The trend of soil seed banks in climax forests in Japan

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Synopsis

The buried viable seeds in the climax forests of Japan decrease in number in proportion to the degree of latitude and altitude. The seed density of woody species clearly decrease from the warm-temperate forest to the subalpine forest. High density of seeds of woody species and rich flora of seed banks in the temperate broad-leaved forests function in the recovery of plant biomass, the rapid recruitement of seedling population, and the maintenance of community diversity. On the other hand, the poor seed bank of the subalpine conifer forest causes slow recovery after forest disturbances.

Climax forests, growth season, Japan, life history, seed banks, vegetation zone

Introduction

A seed bank is defined as seeds buried alive in soil in the plant growth season, producing seedlings when conditions are suitable for germination. It is contrasted with the growing plant population, and is regarded as the potential plant cenopopulation. Studying the seed banks in climax forests is very important for understanding how many seeds are in soils as the successors of climax forests. It also makes possible to estimate the species composition and structure of the initial plant community following a disturbance of climax forests. There are already some papers on the buried seeds in climax forests in which the full data of seed density on every species are listed, and they are as follows: OOSTING & HUMPHREYS (1940), OLMSTED & CURTIS (1947), KARPOV (1960), KELLMAN (1970, 1974), GUEVARA & GÓEZ-POMPA (1972), STRICKLER & EDGERTON (1976), HAYASHI (1977), WHIPPLE (1978), NAKAGOSHI (1981, 1984a, 1984b, 1985b), PETROV (1981), PETROV & PALKINA(1983), GRANSTÖM (1982), and NAKA & YODA (1984).

After these sporadical publication of soil seed banks in forests, LECK et al. (1989) reviewed the ecological studies on soil seed banks. Their conclusion, however, seemed to discuss few on climax forests due to the shortage of papers which record full species composition in soil seed banks. This study deals with the ecological features of the seed banks in several types of climax forests in Japan and their comparisons along an eco-geographical zonation and is a revision of the previous paper (NAKAGOSHI, 1992). Some papers on seed banks in climax forests in other regions are referred in this study to discuss the altitudinal and latitudinal gradients of buried seed populations.

This is my great honor to be able to submit this paper to the occasion of the publishment of the special issue of Gesellschaft für Ökologie which will be dedicated to Prof. Dr. Reinhard Bornkamm in February, 1996. I believe that many of his research activities have made a great influence to the Japanese ecologists.

Study Sites

Three climatic climax forest zones can principally be distinguished in the mainland Japan. They are warm-temperate evergreen broad-leaved forest zone (*Camellietea japonicae* MIYAWAKI et OHBA 1963), temperate deciduous broad-leaved forest zone (*Fagetea crenatae* MIYAWAKI et al. 1964) and subarctic or subalpine evergreen coniferous forest zone (*Vaccinio-Piceetea* BR.-BL. 1939). In addition, there are climax conifer forests on the steep slopes of mountains between the warm-temperate zone and the temperate zone. In this study, following 7 stands of climax forests in Japan are selected to study the buried seed populations in soils (Fig. 1).

1. *Castanopsis cuspidata* (Thunb.) Schottky forest located at Moto-ujina in Hiroshima City (40m in altitude, 34° 19' N lat., 132° 29' E long.) surrounded by Hiroshima Bay. Soil was collected in July, 1981.

2. *Castanopsis cuspidata* var. *sieboldii* (Makino) Nakai forest on Mt. Futatabi in Kobe City (350m alt., 34° 43'N lat., 135° 11' E long.) as the protected forest of the Tairyu-ji temple surrounded by the old-growth *Pinus densiflora* forest. Soil was collected in June, 1980.

3. *Abies firma* Sieb. et Zucc. forest on the foot of Mt. Misen on Miyajima Island (20–90m alts., 34° 16'N lat., 132° 19' E long.). Two plots are separately located in the Forest Reserve as the Misen primary forest which is in the *Camellietea japonicae* zone. Soil was collected in July, 1973.

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* Dedicated to Prof. Dr. Reinhard Bornkamm on the occasion of his 65th birthday.

