ANIMAL INFLUENCES ON JAPANESE PINE SEEDS
OF THE FOREST FLOOR
II. SEED INPUT AND OUTPUT OF SEEDLING WITH SEED COAT

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アカマツの種子におよぼす動物の影響
II. 種子の生産と稚樹の形成

Synopsis

The process from seed input to seedling output of the Japanese red and black pine was investigated in the forests of Iwakura, Tanakami, and Kiryu during the period from seed fall to soil emergence. Pine seeds produced are exposed to enemies such as squirrels on the tree and birds or field mice on the seedbed. A small part of the seeds was consumed by squirrels (2.6-13.9%) and most of the fallen seeds on the forest floor were attacked by birds and field mice (86-97%). Seed relocation due to rain showed remarkable difference between on litter and on naked soil. Seedlings emerged were very small compared with the number of seeds produced. This may be entirely due to animal damage. Seed-glueing method to catch clues responsible for animal agents seemed to be available.

Introduction
There are perhaps few studies on the process from seed production (seed input) to seedling emergence (seedling output) in different types of forests. In various trees as well as pines, the survival of the offspring is generally associated with internal and external factors. There are physiological and hereditary factors as internal ones, and biotic or abiotic factors seem to be the external factors. In case of pines good seed production has not been always contributory to many seedling emergence. As a part of the above factors, damage due to animals on pine seeds was emphasized (Taylor &

Accepted June 13, 1975

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To understand the natural regeneration of pine forests as well as other forests, seed crop estimation, biotic or abiotic influences on the pine seed of the seedbed, and the germination rate on the natural seedbed should be studied as the main investigations. Seed crop estimation by the seed trap will provide reliable information regardless of the good or bad seed crop and of site quality, while it costs much time and efforts compared with the allometric method such as D²H (or D³)-cone number. A representative study on seed production, adopting the seed trap, was carried out by Tagawa (1969) in the evergreen forests in Japan.
Pine seeds are comparatively small and their color is similar to litter or soil. And they are rich in nutrients such as carbohydrates and fats (Mikov, 1967). The former makes it difficult to trace the whereabouts of the pine seeds on the forest floor and the latter is one of the reasons responsible for animal damage. Most pine seeds on the forest are attacked by animals, birds and small mammals throughout the year (Rim & Shidei, 1974). Thus, it is necessary to investigate the animal damage quantitatively. This study is an attempt to make clear the process from seed input to seedling output in some Japanese pine forests.

**Site Description and Methods**

The Japanese red pine forests of Iwakura (Kyoto Prefecture), Kiryu (Shiga Prefecture), and the Japanese black pine forest of Tanakami (Shiga Prefecture) were selected for this study. Pine trees seen in the sample areas are shown in Table 1. As shown in the typical pine forests in Japan, undergrowth is developed well in each site. The main trees of the undergrowth were 31 species and the ground flora is dominated by *Rhododendron* species and *Ilex pedunclosa*. The vegetation of the Tanakami site was comparatively simple and poor in leaf litter.

Seed crop estimation was carried out by a seed trap. To protect seeds from animals such as squirrels, doves, and field mice, a wire netting cover was used. The seed trap designed for use in the pine forest consists essentially of a large polythene bag hung mouth upwards from a square wood frame measuring 40-40 cm in size and mounted on a wood stake.

To test if the pine seeds falling from the trees would bounce out of the traps, 100 pine seeds were thrown in the trap three times from various angles. No loss of the seeds was observed. The polythene bag tends to move slightly with the wind, but the contents of the seed bag was observed to be safe because of the top cover. Sixteen traps at the Iwakura sample area, 36 at Tanakami, and 64 at Kiryu were set up in parallel within a quadrant of 20-20 meters respectively. As the pine seeds fall in late October, the seed trap was set up during the period from the 17th to 20th in October 1973. The first seed collection was done in late November and further collections were carried out by opening a part of the trap cover and collecting the whole contents with a beaker. All seeds collected were classified into three groups; sound seeds, un-matured seeds, and destroyed seeds. Sound seeds are lustrous and gray in color, whereas the un-matured ones are light colored. The unmatured seeds were dissected to confirm the contents of the

