Nat. Hist. Res., Special Issue No. 4: 127–131. March 1997.

Some Features of the Forest Dynamics of Warm-temperate Evergreen Broad-leaved Forests in Japan

Shin-Ichi Yamamoto

Department of Environment and Resources Management, Faculty of Agriculture, Okayama University, Okayama 700, Japan
Present address: Laboratory of Forest Ecology and Physiology, School of Agricultural Sciences, Nagoya University, Nagoya 464–01, Japan

Abstract Gap regeneration is an important mode of forest regeneration in the warm-temperate evergreen broad-leaved forests of Japan. This paper characterizes the gap-disturbance regime and gap-regeneration behaviors of major tree species of warm-temperate evergreen broad-leaved forests compared with those of other forest types in Japan, using results obtained from recent studies. The gap-disturbance regime was similar to that of cool-temperate forests, but not similar to that of subalpine forests. On the basis of the gap-phase replacement pattern, major tree species of warm-temperate evergreen broad-leaved forests were divided into four typical types of gap-regeneration behavior, and these four types were evident for major tree species of cool-temperate forests. For major tree species of subalpine forests, only two types of gap-regeneration behavior were found.

Key words: *Castanopsis, Distylium,* evergreen broad-leaved forest, forest dynamics, gap regeneration, natural disturbance, typhoon, *Quercus.*

Evergreen broad-leaved (lucidophyllous or laurel-leaved) forests are thought to be a climax forest community in the warm-temperate zone of Japan (Kira, 1978). Most of the present forests are secondary ones due to previous past human disturbance, but relatively undisturbed primary forests remain in mountainous regions or islands of southwestern Japan, even though they occupy a small area (Numata *et al.*, 1972; Miyawaki, 1981). Recent studies have revealed the dynamics of these primary forests from various viewpoints; modeling of the dynamics of tree size distribution (Nagano, 1978; Kohyama, 1986, 1987, 1988, 1989, 1991), tree seedling demography (Tagawa, 1978; Sato *et al.*, 1994; Shimoda *et al.*, 1994; Tanouchi *et al.*, 1994), gap dynamics (Morita and Tagawa, 1981; Naka, 1982; Naka and Yoda, 1984; Naka and Yoneda, 1984; Yamamoto, 1992a), successional dynamics (Taoda, 1981) and spatial pattern of canopy trees (Tanouchi and Yamamoto, 1995).

The warm-temperate zone in which evergreen broad-leaved forests are distributed is frequently swept by typhoons, which are an important agent of natural disturbance affecting forest dynamics (e.g. Naka, 1982; Yamamoto, 1992a). Despite this disturbance, the damage is not severe or extensive in comparison with subalpine or boreal forest, but small openings (area$<$0.1 ha, called "gaps") are formed in the forest canopy. Regeneration in gaps is an important mechanism maintaining the composition and structure of mature or old-growth stands (e.g. Watt, 1947; Brokaw, 1985; Runkle, 1985; Yamamoto, 1992b), and also an important mode of forest regeneration in the warm-temperate evergreen broad-leaved forests of Japan, which are not susceptible to large-scale natural disturbances (Yamamoto, 1984). In this paper, I characterize the gap-disturbance regime and gap-regeneration behaviors of major tree species in warm-temperate evergreen broad-leaved forests in comparison with those of other forest types in Japan, using results obtained from recent studies (Yamamoto, 1992 a, 1994, 1996, in press; Tanouchi and Yamamoto, 1995). I also discuss the regeneration

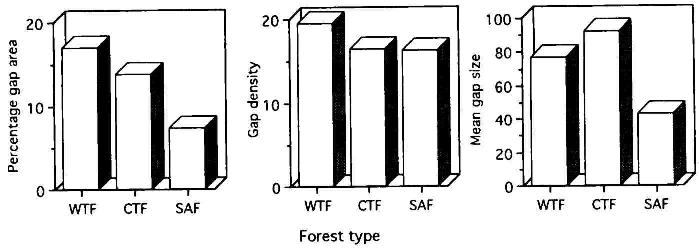

Fig. 1. Percentage gap area (percentage of total gap area to total forested area surveyed), gap density (/ha) and mean gap size (m^2) of the different forest types in Japan. WTF = warm-temperate forest, CTF = cool-temperate forest, and SAF = subalpine forest.

dynamics characteristic of warm-temperate evergreen broad-leaved forests.

