Transient structures of wave patterns arising in the wave regeneration of subalpine coniferous forests

Shin-ichi Ichinose
Department of Environmental Education, Fukuoka University of Education, Akama 729-1, Munakata City, Fukuoka Prefecture, 811-4192 Japan
(Received 19 April 2001; published 13 November 2001)

In wave-regeneration phenomena observed in the subalpine coniferous forests, mainly consisting of *Abies* species, the blighted forests present various shapes in the course of development, spots at the initial stage turning into arches and finally into long whitish stripes. Because the wave-regeneration could not be followed in the field without long term studies, a simple model has been elaborated to simulate the various different dieback structures observed in the real forests. This model, based on cellular automata, is employed to analyze the power spectral density of canopy tree height fluctuations in the wave-regenerated forests. The results demonstrate that almost all the dieback structures observed in the field can be generated by this simple model, by varying the wind direction and its strength by some stochasticity. The power spectrum density presents various shapes in the course of development, white noise type at the initial stage turning into Lorentz type and finally into $1/f$ type power spectrum (spatial Fourier frequency).

DOI: 10.1103/PhysRevE.64.061903 PACS number(s): 87.23.−n

I. INTRODUCTION

There are numerous examples of self-organization phenomena observed in ecological nature, among the most impressive being pattern formation in communities of forests, such as wave regeneration and gap regeneration phenomena. Both of them have demonstrated that new gaps are more likely to occur adjacent to pre-existing gap, and trees in the border of gaps tend to have a higher rate of disturbances. Among other things, the wave-regeneration phenomenon is an exceptionally clear example of large scaled spatiotemporal pattern formation of forests [1–9]. It is uniquely observed in the subalpine coniferous forests, mainly consisting of *Abies veitchii* and *Abies mariesii*. From a distance, such a forest is seen to be highly heterogeneous, with large areas of green canopy broken by numerous more or less ''crescent'' shaped bands of dead trees whose exposed trunks appear silver in side view. Closer examination, however, reveals that each area is actually a band of standing dead trees, with mature forest on one side and young, vigorously wave-regenerating forest on the other. Each band is regularly spaced off from the other (the interval is between 100 and 150 m). There is actually a ''wave'' moving slowly through the forest, with trees dying at the wave's leading edge and being replaced by seedings. These waves move in the general direction of the prevailing wind at speeds of 0.75–3.3 m/yr [7].

After a regeneration wave moves through an old stand and trees in a site show dieback, more light and heat penetrate to the forest floor. Then, the site will be filled quickly by short trees because in a forest floor there are many seedlings capable of responding to canopy opening created by the death of tall trees. The seedlings grow rapidly, leading to intense competition and rapid thinning. Their density is typically reduced to 10% in the first few years after a wave passes through. Five to ten years after the old overstory disappears, the seedlings form a dense stand that shades out the herb layer of the regeneration zone. These phases recur after a period of about 60 yr; thus the ecosystem at any fixed point is in a constant state of change as it undergoes the cycle of regeneration. A wave-regenerated forest with a large number of dead tree's strips normally contains all states of development [2]. Many of these small dead tree's strips have a characteristic shape of ''crescent'' of different sizes, and sometime two or three of them combine, forming a wavelike stripe. The crescent strips may be the earlier stages of development of the long, conspicuous dead tree's stripe.

One of the most interesting points in such forests is concerned with the problem of how the long whitish stripes were formed, and what relationship is there between such stripes and the ''crescent'' shape of dead tree's strips. Such problems were already pointed out by many authors from the vegetative point of view [1,2,3]. Actually, if the *Avies* trees remain standing for 10 yr after their death, the whitish zone formed by the dead tree's trunks may have a shape of ''crescent'' after about 60 yr. In a case that several spots of dead trees occur at interval of ca. 40 m. at the same altitude, these ''crescent'' strips will combine with each other to form a wavelike stripe within 70–80 yr after their start. At the site where an original spot of dead trees occurred, there is established the young extremely overcrowded growth of *Abies veitchii*, which will continue their growth to mature and overmature trees, creating again the inner condition for their own death in groups. New spots of dead trees will occur again at the original sites within 100–120 yr after the initial occurrence of the spot, and these new spots will develop into the long dead tree's stripes with the lapse of time. It is quite possible on such long and wide slope that several long stripes of dead trees are formed by the recurrence of this process. The purpose of this study is to show that the fluctuating nature of the prevailing wind plays a crucial role in converting the dead tree's strips to various types of banded stripes combining with each other as seen in the real subalpine coniferous forests.