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**Table 1. Tree inventory at each sample area (20 × 20 m).**

<table>
<thead>
<tr>
<th></th>
<th>Iwakura</th>
<th>Tanakami</th>
<th>Kiryu</th>
</tr>
</thead>
<tbody>
<tr>
<td>DBH range (cm)</td>
<td>6.9-28.8</td>
<td>1.6-12.0</td>
<td>4.0-48.8</td>
</tr>
<tr>
<td>No. of trees</td>
<td>38</td>
<td>106</td>
<td>32</td>
</tr>
<tr>
<td>Height (m)</td>
<td>5.6-16.0</td>
<td>1.7-7.8</td>
<td>6.5-23.0</td>
</tr>
<tr>
<td>Owners</td>
<td>private</td>
<td>national</td>
<td>national</td>
</tr>
<tr>
<td>Main species</td>
<td><em>Pinus densiflora</em></td>
<td><em>Pinus thunbergii</em></td>
<td><em>Pinus densiflora</em></td>
</tr>
<tr>
<td>Dominant ground flora</td>
<td><em>Rhododendron</em> spp.</td>
<td><em>Rhododendron</em> spp.</td>
<td><em>I. pedunclosa</em></td>
</tr>
<tr>
<td>No. of ground flora spp.</td>
<td>22</td>
<td>17</td>
<td>31</td>
</tr>
</tbody>
</table>

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**Fig. 1. Seed trap covered with wire netting to protect the seeds from animals.**
seeds. Seeds destroyed by the animals are shown in Photo 1.

To confirm the animal damage of pine seeds on the forest ground, the thin thread-glueing method (Rim & Shidei, 1974) was adopted. This method is effective for about three months on moisture soil or litter and for one year or more under natural conditions. Squirrel damage on the tree and field mice damage on the seedbed were confirmed by the hulls of the destroyed seeds. Considering the decreasing rate in seed fall in the course of time, the seed density for observing animal damage was treated as follows; 20 seeds per square meter in November 1973, and 10 seeds in December were placed on the forest floor. In other months 5 seeds were treated in the same way. The germination rate on the forest floor was observed by using a polyvinyl beaker without the bottom. The above-ground part of the beaker, had many small holes for ventilation at the side wall and the top was covered with wire netting to protect it from animals. Seeds for the germination test on the forest floor were placed on or under litter and on naked soil during the period from late December to late April 1974. The germination rate in the laboratory was obtained by placing the sample seeds on wet filter paper for a month. Seeds for the germination test were collected from each sample area. The test for seed relocation due to rain was carried out only at Tanakami site. The first test for relocation due to rain was done by using coated seeds under natural conditions, but this failed because of field mice damage. Therefore to protect the seeds from field mice, a wire netting was fenced at the site. This experiment was carried out twice; April and May, in 1974.

Results and Discussion

1. Seed production

The seed traps showed a distribution in the sample area of 28,700 seeds at Iwakura, 16,200 at Tanakami, and 14,000 at Kiryu. The seed fall before December was 67 per cent at Iwakura, 51 at Tanakami, and 62 Kiryu, of the yearly crops respectively. The Japanese red pine showed a higher rate in seed fall than the Japanese black pine in the same period. This result coincided with that of the previous report (Rim & Shidei, 1973c). This phenomenon seemed to be a serotinous problem, especially in the Japanese black pine. The monthly distribution for the Japanese red and black pine seed fall is shown in Fig. 2. Seed fall decreased suddenly in December and thereafter slowly. Seed fall was over in July in the Japanese red pine, and more protracted in the Japanese black pine than in the red pine. One of the reasons seems to be cone serotiny.

The Iwakura site showed the maximum seed production among the three sample areas, and Kiryu was the least even though it had the tallest trees.

