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Ewa PIROŻNIKOW

Białowieża Geobotanical Station of Warsaw University,
17-230 Białowieża, Poland

SEED BANK IN THE SOIL OF STABILIZED ECOSYSTEM OF A DECIDUOUS FOREST (TILIO-CARPINETUM) IN THE BIAŁOWIEŻA NATIONAL PARK

ABSTRACT: Species composition and distribution of seeds in soil of the Tilio-Carpinetum ecosystem have been investigated during two vegetation seasons. The seed bank has a similar number of species as the plant cover. But the diaspores of many herb layer components are not included in the bank. Seeds of early succession stages are the most abundant in the seed bank. The seed bank is relatively small, similarly as in other stabilized forest ecosystems. The contribution of particular species of herbaceous plants to the bank is quite constant from year to year; about $\frac{2}{3}$ of seeds are in the top soil layer.

KEY WORDS: Seed bank, diaspores in soil, species composition, numbers, distribution in soil, germination capacity.

C o n t e n t s

1. INTRODUCTION

Diaspores in the soil of ecosystem are the seed bank. They are from two sources (1) local, i.e., produced by plants living in the phytocoenosis examined (seed fall), (2) from closer or farther neighbourhood transported by means of animals, wind, water and also man (Harper 1977).

The seed bank has been for a long time an object of investigations of many authors. The seed bank in soils of simple ecosystems, consisting of a small number of species, has been more thoroughly investigated (Branchley and Warington 1930, 1964 after Harper 1977, Wilkoń-Michalska 1976, Symonides 1978). Less frequently investigated are forest ecosystems (Olmsted and Curtis, 1947, Karpov 1960).

In all investigations on the composition and density of seeds in soils there have been three main problems: distribution of seeds at various depths; differentiation of seed bank depending on the plant cover; the role of seed bank in plant succession.

In stabilized forest ecosystems the majority of herbaceous plants reproduce vegetatively. A very low per cent of individuals attain the generative stage - 3-30% of shoots (Falińska 1968). The plants in ecosystems under discussion do not produce many seeds (F a l i ń s k a 1971a). Very few seeds germinate under natural conditions. Thus is has been considered necessary to examine the numbers and species composition, and the germination capacity of seeds in the soil of Tilio-Carpinetum ecosystem.

2. OBJECT AND METHODS

The studies on the seed bank have been conducted in the strict nature reserve of the Białowieża National Park, in a well developed Tilio-Carpinetum ecosystem.

Mesophilous deciduous linden-hornbeam-oak forests are the most common in the Białowieża Forest community connected with fertile sites on soils of lessive or brown type. Multilayer, multispecific and of different age forest stand creates specific conditions of the forest floor. In summer, hardly 10% of full ligth reaches it (S ł o m k a 1967). The Tilio-Carpinetum herb layer is formed by early blossoming, shade-enduring species, which mainly reproduce vegetatively. These species occur almost exclusively in deciduous forests (M a t u s z k i e w i c z 1952, F a l i ń s k i and H e r e ź n i a k 1977, E l l e n b e r g 1978).

These studies were conducted on a constant research area of the Białowieża Geobotanical Station chosen for studies within the International Biological Programme (F a l i ń s k i 1966). On this area conducted were, amongst others, studies on the productivity of seeds in the herb layer and the tree stand (F a l i ń s k a 1968, 1971a, 1971b), on the energetic value of diaspores of chosen species (F a l i ń s k a 1968, 1969), and also on the seed consumption (G ę b c z y ń s k a 1976).

The research area is square, 100 × 100 m, and is divided into 100 identical squares.

Studies on the seed bank were conducted during two vegetation seasons - 1979 and 1980. In order to examine the seed bank in soil two methods were applied parallelly (1) direct choice and selection of seeds from soil and (2) keeping soil samples under laboratory conditions for germination of seeds from the bank and the identification of seedlings.

A line, 100 m in length, cutting the phytocoenosis examined from the north to the south, was made in order to take soil samples. In the first year of investigations, late in autumn, 100 soil samples were being taken systematically every 1 m. In the second year - in spring and autumn - 30 samples were taken. In both years the soil was sampled using a cylinder for taking undisturbed soil cores (Kopecky cylinder) (100 ml) in one place at two depths - 0-4 cm and 4-8 cm. In the laboratory the soil was rinsed on sieves of a mesh size 0.25 mm to remove the smallest fractions. The soil remaining on the sieve was analysed under an eye-piece. Seeds selected from soil were identified on the basis of a comparative collection of diaspores of oak-linden-hornbeam forest species and the atlas (S c h e r m a n n 1966). The seeds were segregated into damaged and undamaged ones, also the hulls of seeds and fragments of seed-vessel (pericarp) were isolated. The isolated seeds were placed on Petri dishes to check their germination capacity. The remaining soil was placed in cuvettes and was left in conditions allowing for the germination of seeds not taken into account in the analysis. Diaspores of the genera Betula and Carex were not divided into species.

In spring and autumn of 1980, the top soil layer (down to the depth of 3-4 cm) was taken additionally from 26 squares of a surface area 0.25 m^2 to cuvettes measuring 30 × 40 cm. The cuvettes with soil were taken to the laboratory and left for germination under natural ligth conditions and at moderate moisture. The seedlings were marked and identified according to the herbarium of seedlings and the atlas (C s a p o d y 1968).

In order to observe the reaction of seeds to cooling and drying in soil, 20 samples of a volume 350 ml each were collected from the top soil layer in autumn 1980. Ten were left for the winter in an unheated chamber (at 0-10°C), other were kept dry at room temperature. In spring, the germination capacity of seeds in soil, under laboratory conditions, was checked.

For purposes of comparison the appearance of seedlings was observed in the phytocoenosis under natural conditions. Therefore, 50 evenly distributed (every 3 and 4 m) squares, 1 × 1 m, were delimited in the herb layer. Every 10 days, in both seasons, the number of seedlings of particular species found among the plants of herb layer was recorded.

3. RESULTS

3.1. Species composition and abundance of seed bank

In the soil examined under an eye-piece seeds of 32 species were identified. The greatest contribution was that of herbaceous plants and shrubs - 27 species were identified, whereas 5 species of trees were found (Table I). Five per cent of the total number of seeds was not identified.

Out of the soil examined during two seasons the total of 8375 undamaged seeds were segregated. This calculated per m^2 of soil gave for particular seasons from 3988 ± 789 to 8115 ± 1964 of undamaged seeds.

Particular samples contained 1-93 seeds. The greatest number of samples contained from few to several seeds (Fig. 1). Particular species were much differentiated as regards numbers. Sligh-

