawa (1990) also applied these indices to the study of vegetational patterns in humid East Asia. More recently, researchers in plant ecology have also produced numerous theoretical and mechanistic

studies of vegetation patterns (e.g., Nakamura 1990; Hiura 1995; Kikuzawa 1996; Homma 1997; Okitsu 1999; Nakashizuka 2001; Kohyama 2005).

Unfortunately, a small number of geographers in Japan primarily study vegetation or plant communities, making vegetation science a relatively minor sub-field of geography in Japan. Given the relative lack of studies of vegetation patterns and processes in Japanese geography, geographers have referred to reports by plant ecologists and have incorporated the fundamental theories and field survey methods of these disciplines. Consequently, many geographers consider the disciplinary boundaries between geography and plant ecology to be ambiguous in this study field.

Here, I review the recent research on vegetation science by Japanese geographers, with reference to similar studies conducted by plant ecologists. In particular, I will focus on vegetation-environment relationships, which have been discussed in relative detail in Japanese geography.

Geoecological Studies

Since the beginning of vegetation science in Japan, its practitioners in geography have functionally and quantitatively analyzed a full range of interrelations between vegetation and environmental elements including geology, landforms, soil, and climate. These studies have generally not used theoretical or experimental approaches, but have instead examined the correlations between environmental factors and vegetation patterns and provided detailed descriptions of vegetation and environmental factors of specific areas (e.g., Takeuchi et al. 1986). These studies, which comprehensively examined the relationships between vegetation and environmental factors, were developed as part of the geoecological research thrust in Japan during the 1980s and 1990s.

Geoecology examines the full and complex set of interrelations between organisms or a biocoenosis and environmental factors (Troll 1972). Geoecology was introduced to Japan in the 1970s (Koizumi 1996), and geoecological studies examined mainly alpine and subalpine areas. Watanabe (1986) reported that landform, geology, and various conditions such as the snowmelt pattern or grain size of surface materials is correlated with the vegetation pattern of a cirque in the northern Japanese Alps. In another study, Mizuno (1990) examined the effect of landform on vegetation patterns in cirques of the northern Japanese Alps. Koizumi (1996) and Watanabe (2004) have reviewed and summarized most of the geoecological studies conducted in Japan. However, despite research advances in the 1980s and 1990s, relatively few recent geoecological studies have continued this avenue of research, a trend that can be explained by the greater importance given by geoecologists to the spatial associations between vegetation and related environmental factors.

Landform and Vegetation Pattern

The vegetation patterns in relation to micro-scale landforms could be easily observed in hilly and mountainous regions, and were a major theme of vegetation science in Japan. The vege-

tation patterns are affected by two factors, the environmental factors mediated by landforms and geomorphic processes (Kikuchi 2001).

Landform-mediated environmental factors

The vegetation patterns are changed correspondingly along the landform gradients, because the environmental factors which directly affect the vegetation patterns can covary with landforms. The indirect effects of landforms on vegetation pattern typically result from variations in micro-climate, soil condition, and natural disturbance.

The differences in solar radiation on north- and south-facing slope cause changes in micro-climate which may affect the forest structure and species composition (Jones 1992). The warmer temperature in winter on the south-facing slope mainly formed the evergreen broad-leaved secondary forests at the border with deciduous secondary forests (Isogai 1994). Orito and Hoshino (1997) also showed the differences in forest structure and composition of cool-temperature forests due to late snow melting on the north-facing slopes. The wind direction and speed can also be strongly influenced by local landforms, where they change the vegetation patterns (e.g., Mizuno 1984).

The spatial distribution of soil characteristics, e.g., soil moisture, are highly correlated to topography at the local scale (Tamura 1987), and may affect vegetation patterns (Ishizuka 1977). The spatial distributions of vegetation types were often explained by the differences in soil moisture along a ridge-valley gradient in hilly and mountainous regions (e.g., Yanagisawa and Fujita 1999; Sawada et al. 2005). In particular, the groundwater flow provides a habitat for wetland forest development at the bottom of slopes (Kikuchi et al. 2002). Gotoh and Kikuchi (1997) similarly reported that *Magnolia tomentosa*, an indigenous wetland tree in Japan, always inhabits wet sites on the bottom of valleys in hilly land.

Natural disturbance regimes are considered important environmental factors controlling vegetation patterns and processes (Pickett and White 1985; Nakashizuka and Yamamoto 1987). Landforms also affect the formation of vegetation patterns by controlling natural disturbance

regimes (Swanson et al. 1988). Takaoka and Sasa (1996) examined the relationship between fire history and present vegetation in the mixed forests of northern Japan, and found the vegetation patterns were caused by the difference of fire regime among slope aspects and topographic positions. Bellingham et al. (1996) reported the effects of a powerful typhoon on the primary warm temperate rainforest in Yakushima, and suggested that the spatial heterogeneity of the damage by typhoon caused by the vegetation pattern related to the topographic positions, as well as the patterns in Jamaican montane forests (Bellingham et al. 1995).