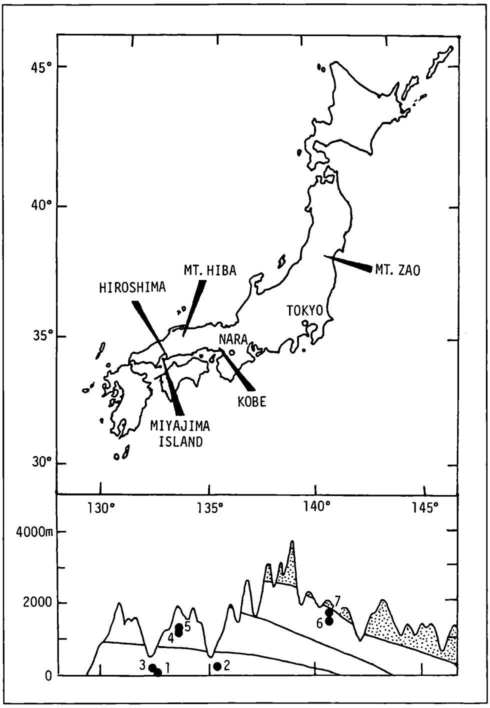

Fig. 1

Map of Japan showing the study sites, Nara and Tokyo. The numbers are the locations of investigated stands in three main forest zones.

4. *Fagus crenata* Blume forest subordinated as the typical type (NAKAGOSHI 1984b) on the slope of Mt. Hiba in southwestern Japan (1180m alt., 35° 04'N lat., 133° 04'E long.). This site is in the wide forest reserve. Soil was collected in May to June, 1978.

5. *Fagus crenata* forest subordinated as the *Dryopteris austriaca* type (NAKAGOSHI 1984b) in the humid hollow on Mt. Hiba (1250m alt., 35° 04'N, 133° 04'E long.) where continuously covered with forest vegetation. Soil was collected in May to June, 1978.

6. *Abies mariesii* Masters forest with moss type floor on the middle part of long slope of Mt. Zao in northeastern Japan (1380m alt., 38° 08'N lat., 140° 29' E long.). This forest locates in the primary conifer forest. Soil was collected in August 1979.

7. *Abies mariesii* Masters forest with floor covered by *Sasa kurilensis* near a flat ridge on Mt. Zao (1540 m alt., 38° 07'N lat., 140° 28'E long.). Soil was collected in August 1979.

Methods

A large number of seeds were detected between 0 and 10 cm depth in the soil of the temperate broad-leaved forests of Japan (NAKAGOSHI 1981, 1984a,b). A soil volume of 80 litres (0.8 m^2 surface area x 10 cm depth) was collected from a climax *Fagus* forest and from a secondary *Quercus-Castanea* forest respectively after the seed dispersal season. Curves relating the number of species retrieved to soil volume were constructed from increasing the number of this 80 litres sample (NAKAGOSHI 1984b). The numbers of species producing seed in the *Fagus* forest and the *Quercus-Castanea* forest (15 m x 15 m size quadrat) were 15 and 35 respectively. These numbers of species were represented in the buried seed populations obtained from 12 litres (0.12 m^2 x 10 cm) and 36 litres (0.36 m^2 x 10 cm) of soil respectively. (NAKAGOSHI 1984b).

After these procedures, the volume of soil sample was fixed at 0.4 m^2 surface area and 10 cm depth (40 litres in volume) at 3 stands. At the other 4 stands, the soil above 5 cm depth was collected and the density of seeds in soil between 5 to 10 cm depth were estimated by the data from a core sample in each stand. It was noticed that the root length of emerged seedlings was shorter than 10 cm in the temperate forests (NAKAGOSHI 1985a). Ten random soil samples of equal size were collected in both the growth season and the dormant season after seed dispersal.

The buried seeds were separated from the soil in order of size by using different mesh (4,2,1.5,1 mm) sieves. It was difficult to identify woody species by germination tests because of their low germination rates (NAKAGOSHI 1985a), therefore, those seeds were identified by external morphology and their viability by the existence/of an embryo or an endosperm. It was not possible to identify the viability of some seeds, so tetrazolium chloride staining (TTC test) was also used to check the viablity of those seeds.

