Stand Structure and Litter Production of Deciduous Broad-leaved Forests and Evergreen Coniferous Forests in Northern Hokkaido

By

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落葉広葉樹林と常緑針葉樹林の林分構造及びリターフォール

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Abstract

Stand structure and litter production of forest ecosystems in the Uryu Experiment Forest were studied by establishing four study plots (P1, P2, P3 and P4) in May, 1988. There were 8 tree species in P1, 5 species in P2, 9 species in P3 and 12 species in P4. Based on the relative basal area and the dominant tree sepcies in the upper story, P1 could be classified as a *Quercus mongolica* FISCH. var. *grosseserrata* REHD. et WILS forest, P2 as *Betula platyphylla* SUKATCHEV var. *japonica* HARA forest, P3 as an *Abies sachalinensis* FR. SCHM. forest, and P4 as a *Picea glehnii* MASTERS forest.

Frequency distribution of diameter [DBH] and height of *B. platyphylla* var. *japonica* in P2 was more or less bell-shaped, while that of *Q. mongolica* var. *grosseserrata* in P1 and *P. glehnii* in P4 had a tendency to be J-shaped. The frequency distribution of diameter [DBH] and height of the *A. sachalinensis* tended to be L-shaped in the four forests. *B. platyphylla* var. *japonica* in P2, tended to be distributed randomly, while the most common distributional pattern was clump distribution which occurred in P1, P3 and P4.

The mean annual litter production of the deciduous broad-leaved forests (DBF), 3.43 t/ha. yr in P1 and 3.06 t/ha. yr in P2, was lower compared with that of the evergreen coniferous forests (ECF), 3.52 t/ha. yr in P3 and 3.69 t/ha. yr in P4. The litter production significantly correlated with the basal area, with coefficient of correlation (r)=0.99 ($P \leq 0.01$). Leaves were the major contributor to the total litter production, accounting for 69-77% in P1, 72-73% in P2, 76-79% in P3 and 70-71% in P4. Seasonal changes of litterfall, seed production, time of seed fall and organic materials accumulated on the forest floor are also discussed in this paper, with respect to the stand structure and litter production.

Received September 29, 1990.

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Key words: Stand structure, Deciduous broad-leaved forests, Evergreen coniferous forests, Litter production.

1. Introduction

The vegetation of the Earth as we know it today is the result of a long process of development under the influence of environmental factors (WALTER, 1973). The forest vegetation of the Japanese archipelago is a continuous band from the sub-tropical to the sub-frigid zone. There are four types of forests, sub-frigid, cool-temperate, warm- temperate, and sub-tropical forests (HACHIYA, 1981). In Hokkaido, evergreen coniferous trees of the sub-frigid zone type and broad-leaved trees of cool-temerate zone type are distributed from tre lowland to the mountainous areas (TATEWAKI, 1958).

In the Uryu Experiment Forest, in the northern part of Hokkaido, *Abies sachalinensis* and *Picea glehnii* are widely distributed. Such broad-leaved tree species as *Fraxinus mandshurica* var. *japonica*, *Ulmus davidiana* var. *japonica*, *Alnus hirsuta* grow in the lowland forests together with the pure forest of *Picea glehnii* in the wetland areas, while the forests of the hillside are composed of *Quercus mongolica* var. *grosseserrata*, *Tilia japonica* and *Betula* spp. (TATEWAKI, 1932; EXPERIMENT FORESTS OF HOKKAIDO UNIVERSITY, 1987).

Forest tree species require many chemical elements to live and grow. The minerals that are taken up into the forest trees, are eventually returned to the surface of the forest soil by litterfall and through the washing and leaching effects of rain on tree foliage and stems (SPURR and BARNES, 1980). Litterfall is a major nutrient cycling pathway which tranfers a significant proportion of the nutrient uptake and net primary production of forests to the forest floor (MAGGS, 1985).

Litter production studies in various forest ecosystems have been carried out in many parts of the world. In Japan, many researchers also have long attempted to quantify the rate of litter production in many types of forests. Among them are ANDO et al. (1977), NISHIOKA and KIRITA (1978), FURUNO and SAITO (1981), SAITO (1977, 1981), KIMURA et al. (1984), HIRABUKI (1985), KAWAHARA and MARUYAMA (1986), SAKAI and TSUTSUMI (1986), KISHIMOTO et al. (1987), and HARDIWINOTO et al. (1989).

In Hokkaido, the northernmost main island of Japan, SIMARANGKIR and IGARASHI (1986, 1987) reported the litter production of an evergreen coniferous forest in a subarctic zone. It is still necessary for more detailed data to be obtained in order to gain further insight into litter production of forest ecosystems in the island. The purposes of this paper are1) to analyze the stand structure2) to quantify litter production and its seasonal changes, including seed production and time of seed fall, and3) to estimate the organic materials accumulated on the forest floor of the deciduous broad-leaved forests and the evergreen coniferous forests in the northern part of the island.

2. Study area

This study was carried out in the Moshiri district, at the Uryu Experiment Forest of Hokkaido University. The district belongs to the Pan Mixed Forest Zone, which is composed of *A. sachalinensis*, *P. glehnii*, *Q. mongolica* var. *grosseserrata* and *Betula* spp. The total area of the forest is about 24,800 ha. The forest is located in the administrative area of Horokanai Town, Sorachi District, in the northern part of Hokkaido (EXPERIMENT FORESTS OF HOKKAIDO UNIVERSITY, 1987). It is situated approximately at E 142° 1′-20′, N 44° 3′-29′ (Fig. 1), and has an elevation range of about 175-900 m above sea level.

General climatic conditions, as measured in the climatological observation in the Moshiri Branch Station from 1979 to 1988 are shown in Table 1. The daily mean air temperature was 2.4℃, with a maximum of 33.7℃ occurring on August 16, 1984, and a minimum of −42.9℃ on February 5, 1982. The annual mean precipitation was 1,339 mm, mainly in the form of snow which falls from late October to the end of following April. The study area was covered by snow for about 7 months, from November to the following May, with a maximum accumulation of up to 2.67 m recorded on March 11, 1982. This district is said to be one of the snowiest and coldest regions in Hokkaido.

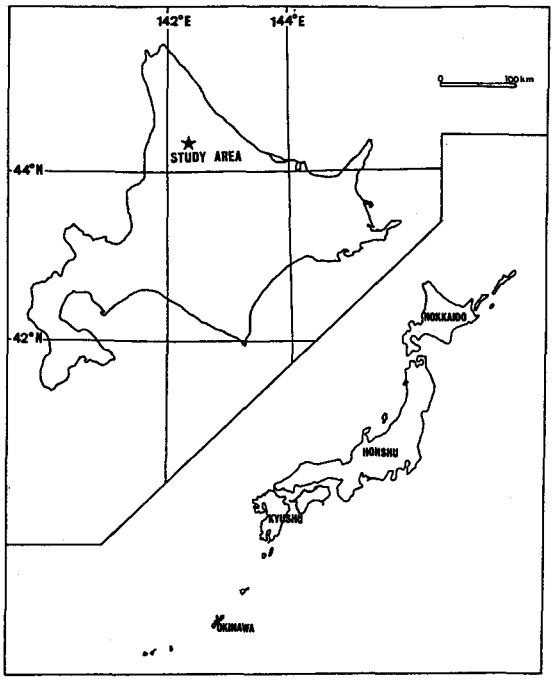

Fig. 1. Map of Japan, showing location of the study area in the Uryu Experiment forest, Hokkaido.

Table 1. General climatic conditions of the study area (from 1978 to 1988)

	Mean temp. (℃)			Snow depth (cm)	Precipitation (mm)
	daily	daily max.	daily min.		
Jan.	−13.0	− 7.2	−21.2	138.7	117.1
Feb.	−13.3	− 6.3	−22.8	169.0	76.0
Mar.	− 7.6	− 1.5	−16.3	181.4	78.9
Apr.	− 0.1	5.9	− 5.9	119.1	56.4
May	6.9	13.4	0.0	9.1	70.2
Jun.	13.0	19.6	6.1	0.0	60.8
Jul.	16.6	22.6	10.8	0.0	94.4
Aug.	18.3	23.8	12.9	0.0	149.4
Sep.	11.9	18.4	5.6	0.0	134.9
Oct.	5.2	10.9	− 0.7	1.3	187.3
Nov.	− 1.9	2.1	− 6.5	27.5	163.1
Dec.	− 7.5	− 3.3	−13.5	89.9	150.2
Year	2.4	8.2	− 4.3		1338.7

3. Study plots and Methods

Four permanent plots, P1 (30 m×30 m), P2 (20 m×20 m), P3 (20 m×20 m) and P4 (20 m×50 m) were established in May, 1988. All trees with height of more than 2 m in the study plots were numbered, their diameter at breast height [DBH], height [H], position, as well as crown position were measured. Based on their height, the trees were classified into three stories, namely: lower story (H<8 m), middle story (8 m≦H≦16 m), and upper story (H>16 m). Distributional patterns of the tree species were analyzed by the change of Morishita Iδ-index corresponding to the change in quadrat size (Morishita, 1959a).

In order to catch litterfall, 10 littertraps each in P1 and P4, and 8 littertraps each in P2 and P3 were set up. The traps were made from wood, 85 cm×85 cm in size, and with a 1-mm mesh screen bottom. On the forest floor of the plots, the littertraps were placed randomly on May 31, 1988. To protect the accumulated litterfall from the decomposition process, the forest floor under each trap was covered with plastic sheet, and the mesh screen bottom was set up at about 5 cm above the sheet (Photo 1).

All accumulated organic materials (litterfall) in the traps were collected monthly at the end of every month during the snow uncovered season (from June to October). Because of the accumulation of snow, it was very difficult to collect the litterfall during the snow covered season (from November to the following May), therefore, for that period it was collected only once at the end of May. In the first year (from June, 1988 to May, 1989), the collected materials were separated into leaves, branches, barks, seeds and other materials (insect bodies and feces, cones, flowers, bud scales and unidentified materials). The leaves and seeds were further sorted by species. FYLES et

al. (1986) considered that small litter traps were inappropriate for measuring the production of large wood litter. NISHIOKA and KIRITA (1978) defined the large litter as branches with diameter at basal end larger than 1.5 cm. In this study, only branches less than 1.5 cm in diameter were collected. In order to clarify seed production and time of seed fall, the seeds were counted. In the second year (from June, 1989 to May, 1990), the materials were sorted only into broad-leaved species leaves, coniferous species leaves, branches and other materials. The sorted materials were then oven-dried at 80℃ for more than 48 hours to determine the dry weight.

To quantify the accumulated organic materials on the forest floor, a smaller plot of 2 m×10 m each inside P1, P2, P3, and P4 was set up. The small plots were further divided into 5 small quadrats of 2 m×2 m, Q1-Q5. After eliminating the undergrowth of *Sasa senanensis*, all the accumulated organic materials (litter) on the L-layer of Q1, Q3, and Q5 were collected and brought to the laboratory at the end of September, 1988. Samples of more than 25% of the collected litter were separated into woody materials, *Sasa* litter (leaves and culms) and, leaves and other material litter. Before weighing, the separated materials were oven-dried at 80℃ for about one week to determine the dry weight.

4. Results

4. 1 Stand structure

The stand structure of P1 is presented in Table 2. There were 684 stems/ha, with basal area=50.73 m²/ha, and composed of 8 species. The relative basal area of the P1 was 84.1% of *Quercus mongolica* var. *grosseserrata*, 6.9% of *Acer mono*, 5.2% of *Betula platyphylla* var. *japonica*, 3.0% of *Abies sachalinensis*, 0.5% of *Magnolia obovata*, 0.3% of *Acer japonicum*, *Kalopanax pictus* and *Ulmus laciniata*. In Table 3, the stand

Table 2. Stand structure of P1

Scientific name	Japanese name	N/ha	Mth [m]	Mtd [cm]	Ba [cm²/ha]	Rba [%]
Quercus mongolica var. *grosseserrata*	Mizunara	231	20.46	43.10	423852.11	84.14
Acer mono	Itayakaede	99	9.74	16.59	34538.13	6.86
Betula platyphylla var. *japonica*	Shirakanba	11	29.00	55.20	26324.65	5.23
Abies sachalinensis	Todomatsu	266	5.31	7.75	15027.76	2.98
Magnolia obovata	Hoonoki	33	8.87	8.80	2451.02	0.49
Acer japonicum	Hauchiwakaede	22	5.10	6.70	778.47	0.15
Kalopanax pictus	Harigiri	11	7.80	8.40	609.62	0.12
Ulmus laciniata	Ohyou	11	3.90	4.30	159.72	0.03
Total	8 species	684			503741.48	100.00

Notes:
N/ha=Number of stems per hectar, Mth=Mean tree height, Mtd=Mean tree diameter at breast height, Ba=Basal area, Rba=Relative basal area.