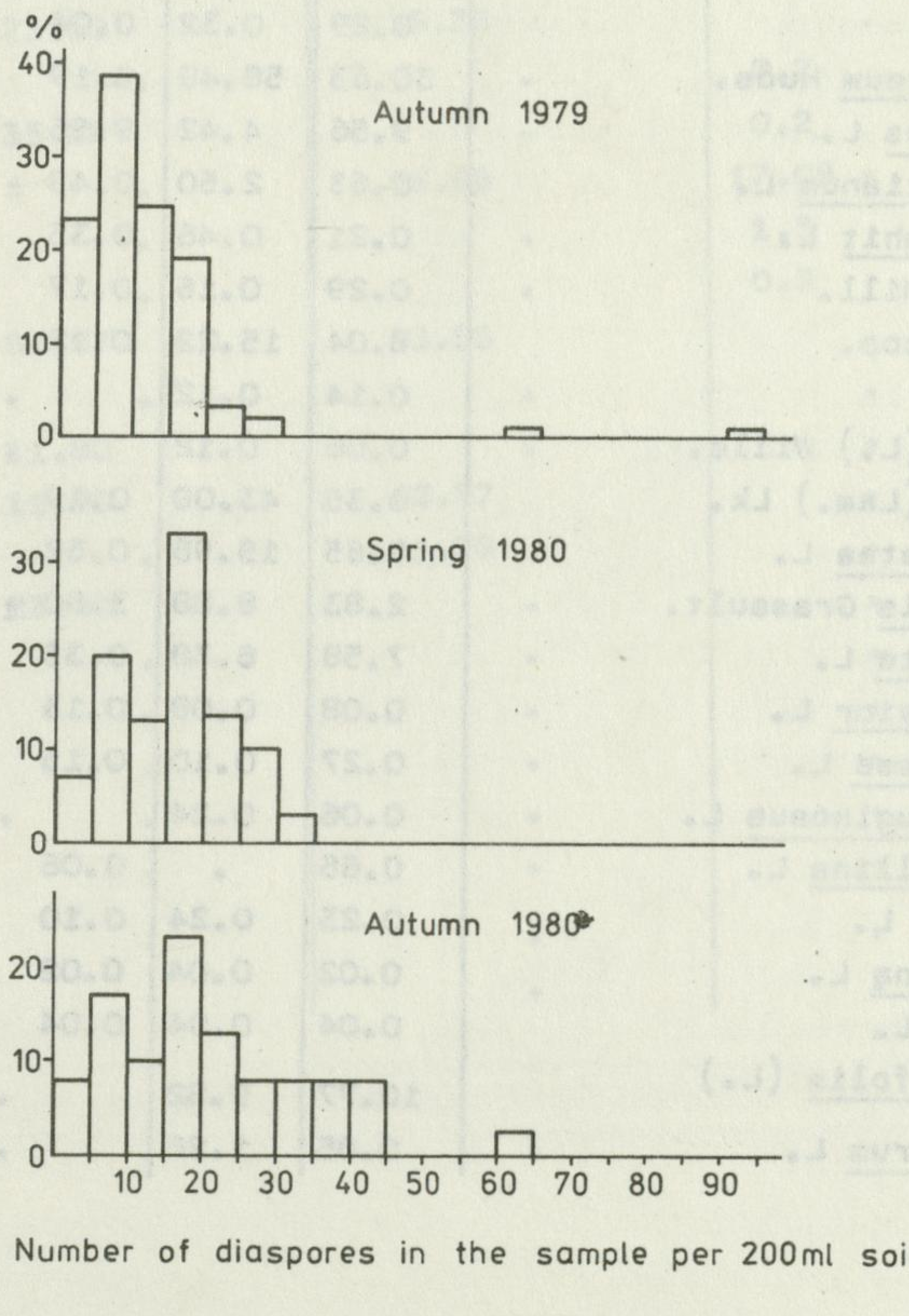

Fig. 1. Frequency of samples (in per cents) with a different nummer of diaspores

Table I. Density of shoots and seedlings in the herb
Standard deviation for

Species	Number of aboveground shoots per m^2		Number of seedlings per m^2	
	1980	1981	1980	1981
Anemone nemorosa L.	262.4	162.42	4.75 ± 1.47	12.88 ± 3.95
Oxalis acetosella L.	144.4	226.8	36.30 ± 4.69	56.48 ± 8.58
Impatiens noli-tangere L.	62.4	49.2	62.40 ± 19.40	49.2 ± 12.84
Carpinus betulus L.	17.23	46.70	17.23 ± 2.49	46.70 ± 7.81
Milium effusum L.	15.90	38.82	1.38 ± 0.71	7.08 ± 3.51
Moechringia trinervia (L.) Clarv.	3.19	2.24	4.65 ± 2.86	5.04 ± 3.57
Viola sp.	1.75	2.40	1.98 ± 1.02	1.48 ± 1.21
Urtica dioica L.	0.94	0.74	0.58	0.54
Mycelis muralis (L.) Dum.	0.75	0.88	0.42 ± 0.28	1.18 ± 0.63
Rubus idaeus L.	0.29	0.32	0.04	0.06
Galeobdolon luteum Huds.	30.63	58.40	0.19	2.80 ± 1.29
Acer platanoides L.	9.56	4.42	9.56	0.12
Geranium robertianum L.	0.63	2.50	0.48 ± 0.44	5.36 ± 4.80
Galeopsis tetrahit L.	0.21	0.46	0.35	0.56
Tilia cordata Mill.	0.29	0.16	0.17	0.08
Carex pilosa Scop.	8.04	15.22	0.12	•
C. digitata L.	0.14	0.12	•	•
Luzula pilosa (L.) Willd.	0.06	0.12	•	•
Picea excelsa (Lam.) Lk.	0.35	43.00	0.19	43.00 ± 13.87
Stellaria holostea L.	9.65	15.96	0.62	0.02
Hepatica nobilis Grasault.	2.83	8.88	3.60 ± 1.65	3.92 ± 1.65
Asperula odorata L.	7.58	6.38	0.35	0.14
Fraxinus excelsior L.	0.08	0.08	0.13	•
Sanicula europaea L.	0.27	0.10	0.15	0.02
Ranunculus lanuginosus L.	0.06	0.24	•	0.24
Adoxa moschatellina L.	0.65	•	0.06	•
Circaea alpina L.	0.23	0.24	0.10	0.06
Corylus avellana L.	0.02	0.04	0.02	0.02
Quercus robur L.	0.04	0.04	0.04	0.02
Majanthemum bifolim (L.) F.W. Schm.	10.77	9.82	•	•
Stellaria nemorum L.	0.85	1.26	•	•

layer and seed bank in the soil of Tilio-Carpinetum ecosystem
semple frequency 40% only

Seed bank, number of diaspores per m^2			Number of seedlings from seed bank per m^2	
1979 autumn	1980 spring	1980 autumn	1980 spring	1980 autumn
14.15	82.57	35.38	0.20	
424.63 ± 102.62	601.56 ± 276.01	790.28 ± 268.93	27.04 ± 6.16	1.76 ± 3.28
95.54 ± 60.16	117.95 ± 145.08	188.72	11.84 ± 8.08	1.00
1277.42 ± 230.01	1521.59 ± 552.02	2264.69 ± 1135.88	36.76 ± 6.32	1.52 ± 1.24
14.15	58.98	58.98	1.20	1.00
668.79 ± 509.55	448.22 ± 350.32	743.10 ± 675.87	20.00 ± 20.02	1.76 ± 1.60
10.61	11.80	11.80	1.1	.
49.53	117.29	224.11	2.5	0.5
21.23	58.98	23.59	0.3	0.25
300.78 ± 353.86	252.86 ± 233.55	1085.16 ± 304.32	29.40 ± 11.08	3.24 ± 3.08
.	23.59	82.51	0.6	
42.46	271.29	176.93	0.6	.
.	23.60	35.38	.	0.25
10.61	.	.	0.2	.
88.46	35.39		0.2	.
.	.	58.98	17.08 ± 8.72	1.25
.	.	.	1.5	
31.85	.	.	0.3	0.25
10.61	82.57	23.56	.	.
.	.	.	.	.
35.39	11.80	.	.	.
17.69	11.80	82.57	.	.
.	.	11.79	.	.
.	23.60	.	.	.
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.
.	.	.	.	.