Geomorphic processes

Geomorphic processes are natural disturbances that directly influence vegetation patterns (Ito and Nakamura 1994). The vegetation patterns related to geomorphic processes have been recorded at many forest types in Japan (Kikuchi 2002).

Since slopes steeper than 30 degrees are widely distributed, slope processes are important natural disturbances that directly influence vegetation patterns in hilly and montane regions of Japan (Nakamura 1990). Slope processes can change in relative intensity and frequency along topographic gradients, and in particular, the lower slope is characterized by relatively active processes of soil erosion, landslides and slope failure (Kikuchi and Miura 1993). Since the slope stability can strongly affect the vegetation patterns (Shimokawa and Jitosono 1984; Nakamura 1990), the transition in the vegetation mostly corresponded to the convex break between upper and lower slopes (Matsubayashi 1997; Takaoka 2001). Sakai and Ohsawa (1994) reported the vegetation pattern coincided with erosional condition in a warm-temperate hilly region, and also indicated that the vegetation was separated topographically into two species groups; late successional species dominated on the relatively stable slopes and pioneer species dominated on the unstable slopes. Hara et al. (1996) also found that the poorly developed vegetation consisting of pioneer broad-leaved species was seen on the lower slope in an evergreen broad-leaved forest, and suggested that the difference in stability of the land surface was

the major cause of the differences in forest structure between the upper and lower slopes.

Natural disturbances are also key factors for the maintenance and regeneration of riparian forests in mountain regions (Kaneko 1995; Sakio 1997). The intensity and frequency of natural disturbances caused by fluvial processes can strongly affect the vegetation pattern and species coexistence in riparian forest (Nakamura 1995; Nakamura et al. 1997). Shin et al. (1999) reported that the mosaic pattern of riparian forests was developed by the frequent channel shifts in floodplain along the Azusa River in central Japan. Suzuki et al. (2002) also suggested that the heterogeneous site condition created by multiple disturbance regimes formed the vegetational mosaics in the Kanumazawa Riparian Research Forest, northern Japan.

Given the correspondence of spatial and temporal scales of topographic processes to forest dynamics (Nakamura 1990), many studies of plant ecology have demonstrated the relationships between geomorphic processes and vegetation patterns in the last two decades. However, over the same period, relatively few geographers examined the effects of topography-related natural disturbances on vegetation patterns (e.g., Shin et al. 1999; Takaoka 2001; Ogata 2003).

Climate and Vegetation Pattern

Geographical patterns of vegetation types in Japan are largely determined by the present climatic conditions, particularly temperature (Kira 1948; Ohsawa 1993; Matsui et al. 2004). For example, the northern (upper) limit of evergreen broad-leaved forests coincides closely to the -1°C isotherm of monthly mean temperature in the coldest month (Ohsawa 1990). Several studies implied that these vegetation patterns were related to the physiological characteristics of the evergreen broad-leaved trees, such as freezing resistance (Sakai 1972), freeze-thaw embolism (Taneda and Tateno 2005), and leaf water relation (Harayama 2006).

Ecological responses to recent climate change are already clearly visible in many regions of the world (Walther et al. 2002), and the effects of climate change on forest ecosystems have become a major concern of many scientists since

the turn of the 21st century (McCarthy et al. 2001). In Japan, potential plant distributions under climate change scenarios have been predicted in many studies (e.g., Kohyama and Shigesada 1995; Tsunekawa et al. 1996; Ishigami et al. 2003, 2005; Matsui et al. 2004). Most of these studies have predicted the potential distribution of natural vegetation under predicted climate change based mainly on the relationships between the dominant species and present climatic factors. However, effects of climate change on vegetation pattern will not only induce a shift of vegetation zone toward the north and higher elevations in a macro-scale, but also complex changes depending on the diverse controlling environmental factors in fine scales (Tanaka et al. 1998). Furthermore, the differential physiologic response of tree species to climate change should reflect the differences in species traits such as dispersal capacity and environmental-dependent responses of demographic processes (Kohyama and Shigesada 1995; Takenaka 2005). Therefore, further on-site observations and field experiments on the relationships between vegetation patterns and climatic factors are needed to predict more accurately the effects of climate change on vegetation (Kohyama 1996).

