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Analysis of dispersion structure in Japanese red pine populations with reference to topography

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Dispersion structure with reference to topography was analyzed by Iδ-method in the natural populations of Japanese red pine (*Pinus densiflora* SIEB. & ZUCC.). Most of stands less than 10 years old on the bank-slopes along a sunny road exhibited the aggregated distribution, regardless of the inclination and the direction of slopes. This contagiousness was seemed to closely relate with micro-topography of the stands and behavior of seeds with wings after landing onto the ground. All the stands more than 10 years old denoted even-spacing. The change of pattern from the aggregated distribution to the uniform suggested that mortality process operates density-dependently in local among trees. From the standpoint of dispersion structure, there was suggested a possibility of predicting the exact time when self-thinning would start.

INTRODUCTION

Japanese red pine (*Pinus densiflora* SIEB. & ZUCC.) is commonly known as an important tree that occurs at the seral stage of succession, because of its heliphytic character. It often forms pure and even-aged stands under the natural condition after the virgin forest or afforestation was clear cut or burned. Such a tree stand may provides us the valuable information concerning with the dispersion structure of populations or communities different from herbs and grasses that the individuality is not always discrete. It is of ecological intrest to determine the extent to which the dispersion structure manifested by a plant assemblage, *population* or *community* may be rigidly held by its intrinsic nature or may be pliably modified by the environmental variables.

The present study aims to clarify the relationships between the dispersion structure of Japanese red pine populations and the topographic condition, and to elucidate mortality process of trees associated with the developement of stands.

STUDY AREA AND METHODS

The main study area was situated at the eastern coast of Shimane Peninsula, Shimane Prefecture, San'in Region (Fig. 1). Quadrat samplings were carried out in the natural forest stands along a sunny road passing through from Kataku to Mitsu of Kashima-cho, Yatsuka-gun. Qaudrats ranged from 30 m to 140 m above sea level.

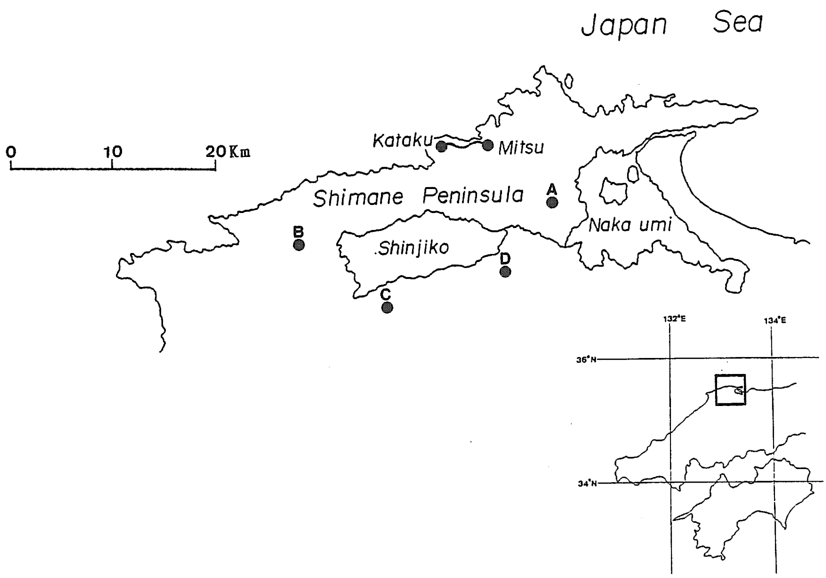

Fig. 1. The main study area was situated between Kataku and Mitsu of Shimane-cho, Yatsuka-gun. A~D are other additional stands. A: Nishimochida, Matsue-shi, B: Higashifu-kumachi, Hirata-shi, C: Ohno, Shinji-cho, D: Shimoinbe, Matsue-shi.

All the young stands less than 10 years old were sampled from seedling or sapling populations on the road-banks. The quadrat size ranged from 16 m^2 through 64 m^2 to 256 m^2 in dimension, properly according to the stand age. The number of stands in which quadrats were set, was twenty-two in total.