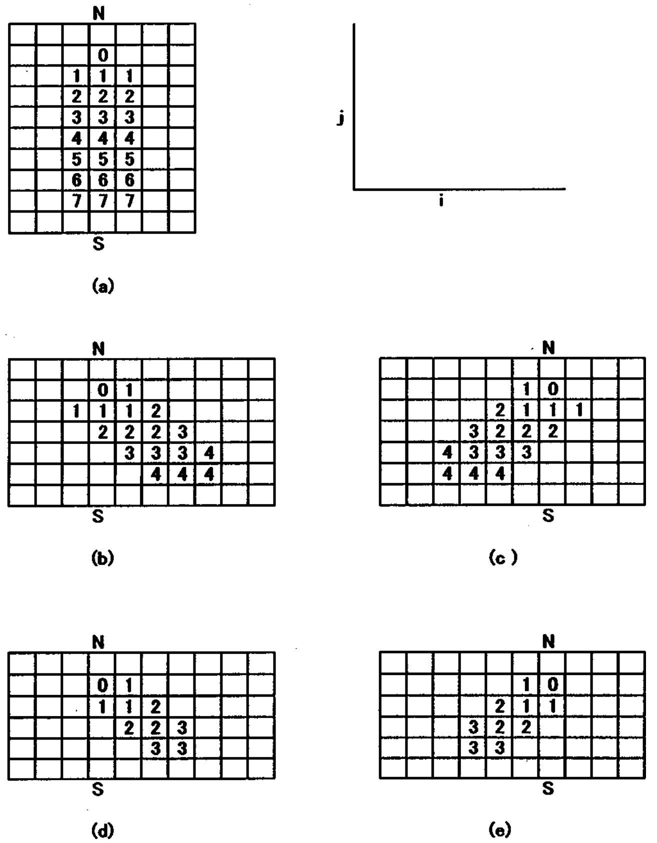

FIG. 1. The variable range of wind-shielding effect of trees. The pattern (a) corresponds to the south wind direction with the interaction range $(w=7)$. The patterns (b) and (c) correspond to the south south-east and south south-west wind direction, respectively, with the range $(w=4)$. The patterns (d) and (e) correspond to the south-east and south-west wind direction with the range $(w=3)$, respectively. The number 0 attached to the figures indicates the tree site (i,j), which is exposed to the prevailing wind. The attached nonzero numbers $(1,2,\ldots,7)$ indicate the range number of wind-shielding effect of tree site (i,j), respectively. $\overline{d}_{\mathrm{cr}}=3.4$, $\sigma=0.000\,01$.

II. MODELING

The numerical simulations are performed with a cellular automaton model specially developed to study the spatiotemporal evolution of wave-regeneration processes. We preserved the main properties of the model proposed in the previous works [10–14], which are essentially determined by the prevailing wind that gives the directionality of the dieback processes. However, we did not assume the stationary conditions of the prevailing wind. In such models, the landscape is modeled as a tessellation or mosaic of rectangular cells. The evolution of the cell properties, such as the average height of cohort, is required to follow a set of rules that reflect the properties of neighboring cells. Because the prevailing wind is suspected to be the major cause of a tree's death in a wave-regenerating forest, a cohort of trees growing in each site is influenced by the windward neighbors and influencing the leeward ones. Trees in a site are assumed to be protected if the height of trees in the windward neighbor is sufficiently higher than their own. If instead the windward