Gap-disturbance Regime

Various parameters of gap-disturbance regimes (percentage gap area, gap density and gap size) affect the structure and dynamics of forests. Percentage gap area (percentage of total gap area to total forested area surveyed) of warm-temperate evergreen broad-leaved forest (WTF) is 17.0%, similar to the figure for cool-temperate deciduous broad-leaved forest (CTF, dominated by *Fagus crenata*), and is larger than the figure for subalpine evergreen coniferous forest (SAF, dominated by *Abies* spp.; Fig. 1). Gap density of WTF is 19.5 gaps ha^{-1}. The mean gap size is 77.1 m^2, similar to the figure for CTF, but is about double that for SAF. The largest gap size surveyed was 568.3 m^2 in WTF, 768.2 m^2 in CTF and 285.0 m^2 in SAF

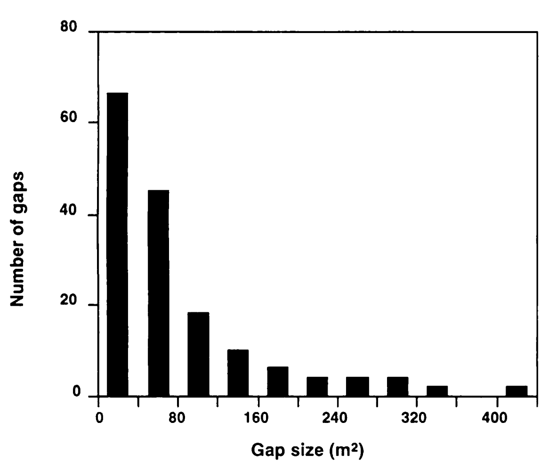

Fig. 2. Gap size distribution of warm-temperate evergreen broad-leaved forest in Japan.

(Yamamoto, 1992a). Gap size distribution has a characteristic inverse-J shape, which indicates that gaps <80 m^2 are much more frequent than those larger than this, and that gaps >400 m^2 are rare (Fig. 2). Gapmaker density of WTF is 25.0 trees ha^{-1}, and is higher than and lower than that of CTF and SAF, respectively (Fig.3). Gaps formed by a single gapmaker are the dominant mode of gap formation in WTF, as in other forest types. Gaps formed by multiple gapmakers are important because they account for most of the larger gaps and constitute 19.9% of the total gaps in WTF. The parameters of the gap-disturbance regime in WTF are nearly the same as those in CTF, but do not correspond to those in SAF.

Death or injury of gapmakers affects the regeneration dynamics after gap formation, and three states – standing-dead, trunk-broken and uprooting – have been recognized in WTF as well as in other forest types (Fig. 4). Standing-dead accounts for 17.3%, trunk-broken 51.5%, and uprooting 22.3% of all gapmakers in WTF. Uprooted gapmakers are uncommon, but uprooting may expose buried viable seeds to the environments re-

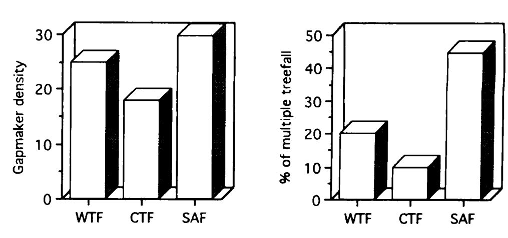

Fig. 3. Density of gapmakers (/ha) and percentage of multiple treefall for different forest types in Japan. See Fig. 1 for abbreviations of forest types.

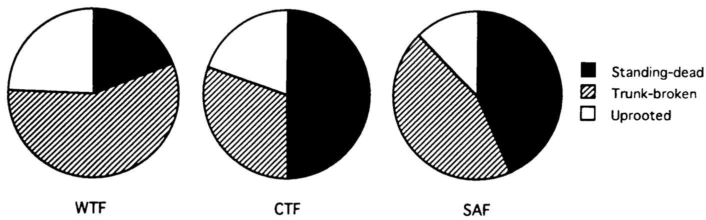

Fig. 4. State of death or injury of gapmakers in the different forest types in Japan. See Fig. 1 for abbreviations of forest types.

quired for germination and provide a suitable substrate for tree species requiring mineral soil for establishment (Putz, 1983; Yamamoto 1992a). Standing-dead is less frequent and trunk-broken more frequent in WTF than in other forest types. One of the reasons seems to be that stems of standing-dead gapmakers are easily broken down by the strong winds generated by typhoons in WTF, which are more frequently exposed to such storms.

Gap-regeneration Behaviors of Major Tree Species

From analysis of the gap-phase tree replacement pattern (Yamamoto, 1992a), four typical gap-regeneration behaviors have been recognized for the major tree species of WTF (Table 1): Type I; canopy trees regenerate in gaps from saplings recruited before gap formation, Type II; canopy trees regenerate in gaps from saplings recruited after gap formation, Type III; "sub-canopy tree species" that regenerates in gaps from saplings recruited before gap formation, but rarely reach the canopy layer, and Type IV; trees can not regenerate in gaps formed under the current gap-disturbance regime.