Table 3. Stand structure of P2

Scientific name	Japanese name	N/ha	Mth [m]	Mtd [cm]	Ba [cm²/ha]	Rba [%]
Betula platyphylla var. *japonica*	Shirakanba	1350	13.36	12.53	196677.25	88.03
Salix hultenii var. *angustifolia*	Ezonobakkoyanagi	50	9.05	18.75	14273.25	6.39
Phellodendron amurense var. *sachalinense*	Hirohanokihada	150	6.77	7.85	10890.25	4.87
Abies sachalinensis	Todomatsu	75	3.73	4.50	1409.50	0.63
Magnolia obovata	Hoonoki	25	4.50	3.00	176.75	0.08
Total	5 species	1650			223427.00	100.00

Notes:
N/ha=Number of stems per hectar, Mth=Mean tree height, Mtd=Mean tree diameter at breast height, Ba=Basal area, Rba=Relative basal area.

Table 4. Stand structure of P3

Scientific name	Japanese name	N/ha	Mth [m]	Mtd [cm]	Ba [cm²/ha]	Rba [%]
Abies sachalinensis	Todomatsu	1475	9.35	13.47	376092.00	66.65
Betula spp.	Kanba rui	150	14.20	27.75	173453.75	30.74
Picea glehnii	Akaezomatsu	150	4.70	7.52	8075.25	1.43
Phellodendron amurense var. *sachalinense*	Hirohanokihada	125	6.44	6.70	5108.00	0.91
Kalopanax pictus	Haragiri	25	5.00	4.70	433.75	0.08
Kalopanax sciadophylloides	Koshiabura	25	5.90	4.70	433.75	0.08
Sorbus alnifolia	Azukinashi	75	4.03	2.63	428.25	0.08
Sorbus commixta	Nanakamado	25	6.70	3.50	240.50	0.04
Total	9 species	2050			564265.25	100.00

Notes:
N/ha=Number of stems per hectar, Mth=Mean tree height, Mtd=Mean tree diameter at breast height, Ba=Basal area, Rba=Relative basal area.
Betula spp.=*B. platyphylla* var. *japonica* and *B. ermanii*.

structure of P2 is illustrated. Five species were recognized in the plot, with basal area=22.34 m²/ha, and number of trees=1,650 stems/ha. The relative basal area of P2 was 88.0% of *Betula platyphylla* var. *japonica*, 6.4% of *Salix hultenii* var. *angustifolia*, 4.9% of *Phellodendron amurense* var. *sachalinense*, 0.6% of *Abies sachalinensis* and 0.1% of *Magnolia obovata*.

Table 4 shows the stand structure of P3. The basal area of P3 was 56.43 m²/ha, consisting of 2,050 stems/ha, belonging to 9 species. The relative basal area of P3 was 66.7% of *Abies sachalinensis*, 30.7% of *Betula* spp., 1.4% of *Picea glehnii*, 0.9% of *Phellodendron amurense* var. *sachalinense*, and 0.2% of *Kalopanax pictus*, *Sorbus alnifolia* and *Sorbus commixta*. The basal area of P4 was 61.16 m²/ha (Table 5), consist-

Table 5. Stand structure of P4

Scientific name	Japanese name	N/ha	Mth [m]	Mtd [cm]	Ba [cm²/ha]	Rba [%]
Picea glehnii	Akaezomatsu	150	21.43	53.22	453552.40	74.16
Abies sachalinensis	Todomatsu	710	7.07	9.68	74074.50	12.11
Betula spp.	Kanba rui	50	12.08	27.32	65808.50	10.76
Quercus mongolica var. *grosseserrata*	Mizunara	100	6.06	6.80	8598.90	1.41
Sorbus commixta	Nanakamado	70	7.21	7.31	3668.10	0.60
Sorbus alnifolia	Azukinashi	320	4.62	3.40	3221.20	0.53
Kalopanax pictus	Harigiri	60	3.67	3.95	829.50	0.14
Kalopanax sciadophylloides	Koshiabura	110	4.27	2.99	802.00	0.13
Tilia japonica	Shinanoki	10	5.70	7.50	441.80	0.07
Acer mono	Itayakaede	20	4.20	4.35	308.60	0.05
Phellodendron amurense var. *sachalinense*	Hirohanokihada	20	5.80	4.25	297.90	0.05
Total	12 species	1620			611603.40	100.00

Notes:
N/ha=Number of stems per hectar, Mth=Mean tree height, Mtd=Mean tree diameter at breast height, Ba=Basal area, Rba=Relative basal area.
Betula spp.=*B. platyphylla* var. *japonica* and *B. ermanii.*

Table 6. Vertical structure [number of stems and its percentages] in P1, P2, P3 and P4

Vertical structure	P1			P2		
	Qm	As	BL	Bp	As	BL
Lower story [%]	1 [3]	20 [65]	10 [32]	8[44]	3 [17]	7 [39]
[%]	[5]	[83]	[59]	[15]	[100]	[78]
Middle story [%]	2 [18]	4 [36]	5 [46]	28[93]	0 [0]	2 [7]
[%]	[9]	[17]	[29]	[52]	[0]	[22]
Upper story [%]	18 [90]	0 [0]	2 [10]	18[100]	0 [0]	0 [0]
[%]	[86]	[0]	[12]	[33]	[0]	[0]
Total	21	24	17	54	3	9
[%]	[100]	[100]	[100]	[100]	[100]	[100]

Vertical structure	P3			P4		
	As	Pg	BL	Pg	As	BL
Lower story [%]	29 [65]	5 [11]	11 [24]	3 [3]	45 [39]	68 [58]
[%]	[49]	[83]	[65]	[20]	[63]	[89]
Middle story [%]	22 [81]	1 [4]	4 [15]	2 [7]	23 [77]	5 [17]
[%]	[37]	[17]	[23]	[13]	[33]	[7]
Upper story [%]	8 [80]	0 [0]	2 [20]	10 [62]	3 [19]	3 [19]
[%]	[14]	[0]	[12]	[67]	[4]	[4]
Total	59	6	17	15	71	76
[%]	[100]	[100]	[100]	[100]	[100]	[100]

Note:
Qm=*Quercus mongolica* var. *grosseserrata,* Bp=*Betula platyphylla* var. *japonica,* As=*Abies sachalinensis,* Pg=*Picea glehnii,* BL=Broad-leaved species (excluding Qm in P1, and Bp in P2).

Table 7. Number of trees in each diameter [DBH] and height class in P1 (0.09 ha)

DC (cm)	Species								Total
	Qm	As	Am	Aj	Kp	Mo	Ul	Bp	
0—5		9	1			1	1		12
5—10	2	7	4	2	1	1			17
10—15		8				1			9
15—20	1								1
20—25			1						1
25—30	3		1						4
30—35	1		1						2
35—40	1		1						2
40—45	4								4
45—50	3								3
50—60	2							1	3
60—70	3								3
70—80									
80—90									
90—100									
>100	1								1
Total	21	24	9	2	1	3	1	1	62

HC (m)	Species								Total
	Qm	As	Am	Aj	Kp	Mo	Ul	Bp	
2—4		10	1			1	1		13
4—6	1	6	1	2					10
6—8		4	3		1				8
8—10	1	2				1			4
10—12		1	1						2
12—14	1	1							2
14—16			2				1		3
16~18	3		1						4
18—20	3								3
20—22	3								3
22—24	4								4
24—26	2								2
26—28	2								2
28—30	1							1	2
Total	21	24	9	2	1	3	1	1	62

Note:
DC=Diameter class, HC=Height class,
Qm=*Quercus mongolica* var. *grosseserrata*, As=*Abies sachalinensis*, Am=*Acer mono*, Aj=*Acer japonicum*, Kp=*Kalopanax pictus*, Mo=*Magnolia obovata*, Ul=*Ulmus laciniata*, Bp=*Betula platyphylla* var. *japonica*.

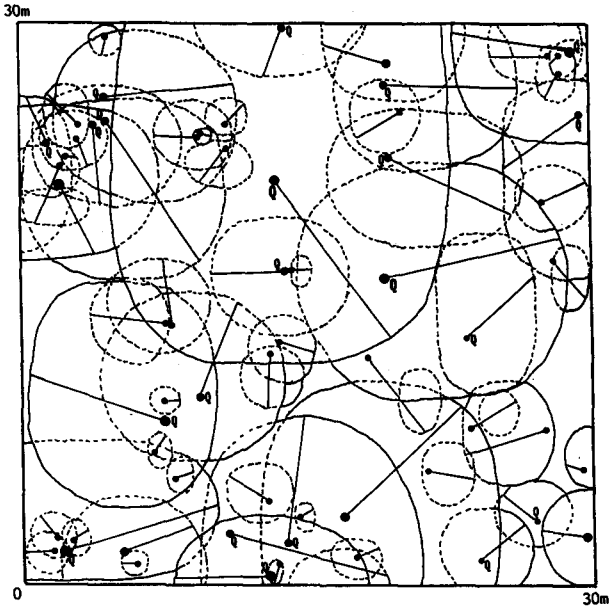

Fig. 2. Distributional map of individual trees and their crown projection in P1; Q=*Quercus mongolica* var. *grosseserrata*.

ing of 1,620 stems/ha, and belonging to 12 species. The relative basal area of P4 was 74.2% of *Picea glehni*, 12.1% of *Abies sachalinensis*, 10.8% of *Betula* spp., 1.4% of *Quercus mongolica* var. *grosseserrata*, 0.6% of *Sorbus commixta*, 0.5% of *Sorbus alnifolia*, 0.4% of *Kalopanax pictus*, *Kalopanax sciadophylloides*, *Tilia japonica*, *Acer mono* and *Phellodendron amurense* var. *sachalinense*.

The vertical structure of the investigated forests is presented in Table 6. As can be seen from the Table the upper story of P1 was dominated by *Q. mongolica* var. *grosseserrata*, P2 by *B. platyphylla* var. *japonica*, P3 by *A. sachalinensis* and P4 by *P. glehnii*.

Frequency distribution of diameter [DBH] and height of P1 is shown in Table 7 and Fig. 2. It can be seen from the Figure that the frequecy distribution of diameter and height of *Q. mongolica* var. *grosseserrata* tended to be J-shaped while that of other broad-leaved species and *A. sachalinensis* tended to be L-shaped. Table 8 and Fig. 3 show that the frequency distribution of diameter and height of *B. platyphylla* var. *japonica* (in P2) tended to be bell-shaped. The frequency distribution of *A. sachalinensis* as well as broad-leaved species in P3 and P4 tended to be L-shaped, while that of *P. glehnii* in P4 had a tendency to be J-shaped (Tables 9, 10 and Figures 4, 5).

Distribution of individual trees and their crown projection of P1, P2, P3 and P4 is shown in Fig. 6, 7, 8 and 9, respectively. The distributional pattern of *Q. mongolica* var. *grosseserrata* as well as other broad-leaved species in P1 was more or less clump distribution. In P2, *B. platyphylla* var. *japonica* had a tendency to be distributed randomly (Fig. 10). In Fig. 11, distributional patterns of tree species in P3 and P4 are shown. The graphs indicate that *A. sachalinensis* and other species in P3, as well as

Table 8. Number of trees in each diameter [DBH] and height class in P2 (0.04 ha)

DC (cm)	Species					Total
	Bp	As	Ps	Mo	Sh	
0—5	4	2	3	1		10
5—10	17	1	1			19
10—15	16		1			17
15—20	11		1		1	13
20—25	6				1	7
Total	54	3	6	1	2	66
HC (m)	**Species**					**Total**
	Bp	As	Ps	Mo	Sh	
2—4	4	2	2			8
4—6	2	1	1	1		5
6—8	2		2		2	5
8—10	3					3
10—12	9				1	10
12—14	8					8
14—16	8					9
16—18	9					9
18—20	8					8
20—22	1					1
Total	54	3	6	1	2	66

Note:
DC=Diameter class, HC=Height class,
Bp=*Betula platyphylla* var. *japonica*. As=*Abies sachalinensis*, Ps=*Phellodendron amurense* var. *sachalinense*, Mo=*Magnolia obovata*, Ul=*Ulmus laciniata*,

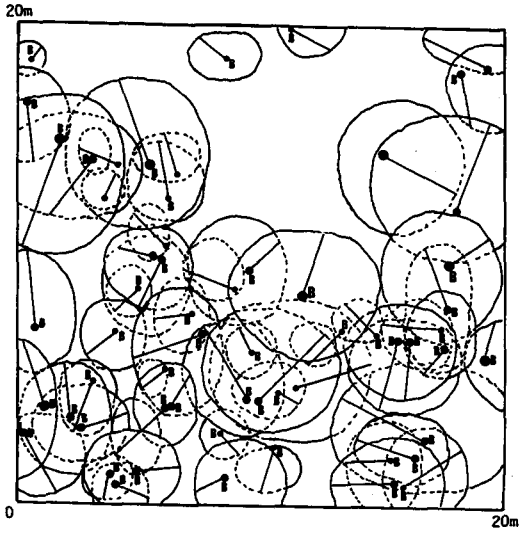

Fig. 3. Distributional map of individual trees and their crown projection in P2; B=*Betula platyphylla* var. *japonica*.