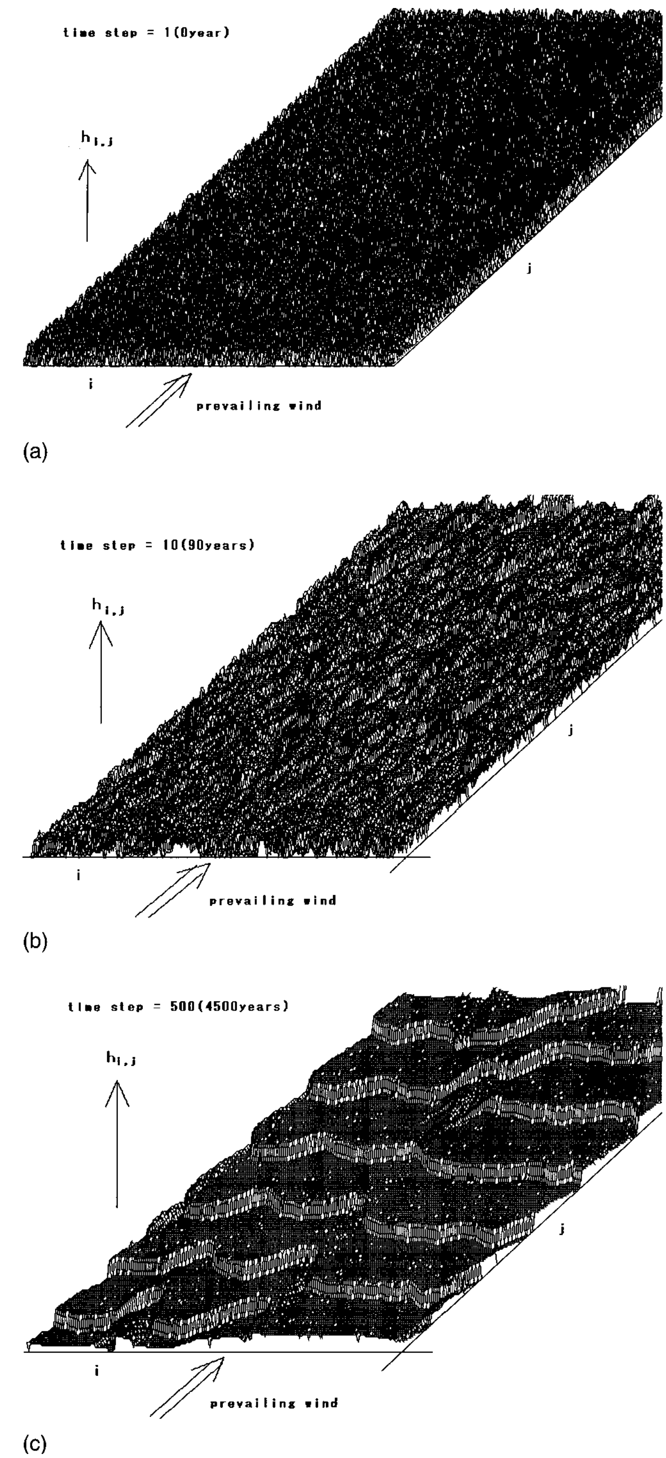

FIG. 2. The pattern on the south slope generated by the two-dimensional model, expressed by the canopy tree height plot. (a) Random initial pattern $(t=1)$, in which the tree height is independent and is chosen randomly between 0 and 10 m with equal probability. (b) The pattern over 10 time steps. (c) The pattern over 500 time steps. Most developed pattern is formed as a banded dieback tree stripe.

neighbor of the cohort is much shorter (by more than some critical height difference d_{cr}), then the trees experience stand-level dieback under the prevailing wind [10,11,14]. After the dieback of the tallest trees, the trees growing next to them become the tallest and fully exposed to the prevailing wind, and thus the dieback zone moves. All the other trees increase their heights at a nearly constant rate. This is the reason why once a wavelike pattern is formed, the same spatial pattern is maintained moving at a constant speed in a direction parallel to the path of the prevailing wind.