According to some reports on pine seed production, 1,800,000–3,000,000 seeds per hectare were produced (Inoue, 1958; Kochi Regional Forest, 1972; Shidei, unpublished data from 1966). Seed crop in the study areas was very small compared with the above results. There should be

![Photo 1. Hulls of Japanese red and black pine seeds destroyed by squirrels and field mice.](image)

![Fig. 2. Monthly distribution of Japanese red and black pine seed fall, Iwakura: red pine, Tanakami: black pine, Kiryu: red pine.](image)
among the sites difference in environmental factors such as precipitation, site quality, temperature, tree age and size, and tree space related to seed crop of the Japanese pines. Besides the environmental factors, internal factors such as heredity characters may be related to cone crop. It has been repeatedly observed that certain trees are consistently heavy producers, while certain trees are consistently barren (Mathews, 1963). Furthermore the quantity of seeds produced by the red and black pines, as in most other conifers, varies from tree to tree, from year to year, and from place to place. Considering from the above results, allometric estimation should also be studied in the present area in more detail.

2. Dispersion of pine seeds

It is worthy to understand the dispersion pattern of fallen pine seeds, because the dispersion pattern seems to be related to the animal damage rate. Some indices for measuring the dispersion pattern of plants and animals were attempted by quadrat counts (Greg-Smith, 1964; Morisita, 1959). In this study, $I_e$-index, which is superior in measuring the aggregation tendency because it is unaffected by the difference in mean density, was adopted. This index was proposed by Morisita, and the value can be calculated by the following formula:

$$I_e = \frac{\sum_{i=1}^{q} n_i(n_i-1)}{N(N-1)}$$

where $n_i$ is the seed number in the $i$th sample unit ($i = 1, 2, 3, \ldots, q$), $q$ is the number of sample units, and

$$N = \sum_{i=1}^{q} n_i$$

$I_e$-index based on the seed sample, collected at monthly intervals, is shown in Fig. 3. The dispersion of fallen seeds on the forest floor, on the whole, showed a clumped distribution.

The seed dispersion on the forest floor is not always uniform in terms of $I_e$-quadrat size relations.

3. Relocation of seeds due to rain

Seed relocation due to rain water is not a simple phenomenon. At least this may be related to the inclination of the site, soil surface conditions, kinds of litter, depth of litter, size of rain drop, and amount of precipitation. It is difficult to obtain reliable data including all of the above factors. This experiment for relocation of the seed due to rain is not sufficient, but this is an attempt for further study. Fig. 4 shows that the distance of relocation of the seeds due to rain water tends to increase remarkably with inclination in case of naked soil, while seeds on litter were relocated only a small distance compared with that of the naked soil. Litter is a good obstructor for pine seeds transported by rain.

4. Animal influences on pine seeds of forest floor at each site

Animals that attacked pine seeds were confirmed to be squirrels on the tree and field mice or birds on the forest floor. Damage by squirrels on cones begins even when unmatured.

This damage was confirmed by binocular observation. Only cone bodies without scales are found from place to place on the forest floor. Squirrels bite pine cones to remove the cone scales and to eat the pine seeds beneath them. Such behaviour has
been observed on the branches of pine trees or on rocks. They left the cone body and scales on the ground. The hull of the seeds attacked by them are too similar to distinguish them from the ones attacked by field mice. The number of seeds damaged by the animals in the areas studied was 1,800 at Iwakura, 2,700 at Tanakami, and 6,200 at Kiryu. In terms of per cent, it was 2.6, 6.7, and 13.0 respectively. As shown above, the damage rate due to squirrels differed from site to site. The main enemies of the pine seeds on the forest floor were the field mice and birds. The hulls of destroyed seeds damaged by the field mice are different from that by birds (Rim & Shidei, 1974). The damage rate due to animals on the forest floor is shown in Fig. 5. November and December, when the seed fall was abundant, showed a low predation rate, while in other months a comparatively high rate of damage was observed. If higher density such as 50 or more seeds per square meter had been treated in November and December, a higher predation rate would have been obtained. The remaining seed number was gained from following formula:

\[ N(t) = N(o) R(t) , \]

where \( N(t) \) is the remaining seed number, \( N(o) \) is the fallen seeds on the seedbed, and \( R(t) \) is the remaining rate for time \( t \).