Table 9. Number of trees in each diameter [DBH] and height class in P3 (0.04 ha)

DC (cm)	Species								Total
	As	Pg	Bs	Ps	Sc	Sa	Kp	Ks	
0—5	18	2	1	2	1	3	1	1	29
5—10	12	3		2					17
10—15	9	1	2	1					13
15—20	8								8
20—25	6								6
25—30									
30—35	1		1						2
35—40	2		1						3
40—45	1								1
45—50	1								1
50—60									
60—70	1								1
70—80									
>80									1
Total	59	6	6	5	1	3	1	1	82

HC (m)	Species								Total
	As	Pg	Bs	Ps	Sc	Sa	Kp	Ks	
2—4	19	3	1			2			25
4—6	7	2		2		1	1		13
6—8	3			2	1			1	7
8—10	2	1		1					4
10—12	2		1						3
12—14	8		1						9
14—16	10		1						11
16~18	5								5
18—20			1						1
20—22	2		1						3
22—24									
24—26	1								1
Total	59	6	6	5	1	3	1	1	82

Note:
DC=Diameter class, HC=Height class,
As=*Abies sachalinensis*, Pg=*Picea glehnii*, Bs=*Betula* spp., Ps=*Phellodendron amurense* var. *sachalinense*, Sc=*Sorbus commixta*, Sa=*Sorbus alnifolia*, Kp=*Kalopanax pictus*, Ks=*Kalopanax sciadophylloides*.

Table 10. Number of trees in each diameter [DBH] and height class in P4 (0.1 ha)

DC (cm)	Species											Total
	Pg	As	Bs	Qm	Sa	Am	Kp	Ks	Sc	Tj	Ps	
0—5		20	2	8	29	1	5	11	3		1	80
5—10	2	21	1	1	3	1	1		1	1	1	33
10—15	1	18							3			22
15—20	1	7										8
20—25	1	3										4
25—30	1											1
30—35		2		1								3
35—40												
40—45			1									1
45—50												
50—60	1											1
60—70	1											1
70—80	3											3
80—90	3		1									4
90—100												
>100	1										1	
Total	15	71	5	10	32	2	6	11	7	1	2	162

HC (m)	Species											Total
	Pg	As	Bs	Qm	Sa	Am	Kp	Ks	Sc	Tj	Ps	
2—4	1	26	1	6	8	1	5	5				52
4—6	2	12	1	2	23	1	1	6	3	1	1	53
6—8		7		1	1				1		1	11
8—10		9	1	1					3			14
10—12	2	5										7
12—14		1										7
14—16		2										2
16—18	1											1
18—20		3	1	1								5
20—22												
22—24	1											1
24—26			1									1
26—28	3											3
28—30	2											2
30—32	1											1
32—34	2											2
Total	15	71	5	10	32	2	6	11	7	1	2	162

Note:
DC=Diameter class, HC=Height class,
Pg=*Picea glehnii*, As=*Abies sachalinensis*, Bs=*Betula* spp., Qm=*Quercus mongolica* var. *grosseserrata*, Sa=*Sorbus alinifolia*, Am=*Acer mono*, Kp=*Kalopanax pictus*, Ks=*Kalopanax sciadophylloides*, Sc=*Sorbus commixta*, Tj=*Tilia japonica*, Ps=*Phellodendron amurense* var. *sachalinense*.

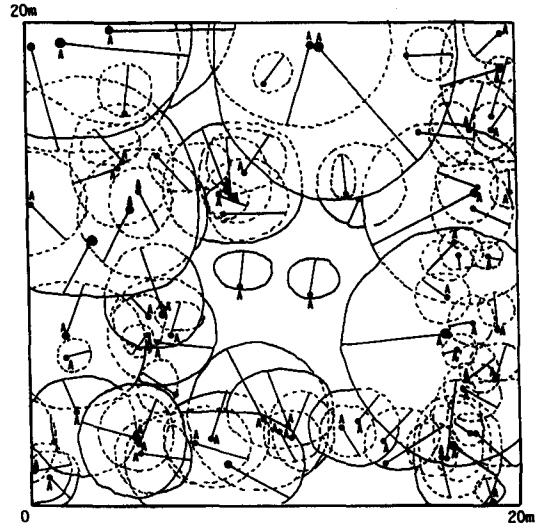

Fig. 4. Distributional map of individual trees and their crown projection in P3; A=*Abies sachalinensis*.

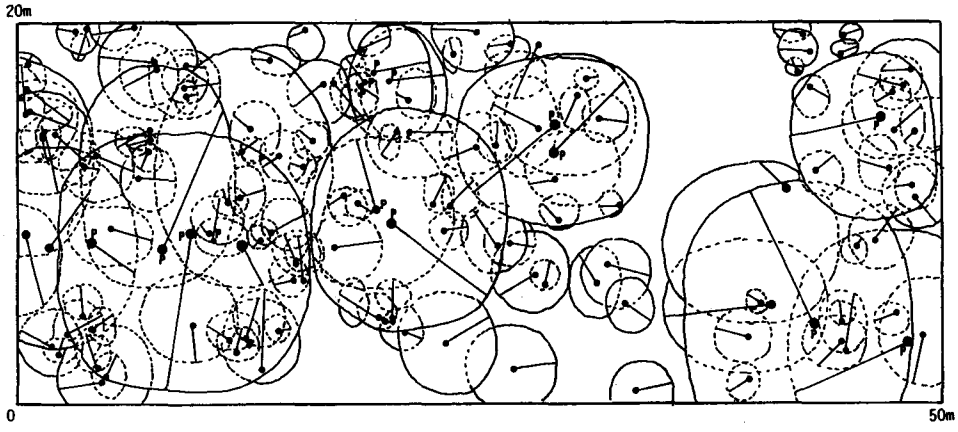

Fig. 5. Distributional map of individual trees and their crown projection in P4; P=*Picea glehnii*.

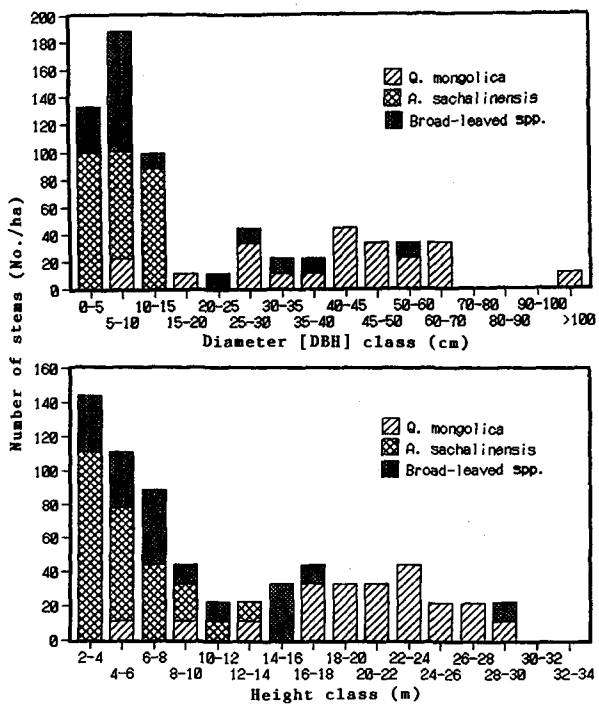

Fig. 6. Frequency distribution of diameter [DBH] and height in P1.

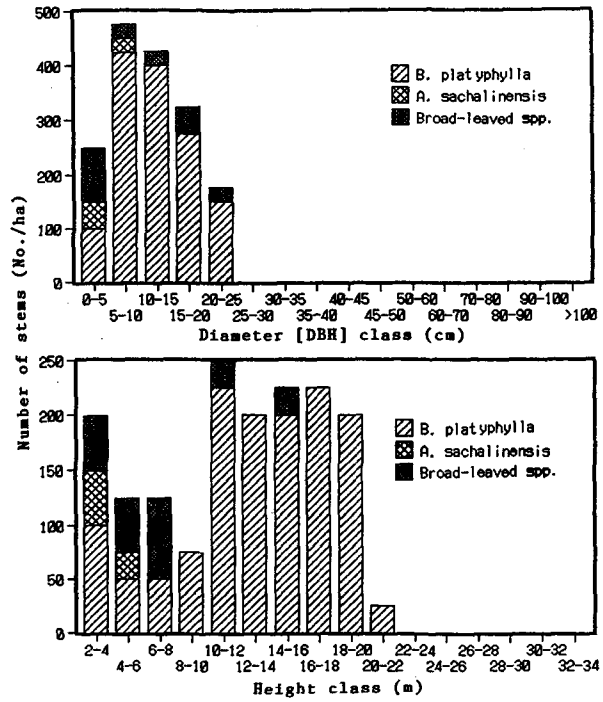

Fig. 7. Frequency distribution of diameter [DBH] and height in P2.

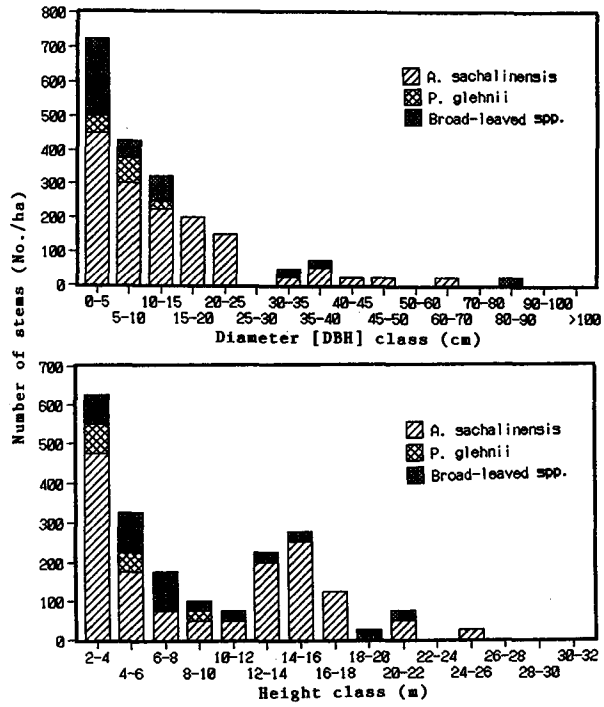

Fig. 8. Frequency distribution of diameter [DBH] and height in P3.

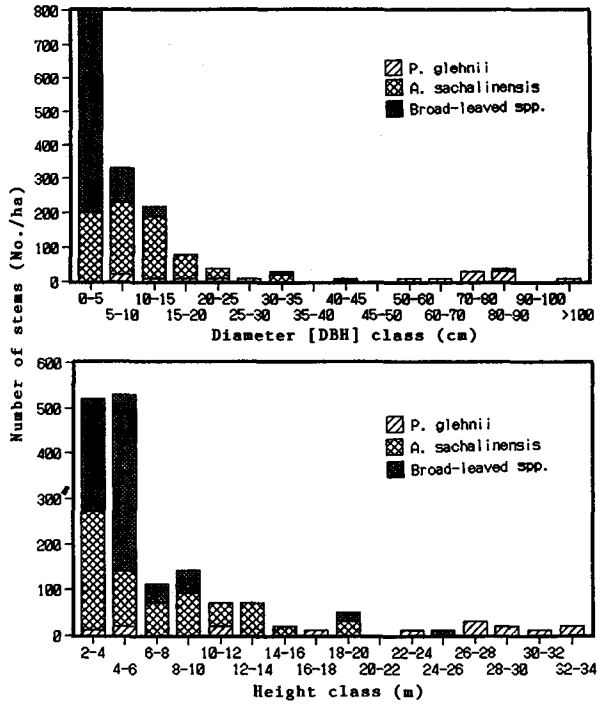

Fig. 9. Frequency distribution of diameter [DBH] and height in P4.

