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THE INFLUENCE OF NATURAL AND EXPERIMENTAL DISTURBANCES ON EMERGENCE AND SURVIVAL OF SEEDLINGS IN AN OAK-LINDEN-HORNBEAM (*TILIO-CARPINETUM*) FOREST

ABSTRACT: It has been demonstrated that gap formation in herb layer following experimental removal of herbs in an oak-linden-hornbeam forest doubled abundance of seedlings of all species in comparison with an undisturbed herb layer. Number of species recolonizing the gaps increased from 24 to 48. Herb removal allowed species rare in oak-linden-hornbeam forests (e.g. *Rubus idaeus*, *Carex remota*) to emerge. As a consequence of a natural disturbance (wild boar feeding, uprooted trees), species number decreased by 1.5 to 2 times. Disturbances resulting from uprooting trees did not contribute to the reduction of seedling density (comparing with the control plots), whereas boar feeding reduced the density by 1.5 to 6 times during successive seasons.

KEY WORDS: herbaceous seedlings, disturbances, germinating power, mesophilous deciduous forest

1. INTRODUCTION

Many authors have claimed that populations of perennials in stabilised communities are continuously regenerating clones (Cook 1985, Harper 1986, Eriksson 1989), since severe competition of herbs and tree roots as well as low light intensity limit generative reproduction (Barkham 1980, Peart 1989). Importance of generative reproduction in stabilised communities consists in population replenishment through replacement of dying individuals and population expansion (Eriksson 1989). Former studies have shown that despite limited seed production by herbs in deciduous forests (Zarzycki 1968, Falińska 1971), seedlings are still present (Czarnecka 1995, Tumidajowicz 1977, 1995, Eriksson 1992). Ecologists agree that percentage of seeds that produce seedlings is very low (Falińska 1990). There is however an open question whether seed production of perennials depends on seedling density (Andersen 1989, Peart 1989). Many authors have noticed that emergence of perennial seedlings in established plant communities is limited by number of sites safe for germination (Grice and Westoby 1987, Flower 1988, Kelly 1989a). In dense plant communities, such safe sites may form after individual plants die or become injured by herbivores, or after a disturbance leading to plant destruction on several square meters of the ground area (Flower 1988, Eriksson 1989, Kelly 1989b). There is little known about the degree to what gaps forming as a consequence of natural disturbances modify chances of seedlings to emerge. Seedling distribution pattern in dense communities determines the type of seed dispersal and arrangement of safe sites for seed germination (Kelly 1989a, Eriksson 1992). Kelly (1989b) reported that certain species in dense grassland communities have emerged every year in the same places, while locality of the sites safe for other species germination have changed year by year. The sites safe for germination and seedling establishment differ as regard convenience degree (Flower 1988). In the case of plants that require light for seeds to germinate, the main factor limiting seedling emergence is ground shading by mature plants (Flower 1988, Eriksson 1989). This is why gaps in plant cover promote seedling emergence. For majority of plants, a factor preventing emergence and establishment of their seedlings is thick litter layer (Flower 1988, Tumidajowicz 1995, Kwiatkowska 1996). In hollows made by windthrow trees and in places where wild boars have fed the soil is devoid of litter. Chances of seedlings to emerge and establish are however different due to different fertility of the sites. The hollows made by uprooted trees contain practically no humus, whereas in the patches digged up by wild boars, upper soil layers contain more nitrogen available to plants due to intensive litter decay (Faliński 1986).

The objective of this work was to find densities and survival rates of seedlings of herbaceous plants and trees in intact herb layer as well as in natural and experimentally made gaps. The following hypotheses were tested: (1) dense plant cover reduces both seed germination and seedling development, (2) a gap formed in the herb layer stimulates seedling emergence and enhances their chances to survive until they approach juvenile phase, (3) density and species diversity of seedlings depends on gap type, (4) arrangement of sites safe for germination in undisturbed herb layer changes from year to year.

2. METHODS AND MATERIAL

2.1. STUDY PLOTS

The studies were carried out in Białowieża Primeval Forest (23°31'–24°21' E and 52°29'–52°57' N). Białowieża Forest is best protected large forest complex in European lowland. In 1978–1984, observations were made at the permanent Białowieża Geobotanical Station area (Faliński 1966) in Białowieża National Park. In order to examine how various gap types affect emergence and development of seedlings, four plot types were established: (1) control, (2) experimental (man-made gaps in herb layer),

(3) hollows made by uprooted trees, (4) places frequently visited by wild boars.