The locations of living trees and dead ones were exactly mapped on a section paper. The stand age was determined by counting annual rings of a stumps or the number of boughs or bough's marks on a trunk. Table 1 shows stand age, density of trees per m^2, cross section at the ground, quadrat size, direction and inclination of stand slope. In addition, the data obtained from other stands (A~D) of Izumo Area were ueed for comparative study (Fig. 1 and Table 1). The field survey was carried out in the summer of 1982.

Analysis of the dipersion structure was made by Morisita's $I\delta$-method (Morisita, 1959) which is universally known today. The mortality process of populations was analyzed using τ, an index of local density dependence (Iwao & Kuno, 1969). This index is given by the following formula;

$$\tau=\frac{\overset{*}{m}}{(1-p)\overset{*}{m}_0}=\frac{\overset{*}{m}}{\overset{*}{m}_0}\cdot\frac{m_0}{m}$$

where p is the average mortality rate, m_0 and $\overset{*}{m}_0$, the mean density and mean crowding in the initial population, and m and $\overset{*}{m}$, those after the operation of mortality. The

Table 1. Outline of established quadrats. Stands with asterik indicate those below 10 years old. A: aggregated distribution, R: random distribution, U: uniform distribution.

Stand	Age	Direction	Inclination	Quadrat Size(m^2)	Density per m^2	D_0^2(cm^2)	Pattern
16*	1–3(2.0)	S66°E(E)	45°	16	2.560	6.90	A
9*	1–6(2.2)	N80°E(E)	40°	16	14.700	99.60	A
2*	3–6(5.3)	N45°E(E)	45°	16	8.250	210.00	U
1*	3–8(5.8)	N45°E(E)	45°	16	8.500	—	A
6	14–18(15.4)	N71°E(E)	18°	256	0.246	—	U
18	27–40(32.8)	N55°E(E)	15°	256	0.137	—	U
4*	1–2(1.0)	N50°W(W)	40°	16	3.130	—	A
15*	1–4(1.3)	N45°W(W)	40°	16	8.560	18.30	A
19*	1–5(1.3)	S80°W(W)	35°	16	14.000	19.60	A
22*	1–5(1.8)	N65°W(W)	40°	16	9.250	9.80	A
21*	1–5(1.9)	N65°W(W)	40°	16	4.440	11.20	U
3*	1–6(2.8)	N80°W(W)	55°	16	15.100	67.90	A
8	28–40(35.6)	N70°W(W)	10°	256	0.125	—	U
10*	1–8(2.0)	S 2°E(E)	50°	16	3.750	68.00	A
5*	1–3(1.1)	N15°W(N)	45°	16	18.500	5.00	A
13*	1–3(1.2)	N 0°W(N)	45°	16	3.250	1.50	U
14*	1–3(1.2)	N 0°W(N)	45°	16	2.810	—	A
17*	1–6(2.0)	N30°W(N)	37°	16	7.880	21.00	A
11	13–18(16.)	N15°E(N)	10°	64	0.516	—	U
12	14–20(17.4)	N40°W(N)	20°	64	0.359	—	U
20	20–24(22.4)	N30°E(N)	8°	64	0.234	—	U
7	18–34(29.3)	N25°E(N)	7°	256	0.074	—	U
A*	1–5(2.6)	E 0°S(N)	56°	16	3.060	3.10	A
B*	1–5(2.3)	N80°W(W)	40°	16	8.560	5.10	A
C*	1–5(1.8)	S15°E(S)	45°	16	7.380	5.00	A
D*	1–5(2.1)	S10°W(S)	35°	16	3.130	3.10	R
E*	1–5(2.3)	N25°E(N)	48°	16	9.000	9.10	A

value of τ is equal to unity when the mortality occurs at random in trees, and is less than or more than unity when its action is density-dependent and inversely density-dependent, respectively.

Results

Figure 2 shows schematically the direction and inclination of stands. The stands occurred in slopes of all directions, but more frequently in both of north and west slopes. All the stands less than 10 years old were more than 35° in the inclination. The distribution pattern of trees is given in the last column of Table 1.