Species	Number of aboveground shoots per m^2		Number of seedlings per m^2	
	1980	1981	1980	1981
Geum urbanum L.	.	0.14	.	.
Polygonatum multiflorum (L.) All.	0.02	0.02	.	.
Rubus saxatilis L.	.	0.02	.	.
Ficaria verna Huds.	.	0.02	.	.
Aegopodium podagraria L.	0.8	0.04	.	.
Phaegopteris dryopteris (L.)F	0.19	0.24	.	.
Equisetum pratense Ehrh.	5.08	2.10	.	.
Dryopteris spinulosa (Müll.) O. Kuntze	0.19	0.24	.	.
Equisetum silvaticum L.	0.65	0.26	.	.
Athyrium filix-femina (L.) Roth.	0.08	0.08	.	.
Lathyrus vernus (L.) Bernh.	.	.	0.02	.
Cardamine amara L.	.	.	.	0.04
Taraxacum officinale Web.	.	.	.	0.02
Betula sp.	.	.	.	.
Melica nutans L.	.	.	.	.
Juncus sp.	.	.	.	.
Epilobium sp.	.	.	.	.
Vicia sp.	.	.	.	.
Fragaria vesca L.	.	.	.	.
Alnus glutinosa (L.) Gaertn.	.	.	.	.
Salix sp.	.	.	.	.
Cirsium sp.	.	.	.	.
Carex remota L.	.	.	.	.
C. silvatica Huds.	.	.	.	.
Deschampsia sp.	.	.	.	.
Ranunculus repens L.	.	.	.	.
Stachys silvatica L.	.	.	.	.
Solanum dulcamara L.	.	.	.	.
Polygonum sp.	.	.	.	.
Festuca rubra L.	.	.	.	.
Species non determinated	.	.	.	.
Total	599.48	701.12	145.88± 14.04	237.54± 23.36

Table I continued

Seed bank, number of diaspores per m^2			Number of seedlings from seed bank per m^2	
1979 autumn	1980 spring	1980 autumn	1980 spring	1980 autumn
•	•	•	•	•
•	•	•	•	•
•	•	•	•	•
•	•	•	•	•
•	•	•	•	•
•	•	•	•	•
•	•	•	•	•
•	•	•	•	•
•	•	•	°	•
•	•	•	•	•
•	•	11.79	•	•
•	•	•	0.2	0.25
•	•	•	0.3	3.24 ± 2.72
365.25 ± 162.77	1969.80 ± 622.79	1887.24 ± 668.79	34.72 ± 13.72	0.25
•	•	11.79	0.2	•
•	•	11.79	0.5	0.5
•	•	58.98	•	0.25
•	•	11.79	0.2	•
17.69	•	•	•	•
•	23.60	•	•	•
•	47.20	•	•	•
•	23.60	•	•	•
•	•	•	1.4	3.00
•	•	•	0.2	0.25
•	•	•	0.2	•
•	•	•	0.2	•
•	•	•	0.2	•
•	•	•	0.2	•
•	•	•	0.3	•
•	•	•	0.2	•
191.33	254.900	224.21	•	3.50
3987.97 ± 789.10	6074.54 ± 1223.3	8115.12 ± 1963.91	189.79 ± 31.52	24.00 ± 7.32

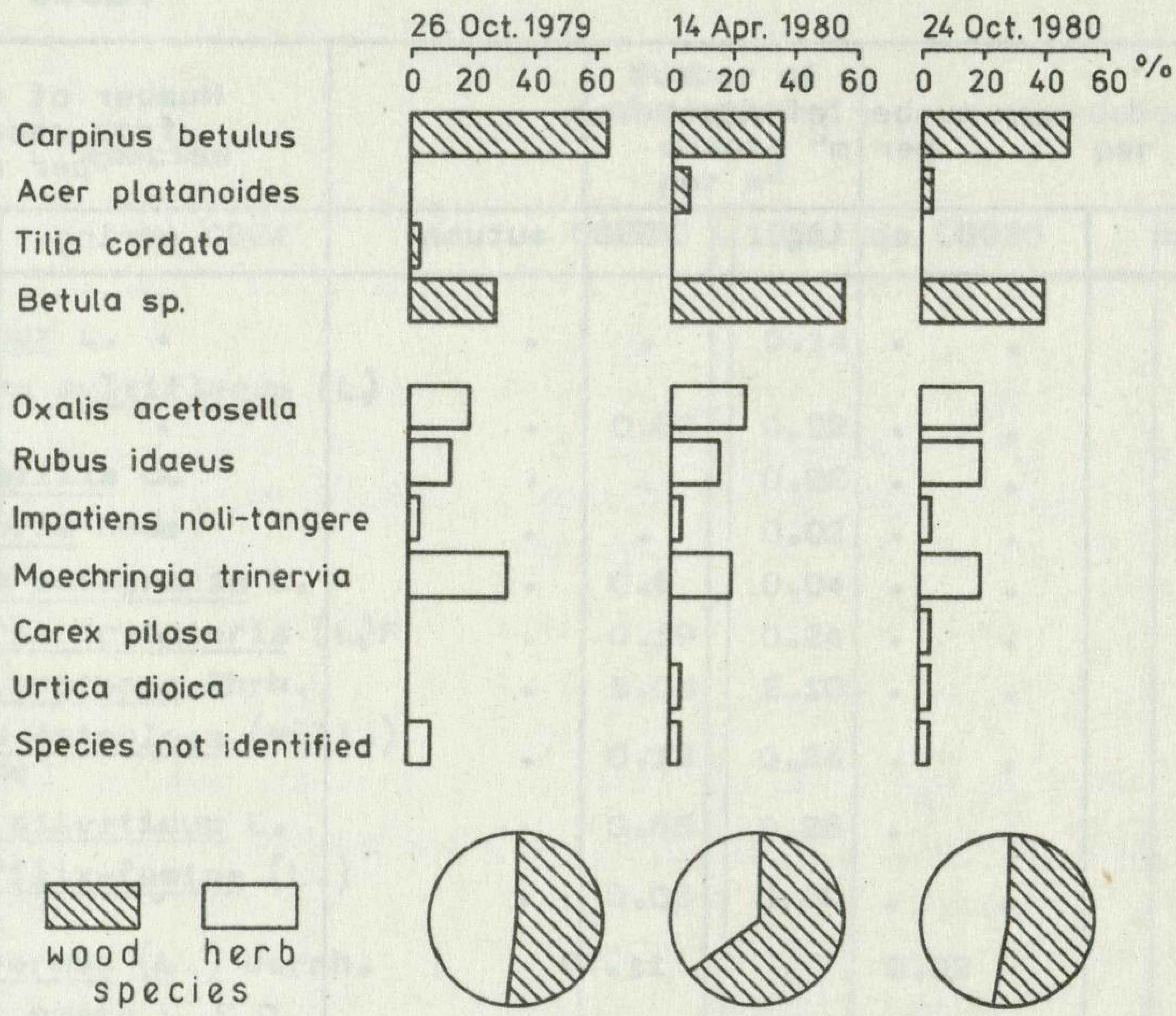

Fig. 2. Percentage participation of diaspores of particular species in the seed bank

tly less than half of all selected diaspores were seeds of herbaceous plants and shrubs. The rest of the seed bank were tree seeds. At all three dates of investigations, among the diaspores of herbaceous plants and shrubs, in the seed bank dominated three species: Oxalis acetosella, Moechringia trinervia and Rubus idaeus. Less numerous were the seeds of Impatiens noli-tangere and Urtica dioica, and in the autumn of 1980 also Carex remota. The similar contribution to the seed bank of species of herbaceous plants and shrubs at all three dates of investigations is striking (Fig. 2).