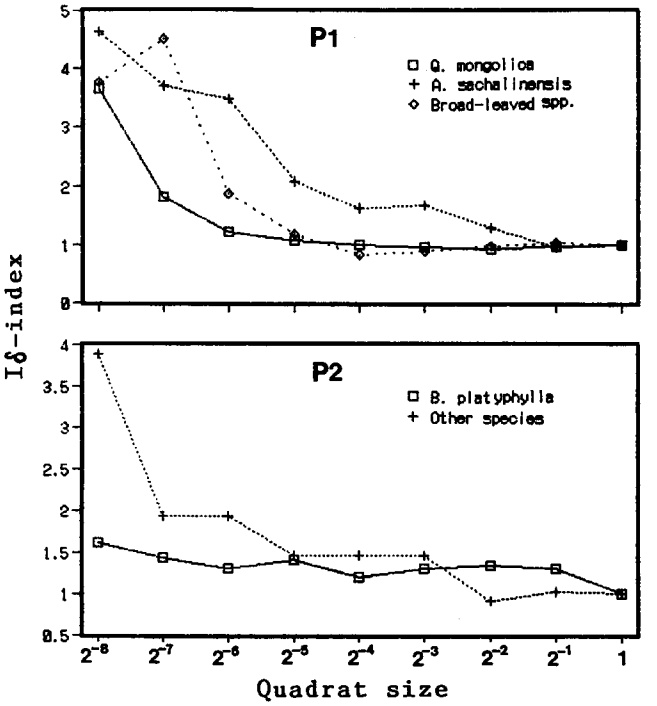

Fig. 10. Distributional patterns [Iδ-quadrat curves] of tree species in P1 and P2.

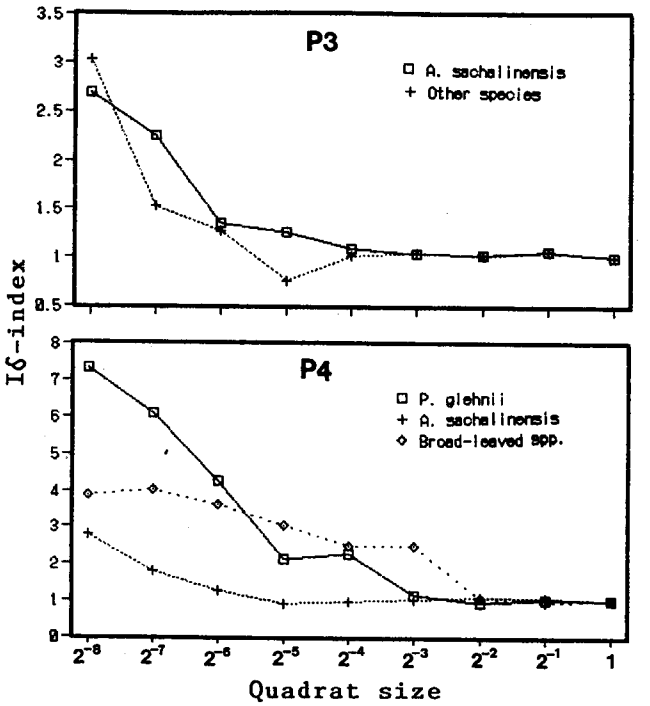

Fig. 11. Distributional patterns [Iδ-quadrat curves] of tree species in P3 and P4.

P. glehnii, *A. sachalinensis* and broad-leaved species in P4 had a similar tendency in their distributional pattern, that is a clump distribution.

4. 2 Litter production

4. 2. 1 First year (from June, 1988 to May, 1989)

Litter production of the DBF is shown in Table 11 and Table 12. In P1, the litter production amounted to 3.20 t/ha. yr, composed of leaves (*Q. mongolica* var. *grosseserrata* leaves=54.4%, other broad-leaved species leaves=7.6%, coniferous species leaves=6.2%), branches (14.7%), bark (4.5%), seeds (0.5%), and other materials (11.8%). The litter production of P2 was 2.68 t/ha.yr, and consisted of leaves (*B. platyphylla* var. *japonica* leaves=64.1%, other broad-leaved species leaves=4.4%, conif-

Table 11. Litter production from June, 1988 to May, 1989 [one year] in P1 ($\times 10^{-2}$t/ha)

	Leaves			Br	Bark	Seeds	Oth	Total	[%]
	Qm	Bl	Cl						
June	0.61	0.07	0.04	1.91	0.13	0.00	10.56	13.32	4.2
July	2.83	0.67	0.03	1.23	0.10	0.00	18.19	23.05	7.2
August	0.99	0.24	0.06	1.18	0.71	0.47	1.71	5.36	1.7
September	2.90	0.95	0.12	1.80	0.32	0.41	1.03	7.53	2.3
October	164.57	23.18	16.56	32.03	2.08	0.54	2.99	241.95	75.5
Nov-May	2.42	0.07	3.23	8.91	11.06	0.08	3.32	29.09	9.1
Total	174.32	25.18	20.04	47.06	14.40	1.50	37.80	320.30	100.0
[%]	54.4	7.9	6.2	14.7	4.5	0.5	11.8	100.0	

Note:
Qm=*Q. mongolica* var. *grosseserrata*, Bl=Broad-leaved species excluding Qm, Cl=Coniferous species, Br=Branches, Oth=Other materials (insect bodies & feces, cones, bud scales, flowers and unidentified materials).

Table 12. Litter production from June, 1988 to May, 1989 [one year] in P2 ($\times 10^{-2}$t/ha)

	Leaves			Br	Bark	Seeds	Oth	Total	[%]
	Bp	Bl	Cl						
June	12.86	0.07	0.07	1.26	0.29	0.00	5.51	20.06	7.5
July	4.78	0.12	0.03	0.72	0.07	0.01	5.04	10.77	4.0
August	8.09	0.37	0.02	0.70	0.20	0.05	1.74	11.17	4.2
September	22.01	0.92	0.05	2.81	0.05	0.26	1.77	27.87	10.4
October	123.65	10.20	7.27	26.78	0.50	0.89	5.97	175.26	65.4
Nov-May	0.45	0.03	2.90	12.39	1.06	0.08	6.03	22.94	8.5
Total	171.84	11.71	10.34	44.66	2.17	1.29	26.06	268.07	100.0
[%]	64.1	4.4	3.8	16.7	0.8	0.5	9.7	100.0	

Note:
Bp=*B. platyphylla* var. *japonica*, Bl=Broad-leaved species excluding Bp, Cl=Coniferous species, Br=Branches, Oth=Other materials (insect bodies & feces, cones, bud scales, flowers and unidentified materials).

erous species leaves=3.8%), branches (16.7%), bark (0.8%), seeds (0.5%), and other materials (9.7%).

In the ECF, the litter production amounted to 3.36 t/ha. yr in P3 (Table 13) and 3.85 t/ha. yr in P4 (Table 14). In P3, it was composed of leaves (*A. sachalinensis* leaves=54.4%, *P. glehnii* leaves=7.2%, broad-leaved species leaves=16.9%), branches (11.3%), bark (1.6%), seeds (0.7%), and other materials (7.9%). The litterfall of P4 consisted of leaves (*P. glehnii* leaves=44.6%, *A. sachalinensis* leaves=10.2%, broad-leaved species leaves=14.5%), branches (10.4%), bark (9.2%), seeds (0.6%), and other materials (10.2%).

The largest proportion of the litter production was the leaf fall, accounting for 68.5% in P1, 72.3% in P2, 78.5% in P3, and 69.5% in P4. The ratios of non-leaf litter to total litter were 31.5% in P1, 27.7% in P2, 21.5% in P3, and 30.5% in P4.

Table 13. Litter production from June, 1988 to May, 1989 [one year] in P3 ($\times 10^{-2}$t/ha)

	Leaves			Br	Bark	Seeds	Oth	Total	[%]
	As	Pg	Bl						
June	1.10	0.23	0.25	0.39	0.05	0.00	1.45	3.47	1.0
July	0.85	0.12	0.69	0.25	0.16	0.00	2.01	4.08	1.2
August	2.03	0.38	1.01	0.28	0.21	0.00	1.83	5.74	1.7
September	2.76	0.86	1.08	0.26	0.41	0.20	1.27	6.84	2.1
October	128.65	12.17	50.63	9.89	0.96	1.34	9.02	212.66	63.3
Nov-May	47.26	10.50	3.14	26.79	3.60	0.79	11.00	103.08	30.7
Total	182.65	24.26	56.80	37.86	5.39	2.33	26.58	335.87	100.0
[%]	54.4	7.2	16.9	11.3	1.6	0.7	7.9	100.0	

Note:
As=*A. sachalinensis*, Pg=*P. glehnii*, Bl=Broad-leaved species, Br=Branches, Oth=Other materials (insect bodies & feces, cones, bud scales, flowers and unidentified materials).

Table 14. Litter production from June, 1988 to May, 1989 [one year] in P4 ($\times 10^{-2}$t/ha)

	Leaves			Br	Bark	Seeds	Oth	Total	[%]
	Pg	As	Bl						
June	5.43	0.52	0.86	0.58	0.44	0.0	1.29	9.12	2.4
July	4.53	0.31	0.49	0.40	0.34	0.00	1.74	7.81	2.0
August	7.40	1.00	0.54	0.76	1.44	0.02	0.86	12.02	3.1
September	10.18	0.51	0.73	0.54	1.32	0.18	0.92	14.38	3.8
October	90.10	28.90	52.04	10.28	5.75	1.08	5.01	193.16	50.2
Nov-May	53.90	9.22	1.03	27.64	26.06	0.86	29.55	148.26	38.5
Total	171.54	40.46	55.69	40.20	35.35	2.14	39.37	384.75	100.0
[%]	44.6	10.5	14.5	10.4	9.2	0.6	10.2	100.0	

Note:
Pg=*P. glehnii*, As=*A. Sachalinensis*, Bl=Broad-leaved species, Br=Branches, Oth=Other materials (insect bodies & feces, cones, bud scales, flowers and unidentified materials).

The amounts of bark litter, 14.40 g/m². yr in P1 and 35.35 g/m². yr in P4, were markedly higher compared with 2.17 g/m². yr in P2 and 5.39 g/m². yr in P3.

Rates of litterfall were seasonal in the four forests (Fig. 12). In spring and summer months (June, July and August), the rates were low, though a slightly higher rate appeared in the DBF communities. Even at the beginning of autumn (September), the rates were still low, except in the *B. platyphylla* var. *japonica* forest. As a result of leaf fall, remarkable increases in litterfall occurred in October (autumn), with all communities showing a great peak at that time.

Seasonal changes in leaf fall of the dominant species in the four forest communities are shown in Fig. 13. A low peak of leaf fall of *B. platyphylla* var. *japonica* occurred in June, and of *Q. mongolica* var. *grosseserrata* in July. A large increase in leaf fall appeared in October, with about 94% of *Q. mongolica* var. *grosseserrata*, 72% of *B. platyphylla* var. *japonica*, 70% of *A. sachalinensis*, and 53% of *P. glehnii* leaf fall occurring in this month. Almost all of the deciduous broad-leaved species leaves have already fallen by October, while those of the evergreen coniferous species still continued to fall during the snow covered season.

Branch litter in the 4 forest during spring and summer months was low. In the DBF, the litter increased greatly in October. Even though there was also an increase in branch fall in the ECF in October, but not as high as in the DBF (Fig. 14). During the winter period, branch fall rates in the ECF were much higher than those in the DBF. In general, bark litter fluctuated similarly in the four forests. The litter was low during spring and summer, and increased in October (Fig. 15). The high rates of bark litter during the winter period might be attributable to the snow fall.

Seed litter was recorded from July in P2, August in P1 and P4, and September in P3 up to the winter months (Fig. 16). Peaks of seed fall rate were in October, with 36.0% (P1), 69.9% (P2), 57.5% (P3), and 50.5% (P4) of seed litter occur-

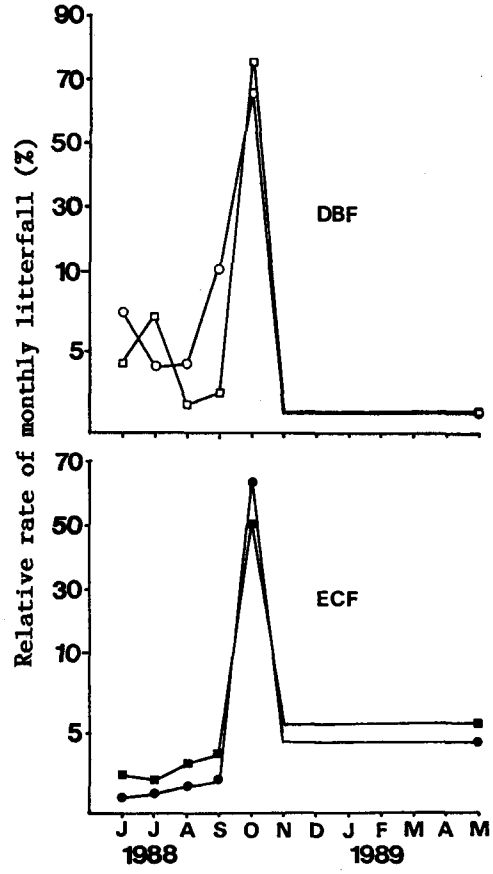

Fig. 12. Seasonal fluctuation of total litterfall in P1, P2, P3 and P4 (from June, 1988 to May, 1989).
Note: clear squares (P1), clear circles (P2), solid circles (P3) and solid squares (P4). DBF=Deciduous broad-leaved forests, ECF=Evergreen coniferous forests. The rates from November, 1988 to May, 1989 are the average values.