In the greenhouse, germination tests were conducted with those seeds which went through the 1.5 or 1 mm mesh sieve. The germination tests were carried out during a 100-day period. This period is considered sufficient to detect almost all the buried viable seeds in the forest soil (NAKA & YODA 1984). Unfortunately, I could not identify some of them due to their immediate death although their seedlings have emerged from soil (NAYLOR 1985).

The species occurred in seed banks were classified into 3 categories reflecting the reproductive aspects in each forest as follows:

1. seeds of the fruiting species in the forest
2. seeds of the vegetative species in the forest
3. seeds of species not presently growing in the forest

The life/dormancy forms (NAKAGOSHI 1985a) of species are as following abbreviation:

MM: meso- and mega-phanerophytes
M: micro-phanerophytes (ML: liana)
N: nano-phanerophytes (NL: liana)
Ch: chamaephytes
H: hemicryptophytes
G: geophytes (cryptophytes)
Th: therophytes

Nomenclature follows OHWI & KITAGAWA (1983).

Results

In Japan, it is found that the numbers of species and seed grains in the growth season decrease compared with those in the dormant season (NAKAGOSHI 1981, 1984a, b, 1985b). On the other hand, adequate portion of buried viable seeds was reserved in the growth season showing in Table 1. Namely, these seeds were dormant even during the growth season, and they composed the permanent seed banks in the climax forests.

In Table 1, two micro-phanerophytes, *Eurya japonica* and *Dendropanax trifidus* were dominant in the seed bank of the *Castanopsis cuspidata* forest in Hiroshima. The density of buried seeds of the *Castanopsis cuspidata* var. *sieboldii* forest in Kobe was lower than that of the *Castanopsis* forest in Hiroshima. On the contrary, the number of species in the seed bank of the Kobe's forest was larger than that of the forest in Hiroshima. In Kobe, the seed of *Eurya japonica* was solely dominant in the seed bank of the *Castanopsis* forest. The seeds of phanerophytes, *Mallotus japonicus, Rhus succedanea, Rh. trichocarpa, Clerodendron trichotomum,* and *Zanthoxylum schinifolium*, were reserved in soils of the *Castanopsis* forests. These species generally emerge from the deposited seed and grow in the substitutional community following disturbances of forests together with *Aralia elata*, *Rhus javanica, Rubus microphyllus* and *R. palmatus.* If there are no disturbances such as wind damage, clear cut and wildfire, these seeds stay in the dormant stage and never germinate. No nuts of *Castanopsis cuspidata, C. cuspidata var. sieboldii* and the evergreen *Quercus* were observed in these climax *Castanopsis* forests in the growth season.

A total of 11 species and 258 seeds per m^2 occurred in the soil of the *Abies firma* forest situated on the warm-temperate slope of Miyajima Island (Table 1). Viable seeds of *Abies firma*, the dominant tree, could not be found in soils of either season. This might be caused by low seed production of *Abies firma* and the unsuitable environment of forest floor including browing by deer to its dispersed seeds (NAKAGOSHI 1985b.) On the contrary, *Cryptomeria japonica* produce seeds despite low dominance of the aboveground vegetation. *Mallotus japonicus* and *Vitis flexuosa* were detected in the seed bank, and they are known to grow in disturbed sites, chiefly felling and fire sites. The results also suggest that *Symplocos glauca, Cinnamomum camphora* and *Cleyera japonica* probably maintain their population by generative reproduction producing seeds in this *Abies firma* forest.

An annual weed, *Crassocephalum crepidioides*, widely disperses its anemochoric seeds in the climax forests of the warm-temperate zone. This weed is a character species of the *Crassocephalo crepidioidis-Erechitetum hieracifoliae* MIYAWAKI 1967 at the open sites such as clear cut or post-fire stands.

In the early spring, seedlings emerge on the floor of the *Fagus crenata* forest owing to the good thermal conditions under the open canopy. As a result, the reserved seeds decrease and the reserve ratio of buried seeds in the *Fagus* forests indicates lower value compared with those of the climax forests of evergreen trees. The seeds of phanerophytes such as *Aralia elata, Rhus ambigua, Rh, javanica, Rh. trichocarpa, Rubus crataegifolius, R. palmatus,* germinate in low rates (NAKAGOSHI 1985a), therefore, they composed the permanent/persistant seed banks in the growth season (NAYLOR 1985). The seeds of *Cacalia nikomontana*, invaded from outside the plots which are under the *Fagus* canopy, were most numerous but they never established seedlings. They were constantly buried in soil throughout a year. On the contrary, the nuts of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* had difficulties to be buried alive in soils of the growth season.