Woody species behaved differently in the seed bank. The numbers and contribution of particular species to the seed bank in the period between autumn 1979 and autumn 1980 greatly fluctuated. But at all three dates 80% of tree seeds in soil were Carpinus betulus and Betula sp. In autumn the contribution of hornbeam was higher than that of birch, and in spring there were more birch seeds. Apart from species mentioned, seeds of Acer platanoides,

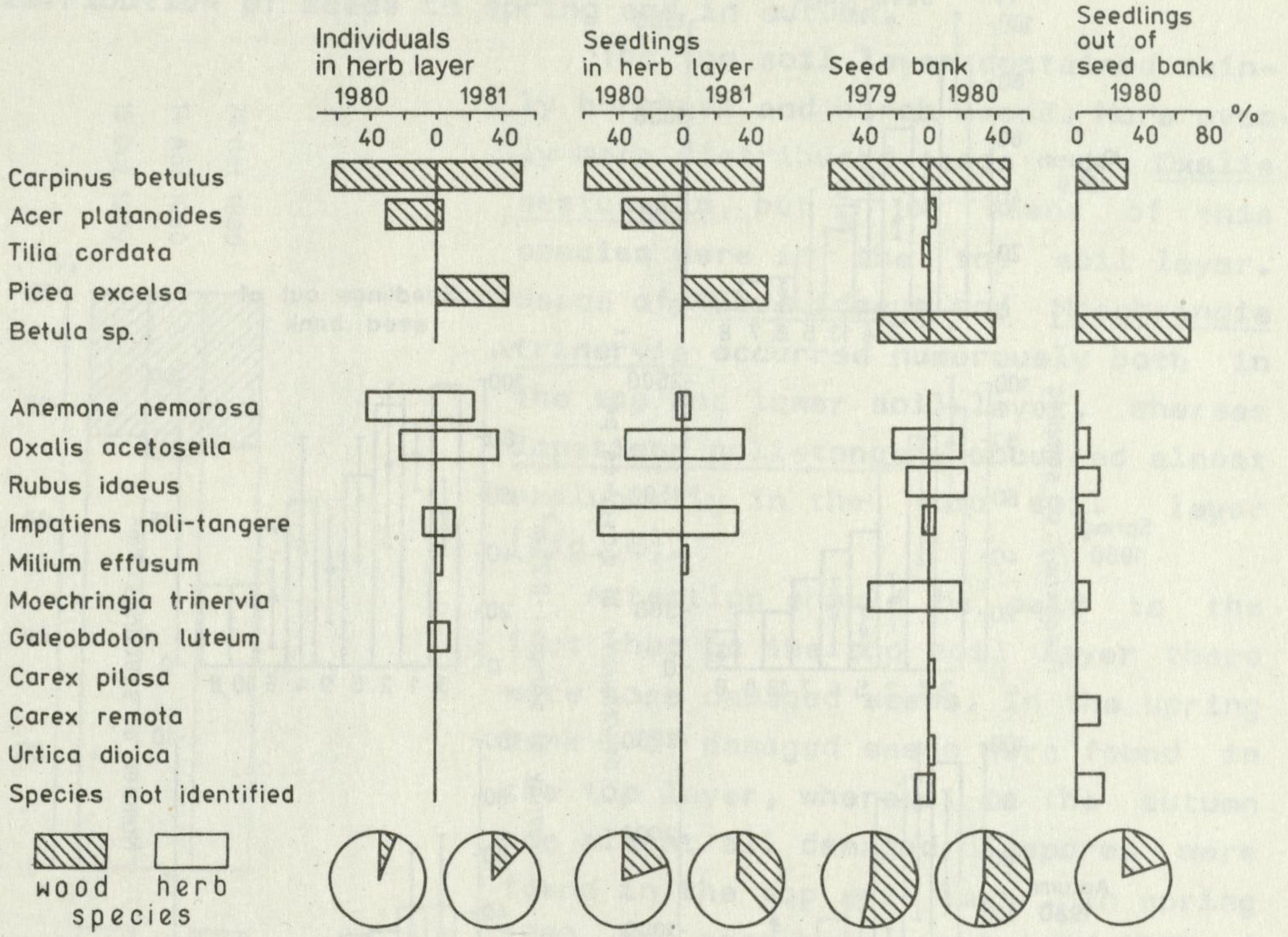

Fig. 3. Contribution of species of flowering plants (in per cents) to the structure of the herb layer, production of offspring (seedlings) and the seed bank
Contribution of seedlings of particular species, which developed from seeds in soil under laboratory conditions (last column)

Tilia cordata, Fraxinus excelsior, Picea excelsa, Alnus glutinosa and Salix sp. were found (Fig. 3, Table I).

3.2. Horizontal and vertical distribution of seeds in soil

The highest frequency in samples was that of seed bank dominants - Carpinus betulus, Betula sp., and Oxalis acetosella. Seeds of birch and hornbeam were found in 67-97% of samples, whereas seeds of Oxalis acetosella in 65-80% samples. This proves the quite even horizontal distribution of seeds of species mentioned. Seeds of Rubus idaeus and Moechringia trinervia had

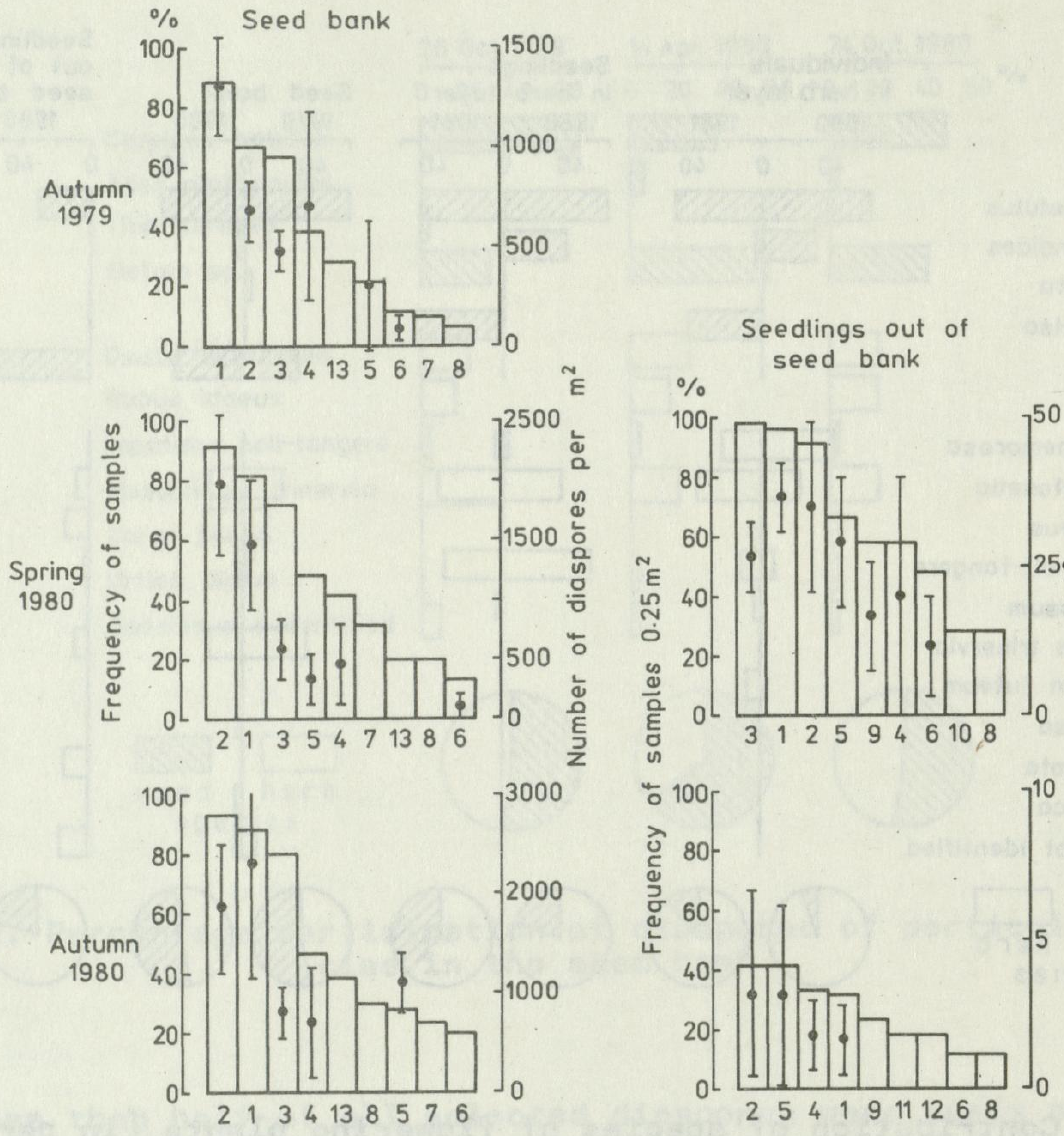

Fig. 4. Frequency and density of diaspores per m^2 of species dominant in the seed bank
1 - Carpinus betulus, 2 - Betula sp., 3 - Oxalis acetosella, 4 - Moechringia trinervia, 5 - Rubus idaeus, 6 - Impatiens noli-tangere, 7 - Acer platanoides, 8 - Urtica dioica, 9 - Carex pilosa 10 - C. digitata, 11 - Millium effusum, 12 - C. remota, 13 - unidentified species

a much lower frequency - 25-50%. Diaspores of Acer platanoides and Impatiens noli-tangere were found in several per cents of samples. Other species from the seed bank had a very low frequency (Fig. 4). The character of the distribution of these species was more or less aggregational. Isolation of seeds from soil samples taken at two different depths (0.4 cm and 4-8 cm) at all dates showed that over 74% of undamaged seeds were from the surface soil layer. In the deeper layer about 26% of diaspores were found

(Fig. 5). There was no significant difference in the vertical distribution of seeds in spring and in autumn.