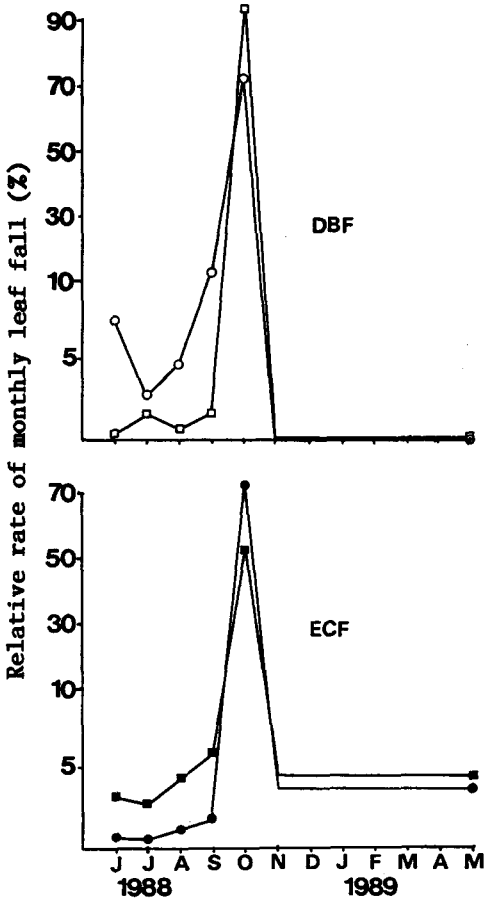

Fig. 13. Seasonal fluctuation of leaf fall of the dominant species in P1, P2, P3 and P4 (from June, 1988 to May, 1989).
Note: see Fig. 12.

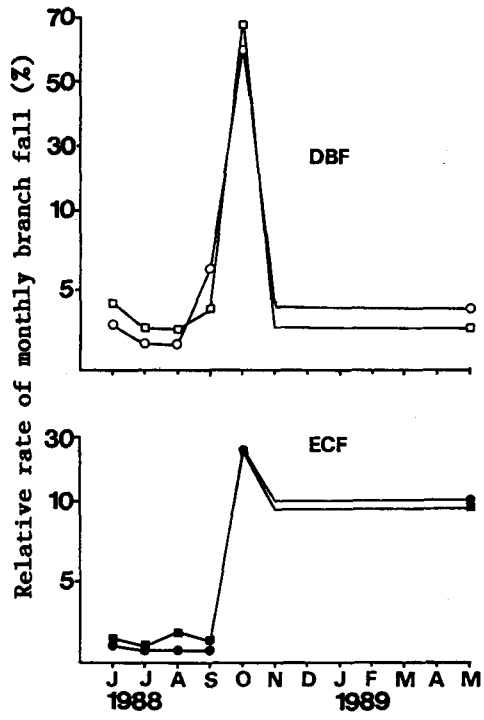

Fig. 14. Seasonal fluctuation of branch fall in P1, P2, P3 and P4 (from June, 1988 to May, 1989).
Note: see Fig. 12.

ring in this month. In the ECF, as a result of *A. sachalinensis* and *P. glehnii* seed fall, the rates were still high during the winter months.

Other material litter was composed of bud scales, flowers, cones, insect bodies and feces, and very small materials which were difficult to identify. In general, the litter had a similar fluctuation in the four forests (Fig. 17). The first peak appeared in spring as a result of bud scale and flower fall. In August and September, the litter was low, increased and reached the second peak in October, due to the fall of cones.

Seed production of the four forests in one year, from June, 1988 to May, 1989 is shown in Table 15. In the DBF, levels of seed fall amounted to 200 grains/m^2. yr of 6 species in P1, and 4,191 grains/m^2. yr belonging to 4 species in P2. Levels of seed fall in the ECF were 376 grains/m^2. yr of 4 species in P3, and 369 grains/m^2. yr belonging to 5 species in P4. Except in the *Q. mongolica* var. *grosseserrata* forest, the dominant species were the major contributor to the seed production, namely *B. platyphylla* var. *japonica*=96.7% in P2, *A. sachalinensis*=75.5% in P3 and *P. glehnii*=70.4% in P4.

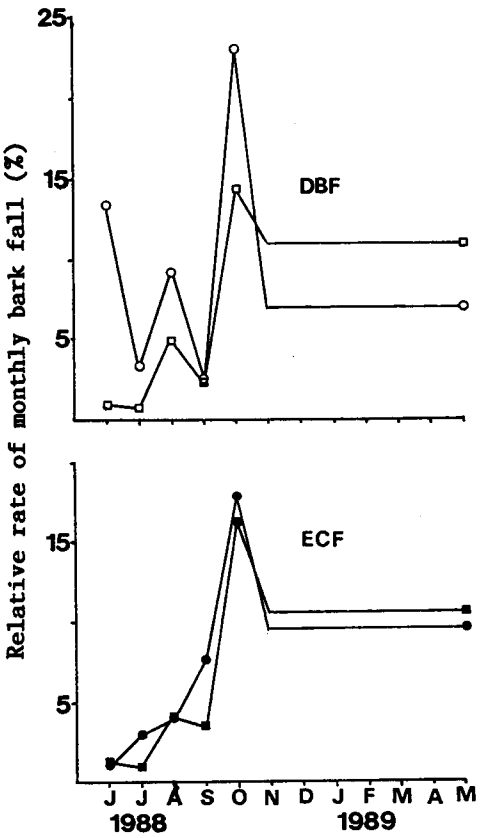

Fig. 15. Seasonal fluctuation of bark fall in P1, P2, P3 and P4 (from June, 1988 to May, 1989).
Note: see Fig. 12.

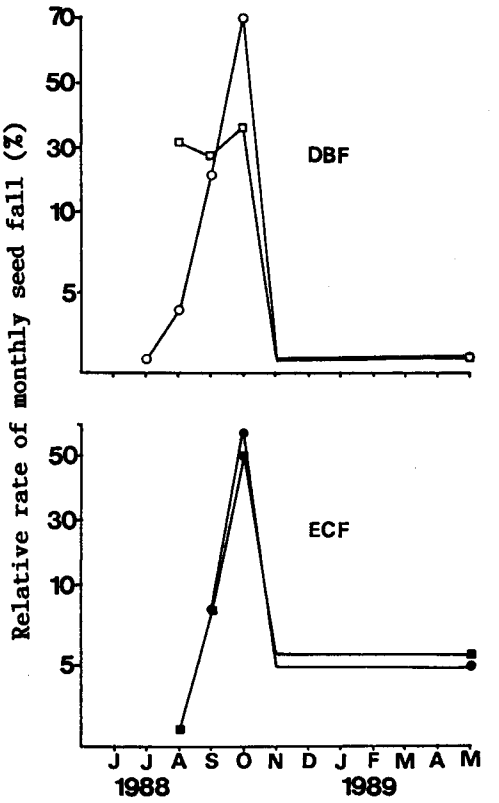

Fig. 16. Seasonal fluctuation of seed fall in P1, P2, P3 and P4 (from June, 1988 to May, 1989).
Note: see Fig. 12.

Table 16 illustrates the time of seed fall of the five species in the study plots. Seeds of *Q. mongolica* var. *grosseserrata* began to fall and reached a maximum of 64.7% in August, decreased in September (29.4%) and October (5.3%), but the fallen seeds were still small and immature. Although with a very low percentage (0.8%), seeds of *B. platyphylla* var. *japonica* had already begun to disperse in July, increased gradually in August (6.5%) and September (31.7%), and led to a maximum of 57.4% in October. Seed fall of *B. ermanii* also reached the maximum in October, but it started two months later than that of *B. platyphylla* var. *japonica*. During the winter period, the rate of *B. platyphylla* var. *japonica* seed fall (3.4%) was much lower than that of *B. ermanii* (17.1%). It is suggested that the time of seed fall of *B. platyphylla* var. *japonica* was slightly earlier than that of *B. ermanii*.

A percentage of 8.3% of *A. sachalinensis* seed fall was recorded in September. The rate increased greatly leading to a peak in October (61.5%), and decreasing during the winter period (31.7%). The first presence of *P. glehnii* seeds in the traps was also in September, but with a very low rate of 0.6%. The rate increased in October to 37.1%, leading to a maximum of 62.3% during the winter period. There was an

indication that the time of *P. glehnii* seed fall was somewhat later than that of *A. sachalinensis*.

4. 2. 2 Second year (from June, 1989 to May, 1990)

In the second year, annual litter production of the DBF was 3.66 t/ha. yr in P1 (Table 17) and 3.37 t/ha. yr in P2 (Table 18). In the ECF the litterfall amounted to 3.01 t/ha. yr in P3 (Table 19) and 3.52 t/ha. yr in P4 (Table 20). Except in P4, the 2nd year production was higher than the lst year, with the 2nd/lst year ratios of 1.1 in P1 and P3, 1.2 in P2, and 0.9 in P4 (Table 21).

Although with a low peak in June, the litterfall rates in the DBF were low during spring and summer, and their outstanding peak occurred in October. In the ECF, the first peak of litterfall appeared in August, with high rates in October and the winter months.

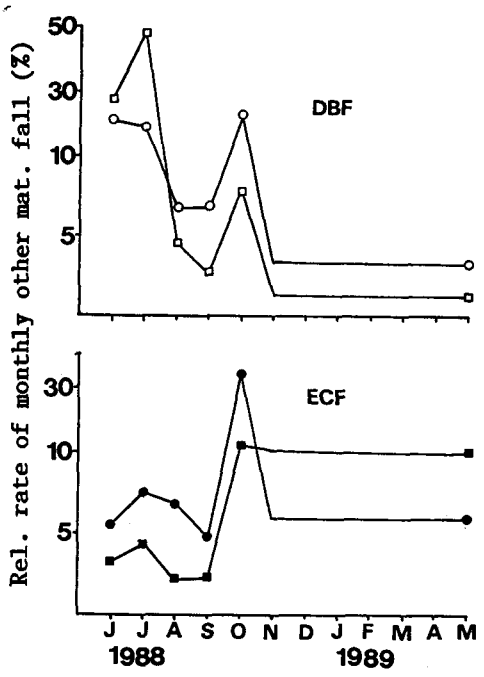

Fig. 17. Seasonal fluctuation of other material litter in P1, P2, P3 and P4 (from June, 1988 to May, 1989).
Note: see Fig. 12.

Almost all of the deciduous broad-leaved species leaf fall in the DBF was in autumn, in P1 it accounted for 96.1% in October, and 91.6% in September and October in P2. In the ECF, as a result of needle leaf fall, a peak of leaf fall in P3 and P4 appeared in August. In both plots, P3 and P4, the high rates were in October and the winter months, with total rates of 78.5% in P3 and 84.5% in P4.

Seasonality of branch fall in the DBF was not specially obvious. The rates were high in June, in both plots. In P1, the rates reached a maximum in October, and were low during the winter months. On the other hand, the lowest rate in P2 was in October, and the rates were relatively high during the winter months. In the ECF, the seasonality was more obvious with very low rates during the snow uncovered season, and almost all of the branch fall was during the snow covered season, with 91.3% in P3 and 88.4% in P4 occurring in this season.