The density of seeds in the *Dryopteris* type forest was higher than that of the typical type, on the other hand, the seed bank in the latter type showed higher diversity in the floristic composition and in the relative seed density compared with that of the former type. It is,however, already found that the features of seed banks of these two types do not have much differences in species diversity and in seed density in the other years (NAKAGOSHI 1984b).

The viable seeds of *Abies mariesii* were not found in the soil during the growth season of the subalpine *Abies mariesii* forest. Instead, the seeds of hemicryptophytes such as *Deschampsia flexuosa, Anaphalis margaritacea* var. *angustior*, and *Epilobium* sp. had dominated the seed bank. The seeds of phanerophytes constituted 35 % of the seed bank in the moss type forest and only 15 % of that in *Sasa* type. *Betula ermanii* which is the only tall tree of successional species unexpectedly reserved its viable seeds in the climax *Abies* forests. The moss type forest in lower altitude had apparently rich seed bank compared with that of the *Sasa* type in higher altitude.

Tab. 1

The seed banks in soils of climax forests in Japan during the plant growth season and number of species are corresponded to real soil size, but total seeds are multipled per sq.m.

Forest types:

Cc: *Castanopsis cuspidata*, Ccs; *Castanopsis cuspidata* var. *seiboldii*,

Af: *Abies firma*,

Fc: Typical type of *Fagus crenata*,

FcD: *Dryopteris* type of *Fagus crenata*,

Am: Moss type of *Abies mariesii*, and

AmS: *Sasa* type of *Abies mariesii* forest.

	Forest type	Cc	Ccs	Af	Fc	FcD	Am	AmS
	Number of species/ 0.4 m^2 x 10 cm	15	19	11	17	13	15	11
	Total seed per m^2 x 10 cm	590.7	416.5	257.5	217.5	350	357.6	257
Life form	Species							
M	*Dendropanax trifidus*	111.6						
M	*Symplocos lucida*	27.2						
NL	*Smilax china*	8.2						
MM	*Ilex integra*	5.4						
M	*Aralia elata*	2.7			2.5	2.5		
ML	*Hedera rhombea*	2.7						
ML	*Akebia trifoliata*	2.7						
N	*Pittosporum tobira*	2.7						
-	Unidentified species 1	2.7						
M	*Eurya japonica*	378.4	204.2					
MM	*Rhus succedanea*	19.1	10.9					
N	*Zanthoxylum schinifolium*	8.2	16.3					
N	*Clerodendron trichotomum*	2.7	2.7					
M	*Mallotus japonicus*	5.4	27.2	35				
M	*Rhus trichocarpa*	10.9	2.7		2.5	2.5		
Th	*Crassocephalum crepidioides*		21.8	70				
N	*Rubus microphyllus*		13.6					
G	*Phytolacca americana*		13.6					
MM	*Prunus jamasakura*		10.9					
ML	*Vitis saccarifera*		10.9					
-	Monocotyledoneae sp.		5.4					
H	*Miscanthus sinensis*		2.7					
M	*Ilex pedunculosa*		5.4	2.5				
MM	*Carpinus tschonoskii*		46.3		2.5			
M	*Rhus javanica*		5.4		5			
N	*Rubus palmatus*		5.4		57.5			
H	*Viola grypoceras*		8.2			5		
M	*Acer palmatum* var. *matsumurae*		2.7	2.5				
M	*Symplocos glauca*			50				
MM	*Cryptomeria japonica*			47.5				
MM	*Cinnamomum camphora*			30				
MM	*Cleyera japonica*			10				
-	Gramineae sp.			5				
ML	*Vitis flexuosa*			2.5				
-	Unidentified species 2			2.5				
M	*Acanthopanax sciadophylloides*				5			
N	*Symplocos coreana*				2.5			
MM	*Kalopanax pictus*				2.5			
MM	*Magnolia obovata*				2.5			
M	*Cornus kousa*				2.5			
N	*Meliosma tenuis*				2.5			
N	*Ligustrum tschonoskii*				2.5			
G	*Cacalia nikomontana*				77.5	152.5		
N	*Lindera umbellata*				10	5		
M	*Prunus grayana*				5	2.5		
N	*Rubus crataegifolius*				5	2.5		
ML	*Rhus ambigua*			/	30	132.5		3.4
Ch	*Rubus pectinellus*					35		
M	*Ilex macropoda*					2.5		
ML	*Actinidia arguta*					2.5		
G	*Viola vaginata*					2.5		
MM	*Taxus cuspidata*					2.5	3.7	
H	*Anaphalis margaritacea* var. *augustior*						73.7	
H	*Viola selkirkii*						18.4	
N	*Alnus maximowiczii*						14.7	
H	*Solidago virga-aurea* var. *leiocarpa*						14.7	
N	*Vaccinium* sp.						11.1	
G	*Streptopus streptopoides* var. *japonicus*						11.1	
M	*Sorbus commixta*						7.4	
M	*Viburnum furcatum*						3.7	
N	*Prunus nipponica*						3.7	
H	*Deschampsia flexuosa*						92.2	140.5
Ch	*Empetrum nigrum* var. *japonicum*						25.8	30.8
N	*Hydrangea paniculata*						22.1	20.6
N	*Ilex sugerokii* var. *brevipedunculata*						29.5	6.9
MM	*Betula ermanii*						25.8	3.4
H	*Epilobium* sp.							34.3
H	*Polygonum cuspidatum*							6.9
G	*Clintonia udensis*							3.4
N	*Vaccinium ovalifolium*							3.4
-	Dicotyledoneae sp.							3.4