The top soil layer contained mainly hornbeam and birch seeds. More evenly were distributed seeds of Oxalis acetosella, but $\frac{2}{3}$ of seeds of this species were in the top soil layer. Seeds of Rubus idaeus and Moechringia trinervia occurred numerously both in the top and lower soil layer, whereas Impatiens noli-tangere occurred almost exclusively in the top soil layer (Fig. 6).

Attention should be paid to the fact that in the top soil layer there were more damaged seeds. In the spring bank $\frac{2}{3}$ of damaged seeds were found in the top layer, whereas in the autumn one almost all damaged diaspores were found in the top soil layer. In spring 1980, the seed bank contained 5355 of damaged diaspores per m^2 of soil, whereas in autumn of the same year - 5744. At both dates almost 50% of all segregated diaspores were damaged - 53% in spring and 41% in autumn.

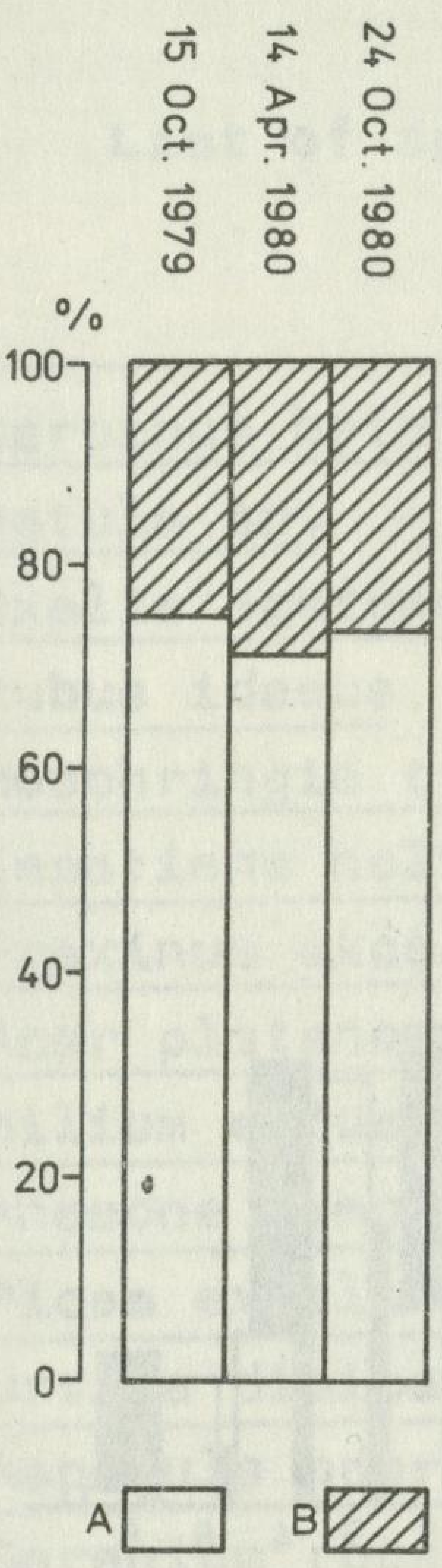

Fig. 5. Vertical distribution of seeds in soil (in per cents) at different dates
A - depth 0-4 cm, B - depth 4-8 cm

3.3. Germination capacity of seeds from dried and cooled soil

In ten soil samples, each of a volume 350 ml, kept at negative temperature (0- -10°C), seedlings of 7 species appeared. The most numerous were seedlings of Betula sp. Quite numerous were seedlings of Rubus idaeus and Carpinus betulus (Table II). Other species occurred in small numbers. From seeds in soil dried at room temperature 50% less seedlings were obtained than from the cooled soil. These were seedlings to six species. Seeds of Impatiens noli-tangere and Carpinus betulus did not germinate (Table II).

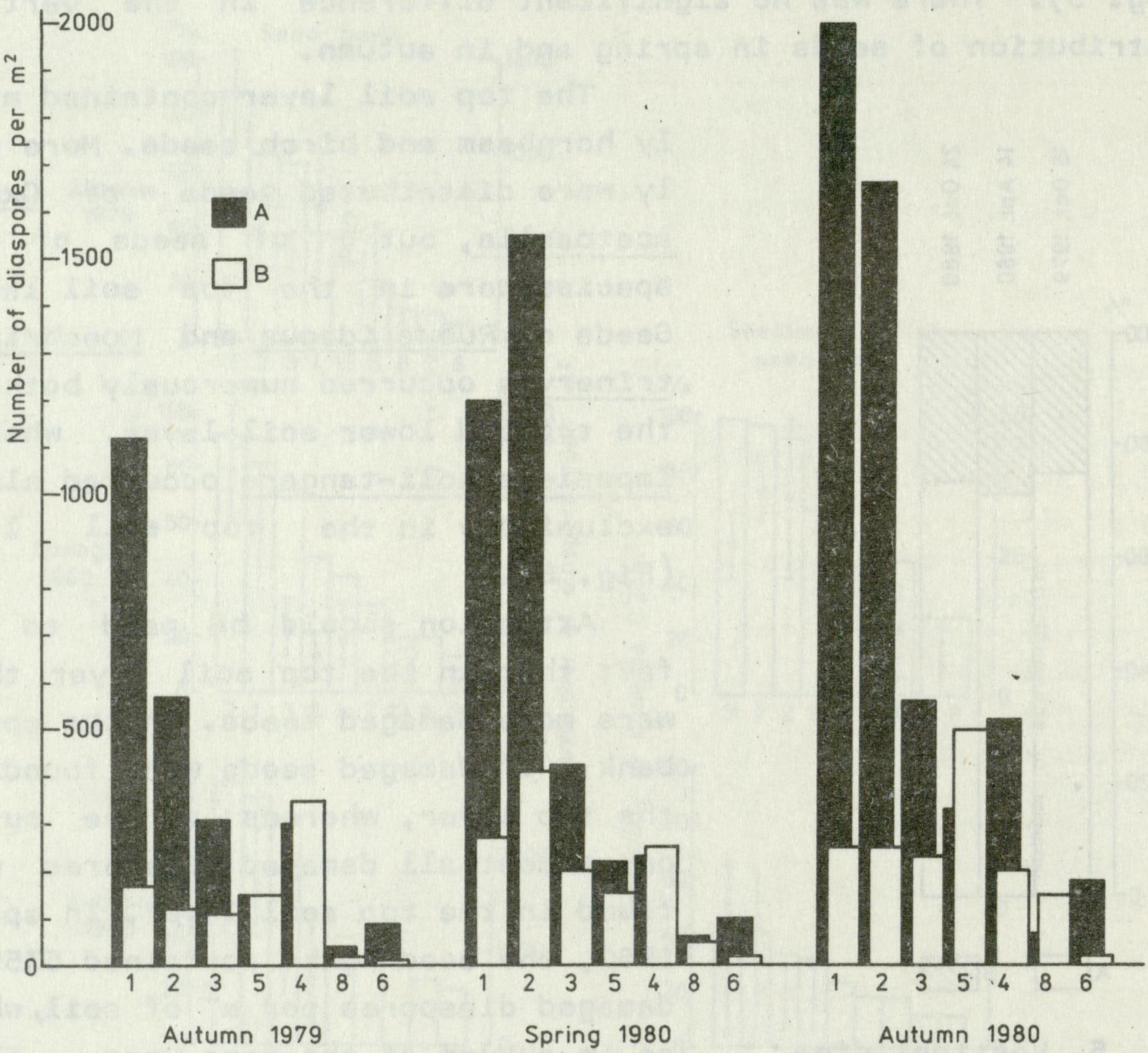

Fig. 6. Number of diaspores of chosen species in soil at different depths

1 - Carpinus betulus, 2 - Betula sp., 3 - Oxalis acetosella, 4 - Moechringia trinervia, 5 - Rubus idaeus, 6 - Impatiens noli-tangere, 8 - Urtica dioica, A - depth 0-4 cm, B - depth 4-8 cm. Ordinal numbers as in Figure 4