1. 50 control plots, each of 1 m^2 area, were established in 1978 in undisturbed herb layer in 3×4 m grid (Fig. 1).

2. 50 experimental plots, each of 1 m^2 area, arranged in the same manner as the control plots (Fig. 1). In 1978, all plants together with their below-ground parts were removed from the plots in order to create gaps in herb layer.

3. 10 plots, each of 0.25 m^2 area, were established in 1980, in hollows made by newly uprooted spruces.

4. 30 plots, each of 0.25 m^2 area, were established in 1980, in a patch of the oak-linden-hornbeam forest systematically visited by wild boars.

2.2. OBSERVATIONS

In the control and experimental plots, seedling emergence was recorded every 5 days in spring, and every 10 days in summer and autumn 1978–1981, whereas in the period 1982–1984 – once a year, in spring, at the time of maximum seedling abundance. Emerging seedlings were marked with plastic tubes. In the plots in hollows made by fallen trees and those in places of wild boar feeding the seedlings were counted at their abundance peaks only, in 1980–1981.

In order to estimate fraction of fruiting individuals, all shoots subdivided into generative and vegetative ones were surveyed in the control plots twice a year – in the period of phenological spring, i.e. at full fruiting of *Anemone nemorosa*, and in early summer.

To find per cent of seeds that further develops into seedlings, 11 species of perennials were selected of different reproduction biology (Table 1). To assess fertility of those species in undisturbed herb layer, 100 individual plants bearing fruits in the vicinity of each control plot were randomly chosen, and then seeds were counted in 100 fruits.

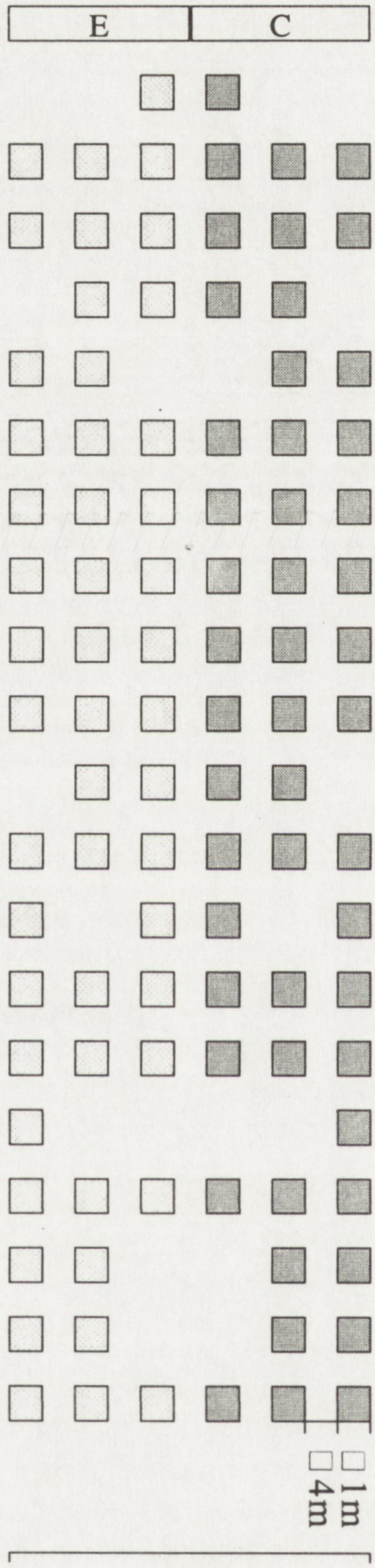

Fig. 1. Arrangement of observation plots in the study area in an oak-linden-hornbeam forest of Białowieża National Park. C – control plots, E – experimental plots

Table 1. Reproduction types of flowering herbaceous plants in undisturbed herb layer of an oak-linden-hornbeam forest of Białowieża National Park. G – generative reproduction, W – vegetative reproduction, * – species included into the studies on seed ability to develop into seedlings