Abbreviations of life form are shown in the text.
Figures indicate the number of seeds of fruiting species, the figures with broken underlines show the number of seeds of vegetative species, and with underlines are the number of seeds of species not presently growing in the forest.

There were several species whose buried viable seeds distributed transzonally. They were *Aralia elata, Rhus javanica, Rh. trichocarpa* and *Rubus palmatus* both in the warm-temperate zone and in the temperate zone. All of these species are the dominant species of the successional community at disturbed sites. The seeds of a micro-phanerophyte liana, *Rhus ambigua*, were buried in the temperate soil and in the subalpine soil.

Discussion

In the same site, the buried seed contents of the secondary forests are always richer than those of the climax broad-leaved forest in the temperate zones of Japan (HAYASHI 1977, NAKAGOSHI 1981, 1984b). This may be caused by the large number of seeds produced by the dominant species in the successional communities, and the low seed production of the species under the shade stress and the unfavorable floor environments in the climax forests. Similar phenomena were reported by OOSTING & HUMPHREYS (1940) and by OLMSTED & CURTIS (1947) in the temperate forests of the United States, and by GUEVARA and GÓMEZ-POMPA (1972) in the tropical forests in Mexico. But the high density of buried seeds in the seral forest did not exist in the boreal forests of Sweden (GRANSTRÖM 1981). This suggests the bad conditions of seed production and soil seed bank under the bareal climate and soil type.

Even in the tropical rain forest, the density of buried viable seeds in soil fluctuated showing seasonality. Namely, higher (689–862 seeds per m^2) and lower (175–344 seeds) densities of seed banks were observed in the period from January to May and also from June to November respectively. GUEVARA and GÓMEZ-POMPA (1972) estimated that the meteorological factor such as soil temperature possibly controles this seasonal changes.

A distinct seasonal decrease in the number of species in the buried seed populations had been found in the climax forests of Japan. This decrease in the growth season may be ascribed to short-lived seeds, damage by birds, rodents and soil animals, rotting by fungi and bacteria, chilling in the cold winter, and unsuitable conditions at the soil surface. A comparison of the densities of buried viable seeds between dormant season and the next growth season, and the emerged seedlings in the next growth season, has also proved that most of the seeds die without germination in the climax forest (NAKAGOSHI 1985a).