Figure 3 illustrates $I\delta$-curves and clump sizes of the most typical ones out of stands less than 10 years old. Only one stand having the highest density was chosen from every direction. Irrespective of some difference in the degree, all the stands indicated

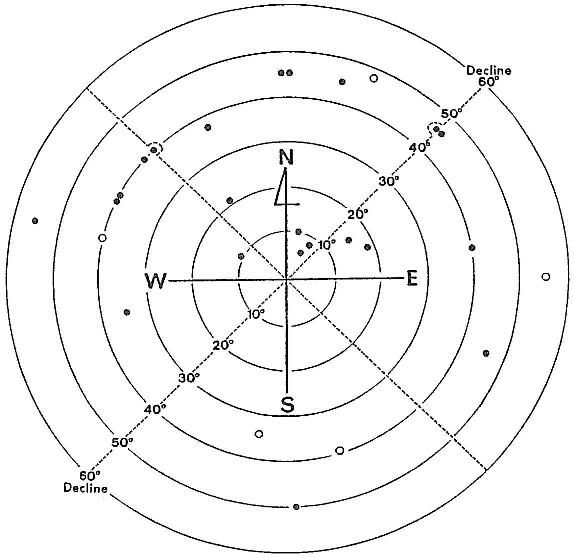

Fig. 2. Showing the direction and inclination of stands. Solid and open circles indicate stands from the main study area and the other additional areas, respectively.

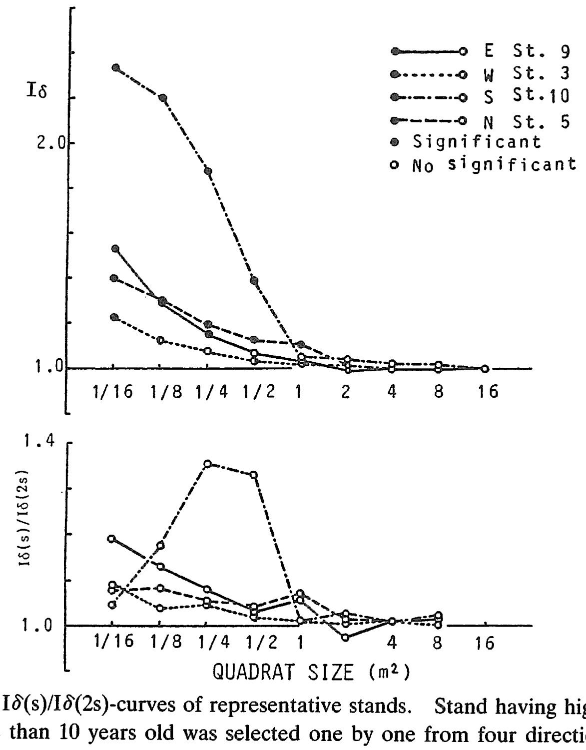

Fig. 3. Iδ- and Iδ(s)/Iδ(2s)-curves of representative stands. Stand having highest tree-density and less than 10 years old was selected one by one from four directions, i.e. east(E), south(S), west(W) and north(N). Solid and open circles in Iδ-curves indicate significant departure from randomness and no sigificance, respectively.

the significantly aggregated distribution. Clump size, which can be estimated by Iδ(s)/Iδ(2s)-curve, ranged from 1/4 m^2 to 1 m^2 in size. The similar trend was recognized in the other stands of which Iδ-curves were not illustrated. For example, with regard to the east slope, the three out of the four stands indicated the aggregated distribution, though there was observed larger differences in the density and the total D_0^2.

Similarly, the five out of six stands facing to the west slope, indicated the aggregated distribution, while the remainning one showed even-spacing. In the north slopes, the three out of the four stands showed the aggregated distribution. A stand facing to the south also showed the aggregated distribution. Additional data (stand A ~D) from other areas also indicated almost similar trend (Table 1).

The distribution pattern associated with the development of stands was examined in every direction of slopes. In the three directions, except for the south, which the data on older stands could not be obtained, the pattern showed a transition from the contagious distribution toward the uniform. As the most typical example, the pattern changes in the north slope are given in Fig. 4. It is worthy notice that there is not found a case of the random distribution, except for stand D.