4. 3 Forest floor litter

Table 22 shows the organic materials (litter) accumulated on the forest floor of the DBF and ECF. The accumulated litter in P1 was 7.85 t/ha, composed of woody materials (25.0%), *Sasa* litter (50.7%) and, leaf and other litter (24.3%). In P2, the litter amounted to 7.62 t/ha, consisting of woody materials (19.2%), *Sasa* litter (49.1%) and, leaf and other litter (31.7%). In the ECF, the total litter accumulated on the forest floor of P3 was estimated of 8.53 t/ha which was composed of woody materials

Table 15. Seed production from june, 1988 to May, 1989 in P1, P2, P3 and P4 (grains/m^{-2})

	Species	Jun	Jul	Aug	Sep	Oct	N—M	Total	[%]
P1	*Q. mongolica* var. *grosseserrata*	0	0	10	4	1	0	15	7.50
	B. platyphylla var. *japonica*	0	0	1	17	113	4	135	67.50
	B. ermanii	0	0	0	0	6	7	13	6.50
	A. mono	0	0	0	0	1	1	2	1.00
	A. sachalinensis	0	0	0	0	25	5	34	17.00
	P. glehnii	0	0	0	0	1	0	1	0.50
	Total	0	0	11	25	147	17	200	100.00
P2	*B. Platyphylla* var. *japonica*	0	35	273	1309	2295	139	4051	96.66
	B. ermanii	0	0	0	3	50	5	58	1.38
	A. sachalinensis	0	0	0	5	63	7	75	1.79
	P. glehnii	0	0	0	0	6	1	7	0.17
	Total	0	35	273	1317	2414	152	4191	100.00
P3	*A. sachalinensis*	0	0	0	21	157	106	284	75.53
	P. glehnii	0	0	0	1	58	6	65	17.29
	B. platyphylla var. *japonica*	0	0	0	3	1	0	4	1.06
	B. ermanii	0	0	0	1	16	6	23	6.12
	Total	0	0	0	26	232	118	376	100.00
P4	*P. glehnii*	0	0	0	2	129	319	450	70.42
	A. sachalinensis	0	0	0	16	95	48	159	24.88
	B. platyphylla var. *japonica*	0	0	0	2	1	2	5	0.78
	B. ermanii	0	0	0	0	21	2	23	3.60
	Q. mongolica var. *grosseserrata*	0	0	1	1	0	0	2	0.31
	Total	0	0	1	21	246	371	639	100.00

(42.8%), *Sasa* litter (15.4%) and, leaf and other litter (41.8%). In P4, the litter amounted to 8.01 t/ha, consisted of woody materials (41.4%), *Sasa* litter (5.0%) and, leaf and other litter (53.5%).

5. Discussion

5. 1 Stand structure

Based on the relative basal area and the vertical structure of the forests, P1 could be classified as a *Quercus mongolica* FISCH. var. *grosseserrata* REHD. et al WILLS. forest (Photos 2, 3, 4), P2 as a *Betula platyphylla* SUKATCHEV var. *japonica* HARA forest (Photos 5, 6), P3 as an *Abies sachalinensis* FR. SCHM. forest (Photos 7, 8) and P4 as a *Picea glehnii* MASTERS forest (Photos 9, 10). The first and the second forests were classified as deciduous broad-leaved forests (DBF), while the third and the fourth ones were classified as evergreen coniferous forests (ECF).

Basal area is a fundamental measure of forest structure, and roughly parallels

Table 16. The time of seed fall of five species in P1, P2, P3 and P4 during 1988—1989 [%]

Species		Jun	Jul	Eug	Sep	Oct	N—M	Total
Q. mongolica var. *grosseserrata*	P1	0	0	10	4	1	0	15
	P2	0	0	0	0	0	0	0
	P3	0	0	0	0	0	0	0
	P4	0	0	1	1	0	0	2
	Total	0	0	11	5	1	0	17
	[%]	0.0	0.0	64.7	29.4	5.9	0.0	100.0
B. platyphylla var. *japonica*	P1	0	0	1	17	113	4	135
	P2	0	35	273	1309	2295	139	4051
	P3	0	0	0	3	1	0	4
	P4	0	0	0	2	1	2	5
	Total	0	35	274	1331	2410	145	4195
	[%]	0.0	0.8	6.5	31.7	57.5	3.5	100.0
B. ermanii	P1	0	0	0	0	6	7	13
	P2	0	0	0	3	50	5	58
	P3	0	0	0	1	16	6	23
	P4	0	0	0	0	21	2	23
	Total	0	0	0	4	93	20	117
	[%]	0.0	0.0	0.0	3.4	79.5	17.1	100.0
A. Sachalinensis	P1	0	0	0	4	25	5	34
	P2	0	0	0	5	63	7	75
	P3	0	0	0	21	157	106	284
	P4	0	0	0	16	95	48	159
	Total	0	0	0	46	340	166	552
	[%]	0.0	0.0	0.0	8.3	61.6	30.1	100.0
P. glehnii	P1	0	0	0	0	1	0	1
	P2	0	0	0	0	6	1	7
	P3	0	0	0	1	58	6	65
	P4	0	0	0	2	129	319	450
	Total	0	0	0	3	194	326	523
	[%]	0.0	0.0	0.0	0.6	37.1	62.3	100.0

Table 17. Litter production from June, 1989 to May, 1990 [one year] in P1 ($\times 10^{-2}$t/ha)

	Leaves		Br	Oth	Total	[%]
	Bl	Cl				
June	1.96	0.16	4.58	13.56	20.26	5.5
July	1.63	0.12	0.90	3.35	6.00	1.6
August	2.61	0.13	5.61	2.31	10.66	2.9
September	3.01	0.21	4.15	2.72	10.09	2.8
October	255.90	11.77	12.98	4.42	285.07	77.9
Nov-May	1.18	2.82	17.06	12.93	33.99	9.3
Total	266.29	15.21	45.28	39.29	366.07	100.0
[%]	72.7	4.2	12.4	10.7	100.0	

Note:
Bl=Broad-leaved species, Cl=Coniferous species, Br=Branches, Oth=Other materials (bark, cones, insect bodies & feces, bud scales, flowers and unidentified materials).

Table 18. Litter production from June, 1989 to May, 1990 [one year] in P2 ($\times 10^{-2}$t/ha)

	Leaves		Br	Oth	Total	[%]
	Bl	Cl				
June	8.67	0.11	9.15	6.07	24.00	7.2
July	4.21	0.07	4.14	1.80	10.22	3.1
August	4.31	0.05	5.90	0.75	11.01	3.3
September	44.98	0.10	6.35	0.59	52.02	15.6
October	169.81	5.81	1.77	1.40	178.79	53.7
Nov-May	2.62	4.51	34.77	15.24	57.14	17.1
Total	234.60	10.65	62.08	25.85	333.18	100.0
[%]	69.6	3.2	19.5	7.7	100.0	

Note: see Table 17.

Table 19. Litter production from June, 1989 to May, 1990 [one year] in P3 ($\times 10^{-2}$t/ha)

	Leaves		Br	Oth	Total	[%]
	Cl	Bl				
June	3.74	0.42	1.16	2.32	7.64	2.1
July	6.29	1.50	1.26	1.50	10.55	2.9
August	30.07	0.78	0.66	1.36	32.87	8.9
September	7.21	1.56	0.66	1.71	11.14	3.0
October	99.58	55.57	2.71	2.82	160.68	43.6
Nov-May	73.18	1.82	51.79	19.08	145.87	39.6
Total	220.07	61.65	58.24	28.79	368.75	100.0
[%]	59.7	16.7	15.8	7.8	100.0	

Note:
Cl=Coniferous species, Bl=Broad-leaved species, Br=Branches, Oth=Other materials (bark, cones, insect bodies & feces, bud scales, flowers and unidentified materials).

Table 20. Litter production from June, 1989 to May, 1990 [one year] in P4 ($\times 10^{-2}$t/ha)

	Leaves		Br	Oth	Total	[%]
	Cl	Bl				
June	7.48	0.18	1.23	3.99	12.88	3.7
July	6.54	0.62	1.15	2.62	10.93	3.1
August	10.08	0.24	0.58	3.00	13.90	39
September	5.96	2.80	0.65	3.22	12.63	3.6
October	76.75	50.34	2.42	4.06	133.57	37.8
Nov-May	87.26	0.92	45.73	35.39	169.30	47.9
Total	194.07	55.10	51.76	52.28	353.21	100.0
[%]	55.0	15.5	14.7	14.8	100.0	

Note: see Table 19.

Table 21. Annual litter production ($\times 10^{-2}$t/ha. yr) in P1, P2, P3 and P4

Study Plots	Fractions	1 st Year	(%)	2 nd Year	(%)	Mean	(%)	2 nd/1 st Ratio
P1	DBS L	199.50	62.3	266.29	72.7	232.90	67.5	1.3
	ECS L	20.04	6.2	15.21	4.2	17.63	5.2	0.8
	Br	47.06	14.7	45.28	12.4	46.17	13.5	1.0
	Oth	53.70	16.8	39.29	10.7	46.50	13.8	0.7
	Total	320.30	100.0	366.07	100.0	343.19	100.0	1.1
P2	DBS L	183.55	68.5	234.60	70.4	209.08	69.5	1.3
	ECS L	10.34	3.8	10.65	3.2	10.50	3.5	1.0
	Br	44.66	16.7	62.08	18.6	53.37	17.7	1.4
	Oth	29.52	11.0	25.85	7.8	27.69	9.3	0.9
	Total	268.07	100.0	333.18	100.0	300.63	100.0	1.2
P3	DBS L	206.91	61.6	220.07	59.7	213.49	60.6	1.1
	ECS L	56.80	16.9	61.65	16.7	59.23	16.8	1.1
	Br	37.86	11.3	58.24	15.8	48.05	13.5	1.5
	Oth	34.30	100.2	28.79	7.8	31.55	8.8	0.8
	Total	335.87	100.0	368.75	100.0	352.31	99.8	1.1
P4	DBS L	212.00	55.1	194.07	55.0	203.04	55.1	0.9
	ECS L	55.69	14.5	55.10	15.5	55.40	15.0	1.0
	Br	40.20	10.4	51.76	14.7	45.98	12.5	1.3
	Oth	76.86	20.0	52.28	14.8	64.57	17.4	0.7
	Total	384.75	100.0	353.21	100.0	368.98	100.0	0.9

Note:
DBS L=Deciduous broad-leaved species leaves, ECS L=Evergreen coniferuous species leaves, Br=Branches, Oth=Other material litter.

Table 22. Accumulated organic materials on the forest floor of P1, P2, P3 and P4 ($\times 10^{-2}$ton/ha)

Quadrat	Deciduous Broad-leaved Forests							
	Wm	Qm Forest [P1]			Wm	Bp Forest [P2]		
		Ss	L & Om	Total		Ss	L & Om	Total
Q1	138.70	419.67	148.05	706.42	108.87	361.03	237.18	707.08
Q3	293.64	357.24	212.33	863.21	197.47	357.92	228.63	784.02
Q5	156.36	415.60	212.18	784.14	132.61	403.27	258.17	794.05
Average	196.23	397.50	190.85	784.59	146.32	374.07	241.33	761.71
[%]	25.01	50.66	24.33	100.00	19.21	49.11	31.68	100.00

Quadrat	Evergreen Coniferous Forests							
	Wm	As Forest [P3]			Wm	Pg Forest [P4]		
		Ss	L & Om	Total		Ss	L & Om	Total
Q1	242.22	193.36	371.43	807.01	277.55	77.88	423.78	779.21
Q3	303.39	80.60	423.33	807.32	173.34	39.37	457.18	669.89
Q3	549.21	119.40	275.33	943.94	544.60	3.68	404.69	952.97
Average	364.94	131.12	356.70	852.76	331.83	40.31	428.55	800.69
[%]	42.79	15.38	41.83	100.00	41.44	5.04	53.52	100.00

Note;
Qm=*Q. mongolica* var. *grosseserrata*, Bp=*B. platyphylla* var. *japonica*, As=*Abies sachalinensis*, Pg=*P. glehnii*, Wm=woody materials, Ss=*Sasa* litter, L & Om=leaf and other material litter.

biomass and production (REINERS, 1972). SATOO (1971) recognized that the net production of coniferous plantation forests was larger than that of deciduous broad-leaved forests. According to KIRA (1977), who summarized net production data of 316 forest stands throughout Japan, the evergreen forests tended to be more productive than the deciduous forests. This tendency was also found in the present study. The basal area of the ECF, 61.16 m^2/ha in P4 and 56.43 m^2/ha in P3, was higher in comparison with that of the BDF (50.73 m^2/ha in P1 and 22.34 m^2/ha in P2). As the leaves of the ECF are green all the year round, it is possible that the ECF have a longer period of photosynthesis. This might be one of the factors which caused the higher basal area of the ECF.

A. sachalinensis seemed to be a shade-bearing tree species whose seeds are able to germinate and manage to grow under the shade of their parent or other trees, and even among the *Sasa* community. It is suggested that due to the characteristic of *A. sachalinensis* as a tolerant species, its frequency distribution of DBH and height tended to be L-shape in the DBF as well as in the ECF.