For the buried seeds in the dormant season, average 1058 seeds per m^2 in the *Castanopsis* forests, 919 seeds in the *Fagus* forests and 905 seeds in the subalpine *Abies* forests were counted in the climax forest soils of Japan. The warm-temperate *Abies firma* forest had 425 seeds per m^2. These densities are similar order compared with those in the climax forest

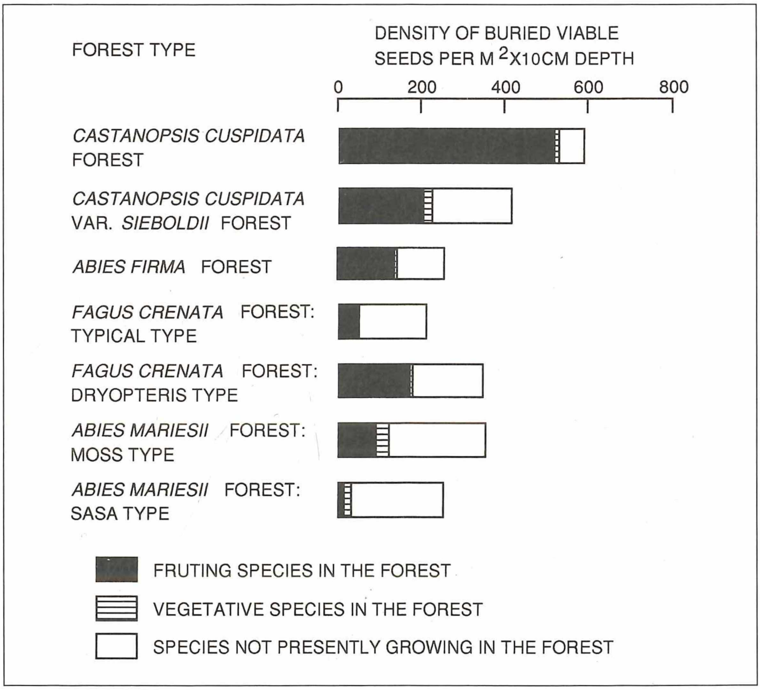

Fig. 2

Densities of seed banks in soils of the climax forests in the plant growth season. Seeds were classified into three species groups which reflect the reproductive aspect in the forest.

of the United States: 1181 seeds per m^2 in the oak-hickory forest in North Carolina (OOSTING & HUMPHREYS 1940), 121 and 990 seeds in the maple forests in Maine (OLMSTED & CURTIS 1947), and 421, 1863 and 3447 seeds in the Pacific conifer forests in Oregon (STRICKLER & EDGERTON 1976).

Among the seed banks of the *Castanopsis* forests in the growth season, 591 seeds per m^2 in the forest of Hiroshima, 417 seeds in Kobe, 2750 seeds in Nara (NAKA & YODA 1984) and 5575 seeds in Tokyo (HAYASHI 1977) were extracted as the viable seeds in soils. In the seed population of Nara, *Eurya japonica* largely occupied 1688 seeds per m^2. In Tokyo, the study forest is in an urban area like a forest island, and the seeds of *Idesia polycarpa* (2725 seeds per m^2) were probably dispersed by birds and accumulated richly in soil. Thus, the small seeds in sap fruits of these two species contribute largely to the density of seed banks in these *Castanopsis* forests.

The densities of seed banks in the climax forests decrease from the *Castanopsis* forests to the subalpine *Abies* forests: average 1253 seeds per m^2 in the *Castanopsis* forests excluded the forest in Tokyo, 425 seeds in the mountainous conifer forests, 285 seeds in the *Fagus* forests and 308 seeds in the subalpine *Abies* forests. This tendency is clear in the seeds of fruiting species (Fig. 2). The densities of seed banks in the Pacific conifer forests in British Columbia were 206 seeds per m^2 (KELLMAN 1974) and 1016 seeds (KELLMAN 1970). The boreal *Picea* forests (two stands over 120 years old) in Sweden had 695 seeds on average (GRANSTRÖM 1981). The subalpine conifer forests in Colorado (ca. 3000m in altitude) had only 28 seeds on average (WHIPPLE 1978). In the subarctic conifer woodlands in Northwest Territories of Canada, seed banks were absent (JOHNSON 1975). JOHNSON(1975) concluded that the lack of viable seeds was caused by the short growing period (ripening condition might not be good) and its effect on germination. These data suggest that the densities of seed banks decrease in number in proportion to the degree of latitude and altitude.