In line with this need, a number of geographical studies involving direct, on-site meteorological observation have provided information on the responses of vegetation to recent climate changes in several vegetation types. Because vegetation in tree line and alpine zones is particularly vulnerable and sensitive to climate conditions (Kullman 2001), several studies have conducted periodic and detailed meteorological observations in alpine and subalpine regions (Takahashi and Hasegawa 2003; Hamada et al. 2000). To predict the changes in community dynamics caused by climate change, a number of temperature manipulation studies have also been conducted mainly in alpine region of Japan (e.g., Kudo and Suzuki 2003; Zaiki et al. 2003; Takahashi 2005). A lot of moors with peat layer are distributed in the mountainous area of Tohoku and Kanto districts along the Sea of Japan, and their vegetation has been reduced recently (Yasuda and Okitsu 2007). Yasuda and Okitsu (2006) pointed out that the reduction of alpine moor on Mt. Hiragatake was associated

with the recent decline in snow accumulation in the mountainous area. Recent studies at subtropical island sites have also suggested the effects of climate change on native vegetation. Japan's subtropical Ogasawara (Bonin) Islands showed a warming and drying trend in the twentieth century (Yoshida et al. 2006). Based on continual meteorological observations, Yoshida et al. (2002) reported that the seasonally dry edaphic conditions strongly affected the vegetation patterns of these subtropical islands. Their findings further implied that predicted climate changes would lead to significant vegetation changes on the Ogasawara (Bonin) Islands.

However, although they provide useful information, such studies of the relationships between climate change and vegetation have only demonstrated the covariation of climate conditions with vegetation patterns and have not elucidated the processes of vegetational changes in response to climate changes. In contrast, plant physiological ecologists have intensively studied the physiological processes underlying plant responses to environmental factors for many years (e.g., Lambers et al. 1998). Future studies of the mechanisms underlying climate-vegetation relationships combined with plant physiological knowledge are necessary to accurately comprehend vegetation changes in relation to climate changes.

Geographical Comparative Studies

Comparative studies have provided empirical evidence supporting the basic theories and principles of vegetation science. Using a comparative approach, a number of studies have attempted to clarify vegetation patterns and processes at relatively large spatial scales. Kitayama (1996) examined the relationships between regional floristic richness and species diversification by comparing an oceanic island with a continental island. He suggested from the results that sympatric and parapatric species radiation was less on the oceanic island than on the continental island, because of the initially poor and disharmonic flora on the oceanic island. Maruoka et al. (2003) compared vegetation along an altitude belt in spatially noncontiguous mountains to investigate geographic variation and habitat

differentiation. They also suggested that multi-dimensional habitat differentiation increased with interspecific competition arising from species packing. Focusing on biological invasion, Yoshida (2001) compared successional paths in abandoned fields invaded by *Leucaena leucocephala* at oceanic and continental island sites. On the oceanic island, the invasion of this alien species altered the secondary successional path irreversibly (Yoshida and Oka 2004); in contrast, biological invasion did not affect the secondary successional path as seriously on the continental island, where dense thickets of *Leucaena leucocephala* were replaced directly by indigenous species of fast-growing secondary trees (Yoshida and Oka 2001). These results suggest that simple communities on oceanic islands are more susceptible to biological invasion than are diverse communities on continental islands (Yoshida 2001).

More recently, comparative geographical studies using research data on large plots (>1 ha) of various forest types have been increasing especially in plant ecology. For example, Kanzaki et al. (2000) compared a tropical montane forest in Thailand with a temperate lucidophyll forest in Japan to examine the pattern of niche differentiation. They came to the preliminary conclusion that high species richness in a tropical forest was associated with fine topographical niche differentiation among the canopy tree species. Takyu et al. (2005) also examined how climate seasonality and the dominant life form affects the attributes of forest ecosystems by comparing these patterns along an altitudinal gradient from tropical to temperate regions of humid East Asia. Similarly, Aiba et al. (2007) compared forest ecosystems along elevational gradients at two World Natural Heritage Sites in eastern Asia, i.e., Yakushima Island, Japan, and Mount Kinabalu, Malaysia, and discussed the consequences of additive basal area for forest ecosystem function. Some vegetation science databases have also been developed in Japan (e.g., Forestry and Forest Products Research Institute 2003). These databases will likely be increasingly used in further comparative geographic studies in vegetation science and plant ecology.

Conclusion

Geographers specializing in vegetation science have long explored the relationships between vegetation and environmental factors at various spatial and temporal scales. However, most studies have provided descriptive reports without an explicit mechanistic basis, with only a few examining the processes underlying vegetation changes. On the other hand, plant ecologists have undertaken numerous theoretical and empirical studies of the mechanistic aspects of the relationships between biotic and abiotic factors within plants, plant communities, and ecosystems. Thus, to better understand the relationship between vegetation and environmental factors and thus enhance predictions of vegetation change in response to environmental change, future studies of vegetation in Japanese geography require collaborative approaches to plant ecology developed over several decades.

The recent improvements in networks among the ecological research sites and the accumulation of forest inventory data in plant ecology have promoted synthesis and comparative studies across sites and ecosystems in Japan (Tanaka and Hori 2001). Geographical comparative study is useful for an elucidation of the importance of various environmental and historical factors that operate at larger spatial and temporal scales, by which vegetation patterns have been shaped (Aiba et al. 2007). Although comparative studies have been traditionally conducted in geography, Japanese geographers have lagged behind in programs focusing on plant ecology. In the understanding of the vegetation patterns and processes in various spatial and temporal scales, we should pay attention to the insights from similar studies and the approaches of plant ecology.

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