The most resistant to unfavourable conditions were seeds of Betula sp., Rubus idaeus, Moechringia trinervia, Urtica dioica and Carex sp. - species which are not connected with the phytocoenosis of hornbeam forest. From soil dried at negative temperature also seeds of Carpinus betulus germinated. The cooling and drying of soil over the period of three months resulted in death of all seeds of the species of the Tilio-Carpinetum community. Other species of the seed bank germinated better under laboratory conditions immediately after being brought from the forest than in the soil exposed for germination.

Table II. Seedlings from seed bank developing under different conditions

List of species	Number of seeds in 3000 ml of soil	Number of seedlings obtained from seeds		
		3000 ml soil left for germination	3000 ml of cooled soil	3000 ml of dried soil
Carpinus betulus	169	1.1	7.7	
Betula sp.	137	2.4	32.6	8.6
Oxalis acetosella	47	1.3		
Rubus idaeus	29	2.4	11.1	3.4
Moechringia trinervia	44	1.3	1.7	4.3
Impatiens noli-tangere	15	0.8	1.7	
Fraxinus excelsior	1			
Acer platanoides	14			
Milium effusum	3	0.8		
Anemone nemorosa	2		-	
Picea excelsa	2			
Urtica dioica	5	0.4	1.7	1.0
Asperula odorata	7			
Geranium robertianum	5	0.4		1.0
Galeobdolon luteum	3			
Carex pilosa	4	0.9	1.7	1.0
Taraxacum officinale		0.2		
Carex remota		2.3		
Luzula pilosa		0.2		
Mycelis muralis		0.2		
Melica nutans		0.2		
Epilobium montanus		0.4		
Stachys silvatica		0.2		
Unidentified species		2.6		1.0
Number of species	16	17	7	6
Total	504	18	58.2	20.3

3.4. Development of seedlings from the seed bank under laboratory conditions

Seedlings in cuvettes with soil samples from the phytocoenosis investigated were under observation in order to examine the abilities of seedlings development from seeds in the soil.

In the soil under conditions allowing for seed germination seedlings of 32 species appeared. The proportion betwen the number of herbaceous plant species and tree species was similar to that in the seed bank obtained by isolating the diaspores from soil (Table I).

Under laboratory conditions 24-190 seeds per m^2 germinated from soil in particular seasons. Similarly as in the case of seed isolation, among herbaceous plants and shrubs dominated: Rubus idaeus, Moechringia trinervia and Oxalis acetosella. But almost as numerous were the seedlings of Carex pilosa, C. remota and C. digitata. Only some per cent of seeds in soil procuded sedlings under laboratory conditions. Seeds of accessory species in the stabilized Tilio-Carpinetum phytocoenosis - Rubus idaeus and Carex remota - germinated abundantly under laboratory conditions and very rarely germinated under natural conditions. A relatively high number of tree seedlings were found in cuvettes. Similarly as among selected seeds decidedly most numerous were the seedlings of Carpinus betulus and Betula sp. (Table I, Fig. 4). Single seedlings of Acer platanoides and Tilia cordata germinated in laboratory soil samples.

The frequency of seedlings in cuvettes with soil sampled from plots of a surface area 0.25 m^2 varied at both dates. In the spring seed bank in 1980 seedlings of Carpinus betulus and Oxalis acetosella had frequency of almost 100%, whereas of Betula sp. - over 90%. In about 60% of samples, seedlings of Moechringia trinervia, Rubus idaeus and Carex pilosa appeared, whereas in about 50% of samples - Impatiens noli-tangere. Carex digitata, Urtica dioica, Viola sp. and Anemone nemorosa occurred in over 20% of samples. In soil sampled in autumn 1980 the seeds germinated very poorly under laboratory conditions, which explains the rather low frequency of particular species (Fig. 4).

3.5. Appearance of seedlings in the herb layer

During the two seasons of investigations in the herb layer of Tilio-Carpinetum phytocoenosis seedlings of 31 species of herbaceous plants and of 6 woody species were found (Table I).

In 1980, in the herb layer there was 141 ± 24 seedlings of all species per m^2, and in 1981 - 238 ± 23. The percentage of seedlings of herbaceous plants in the herb layer was much different from the seed bank composition (Fig. 3). Over 50% of seedlings in both vegetation seasons were Impatiens noli-tangere and Oxalis acetosella. Less abundantly occurred seedlings of Anemone nemorosa and Moechringia trinervia (Fig. 3).

In the herb layer of phytocoenosis examined tree seedlings were less than half of all seedlings, although the soil contained more diaspores of trees than of herbaceous plants. This difference was due to total lack of birch seedlings under natural conditions. In the vegetation season 1981, apart from seedlings of Carpinus betulus, there were also quite numerous seedlings of Picea excelsa.

3.6. Comparison of the seed bank with the species structure of phytocoenosis

The herb layer of Tilio-Carpinetum ecosystem consisted of 36 species of seed plants. The seed bank contained 33 species, in cuvettes under laboratory conditions seedlings of 32 species germinated from the seed bank and in the herb layer seedlings of 31 species appeared. The highest density in the herb layer had the following populations: Anemone nemorosa, Oxalis acetosella, Impatiens noli-tangere and Carpinus betulus. The seeds of these species were in the soil, but no correlation was observed between the population density and the density of the seed bank. Two species are worth pointing out - Carpinus betulus and Oxalis acetosella. They were dominants in the herb layer and in the seed bank.

In the herb layer a group of plant species could be distinguished, the seed of which were not found in soil, but few seedlings occurred under natural conditions. These were Ranunculus lanuginosus, Adoxa moschatellina, Circaea alpina, Corylus avellana and Quercus robur (Table I).

Furthermore, there was a distinct group of seed plants, not represented either in the seed bank nor producing seedlings under natural conditions in the ecosystem. These were Majanthemum bifolium, Stellaria nemorum, Geum urbanum, Polygonatum multiflorum, Rubus saxatilis, Ficaria verna and Aegopodium podagraria.

In the seed bank diaspores of 17 species were identified, which did not occur in the herb layer of the ecosystem examined. Most numerous were the seeds of the genus Betula. The diaspores of other species occurred sporadically.

4. DISCUSSION

Numerous studies on the seed bank have shown the seed reserve in the soil depends to a considerable extent on the production rate of diaspores in the ecosystem examined. Thus the ecosystems abundant in therophytes have a much richer bank: midland dunes - 48 thous. seeds per m^2 (S y m o n i d e s 1978), arable fields - 38 thous. per m^2 (Branchley and Warington 1930 after H a r p e r 1977). Ecosystems more abundant in perennial plants have a smaller seed bank. On meadows with Geranium pratense the reserves of seeds have been estimated as 17 thous. seeds per m^2 (R a b o t n o v 1956). Equally abundant seed banks are found in non-stabilized forest ecosystems. K a r p o v (1969) has found in the birch bush woods of southern part of the taiga 14 thous. seeds of herbaceous plants per m^2.