	No	Species	Reproduction type
		PERENNIALS	
*	1.	*Anemone nemorosa* L.	GV
	2.	*Carex pilosa* Scop.	GV
*	3.	*Galium odoratum* (L.) Scop.	GV
*	4.	*Lamiastrum galeobdolon* (L.) Ehrend.	GV
*	5.	*Milium effusum* L.	GV
*	6.	*Oxalis acetosella* L.	GV
	7.	*Rubus idaeus* L.	GV
*	8.	*Stellaria holostea* L.	GV
	9.	*Stellaria nemorum* L.	GV
	10.	*Urtica dioica* L.	GV
	11.	*Cardamine amara* L.	GV
*	12.	*Hepatica nobilis* Schreb.	G
*	13.	*Lathyrus vernus* (L.) Bernh.	G
*	14.	*Mycelis muralis* (L.) Dum.	G
*	15.	*Ranunculus lanuginosus* L.	G
*	16.	*Sanicula europaea* L.	G
	17.	*Taraxacum officinale* Web.	G
	18.	*Geum urbanum* L.	G
	19.	*Viola riviniana* Rchb. X *Viola reichenbachiana* Jord. ex Boreau	G
	20.	*Adoxa moschatellina* L.	V
	21.	*Aegopodium podagraria* L.	V
	22.	*Carex digitata* L.	V
	23.	*Luzula pilosa* (L.) Willd.	V
	24.	*Majanthemum bifolium* (L.) F. W. Schmitdt	V
	25.	*Polygonatum multiflorum* (L.) All.	V
	26.	*Ranunculus ficaria* L.	V
		ANNUAL AND BIENNIAL PLANTS	
	27.	*Circaea alpina* L.	G
	28.	*Galeopsis tetrahit* L.	G
	29.	*Geranium robertianum* L.	G
	30.	*Impatiens noli-tangere* L.	G
	31.	*Moehringia trinervia* (L.) Clairv.	G

2.3. DATA PROCESSING

Mean seedling densities per 1 m^2 were calculated for the four plot types, i.e. control, experimental, rooted about, and under uprooted trees. Significance of differences between the mean values was assessed using one-factor analysis of variance at 95% confidence intervals.

To assess percentage of produced seeds that further develop into seedlings in populations of chosen species, seed production (per 1 m^2) was compared with density of seedlings of the species in the next season. Seed production was calculated as the product of fecundity of eleven selected species and densities of their generative shoots.

In order to find locality of sites safe for germination and establishment of seedlings in 1979–1981, interpolation maps of densities were drawn for species characterised by high seedling densities on the basis of seedling number in particular plots. Locality of sites safe for germination of other species was determined on the basis of distribution plans of their seedlings and generative shoots, in the scale of 1:10.

3. RESULTS

3.1. PLANT FECUNDITY IN HERB LAYER

During the six-year period of the studies, fruit bearing by populations of 29 species from among 31 species forming herb layer was observed. Fraction of individuals approaching reproduction phase in the plant populations examined amounted to 3–30% (Fig. 2).

Fecundity of the plants varied. The highest fecundity was characteristic of individuals of *Mycelis muralis* (208 seeds shoot^{-1}) and *Milium effusum* (165 seeds shoot^{-1}), and the lowest – of *Galium odoratum* individuals (2–4 seeds shoot^{-1}) (Table 2). Fecundity of individuals changed from season to season: e.g. in 1980, in populations of *Mycelis muralis*, *Stellaria holostea*, *Lamiastrum galeobdolon*, *Sanicula europaea* and *Galium odoratum* the fecundity was twice that reported in 1981 (Table 2). In populations of other species, the between-year variation in fecundity was rather small, with the fecundiy being almost always higher in 1980 than 1981.

3.2. DENSITY AND DISTRIBUTION OF SEEDLINGS

Control plots

From among 31 species of flowering herbaceous plant species, seedlings of 24 species characteristic of herb layer of the oak-linden-hornbeam forest were reported to occur during the six successive seasons, with seedlings of only nine species emerging in a given season (Tables 3 and 4). From eighteen species of perennials reproducing vegetatively, seedlings of eleven species emerged. Neither did seedlings of *Adoxa moschatellina*, *Aegopodium podagraria*, *Carex digitata*, *Luzula pilosa*, *Ranunculus ficaria*, *Polygonatum multiflorum* nor those of *Majanthemum bifolium*, a species abundant in the herb layer, emerge in either season.

Overall density of seedlings of all species varied among seasons. The highest density was recorded in 1981 – 238 seedlings m^{-2}, and the lowest – in 1983 – 43 seedlings m^{-2} (Fig. 3). Number of seedlings emerging varied considerably among the plots – from several to 450.

Among the herbaceous plants, *Oxalis acetosella* and *Impatiens noli-tangere* had the highest seedling densities (Fig. 4). Seedlings of these species occurred in each of the 50 plots. Number of *Oxalis acetosella* seedlings in some groups of the plots amounted to 81–100, whereas in some others – to 1–20 (Fig. 5). Neither area nor location of very dense patches of the seedlings of the two species changed over 3 years, though the mean density varied (Fig. 4). The same was true for one of the main components of the forest herb layer, namely *Anemone nemorosa.* Number of seedlings of this population was however much smaller than that of *O. acetosella* population (less than twenty seedlings per m^2).