Such benefits from cellular modeling have been demonstrated by many authors who were able to explore the processes affecting tree death and regrowth and successfully modeled the wave phenomenon within the cellular model paradigm. The model contains a tessellation of 262 144 cells (512×512). In developing the model, each cell is thought of as representing 10 m^2 of surface. The tree height in a site just after canopy tree dieback is simply assumed to be zero in the model. Time unit in the model is chosen to be the average length of time for newly exposed trees to show dieback. The average increment of the mean height of vegetation in wave-regenerating forest is assumed to be a constant independent of the age of the stand (0.11 m/yr). Hence, in the model, the growth rate is assumed as unity and the unit height is chosen to be the height increment in a unit time step. A variable initial state of cells was denoted as a random pattern, in which the tree height is independent and is chosen randomly between 0 and 10 m with equal probability. In the present model, however, we assume that the direction of the prevailing wind may fluctuate around its mean direction and the velocity always changes around its mean velocity. To follow the dynamics of such systems, we have to make hypotheses on transition between the states. We simply assume that changes in the state of site (i, j) at iteration $t+1$ depend only on the states of the windward neighboring sites at iteration t. How can it be possible for a synchronous renewal of trees to develop from a random initial pattern?

Consider the case in which the prevailing wind mainly blows from the south, but sometimes it blows from the south east or south west and so on. In the present model, these fluctuating variety of the prevailing wind directions is expressed as the variable ranges of wind-shielding effect by several neighboring tree sites as shown in Fig. 1. When the wind happens to come from the south, then the wind-shielding pattern [Fig. 1(a)] is adopted with probability $\frac{1}{2}$ and Eq. (1a) is used there.

$$\overline{h}_{i,j}(t)=\frac{1}{3w}\sum_{l=1}^{w}\sum_{k=-1}^{+1}h_{i+k,j-l}, \tag{1a}$$

where $h_{i,j}(t)$ and $\overline{h}_{i,j}(t)$ are the tree height of the cohort growing and the average height of neighboring sites that has the wind-shielding effect on the site (i,j) at time t, respectively. The parameter w indicates the width of the interaction range as shown in Fig. 1. On the other hand, in the case of south south-east and south south-west direction, the relevant patterns [Fig. 1(b) and Fig. 1(c)] are adopted with probability $\frac{1}{6}$, respectively. The corresponding equations (1b) and (1c) are used there.

$$\overline{h}_{i,j}(t)=\frac{1}{4w}\sum_{k=1}^{w}\{h_{i+k,j-k}+h_{i+k-1,j-k}+h_{i+k-2,j-k}+h_{i+k,j-k+1}\}, \tag{1b}$$

$$\overline{h}_{i,j}(t)=\frac{1}{4w}\sum_{k=1}^{w}\{h_{i-k,j-k}+h_{i-k,j-k+1}+h_{i-k+1,j-k}+h_{i-k+2,j-k}\}. \tag{1c}$$

Finally, in the case of south-east and south-west direction, the relevant patterns (Fig. 1(d) and Fig. 1(e)) are adopted with probability $\frac{1}{12}$, respectively. Then, Eqs. (1d) and (1e) are used there.

$$\overline{h}_{i,j}(t)=\frac{1}{3w}\sum_{k=1}^{w}\{h_{i+k,j-k}+h_{i+k-1,j-k}+h_{i+k,j-k+1}\}, \tag{1d}$$

$$\overline{h}_{i,j}(t)=\frac{1}{3w}\sum_{k=1}^{w}\{h_{i-k,j-k}+h_{i-k,j-k+1}+h_{t-k+1,j-k}\}. \tag{1e}$$

In a similar way, the fluctuating variety of the prevailing wind velocity is expressed as the variable critical height difference d_{cr}. It is assumed that the deviation from the mean critical height difference $\overline{d}_{\mathrm{cr}}$ simply shows a normal distribution with some standard deviations. In a real situation, however, we note that the growth dieback is always accompanied by some stochasticity [14]. Combining the variable nature of prevailing wind with the stochastic behaviors of the growth-dieback phenomena in the wave-regenerated forests, it is assumed that the growth-dieback probability may be a smooth sigmoidal curve of the height difference $h_{i,j}(t)-\overline{h}_{i,j}(t)$.

$$h_{i,j}(t+1)=\begin{cases}0, & \text{with probability } f(h_{i,j}(t)-\overline{h}_{i,j}(t)),\\ h_{i,j}(t)+1, & \text{with probability } 1-f(h_{i,j}(t)-\overline{h}_{i,j}(t))\end{cases} \tag{2}$$

where $f(h_{i,j}(t)-\overline{f}_{i,j}(t))$ is given by

$$f(x)=\frac{1}{1+\exp[-(x-d_{\mathrm{cr}})/\sigma]}, \tag{3}$$

where σ is the strength of stochasticity.