In response to their environmental factors, tree species will be distributed in many patterns. Random distribution was found only in *B. platyphylla* var. *japonica* species of P2. ODUM (1971) described that random distribution as occurring where the environment is very uniform and there is no tendency to aggregate. It is supposed that in the area (P2), a natural disturbance [perhaps a forest fire] happened in some previous year, which caused the environmental conditions to become uniform. At that time, *B. platyphylla* var. *japonica* invaded the area, in the form of random distribution.

TATEWAKI (1958) reported that *B. platyphylla* var. *japonica* forests are generally developed after forest fires, forming pure stands. In this study, an almost pure forest of *B. platyphylla* var. *japonica* was found in P2, with a relative basal area of 88% belonging to the species. The number of *B. platyphylla* var. *japonica* seed fall in P2 during the year of 1988-1989 was 4,051 grains/m^2. yr, indicating that the seeds were produced in very large numbers. The seeds were very small and light, about 5,814 grains/gram dry weight, and they have a pair of wings. Therefore, the seeds are able to be disseminated by the wind effectively over a very long distance from their parent trees. After natural disturbances such as fire and land-slide happened, a large number of *B. platyphylla* var. *japonica* seeds seemed to be disseminated more rapidly than the other species seeds. As a pioneer species, it has a quick growth. Therefore, the species is able to establish a pure stand, as can be seen in the almost pure stand of *B. platyphylla* var. *japonica* in P2.

In the DBF, though the relative light intensities were sufficient, the density and the above ground biomass of the undergrowth of *Sasa* communities were high. On the other hand, in the ECF, the density and above ground biomass of *Sasa* were not high but the relative light intensities were insufficient (HARDIWINOTO et al., 1989). The organic materials accumulated on the forest floor were 7.8 t/ha in P1, 7.6 t/ha in P2, 8.5 t/ha in P3 and 8.0 t/ha in P4. As was reported by IGARASHI and CHENG (1988), CHENG (1989) the major population of *Racodium therryanum*, the causal fungus of dark snow blight, inhabits the surface organic layers. These conditions are not favorable

for the establishment of seedlings. Such favorable habitat as fallen logs, root bases, stumps (SUZUKI et al, 1987, MATSUDA, 1989) were provided when the trees fell, but the habitats provided seemed to be limited. The limited habitats may be able to stimulate the establishment of seedlings into the form of groups. As is shown in this study the most common distributional pattern was clump distribution, which occurred in P1, P3 and P4.

5. 2 Litter production

Species composition is one of factors influencing the annual litter production. Evergreen trees produced more litter than deciduous trees (BRAY and GORHAM, 1964). In the present study, mean annual litter production of the DBF, 3.43 t/ha. yr in P1 and 3.02 t/ha. yr in P2, was also lower in comparison with that of the ECF, 3.60 t/ha. yr in P3 and 3.69 t/ha. yr in P4. Basal area of the investigated forests was 50.73 m^2/ha in P1, 22.34 m^2/ha in P2, 56.43 m^2/ha in P3 and 61.16 m^2/ha in P4. The basal area was significantly correlated to the mean annual litter production, with a coefficient of correlation (r)=0.99, $p \leq 0.01$. FYLES et al. (1986) also reported that the differences in litter production between jack pine stands in northern Alberta, Canada are related primarily to differences in basal area.

In tropical zones, the average litter production of the mountain rain forest in New Guinea was equivalent to 7.55 t/ha. yr (EDWARDS, 1977); in the lowland forests in Gunung Mulu National Park, Sarawak, it ranged from 8.8 t/ha. yr in heath forest to 12.0 t/ha. yr in forest over limestone (PROCTOR et al., 1983); in Pasoh Research Area, Malaysia, it amounted to 10.6 t/ha. yr (OGAWA, 1978), while that in tropical Australian rain forests ranged from 7.28 to 10.53 t/ha. yr (SPAIN, 1984). In subtropical zones of Japan, the litterfall of mangrove stands amounted to 7.5 t/ha. yr in *Rhizophora stylosa- Bruguiera gymnorrhiza* community, 8.8 t/ha. yr in *Bruguiera gymnorrhiza* community (KISHIMOTO et al., 1986), and 8.7 t/ha. yr in *Kandelia candel* community (HARDIWINOTO et al., 1989).

In temperate forests of Japan, mean annual litter production amounted to 5.78 t/ha. yr in the evergreen broad-leaved forest in Kyushu (NISHIOKA and KIRITA, 1978), 6.33 t/ha. yr in an *Abies firma* forest and 5.24 t/ha. yr in a *Tsuga sieboldi* forest in Shikoku (ANDO et al., 1977). Litterfall of *Quercus serrata* stands in Kyoto, was estimated at 5.8 t/ha. yr in a mature stand and 4.4 t/ha. yr in a young stand (FURUNO and SAITO, 1981). SAKAI and TSUTSUMI (1986) reported that the mean annual litter production of natural deciduous forests in Ashu Experimental Forest of Kyoto University was 4.05 t/ha. yr in the upper part and 4.86 t/ha. yr in the lower part. In northern Honshu, Yamagata Prefecture, mean annual litterfall of a *Fagus crenata* was 5.74 t/ha. yr (KAWADA and MARUYAMA, 1986). In an evergreen coniferous (*Chamaecyparis obtusa*) plantation forest in Mt. Watamuki-yama, Shiga, the amount of litterfall was 4.77 t/ha. yr (SAITO, 1981).

As litter production is related to latitude, with a maximum productivity at the equatorial zone, declining steadily to the northern or southern latitudes (BRAY and GORHAM, 1964), the figures obtained in tropical and subtropical forests were markedly

greater, and those in the temperate forests were higher compared with the figures obtained in the present study. Litter production rates of 2.83-3.16 t/ha. yr in an evergreen coniferous forest in sub-arctic zone of Hokkaido (SIMARANGKIR and IGARASHI, 1986, 1987) are within the range of our results.

FYLES et al. (1986) recognized that the seasonality of litterfall was controlled by random factors such as weather activity, chronic factors such as insect and disease activity, and predictable, seasonal factors such as leaf abscission in autumn. A low peak of leaf fall of dominant species of the DBF in the lst year spring was attributed to insect activity. Because of disease, a *P. glehnii* tree near P3 died in August, 1989, and as a result, an obvious peak of coniferous leaf fall in P3 appeared in this month. A great amount of leaf fall of the dominant species in the DBF as well as in the ECF occurred in October, with 94.4% of *Q. mongolica* var. *grosseserrata*, 72.0% of *B. platyphylla* var. *japonica*, 70.4% of *A. sachalinensis*, and 52.5% of *P. glehnii* leaf fall occurring in this month. FYLES et al. (1986) described the high rate of leaf fall in autumn as being controlled by predictable seasonal factors and generated through the physiological changes that occur in the individual plants.

In the DBF, the branch fall showed an uncertain pattern, during the lst year, the rate being low in spring, summer and winter, with an outstanding peak in October (Fig. 14), but in the 2nd year, the rates were somewhat high in spring and summer, the autumn peak appearing in P1, but not in P2; and in both plots the rates were high during winter, (Tables 19, 20, Photos 11, 12). Since the branch fall is primarily controlled by random factors such as strong wind, typhoon and snow loading, similar results were obtained in many types of forests as was reported by NISHIOKA and KIRITA (1978), KIMURA et al. (1984), HIRABUKI (1985), and HARDIWINOTO et al. (1989). In the ECF, the seasonality of the branch fall was more obvious, with very low rates in spring and summer. The maximum rates were during the snow covered season, with 70.7-88.9% of branch fall in P3 and 68.7-88.4% in P4 occurring in this period. The possibility that needle leaves of the ECF were heavily laden with snow during the winter, is suggested as a main factor contributing to the high rates (Photos 13, 14). This result supports the reports of SIMARANGKIR and IGARASHI (1986, 1987). As the forests investigated are located in a heavy snow area (Table 1), the high rates of winter branch fall are more predictable.

In general, the bark fall fluctuated similarly (Fig. 15), with a peak occurring in October and high rates during winter (Photo 11). It suggested that the seasonality of the bark fall is primarily controlled by random factors, as was reported by FYLES et al. (1984) in *Pinus banksiana* stands in northern Alberta. The character of the dominant species in P1 and P4 which produced a large amount of bark fall, is supposed to be the causative factor of the high rates in the plots (Tables 11, 12, 13, 14).

Abundant flowering and seed production, occurring irregularly in natural stands of forest trees, is not only controlled by the internal environment of the plant, but is also strongly influenced by the external environments such as light particularly, temperature and moisture (SPURR and BARNES, 1980). The fallen seeds of *Q. mongolica* var. *grosseserrata* were few, still small and immature suggesting that the year 1988-1989 was not

an abundant year for *Q. mongolica* var. *grosseserrata* seed production. The high rates of seed fall of the three dominant species, *B. platyphylla* var. *japonica*=4,105 grains/m^2. yr in P2, *A. sachalinensis*=375 grains/m^2. yr in P3, and *P. glehnii*=500 grains/m^2. yr in P4, indicated that the year 1988-1989 was one of abundant seed production for the three species. All seeds of *A. sachalinensis* were found in the traps separately from their cones, indicating that the cones opened shortly after ripening, and the seeds were dispersed rapidly. On the other hand, numbers of *P. glehnii* seeds were collected when they were still in their cones, suggesting that seed dispersal of *P. glehnii* was not as rapid as *A. sachalinensis*.

Annual litter production may fluctuate greatly in different years (BRAY and GORHAM, 1964). HIRABUKI (1985) reported the maximum/minimum ratio of total litter production of 1.2 and 1.4 (ANDO et al., 1977) in an *Abies firma* forest, during a 3 years monitoring. NISHIOKA and KIRITA (1978) found the ratio of 1.5 in warm-temperate evergreen broad-leaved forests, in the Minamata Research Area, over a period of 5 years observation. In a *Chamaecyparis obtusa* plantation forest, with a 10 years period of investigation, the rate reached as high as 2.5 (SAITO, 1981). In the present study, except in P4, the annual litter production in the 2nd year was somewhat higher than in the 1 st year, with the 2nd/lst ratios of 1.1 in P1 and P3, 1.2 in P2 and 0.9 in P4 (Table 21). Leaf fall of broad-leaved species in P1 and P2, increased about 30% in the 2nd year. Though there was a 10% increase in leaf fall of coniferous species in P3, this was brought about by a dying tree which shed all its leaves, while leaf fall in P4, showed a decrease in the 2nd year. The higher rates of other material litter in the lst year were attributed to the high amount of insect feces fall in P1 and the abundance of cone fall in P3 and P4 during that year. As the litter production fluctuated annually, a longer period of observation should be undertaken.

Excluding the *Sasa* litter, the amounts of organic materials on the forest floor of the DBF were lower than those of the ECF (Table 22). Since litterfall is the major contributor of organic materials to the forest floor, the lower litter production in the DBF was in agreement with the lower accumulated organic materials. Beside the higher leaf litter production of the ECF, it is suggested that the higher accumulated leaf and other materials on the forest floor of the ECF may be attributable to the slower decomposition of the leaves of coniferous species. Therefore, an observation on the decomposition process of the coniferous and broad-leaved species leaves should be carried out.

Akcnowledgements

We are grateful to Dr. K. Matsuda, Dr. M. Kadomatsu and Dr. M. Hayashida of the Uryu Experiment Forest, Hokkaido University, for their kind assistance and useful advice during the course of this research. Thanks are also extended to Mr. S. Fujimoto, Mr. M. Shibuya, Mr. T. Tadokoro, Mr. T. Kishimoto and other members of the Laboratory of Silviculture, Hokkaido University, and to Mr. N. Sinden, Mr. Y. Yoshimi, Mr. K. Otsuji and Mr. H. Kamimura of the Department of Forestry, University of the Ryukyus, for their kind help during the field work.