A different distribution pattern was characteristic of *Milium effusum* and *Lamiastrum galeobdolon.* Seedlings of these two species occurred in clumps. Occurrence and abundance of the seedlings were associated with presence of individuals in generative phase in the previous season. In *Milium effusum* population, 10–48 seedlings emerged in those plots where individuals bearing fruits had occurred in the former season, whereas in the remaining plots – 1–2 seedlings. As the individuals of the two species being in

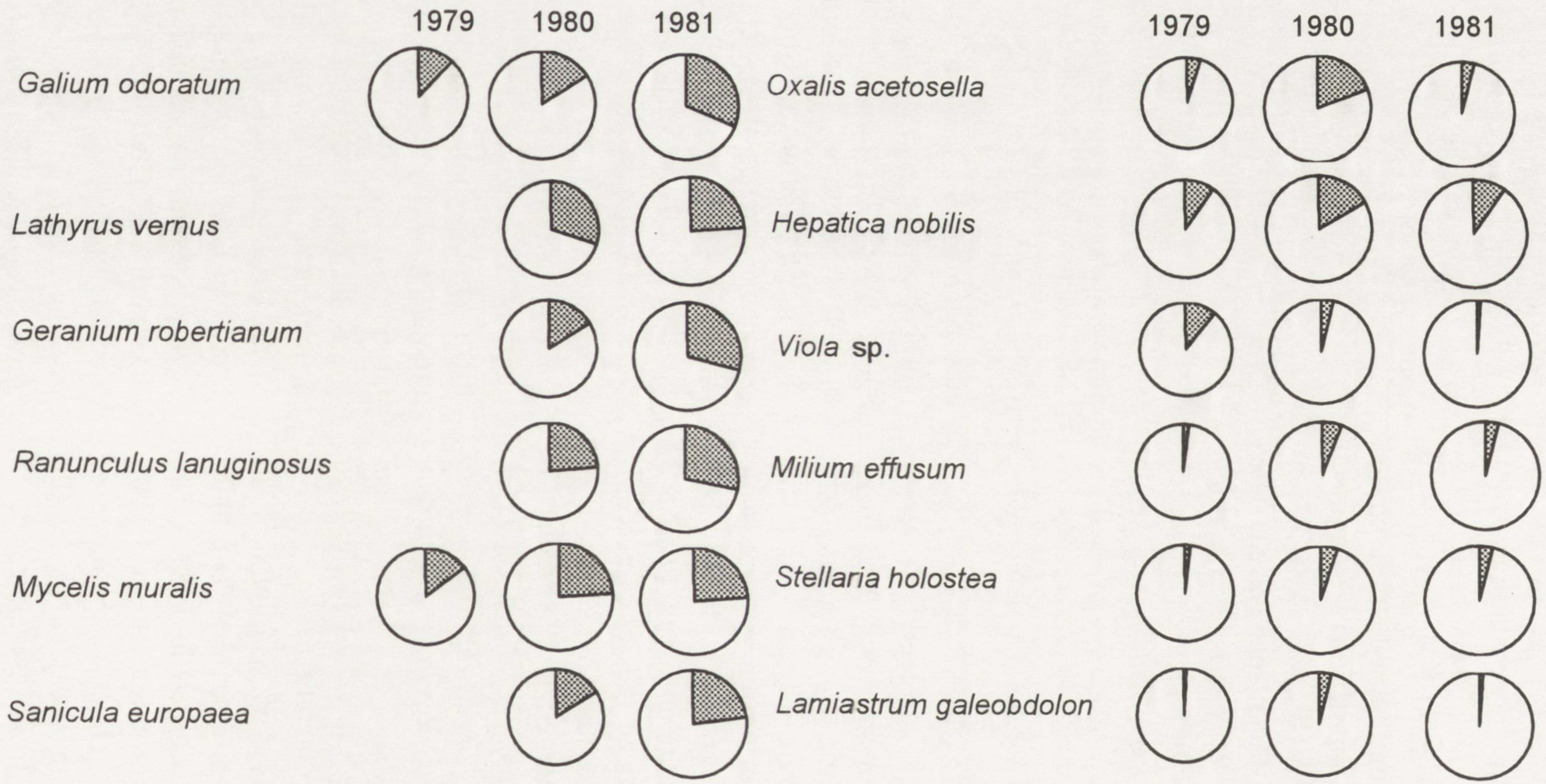

Fig. 2. Participation of fruiting shoots in selected populations of perennials in an oak-linden-hornbeam forest of Białowieża National Park