The seed bank in stabilized forest ecosystems is much smaller than in the above discussed ones. The seed bank of the Tilio-Carpinetum ecosystem (3989-8115 seeds per m^2) has a similar abundance as the banks of other forest ecosystems - alder forest Carici elongatae-Alnetum from 2000 to 3000 per m^2 (F a l i ń s k a 1981) and Carpathian beechwood Dentario glandulosae-Fagetum - from 1770 to 2000 seeds per m^2 (Z a r z y c k i 1964).

A several times higher result has been obtained in the Tilio-Carpinetum ecosystem disturbed by economical management in The Białowieża Forest (Dziermańska 1980)[1]. Numerous observations indi-

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[1] Dziermańska T. 1980 - Seed bank in the soil of oak hornbeam ecosystem (Tilio-Carpinetum) - manuscript.

cate that the cultivation treatments such as thinning the forest stand create better conditions for generative reproduction in the herb layer than in the undisturbed ecosystems.

Studies on the numbers of seedlings developing from seeds in soils of stabilized ecosystems have provided slightly higher results than in the present paper. In mesophilus deciduous forests with linden in the European part of the USSR (Moscow surroundings) 450-900 seedlings germinated per m^2 (R y s i n i n and R y s i n i n a 1965). A similar result has been obtained for the natural forest with Pinus strobus L. in New England - 350 seedlings per m^2 (Livingston and Allessio 1968 after H a r p e r 1977).

The very low numbers of seeds in the soil of stabilized forest ecosystems is mainly due to the relatively low production of generative diaspores (F a l i ń s k a 1971a, 1971b). In the majority of cases these species have a low fraction of generative shoots (5-30%), and studies on the vitality of seeds in soil point to the faint chance of the majority of species to retain their germination capacity for longer than 2-3 years (F a l i ń s k a 1981).

Still, there are stabilized forest ecosystems having a much higher number of seeds with a germination capacity. From the soil of taiga forests 1300-3200 seeds of herbaceous plants germinated per m^2 (K a r p o v 1960, 1969). The most numerous were the seedlings of Rubus sp. - up to 2400 per m^2 of soil.

Many scientists point out that the seed bank is more abundant in species than the plant cover and that its numbers exceed those of the individuals growing in the phytocoenosis (K a r p o v 1969, H a r p e r 1977, S y m o n i d e s 1978). In the case of stabilized forest ecosystems this regularity is not confirmed. In the Tilio-Carpinetum ecosystem in the herb layer, similarly as in the seed bank there was over 30 species - 32 in the bank and 36 in the herb layer.

It is worth pointing out that in all ecosystems examined there have been very few forest species in the seed bank (R y s i n i n and R y s i n i n a 1965, K a r p o v 1969, P e t r o v 1977). In the present paper the main part of seed bank (apart from dominants) consists of forest species. The locality of the Tilio-Carpinetum ecosystem examined in a large, dense and natural forest complex, not much penetrated by people, far from the forest margin, creates a faint possibility for the migration of diaspores from other ecosystems beyond the forest border. The forest is a natural barrier for seed migration.

The results presented confirm the thesis that species proper for communities of early succession stages contribute more to the seed bank than species dominant in communities which attain the stage of maturity (K a r p o v 1969, H a r p e r 1977). Similarly as in other forest ecosystems the seed bank is formed mainly by two species, which are accessory in the ecosystem examined. Numerous seeds of Rubus idaeus are transferred to the Tilio-Carpinetum ecosystem in the alimentary canals of small birds - whitethroats (Sylvia sp.) and thrushes (Turdus sp.). The considerable frequency of penetration of ecosystems of deciduous forests and of shrubs abundant in raspberries by numerous groups of individuals of these genera of birds in late summer results in seed transfer (M. Piotrowska - unpublished data). These seeds do not germinate under natural conditions of linden-hornbeam forest, but cumulate in the soil. Several years of observations on the germination of seeds from the bank in the Tilio-Carpinetum ecosystem indicate that seeds of this species remain in soil many years without losing their germination capacity. The seeds of the second dominant in the bank - Betula sp. - are carried by wind from the closer and further neighbourhood (P a c z o s k i 1951, F a l i ń s k a 1971b).

But many species of the ecosystem examined are not represented in the seed bank. The comparison of the contribution of particular populations of the ecosystem examined to the production of generative diaspores with the contribution of these species to the seed bank is very interesting. The highest production of diaspores in the Tilio-Carpinetum herb layer from year to year is that to Anemone nemorosa and Ranunculus lanuginosus (F a l i ń s k a 1971a). According to this a seed density in soil of several thousands or at least of several hundreds per m^2 can be expected, whereas in the seed bank these species are rare.

In the Tilio-Carpinetum herb layer 10 species produce practically the generative diaspores. In the seed bank 26 species of herbaceous plants have been identified, but only 6 species contribute significantly - some of them do not produce many generative diaspores in the ecosystem examined. These are: Rubus idaeus, Oxalis acetosella, Moechringia trinervia, Impatiens noli-tangere. The reason for such disproportion between the herb layer production and their density in soil is the great seed loss due to consumption by small rodents (G ę b c z y ń s k a 1976). The studies on the gut contents of red bank vole (Clethrionomys glareolus (Schreber)) in the same fragment of the Tilio-Carpinetum ecosystem, where previously the production rate of seeds in the herb layer and tree stand has been determined (F a l i ń s k a 1971a, 1971b), and at present the seed bank has been investigated, indicates that the contribution of seeds of herbaceous plants to the food of this most abundantly occurring rodent in the linden-hornbeam forest ecosystem, is considerable. The gut contents of this rodent contain mostly the seeds of Oxalis acetosella, Anemone nemorosa and Ranunculus lanuginosus. Seeds of herbaceous plants and trees are food components of animals examined in all seasons of the year. Numerous observations confirm the fact that bank voles show preference for seeds of Hepatica nobilis. According to studies of F a l i ń s k a (1969) seeds of this species have a very high energetic value of the order 600 cal per gramme (2512 J per g).

In studies on the seed bank in forest ecosystems the very low contribution of tree seeds of mature succession stages is striking (K a r p o v 1969, H a r p e r 1977, P e t r o v 1977). Studies on the tree seeds production on the discussed surface area of Tilio-Carpinetum point to a quite high tree seeds production from year to year. It is estimated as 829-4235 seeds per m^2 (F a l i ń s k a 1971b). The distinctly highest contribution is that of seeds of Carpinus betulus. Ouite numerous are also the seeds of Tilia cordata and Acer platanoides. The two latter species are not abundant in the seed bank. According to the studies on gut contents of the bank vole, tree seeds, in spring, autumn and winter, are 21-36% of food mass (G ę b c z y ń s k a 1976). Many tree seeds are also consumed by other animals, which probably explains why so few seeds, apart from hornbeam seeds, are found in soil. This may be also due to the fact that the studies on the seed bank did not cover the "seed peak" of none of the trees of the Tilio-Carpinetum ecosystem. Numerous seedlings of Picea excelsa, which appeared in the herb layer in 1981 were from seeds sown in winter of 1980 - already after the soil samples were taken. The low number of tree diaspores in the bank proves the low durability of seeds of these species in soil.

Many scientists point to the considerable variability of the seed bank as a result of many modifying factors (R a b o t n o v 1964, 1972, K a r p o v 1969). The studies presented have not shown such great difference as could be expected judging by the variability of seed production in the herb layer and tree stands of the ecosystem under discussion, and also the fluctuations in numbers of animals living in this ecosystem, as well as the low durability of seeds in soil. However, the too short period of investigations does not allow to give a definite opinion. The latest investigations on the dynamics of the seed bank indicate though a considerable stability of the seed reserves in soils of stabilized ecosystems (T o m p s o n and G r i m e 1979).