III. EVOLUTION OF WAVE-REGENERATED STRUCTURES

In the series of numerical simulations, dieback trees patterns were very clearly and strongly developed. Typical model output is shown in Fig. 2. In these figures, the wind

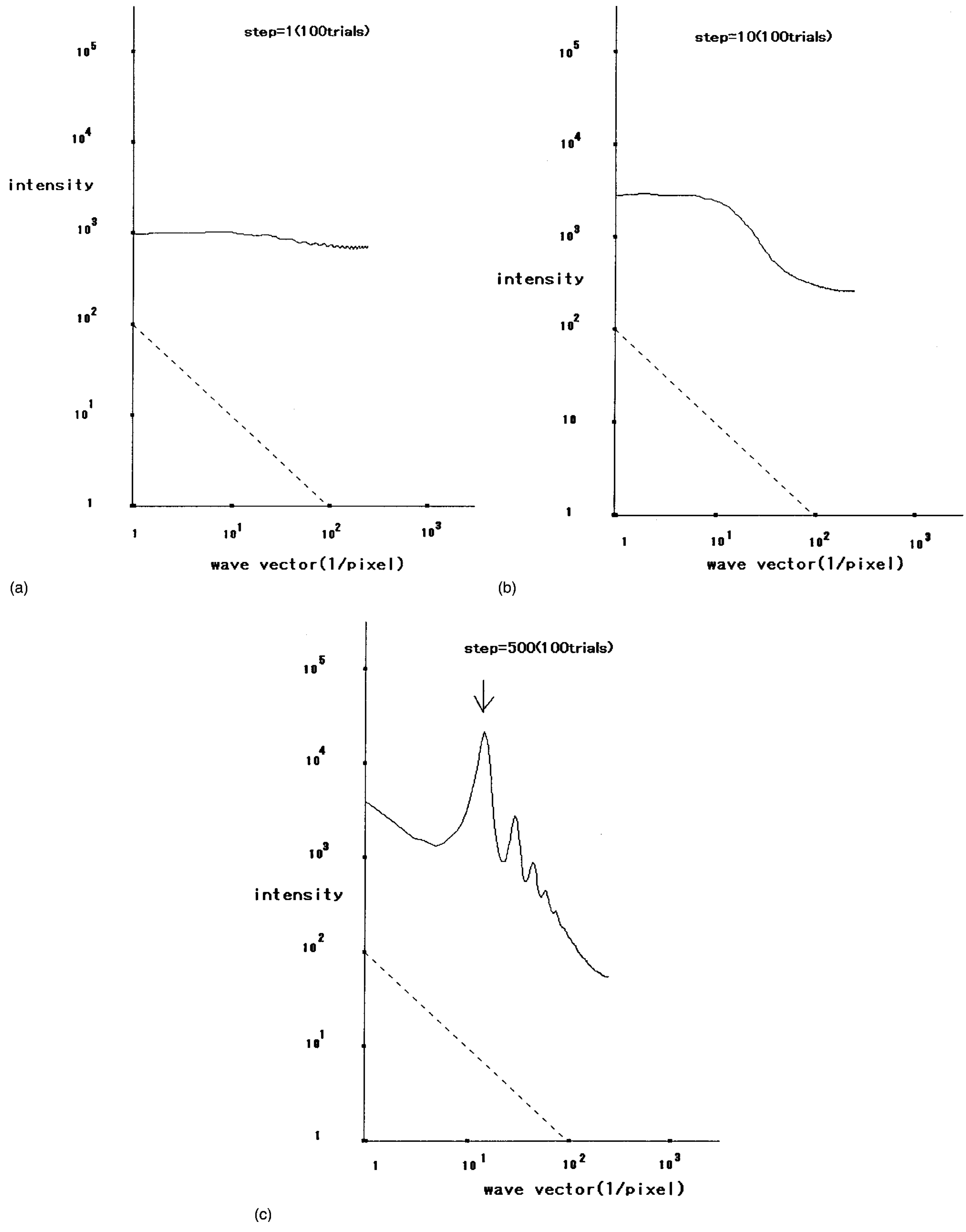

FIG. 3. Power spectra of spatial Fourier transform of the canopy tree height fluctuations in the prevailing wind: panels (a)–(c) correspond, respectively, to the states of Figs. 2(a), 2(b), and 2(c), averaged over 100 samples.