In the previous study, density dependence was observed in the open or adjacent part of the forest, while density independent was done on the forest floor. In other words, the damage rate due to animals on the forest floor was higher than in the open or adjacent parts of the forest. But it seemed that this is not necessarily true of all cases, as there are several known cases in which the population density is apparently quite dependent on the amount of food available. However, should the predator population reach a density where the pine seed resource becomes limited, the density-dependent factors will become the deciding answer to the impossible increase of the population over its supply. Poole (1974) pointed out that the population may be regulated by density independent-factors at one time and density-dependent factors at another. In fact a density-dependent factor in some situation may act as a density-independent factor in others. When especially the pine seed density was low (from March to October), the

![Fig. 4. Relation between inclination and relocated distance of pine seeds due to rain water.](image1)

![Fig. 5. Monthly changes of predation rate of pine seeds due to animals.](image2)
density-independent type was observed on the forest floor. Considering the relationship between seed input and animal damage, the seed number responsible for germination was too small.

5. Germination rate

The seeds which were sown in late December 1973 germinated in late April 1974. The germination rate on the forest floor under various seed-bed conditions was reported in the previous report (Rim & Shidei, 1974). This experiment dealt with the seedbed, on or under litter. The germination rate at Iwakura was higher than that at Kiryu. The authors tried to carry out the germination test as far as possible under natural conditions. But animal damage made it difficult to test germination under natural conditions. Field mice take even color-coated seeds with poison.

In the Japanese black pine the difference in germination rate between the laboratory test and natural conditions was very small, whereas the red pine showed a remarkable difference. High germination at Tanakami seemed to be due to the mineral soil and sufficient light. The germination rate obtained at the Kamigamo site during the period from September to October 1973, revealed a value similar to that gained at Iwakura during the period from December 1973 to April the next year.

6. Seedling emergence and distribution

A seedling map was made to check seedling emergence and changes of seedling number. The disappearance due to damping-off can be confirmed by investigating the dead seedling stem. The seedling number in the sample areas observed from late April to late May was 27 at Iwakura, 60 at Tanakami, and 52 at Kiryu. The expected seedling number was 61, 67, and 62 respectively. The difference between the observed number and expected one was very small except at the Iwakura site.

Seedling distribution on the forest floor at the Kiryu site is shown in Fig. 6 and this $I_r$-index was followed by Morisita to be the same as the seed dispersion. The dispersion of seedlings revealed a high degree of clumped pattern as the pine seed distribution. And this result agreed with those of the Kochi Regional Forest (1972). Though predator density was not investigated in this study, the seedling distribution may probably be related to animal density.

7. Model of seed input and seedling output in Japanese pine forests

A schematic illustration showing the process from seed input to seedling output is sometimes convenient to understand a part of the ecosystem. More important is to realize the variance such as seed crop, size, habitat conditions, viability and mortality among the different species.

There is a further possibility that the seed input of pine species is in the nature of a physiological accident quite independent of the immediate needs of the plant and governed chiefly by hereditary factors with little or any direct relation to the survival value. Among many environmental factors during the germination period, biotic factors such as animals seem to be the most serious to pine seeds according to the results obtained from the authors’ investigations. The efficiency of seed production is a term used by Weaver & Clements (1929) to note the effective seed crop available for germination after a part has been destroyed by birds, animals, insects and by other injuries. If these agencies consume a large part of the seed, the efficiency may be decreased.

Rodents are often so destructive of lodgepole pine seed that efficiency is practically zero every year, so the number of seeds produced by the tree is large but the efficiency is almost nil (Weaver & Clements, 1929).

Table 2. Germination rate at each site (%).

<table>
<thead>
<tr>
<th>Seed bed condition</th>
<th>Iwakura</th>
<th>Tanakami</th>
<th>Kiryu</th>
</tr>
</thead>
<tbody>
<tr>
<td>Removal of litter</td>
<td>53.0±0.0</td>
<td>92.7±2.2</td>
<td>46.0±5.3</td>
</tr>
<tr>
<td>On litter</td>
<td>54.3±4.2</td>
<td>92.0±2.0</td>
<td>48.3±8.3</td>
</tr>
<tr>
<td>Under litter</td>
<td>56.3±5.1</td>
<td>93.0±1.5</td>
<td>40.7±10.2</td>
</tr>
<tr>
<td>No undergrowth area</td>
<td></td>
<td></td>
<td>48.0±6.0</td>
</tr>
<tr>
<td>Lab. test</td>
<td>85.0</td>
<td>98.3</td>
<td>83.7</td>
</tr>
</tbody>
</table>
A schematic illustration revised from the model of Tagawa (1969) is shown in Fig. 7.