Type I gap-regeneration behavior has been termed "primary tree species" (Brokaw, 1985) or "climax (non-pioneer) species" (Whitmore, 1989). *Distylium racemosum* is a typical species showing Type I gap-regeneration behavior. *D. racemosum* can replace not only its own gaps, but also gaps of other species, created by the death of single trees (Yamamoto, 1992a). *Persea thunbergii* also belongs to Type I. There are two types of WTFs, that with and that without *D. racemosum*. In WTF with *D. racemosum*, *Castanopsis cuspidata* is a species with Type II gap-regeneration behavior, but *C. cuspidata* is a Type I species in WTF without *D. racemosum*. *C. cuspidata* regenerates not only from seeds but also by sprouting from in-

Table 1. Gap-regeneration behavior of major tree species in different forest types in Japan. See Fig. 1 for abbreviations of forest types.

Regeneration type	Forest type		
	WTF	CTF	SAF
I	*Distylium racemosum* *Persea thunbergii*	*Fagus crenata* *Acer mono*	*Abies mariesii* *Abies veitchii*
II	*Castanopsis cuspidata** *Fagara ailanthoides*	*Betula grossa*	*Picea jezoensis* *Betula ermanii*
III	*Camellia japonica* *Cleyera japonica*	*Acanthopanax sciadophylloides* *Acer japonicum*	
IV	*Quercus acuta* *Quercus salicina*	*Quercus mongolica*	

* Type I species in forests without *Distylium racemosum*.

jured gapmakers in gaps. Most deciduous broad-leaved tree species including *Fagara ailanthoides* may belong to this type. Some Type II tree species maintain their populations by seedling establishment on exposed mineral soils of root mounds formed by uprooted gapmakers. Type II gap-regeneration behavior has been termed "pioneer tree species" (Brokaw, 1985; Whitmore, 1989). *Camellia japonica* and *Cleyera japonica* show Type III gap-regeneration behavior and are typical "subtree species" without attaining a size of about 30 cm diameter at breast height (Yamamoto 1992a). *Quercus acuta* and *Q. salicina* show Type IV gap-regeneration behavior and have no or very little regeneration. Though there may be old-growth stands dominated by *Quercus acuta* without regeneration, the regeneration mechanism of these stands has not been clarified.

Other Features of Regeneration Dynamics

Dwarf bamboos do not affect the forest dynamics of WTF, and differ from the case in CTF and SAF because WTF with a dwarf-bamboo understory does not occur. Regeneration on logs or stumps is not an important mode of regeneration in WTF, compared with the case in SAF. In old-growth stands of WTF, some major canopy tree species (e.g. *Castanopsis cuspidata* and *Persea thunbergii*) can regenerate by base sprouting, and thus regeneration by sprouting seems to be an important mode of regeneration in WTF.

Acknowledgments

The studies reported in this paper were supported by grants from the Ministry of Education, Science, Sports and Culture, and the Ministry of Agriculture, Fisheries and Forestry, Japan. I thank many persons for their field assistance in various parts of the study. I also thank M. Hara and two anonymous reviewers for their helpful comments on the manuscript. This paper is based on a talk given at the Symposium on "The Character of Laurel-leaved Forest—Its Flora and Vegetation Structure in East Asia" at the 7th Natural History Symposium in Natural History Museum and Institute, Chiba, 17–18 February, 1996.

References

Brokaw, N.V.L. 1985. Treefalls, regrowth, and community structure in tropical forests. *In* Pickett, S.T.A. and P. S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics, pp. 53–69. Academic Press, New York.

Kira, T. 1978. Warm-temperate evergreen broadleaf forest of Eastern Asia. *In* Kira, T., Y. Ono and T. Hosokawa (eds.), Biological Production in a Warm-Temperate Evergreen Oak Forest of Japan (JIBP Synthesis 18), pp. 1–3. University of Tokyo Press, Tokyo.

Kohyama, T. 1986. Tree size structure of stands and each species in primary warm-temperate rain forests of southern Japan. Bot. Mag. Tokyo 99: 267–279.

Kohyama, T. 1987. Stand dynamics in a primary warm-temperate rain forest analyzed by the diffusion equation. Bot. Mag. Tokyo 100: 305–317.

Kohyama, T. 1988. A function describing all-sized trunk diameter distribution in warm-temperate rain forests. Bot. Mag. Tokyo 101: 207–212.

Kohyama, T. 1989. Simulation of the structural development of warm-temperate rain forest stands. Annals of Botany 64: 47–57.

Kohyama, T. 1991. Simulating stationary size distribution of trees in rain forests. Annals of Botany 68: 173–180.

Miyawaki, A. (ed.) 1981. Vegetation of Japan, Vol. 2: Kyushu. 484 pp. Shibundo, Tokyo (In Japanese).