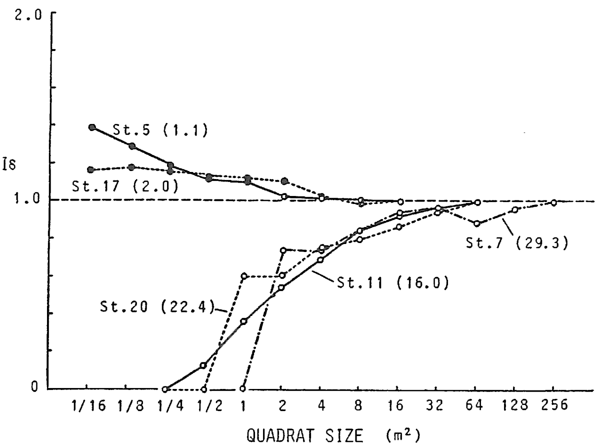

Fig. 4. Successive change of Iδ-curves associated with stand age. All the stands were selected from those facing north.

In both stands including a lot of many dead trees, Nos. 11 (16.0 years old) and 8 (35.6 years old), the mortality process was examined. The transition of the change of pattern in the two stands is shown in Fig. 5. In the former stand, the pattern strengthened the uniformity as time went on, while in the latter, it varied from the significantly contagious distribution to the uniform one. These results may suggest the existence of severe self-thinning among living trees. Therefore, in the three stands including these two, mortality process was analyzed using τ-index (Fig. 6). In the

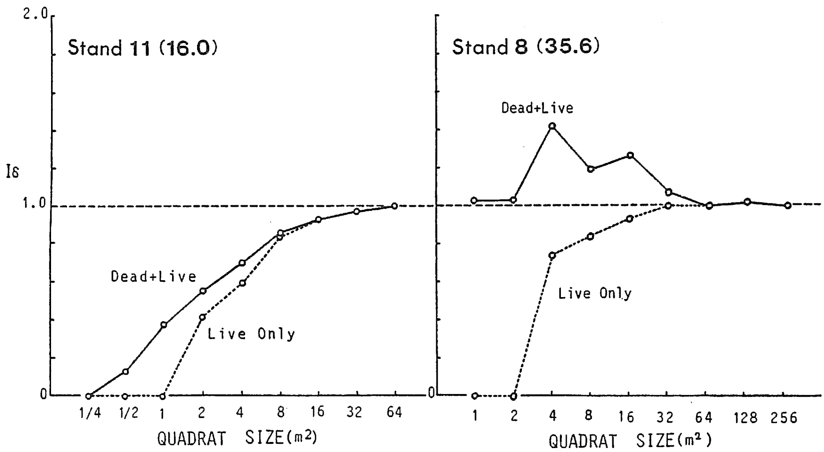

Fig. 5. Distribution patterns in stands including a lot of dead trees. The pattern of all trees including live and dead ones denote that of live trees in a prescribed time of the past.

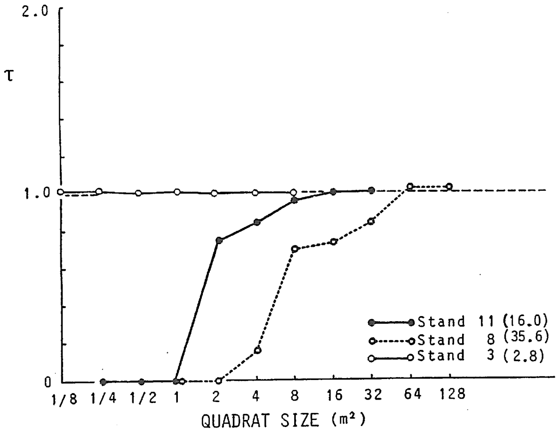

Fig. 6. Analysis of mortality process by means of τ-index. Mortality occurs density-dependently in local.

yougest stand, No. 3, τ kept almost nearly 1.0 with successive changes of the quadrat size. In the other two stands (Nos. 8 and 11), however, it started from null at the quadrat size of 1/4 m^2 or 1 m^2 and approached toward 1.0 at larger grid sizes.