The main factors which may decrease the efficiency of pine seeds on the tree are serotinous cones and animals such as squirrels. Besides squirrels some insects were cited as the seed consumer (Stanley & Thomas, 1969). But in this study the authors failed to detect insects as a pine seed consumer on the pine tree.

Protracted seeds in retarding the release from the cone was about 0.3 per cent in the Japanese red pine and about 1.7 per cent in the Japanese black pine in August 1973. Serotinous cones are a good food resource for squirrels during summer. The remaining seeds attacked by animals fall down on the forest floor. And thus they are always exposed to enemies. Most fallen seeds are consumed by animals and only a small part of them are responsible for germination (Fig. 7). The predation rate depends on the plant species and districts. Gashwiller (1967) noted that during the germination period bird and mammal losses were only one per cent in the Douglas-fir and 15 per cent in the hemlock.

Rain water is certainly responsible for relocation of the seeds on the forest floor. Litter obstructs the flowing of seeds. In the germination period of a little precipitation, the relocated distance of pine seeds due to rain seemed to be small.

The germination rate in the Japanese red and black pine was very high on the natural seedbed, compared with other species such as Chamaecyparis obtusa (Kamo, unpublished data from surveys in 1972-1974). Considering the enormous seed crop and comparatively high germination rate, many seedlings may be expected to emerge. But in fact only a small number of seedlings were observed. Seeds under litter as well as on litter are attacked by field mice. And seeds under litter are comparatively safe to birds but dangerous to field mice. Even the seedlings with seed coat are attacked by animals (Rim & Shidei, 1973a, b).

Among various limiting factors to pine seedling emergence in the Japanese pine forests, animal influence seems to be one of the decisive factors.

Summary

Considering a number of seed crops and a comparatively high germination rate under natural conditions, many seedlings of the pine tree are expected to emerge. This study was carried out to make clear the process between seed fall and the next year seedling emergence. The study areas selected for this study were the forests of Iwakura (red pine), Tanakami (black pine), and Kiryu (red pine). The seed trap and seed-glueing methods were adopted to estimate the seed production and animal influences on the pine seeds. It was difficult to obtain clues responsible for animal damage because of the small size of the pine seeds and their color being similar to that of the soil or leaf litter. To solve this problem, the seed-glueing method was devised by the authors. Namely, a thin thread was glued on the surface of the pine seed with emulsion of polyvinylacrylate. As the relocated distance due to rain seemed to be little on the forest floor during the germination period, this method was attempted. The results obtained in this study are as follows;

1. Among the number of seeds produced, only those that remained in April were responsible for germination.
2. The remaining seeds was obtained from the
seed fall and damage rate due to animals. If we
knew the germination rate in the Japanese red and
black pine under natural conditions, the expected
seeding number could be gained easily.
3. The seed-gluing method gave reliable infor-
mation during the period from seed fall to seedling
emergence, but in the rainy season it was effective
for about two months. This method may not be
available on naked soil during the rainy season.
4. Animal influence as a serious limiting factor to
natural regeneration of pines was confirmed in this
study.

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摘 要
マツの種子が生産されてから発芽に至るまでどの程度
の種子が損耗しているかを、京都盆地と滋賀県周辺の
アカマツ林や滋賀県田上のクロマツ林で調べた。種子の
生産量は有茎種子トラップを使い、また種子に対する動
物の影響は種子揚法によって調べた。その結果は次の
ようである。
1. マツの種子に及ぼす動物の影響をみると種子の落
下以前の状態ではリスによる被害が2.6〜13.9％程度を
示し、落葉後は86〜97％の種子が鳥類や野ネズミ類によ
って食害された。
2. 雨水による種子の流下は衝突の傾斜度や林床にお
けるリターの被覆状態によって大きく影響された。
3. そして種子が生産されてから稚樹が形成されるま
でにおよそ99％以上の種子が主に動物による摂食によ
って損耗していくことが明らかとなった。