Comparison of the data obtained with those of other authors has created some difficulties, because the seed bank in different ecosystems has been investigated using three different methods: isolation of seeds from soil samples having a determined volume, keeping the soil under laboratory conditions allowing for the germination of seeds from the bank, counting and identifying the appearing seedlings, and uncovering soil fragments in the ecosystem and leaving them till they become overgrown by seedlings. Information about the seed reserves obtained using particular methods allows to solve various research problems. The choice and segregation of seed from soil provides information about their species composition and numbers of generative diaspores in soil, and also about their vertical and horizontal distribution. Nevertheless, this method does not give grounds for deciding about the germination capacity of seeds found in the soil. Many times it has been observed that numerous undamaged seeds found in soil are dead (H a r p e r 1977). Also the control of germination capacity of seeds taken from the soil of Tilio-Carpinetum does not provide full information about the number of live seeds in the bank. Out of 500 seeds placed for germination in Petri dishes only several seedlings germinate.

When leaving soil samples under laboratory conditions allowing for germination of seeds it is possible to assess their germination capacity from the seed bank and the germination dynamics. Also this method is useful for discovering species having very fine seeds, difficult to distinguish from sand grains. From the point of view of an ecologist this information is of greater value than the knowledge of the species composition and the numbers of diaspores in soil, because it allows to predict the possibilities of reconstructing the plant cover, when the first one is damaged. Still, this method cannot be considered as the only useful one in investigating the seed bank, because in the laboratory the conditions are not appropriate for the germination of all live seeds simultaneously. When investigating the seed bank for the Tilio-Carpinetum ecosystem, numerous seedlings of accessory species for the phytocoenosis examined have grown in the laboratory, seeds of some species germinating well in the forest did not grow into seedlings under laboratory conditions (Table I). According to H a r p e r (1977) unnatural break of the resting stage of seeds under laboratory conditions is the reason why so few seeds develop into seedlings.

Too low data have been obtained when leaving the soil in the laboratory under conditions allowing for germination of seeds from the bank of autumn 1980. Despite very good light conditions, moisture and thermal ones, mass germination of seeds has not been recorded. Thus the laboratory does not fulfill in this case the conditions necessary for germination. Also the cooling of soil in winter has been unfavourable for the germination of numerous seed species.

Russian scientists have suggested that the seed bank in phytocoenosis conditions could be analysed by uncovering fragments of soil by means of removal of litter and herb layer (K a r p o v 1969, P e t r o v 1977). This allows for obtaining more credible results than in the laboratory. However, in the majority of forest phytocoenoses the tree crowns take so much light that seeds of some species do not germinate at all.

Studies on the seed bank in the Tilio-Carpinetum ecosystem and in other forest ecosystems (F a l i ń s k a 1981) allow to assume that the seed reserve in soil may be estimated adequately only on the basis of an analysis of material collected by the two already discussed methods and completing them with data on the composition and numbers of seedlings appearing in unchanged conditions in the phytocoenosis. The variety of mechanisms interrupting the resting stage of seeds belonging to the seed bank does not allow for the exposure of all species under uniform conditions.

5. SUMMARY

The paper presents results on the numbers and species composition, and also on the distribution of diaspores in the soil of a

stabilized Tilio-Carpinetum ecosystem in the Białowieża National Park.

The aim of the investigation has been to find whether the floristic composition of the herb layer is reflected by the seed bank. The seed reserve in soil has been determined by isolating the diaspores from samples of soil of a volume 200 ml. The number of seedlings, which developed in the seed bank, has been determined by leaving the soil from plots of a surface area 0.25 m^2 under conditions allowing for the germination of seeds in the laboratory.

The following regularities have been determined:

1. In the soil of the ecosystem examined there are seeds of 32 plant species, 27 species of herbaceous plants, 5 tree species, and in the herb layer there are 36 species of seed plants (including 30 herbaceous plants) (Table I).

2. The list of species from the seed bank differs from the species composition of seedlings in the herb layer of the ecosystem examined, but the bank has relatively many forest species. The contribution of these species is much higher than in forest ecosystems examined by other authors.

3. Some of the species of the herb layer are not components of the seed bank (Table I, Fig. 3).

4. The seed bank of the Tilio-Carpinetum ecosystem, as regards numbers, reminds those of other forest ecosystems. A relatively low number of seeds in the bank of these ecosystems is due to low seed production, their low durability in soil and to the consumption of diaspores by animals.

5. The greatest contribution to the seed bank is that of species characteristic of early succession stages - Rubus idaeus and Betula sp. (Fig. 4).

6. The majority of seeds in soil do not show the capacity to develop seedlings under laboratory conditions (Fig. 4).

7. Cooling of soil in the winter results in the death of seeds of almost all species of herbaceous plants typical of the ecosystem, but has stimulated the germination of tree seeds and seeds of some accessory species in the Tilio-Carpinetum (Table II).

8. In the ecosystem examined $\frac{2}{3}$ of seeds are in the top soil layer (0-4 cm). The seeds have not shifted down to lower parts of soil between the autumn and spring (Fig. 5).

9. The contribution of particular species of herbaceous plants in the seed bank is quite constant from year to year, despite considerable fluctuations in the seed production of particular populations in different seasons of the year (Fig. 2).

6. POLISH SUMMARY

Praca zawiera wyniki badań nad liczebnością i składem gatunkowym oraz rozmieszczeniem diaspor w glebie ustabilizowanego ekosystemu Tilio-Carpinetum w Białowieskim Parku Narodowym.

Celem badań było stwierdzenie czy skład florystyczny runa jest odzwierciedlony w banku nasion. Zapas nasion w glebie określono na podstawie izolowania diaspor z prób gleby o objętości 200 ml. Liczbę siewek, które rozwinęły się w banku nasion, określono przez pozostawienie gleby zebranej z poletek o powierzchni 0,25 m^2 w warunkach umożliwiających kiełkowanie nasion w laboratorium.

Ustalono następujące prawidłowości:

1. W glebie badanego ekosystemu znajdują się nasiona 32 gatunków roślin, 27 gatunków zielnych i 5 drzewiastych, zaś w warstwie runa stwierdzono 36 gatunków roślin nasiennych (w tym 30 zielnych) (tab. I).

2. Lista gatunków banku nasion różni się od składu gatunkowego siewek pojawiających się w runie badanego ekosystemu, jednak okazało się, że bank zawiera stosunkowo dużo gatunków leśnych. Stwierdzono znacznie wyższy udział tych gatunków niż w ekosystemach leśnych badanych przez innych autorów.

3. Część gatunków warstwy runa nie wchodzi jednak do banku nasion (tab. I, rys. 3).

4. Bank nasion ekosystemu Tilio-Carpinetum nawiązuje liczebnością do innych ekosystemów leśnych. Stosunkowo niska liczebność nasion w banku tych ekosystemów jest spowodowana małą produkcją nasion, ich niewielką trwałością w glebie oraz konsumpcją diaspor przez zwierzęta.

5. Największy wkład do banku nasion wnoszą gatunki charakterystyczne dla wczesnych faz sukcesji - Rubus idaeus i Betula sp. (rys. 4).

6. Większość nasion znajdujących się w glebie nie wykazało zdolności do rozwinięcia się w siewki w warunkach laboratoryjnych (rys. 4).

7. Przechładzanie gleby przez okres zimowy spowodowało obumarcie nasion prawie wszystkich gatunków roślin zielnych typowych dla ekosystemu, natomiast okazało się stymulujące dla kiełkowania nasion drzew i niektórych gatunków akcesorycznych w Tilio-Carpinetum (tab. II).

8. W badanym ekosystemie $\frac{2}{3}$ nasion znajduje się w górnej warstwie gleby (od 0 do 4 cm). Nie stwierdzono przemieszczania nasion do dolnych partii gleby od jesieni do wiosny (rys. 5).

9. Stwierdzono, że udział poszczególnych gatunków roślin zielnych w banku nasion jest dość stały z roku na rok, pomimo znacznych wahań produkcji nasion przez poszczególne populacje w rożnych sezonach (rys. 2).

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