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摘　　要

森林生態系の主要な養分移動経路として，リターフォールの定量的研究は重要である（BRAY and GORHAM, 1964)。これまで世界及び日本各地の様々な森林生態系でリターフォールの調査が行われてきた。しかし，日本最北部である北海道ではこれに関する研究はまだ少ない。本研究では北海道北部における落葉広葉樹林と常緑針葉樹林のリターフォール量及び季節変化を検討した。研究期間は2年間で，一年目は1988年6月から1989年5月まで，二年目は1989年6月から1990年5月までであった。

本研究は北海道大学農学部付属雨龍地方演習林で行った。本演習林は，およそ，北緯44度11分，東経142度16分に位置する（Fig. 1)。1988年5月に4つの方形調査区，P1（30 m×30 m)，P2（20 m×20 m)，P3（20 m×20 m)，P4（20 m×50 m）を設定し，プロット内の樹高2 m以上の全樹木について，樹高，胸高直径，立木位置及び樹冠幅を計測した。

P1とP4では10個ずつ，P2とP3では8個ずつ，リタートラップを設置した。トラップは木製で，底に1 mmメッシュの網を張り，間口は0.85 m×0.85 mである（Photo 1)。

6月から10月までの無積雪期には毎月1度，11月から5月までの積雪期については1989年5月末日に1度，リターフォールを回収した。回収したリターは葉，枝，樹皮，種子，その他に分けた。葉はさらに樹種によって分けた。試料は85℃のオーブンで乾燥し，乾燥重量を求めた。

P1で認められた樹種は8種類，胸高断面積合計は50.37 m^2/haで，ミズナラの相対胸高断面積が84.1%，その他は15.9%，であった(Table 2)。P2では5種類，22.34 m^2/haで，シラカンバが88.0%，その他は12.0%，であった(Table 3)。P3では8種類，56.43 m^2/haで，トドマツが66.7%，その他は33.3%，であった（Table 4)。P4では10種類，61.16 m^2/haで，アカエゾマツが74.2%，その他は25.8%，であった(Table 5)。P1の高木の相対密度はミズナラ＝90%, P2はシラカンバ＝100%, P3はトドマツ＝80%, P4はアカエゾマツ＝63%であった。従って，本研究ではP1をミズナラ（*Quercus mongolica* var. *grosseserrata*）優占林分，P2をシラカンバ(*Betula platyphylla* var. *japonica*)優占林分，P3をトドマツ(*Abies sachalinensis*)優占林分，P4をアカエゾマツ（*Picea glehnii*）優占林分とした（Photos 2-10)。

シラカンバの樹高及び胸高直径階別度数分布はほぼ正規分布で，ミズナラやアカエゾマツではJ-型分布の傾向が認められた。トドマツは陰樹の性質を持つと考えられ，樹高及び胸高直径階別度数分布はL-型分布の傾向が現れた（Figures 6-9)。シラカンバの分布様式は機械分布の傾向が現れたが，一般的には集中斑を持つ集中分布の傾向が認められた（Figures 10-11)。

一年目のP1のリターフォール量は3.20 t/haで，葉(68.5%)，枝(14.7%)，樹皮(4.5%)，種子（0.5%)，その他（11.8%）であった（Table 11)。P2は2.68 t/haで，葉（72.3%)，枝（16.7%)，樹皮（0.8%)，種子（0.5%)，その他（9.7%）であった（Table 12)。P3は3.36

t/ha で，葉（78.5%），枝（11.3%），樹皮（1.6%），種子（0.7%），その他（7.9%）であった（Table 13）。P4 は 3.85 t/ha で，葉（69.6%），枝（10.4%），樹皮（9.2%），種子（0.6%），その他（10.2%）であった（Table 14）。葉はリターフォールの最も大きな部分を占めた。

全体のリターフォール量は6月，7月，8月に，低い値を示した。10月には全プロットで大きなピークが認められた(Fig. 12)。内容別にみるとミズナラの落葉は7月に，シラカンバの落葉は6月に小ピークが現れた。10月には全プロットで大量の落葉がみられた。広葉樹林では10月までにほとんど全ての葉が落ち，針葉樹林の場合には積雪期にも落葉がまだ続いていた(Fig. 13)。

落枝は春と夏の間は少なかった。10月には落葉広葉樹林で非常に多く，大きなピークが現れた。常緑針葉樹林の場合は10月にピークを持つが，むしろ積雪期に多いという特徴があった（Fig. 14)。

落下樹皮量は4つの林分でおおむね類似した季節変化が認められた。P2 以外では春と夏の間に落下樹皮が少なく，10月には落葉広葉樹林及び常緑針葉樹林でもピークが現れた。樹皮量は冬の間に多く，P1 で 76.8%，P2 で 48.9%，P3 で 66.8%，P4 で 73.7%が落下した(Fig. 15, Photo 11)。

落下種子は P1 と P4 では8月から，P2 では7月から，P3 では9月から観察され，ピークは何れも 10 月に認められた。積雪期の針葉樹林の落下種子量は広葉樹林より多かった（Fig. 16)。その他のリターは芽鱗，花，種鱗，虫の遺体とふん，などであった。春には多くの芽鱗と花が落ち，10月には多くの種鱗が落下した（Fig. 17)。

一年間の種子生産は Table 15 で示した。落葉広葉樹林の種子生産は P1 では 200 粒/m^2，P2 では 4,191 粒/m^2 であった。常緑針葉樹林の場合 P3 では 376 粒/m^2，P4 では 639 粒/m^2 であった。P1 以外は優占樹種の落下種子が主要な部分を占め，シラカンバ＝96.7%，トドマツ＝75.5%，アカエゾマツ＝70.4%であった。P2 ではシラカンバの種子生産は 4,051 粒/m^2，P3 ではトドマツが 284 粒/m^2，P4 ではアカエゾマツが 450 粒/m^2 と多数であった。

シラカンバ種子の落下は7月に始まり，8月，9月に次第に多くなって，ピークは10月（57.5%)に認められた。トドマツの種子は9月に落下し始め 10 月に最も多くなって(61.6%)，ピークとなった。アカエゾマツ種子の落下は9月に始まり，10月に多くなったが，62.3%は積雪期に観察された（Table 16)。

二年目のリターフォール量は P1 では 3.66 t/ha. yr（Table 17)，P2 では 3.33 t/ha. yr（Table 18)，P3 では 3.69 t/ha. yr（Table 19)，P4 では 3.53 t/ha. yr（Table 20）であった。P1，P2，P3 と P4 の年平均リターフォール量はそれぞれ 3.43，3.01，3.52 と 3.69 t/ha. yr であった（Table 21)。

落葉広葉樹林における年間のリターフォール（P1 では 3.43 t/ha. yr，P2 では 3.01 t/ha. yr）は常緑針葉樹林（P3 は 3.52 t/ha. yr，P4 は 3.69 t/ha. yr）よりやや低かった。また

五十嵐（1986）は北海道北部のアカエゾマツ・トドマツ天然林の環境要因と林分構造の解析を行い，そのリターフォール量は3.0 t/ha. yr（シマランキル・五十嵐，1986，1987）であるとした。この数字は，本研究における落葉広葉樹林のリターフォール量の平均と殆ど同じであったが，常緑針葉樹林の場合はやや高かった。四国のモミ優占林のリターフォールは6.33 t/ha. yr，ツガ優占林では5.24 t/ha. yr と報告されている（ANDO et al., 1977）。これらの結果と比較して，北海道北部の常緑針葉樹林のリターフォール量は少なかった。

落葉広葉樹林の胸高断面積（P1 で 50.37 m^2/ha，P2 で 22.34 m^2/ha）も常緑針葉樹林（P3 で 56.43 m^2/ha，P4 では 61.16 m^2/ha）より低かった。このデータより胸高断面積が高くなると総リターフォールが多くなる傾向がはっきり認められた（$r=0.99$，$P<0.01$）。

P1 と P4 の落下樹皮量は P2 と P3 の値より非常に高かった。ミズナラ，アカエゾマツの樹皮は落ちやすいため，このような結果になったと考えられる。積雪期には常緑針葉樹林の落枝は落葉広葉樹林のものより明かに多かった。常緑針葉樹林では雪重のため，枝が折れやすいと考えられ，このことが常緑針葉樹林の落枝量が多いことの一つの要因であろう（Photos 13, 14）。これはシマランキル・五十嵐（1986，1987）の見解を支持するものである。

リターフォール量の二年目：一年目の比率は P1 では 1.1，P2 では 1.2，P3 では 1.1，P4 では 0.9 であった。研究期間は二年間で短いがリターフォール量の大きな年変動は認められなかった。

Photo 1. One of the littertraps in Plot 4.

Photo 2. Inside view of Plot 1 on June 30, 1989 (summer).

Photo 4. View of Plot 1 on October 30, 1989 (autumn).

Photo 3. View of Plot 1 on June 30, 1989 (summer).

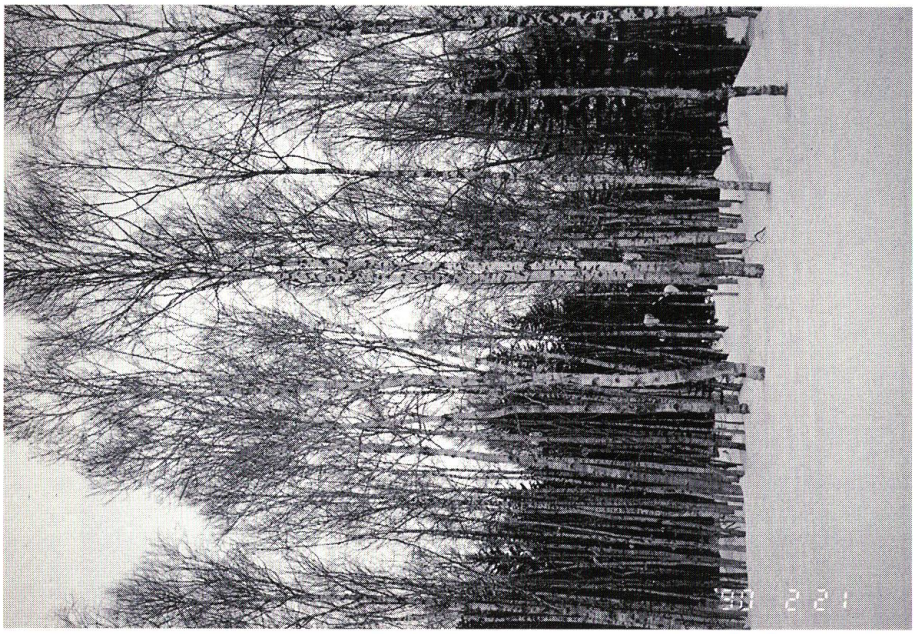

Photo 6. View of Plot 2 on February 21, 1990 (winter).

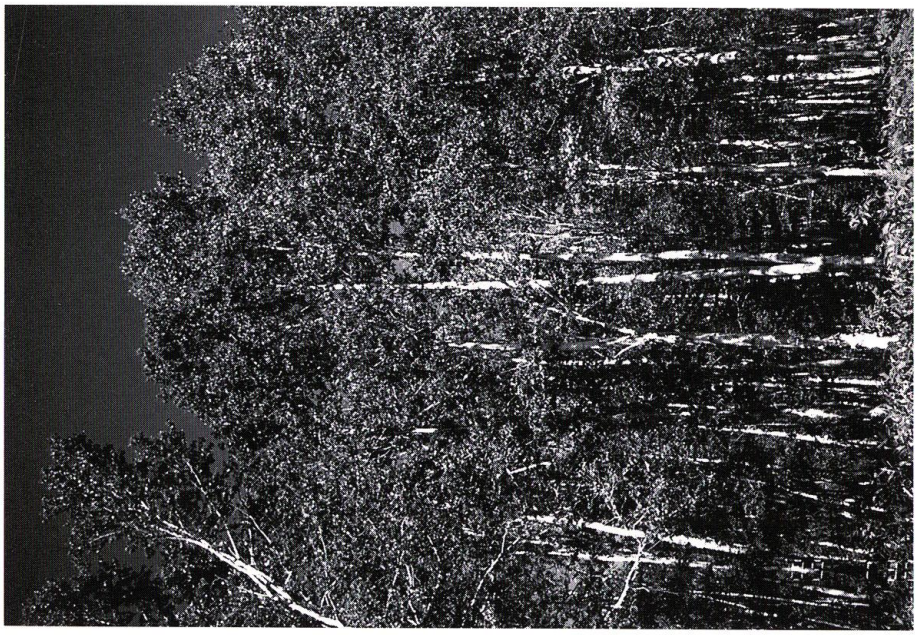

Photo 5. View of Plot 2 on July 30, 1989 (summer).

Photo 8. View of Plot 3 on February 21, 1990 (winter).

Photo 7. View of Plot 3 on July 30, 1989 (summer).

Photo 9. Inside view of Plot 4 on June 30, 1989 (summer).

Photo 10. Inside view of Plot 4 on February 21, 1990 (winter).

Photo 11. Branch and bark litter in *Q. mongolica* var. *grosseserrata* forest during winter.

Photo 12. Branch litter in *B. platyphylla* var. *japonica* forest during winter.

Photo 13. Litterfall in *A. sachalinensis* forest during winter.

Photo 14. Litterfall in *P. glehnii* forest during winter.