In Russia, however, the boreal *Picea* forests contained as many as 1300–1500 seeds per m^2 (KARPOV 1960) and 2799 seeds (PETROV 1981) in the seed banks. Moreover, the *Quercus-Tilia* forest in southern Moskow region had 6500 seeds in soil despite in the growth season (PETROV & PALKINA 1983). But the dominants in these seed banks were *Deschampsia caespitosa, Carex* sp., *Hypericum perforatum* and *Oxalis acetosella* of small herbaceous species, and they are similar to the species in the subalpine *Abies* forest of Japan. Here I see a problem that the result largely depends on what kind of vegetation surround the investigated stand and also the size of the stand.

The maximum size of plant growing from seeds is especially significant to discuss the plant biomass and vegetation structure of the early stage of succession. The life form of species whose seeds were

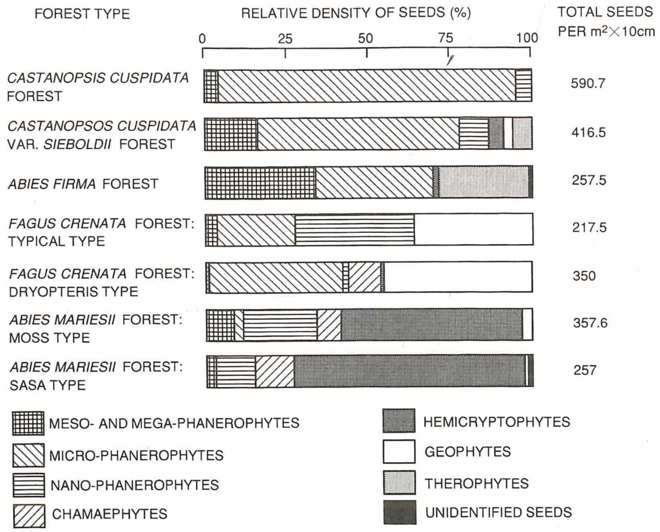

Fig. 3

Composition of seed banks in the plant growth season according to life/dormancy form system.

buried in soil should, therefore, be considered in each seed bank (RABOTNOV 1981, NAKAGOSHI 1985a). Figure 3 shows the compositions of seed banks according to life form analysis.

The *Castanopsis* forests and the mountainous conifer forests had rich seed banks of tree seeds which provide seedlings when the forest canopy is removed (NAKA 1982). These seedlings rapidly grow to reconstruct a substitutional scrub for a few years (NAKAGOSHI 1981). The seeds of therophytes characterize the seed banks of warm-temperate forests.

The *Fagus* forests kept the seed banks consisted in micro-and nano-phanerophytes, chamaephytes and geophytes. Most of the woody species seen in these seed banks can regenerate quickly in forest gaps and felling sites, namely their dormant seeds germinate and establish after the former forest has been destroyed (NAKAGOSHI 1985a). MARQUIS (1975) reported the similar seed bank of woody species in the maple forest in Pennsylvania. Geophytes characterize both in the aboveground vegetation and in the seed bank in the temperate forest.

The seeds of hemicryptophytes were dominant in the seed banks of the subalpine *Abies* forests. These small seeds have difficulty in establishing on the dim floor with thick coniferous litter in the *Abies* forest. The seedlings originated from small seeds can hardly survive on the floor of climax forests(NAKAGOSHI 1985a). They need high temperature and thin organic litter to germinate. Such a condition appears only in the case of erosion or forest fire. In these cases, few seeds remain in the disturbed soil surface. Therefore, the herbaceous seeds in the seed banks of the subalpine forests are not so significant for regeneration of plant community. Thus, the poor seed bank of woody species together with the low temperature climate may retard the succession of subalpine forests after natural and man-made disturbances.

In conclusion, these specific features of seed banks of climax forests influences the rates of regeneration or succession of forests and diversity of forest communities.

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