Discussion

In this study, the present author clarified that most of stands less than 10 years old indicate the aggregated distribution, regardless of stand topography, i.e. the direction and inclination, or biological features i.e. as tree density and D_0^2. Miyata (1977) also recognized that sapling population of 5–7 years old of this species showed a loosely clumped distribution in Ebino Height, South Kyushu.

Many investigators have hitherto demonstrated that a number of plant populations indicated the aggregated distribution in early stages of stand development (Archibald, 1948, 1950, Barnes & Stanbury, 1951, David & Moore, 1955, Kershaw, 1957, Cooper, 1961, Cooper et al., 1959, Tagawa, 1963, 1965, Leassle, 1965, Odani, 1967, Kitamoto, 1972, Kanazawa, 1982b, Miyata & Haramoto, 1986, 1987). Some workers reported that seedlings or saplings forming the understory or groundstory under the canopy are often distributed contagiously (Ogawa et al., 1961, Tagawa, 1965, Miyata et al., 1963, Miyata, 1964, Kitamoto & Shidei, 1972, Kamitani & Maruyama, 1978, Yamamoto & Tsutsumi, 1979, Kanazawa, 1981, Nakashizuka & Numata, 1982, Ishizuka, 1984).

This type of contagiousness may be due to such factors as the vegetative reproduction by rhizomes or stolons, seed dispersal by bolochory or zoochory, allelopathy, heterogeneous distribution of the environmental variables, etc. The Japanese red pine is an anemochore with wings and its seeds are often carried out to a few hundred meters from the parent tree by a wind. According to the definition of Harper (1977) and Grime (1979), Nakagoshi et al. (1982) reported that the current species belongs to D strategy with the newly invaded seeds.

At the present, it is not clear how the seeds of red pine are dispersed on the ground surface of the forest. However, we can expect that seeds would fall onto the forest floor more or less contagiously. Outside the forest, on the other hand, they may make a landing more randomly by a wind as far as becoming more distance from the parent trees. Regardless of such possibility, why do the seedlings or saplings on the bank-slopes of the road are contagiously distributed?

A hypothesis to be elucidated is as follows: Seeds make a landing once on the bank-slopes at random. Then they are gradually blowed together into the micro-concave sites of the slopes, winding thread on spool, because they wear the wings yet. As such the sites are often moderatley moist and fertile, seeds germinate well and seedlings establish quickly. Consequently, seedlings or saplings are distributed contagiously. The concave sites occur widely almost independently of the direction and inclination of the bank-slopes. As this statement is merely a hypothesis, the more detailed study on dynamics of seed dispersal and seedling establishment on the bank-slopes must be reserved for the future.

Some workers has pointed out that the degree of contagiouness of the population is determined by the time length during which species has been present in succession. Tagawa (1965) founded that the distribution pattern of a species population changes, in accordance with certain principle, with its density in the primary and secondary succession. In other words, most species indicate the contagious distribution in the early density-increasing stage while they indicate the other types of the pattern in only the maximum and decrease stage of density. In even-aged stands, such as *P. ponderosa, P. clausa, P. densiflora.* etc., we can often observe a definite change of pattern from the contagious distribution in younger stands through the random distribution in the developmental stage to even-spacing in the mature state (Cooper, 1961, Laessle, 1965, Miyata, 1977).

As mentioned previously, all the stands more than 15–16 years old of the present study areas showed the even spacing without exceptions. This result prefectly coincides with one reported by the present author (1977) in the stands of Ebino Height. Uniform distribution may be resulted from severe competition for light among trees. The foliage biomass in unit land area of even-aged and pure *Pinus* stands reaches to a maximum at early stage of 15–20 years old and then decreases somewhat to reach a more or less constant level. This trend is likely to be maintained for considerably long period, whereas total biomass increases monotonously with the stand age (Sakaguchi et al., 1957). An abrupt decrease of foliage biomass in 15–20 years old stands results from severe and quick self-thinning among trees.

The reason why the cases of the random distribution is fewer may means that the density-dependent mortality proceeds quickly at the fairly limited period of stand development. The analysis by τ-index of mortality process suggested that self-thinning occurs density-dependently in local among trees after 15–16 years of stand development. Accordingly, from the standpoint of dispersion structure, we can predict the exact time when self-thinning would start in the natural stands of Japanese red pine.

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