Morita, Y. and H. Tagawa. 1981. Partial succession in gaps in a *Machilus thunbergii* forest. *In* Kuroiwa, S. (ed.), Ecological Analysis of Regeneration Process and Mechanism of Forest, pp. 47–54, Kyoto University, Kyoto (In Japanese).

Nagano, M. 1978. Dynamics of stand development. *In* Kira, T., Y. Ono and T. Hosokawa (eds.), Biological Production in a Warm-Temperate Evergreen Oak Forest of Japan (JIBP Synthesis 18), pp. 21–32. University of Tokyo Press, Tokyo.

Naka, K. 1982. Community dynamics of evergreen broadleaf forests in southwestern Japan. I. Wind damaged trees and canopy gaps in an evergreen oak forest. Bot. Mag. Tokyo 95: 385–399.

Naka, K. and K. Yoda. 1984. Community dynamics of evergreen broadleaf forests in southwestern Japan. II. Species composition and density of seeds buried in the soil of a climax evergreen oak forest. Bot. Mag. Tokyo 97: 61–79.

Naka, K. and K. Yoneda. 1984. Community dynamics of evergreen broadleaf forests in southwestern Japan. III. Revegetation in gaps in an evergreen oak forest. Bot. Mag. Tokyo 97: 275–286.

Numata, M., A. Miyawaki, and S. Itow. 1972. Natural and semi-natural vegetation in Japan. Blumea 20: 436–496.

Putz, F. E. 1983. Treefall pits and mounds, buried seeds, and the importance of disturbed soil to pioneer trees on Barro Colorado Island, Panama. Ecology 64: 1069–1074.

Runkle, J. R. 1985. Disturbance regimes in temperate forests. *In* Pickett, S.T.A. and P. S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics, pp. 53–69. Academic Press, New York.

Sato, T., H. Tanouchi, and K. Takeshita. 1994. Initial regenerative processes of *Distylium racemosum* and *Persea thunbergii* in an evergreen broad-leaved forest. J. Plant Res. 107: 331–337.

Shimoda, K., K. Kimura, K. Kanzaki, and K. Yoda. 1994. The regeneration of pioneer tree species under browsing pressure of Sika deer in an evergreen oak forest. Ecol. Res. 9: 85–92.

Tagawa, H. 1978. Seed fall and seedling regeneration. *In* Kira, T., Y. Ono and T. Hosokawa (eds.), Biological Production in a Warm-Temperate Evergreen Oak Forest of Japan (JIBP Synthesis 18), pp. 32–46. University of Tokyo Press, Tokyo.

Tanouchi, H., T. Sato and K. Takeshita. 1994. Comparative studies on acorn and seedling dynamics of four *Quercus* species in an evergreen broad-leaved forest. J. Plant Res. 107: 153–159.

Tanouchi, H. and S. Yamamoto. 1995. Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest in Aya district, southwestern Japan. Vegetatio 117: 51–60.

Taoda, H. 1981. A process of succession in *Castanopsis cuspidata* forest. Trans. 92nd Meet. Jpn. For. Soc.: 227–228 (in Japanese).

Watt, A. S. 1947. Pattern and process in the plant community. J. Ecol. 35: 1–22.

Whitmore, T. C. 1989. Canopy gaps and the two major groups of forest trees. Ecology 70: 536–538.

Yamamoto, S. 1984. Regeneration of forests. Its pattern and process. The Heredity (Iden) 38: 43–50 (In Japanese).

Yamamoto, S. 1992a. Gap characteristics and gap regeneration in primary evergreen broad-leaved forests of western Japan. Bot. Mag. Tokyo 105: 29–45.

Yamamoto, S. 1992b. The gap theory in forest dynamics. Bot. Mag. Tokyo 105: 375–383.

Yamamoto, S. 1994. Gap regeneration in primary evergreen broad-leaved forests with or without a major canopy tree, *Distylium racemosum*, southwestern Japan: A comparative analysis. Ecol. Res. 9: 295–302.

Yamamoto, S. 1996. Gap regeneration of major tree species in different forest types of Japan. Vegetatio 127: 203–213.

Yamamoto, S. (in press). Gap-disturbance regimes in different forest types of Japan. Journal of Sustainable Forestry.

照葉樹林の森林動態の特徴

山 本 進 一

岡山大学農学部
〒700 岡山市津島中 1-1-1

わが国の照葉樹林の動態，特に更新動態はギャップ更新に特徴づけられる．このギャップ更新について，照葉樹林のギャップ攪乱体制とその主要構成樹種のギャップ更新特性の特徴をわが国の他の森林タイプ（冷温帯落葉広葉樹林と亜高山帯常緑針葉樹林）との比較から検討した．照葉樹林のギャップ攪乱体制は冷温帯落葉広葉樹林のそれと類似しており，主要構成樹種のギャップ更新特性には冷温帯落葉広葉樹林と同じく大別して４タイプが認められた．