blows from around the downward (south). The dieback of tall trees concentrates on dieback zones, which are spaced almost regularly. Between these zones, cohorts of trees are arranged with continuously changing age and height. The boundary is assumed to be periodic. Note that the dieback areas stretch along the direction perpendicular to the prevailing wind. Figure 2 displays the simulation results after 1 (0 yr), 10 (90 yr), and 500 (4500 yr) iterations, starting always with the same random state distribution in Fig. 2(a). In Fig. 2(b) many dead tree's strips of smaller scale can be seen. Over about 50 iterations (450 yr) many of these small dead tree's strips have a characteristic shape of crescent of different sizes, and sometimes two or three of them combine to form several wavelike strips. Tree clustering in long bands appears after 20 iterations (180 yr) under favorable conditions, whereas at least 100 iterations (900 yr) are necessary to produce such a developed banding patterns.

Through successive iterations, the small dead tree's strips became linked and the crescent type strips emerged. Whitish long stripes take over the whole field [see Fig. 2(c) at 500 iterations]. Such a long whitish stripe may be generally developed within 100–200 iterations (900–1 800 yr), though in some runs pattern evolution was slower. In some model runs, however, departures were noted. Chance linking of growing patches sometimes formed banding that displayed some sinuosity, or bands that divided into two across the slope. This kind of pattern is also evident in the field, and can be seen in the map presented as Fig. 1 in Ref. [1]. In some runs, small partial bands survived, persisting as patches of dead trees zone. Thus, a large variety of images can be obtained by varying both the direction and strength of the prevailing wind. These images reproduce many patterns observed on aerial photographs and include meandering stripe patterns and isolated arched strips.

For a more quantitative discussion, we have computed the statistical quantities such as the canopy tree height fluctuation in the wave-regenerated forests. In order to quantify the wave-regeneration processes through the banding process of dieback tree's strips, we have introduced the notion of the power spectral density of canopy tree height fluctuations in such forests. The power spectral density of canopy tree height fluctuations in the wave-regenerated forests presents various shapes in the course of development as shown in Fig. 3. Though the blighted forests present various types of spots patterns and the spectrum shows white noise type at the initial stage [Fig. 3(a)], they are turning into arches and Lorentz type behavior is appearing in the relatively low spatial frequency region of spectrum [Fig. 3(b)]. Finally, they show long banded whitish stripe and we can see the so called $1/f$ type spectrum at low spatial Fourier frequency region [below 10 units of (1/pixel)]. A peak is observed at about 10(units of 1/pixel), which indicates the width between adjacent of dieback zones in Fig. 3(c). This result shows that the biological fluctuations such as canopy tree height should have a very special stochastic property with basically $1/f$ spectrum. From the viewpoint that most biological processes have their own purpose for better maintaining the living state of a biological community, it is expected that $1/f$ fluctuations play a positive role in stabilizing the complicated biological control of wave-regeneration processes in such forests.

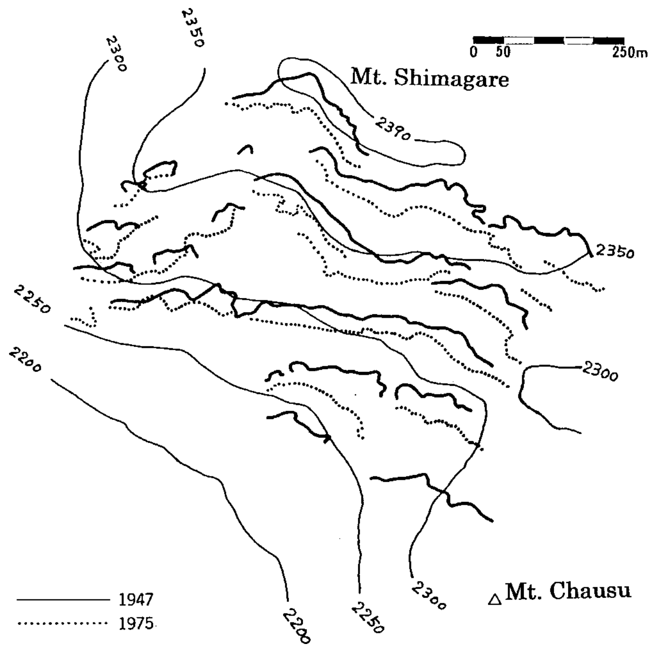

FIG. 4. The movement of borders between the dieback trees zones and the mature trees zones during a 28 yr period in Mt. Shimagare in central Japan. The map sizes are approximately 530 m×530 m. Redrawn from Takahashi [7].

IV. DISCUSSION

In the present paper, the author examined the effect of additional fluctuations to the prevailing wind, which may generate more regular wavelike patterns as seen in the real subalpine coniferous forests. In an attempt to validate the model, the map such as that given in Fig. 4 generated by aerial photography was compared with the patterns generated by the model as shown in Fig. 2. This map presents the movement of the dead tree's stripes during a 28 yr period in Mt. Shimagare in central Japan [7]. We note that dieback trees zones in the map appear either as almost straight lines, or in the various arched form. As a result some differences can be observed in the relative proportions of bands and interbands, but these characters depend mainly upon the mean prevailing wind. According to the model, dead tree's strips occurring at random, possibly as a response to local accidents such as a landslide of a small spatial scale, an infectious disease or herbivore attack, tend gradually to form a dieback stripe oriented perpendicular to the direction of prevailing wind. Observed striped pattern would result from such transitory banding stages. This is the reason why the Lorentz type spectrum is observed in the course of envelopment. The present model indicates that banding can develop from various initial patterns, leading to a number of possible intermediates between such initial patterns and the final banding patterns. Recognition of these intermediates in relation to their occasion may lead to a better understanding of banding processes in such wave-regenerated forests.

The present model calculation here does not describe all the details of the real regeneration process. Nevertheless, the present simulations show that the nonstationary conditions of prevailing wind always plays a central role in the self-organization of regeneration wave patterns with $1/f$ type power spectrum. If a variable wind direction and strength is not included in the model, however, the power spectral density of canopy tree height fluctuations simply shows a peak corresponding to the width between adjacent of dieback zone. As it does not show the $1/f$ type behavior at low spatial Fourier frequency region, then the resulting forest patterns are seen to be more monotonic regular. The variable nature of prevailing wind and the resulting $1/f$ type behavior seen in the power spectral density should be verified in the future field observations on the canopy tree height in the wave-regenerated forest.

ACKNOWLEDGMENTS

The author would like to thank Professor N. Jinno and Miss I. Kawamata for fruitful discussions.

[1] Y. Oshima, M. Kimura, H. Iwaki, and S. Kuroiwa, Bot. Mag. Tokyo **71**, 289 (1958).
[2] H. Iwaki and T. Totsuka, Bot. Mag. Tokyo **72**, 255 (1959).
[3] S. Kuroiwa, Bot. Mag. Tokyo **72**, 413 (1959).
[4] K. Kai, Geogr. Rev. Jpn **47**, 709 (1974) (in Japanese with English summary).
[5] D. G. Sprugel, J. Ecol. **64**, 889 (1976).
[6] W. A. Reiners and G. E. Lang, Ecology **60**, 403 (1979).
[7] F. Takahashi, Shinrin-Kosoku **122**, 10 (1979) (in Japanese).
[8] D. G. Sprugel, Science **211**, 390 (1981).
[9] S. Oka, J. Geogr. Tokyo **92**, 219 (1983) (in Japanese with English summary).
[10] Y. Iwasa, K. Sato, and S. Nakashima, J. Theor. Biol. **152**, 143 (1991).
[11] K. Sato and Y. Iwasa, Ecology **74(5)**, 1538 (1993).
[12] F. Jeltsch and C. Wissel, Ecologic. Model. **5/776**, 111 (1994).
[13] D. L. Dunkerley, Plant Ecology **129**, 103 (1997).
[14] A. Satake, T. Kubo, and Y. Iwasa, J. Theor. Biol. **195**, 465 (1998).