Table 2. Generative reproduction of selected perennial plant species in the oak-linden-hornbeam forest. C – control plots, E – experimental plots, * – no data

	Year	Average number of seeds per shoot	% of seeds producing seedlings C	E
	1979	158.2	*	*
Milium effusum	1980	164.7	6	2
	1981	154.9	5	2
	1982	*	0	1
Oxalis acetosella	1979	10.0	*	*
	1980	10.0	21	20
	1981	10.0	21	23
	1982	10.0	11	13
	1979	12.9	*	*
Anemone nemorosa	1980	14.9	5	8
	1981	12.5	12	5
	1982	*	8	5
Lamiastrum galeobdolon	1979	41.2	*	*
	1980	60.4	4	1
	1981	33.5	4	2
	1982	*	12	13
Mycelis muralis	1979	89.3	*	*
	1980	207.6	2	1
	1981	109.3	2	3
	1982	*	7	3
Hepatica nobilis	1979	16.9	*	*
	1980	17.3	36	2
	1981	16.6	16	1
	1982	*	1	0
Stellaria holostea	1979	12.3	*	*
	1980	27.2	11	3
	1981	10.7	0	0
	1982	*	14	34
Galium odoratum	1979	4.0	*	*
	1980	3.5	4	0
	1981	1.6	3	0
	1982	*	1	1
Lathyrus vernus	1980	10.1	*	*
	1981	8.7	5	0
Sanicula europaea	1980	34.7	*	*
	1981	14.7	1	0
Ranunculus lanuginosus	1980	82.8	*	*
	1981	77.1	3	0

generative phase did not developed flower shoots every year, the sites where the greater number of seedlings emerged changed their locality in successive years.

Among perennials and biennials, a group of species could be distinguished characterised by a slight between-year variation in their seedling densities. No statistically significant differences were found in the seedling densities of *Hepatica nobilis*, *Viola riviniana* X *V. reichenbachiana*, *Mycelis muralis* and *Moehringia trinervia* between the successive seasons (Fig. 4).

Every season, 12–16 species were represented by few seedlings occurring in 1–5 from among 50 plots. Very low densities were characteristic of populations of species dominant in the herb layer, such as *Stellaria holostea*, *Galium odoratum*, *Carex pilosa*, *Lathyrus vernus* and *Ranunculus lanuginosus*, as well as those

Table 3. Trees and shrubs seedling density per $1m^2$ in the oak-linden-hornbeam forest. C – control plots, E – experimental plots, * – no data, frames denote statistically significant differences. Values were rounded to 0.1 seedlings per m^2

Species		Year					
		1979	1980	1981	1982	1983	1984
Carpinus betulus	C	5.5	17.2	46.7	7.4	5.1	46.3
	E	7.5	37.5	90.5	7.1	13.2	29.2
Picea abies	C	1.3	0.2	43.0			
	E	1.8	0.1	51.8		0.1	
Tilia cordata	C	0.4	0.2	0.1			0.6
	E	0.3	0.5	0.1	0.0	2.5	
Fraxinus excelsior	C	0.1	0.1	0.0			0.0
	E	0.1	0.1	0.0			
Acer platanoides	C	0	9.9	0.1		8.3	
	E	0.0	5.2	0.2		3.8	
Quercus robur	C	0.0	0.0	0.0			0.0
	E	0.3	0.0	0.1		0.2	
Corylus avellana	C		0.0	0.0			
	E	0.0		0.0			
Betula sp.	C						
	E	12.4		0.3		1.4	
Sorbus aucuparia	C						
	E	0.2					
Sambucus nigra	C						
	E	0.0					

occurring only rarely in the forest patch considered, e.g. *Circaea alpina*, *Geum urbanum* (Table 4).

Experimental plots (simulated disturbance)

In the first year of the experiment (1978), few seedlings emerged in the plots. In the next season (1979), after herb layer removal, the seedling density was twice that in the control plots (Fig. 3). The difference was found to be statistically significant. In the subsequent years, the densities in the experimental plots were generally only slightly higher than those in the control plots. In 1981, 1983 and 1984, the differences in the seedling density between the two plot types were statistically significant (Fig. 3).

In the year following the experimental herb layer removal (1979), seedling number also doubled in comparison with the control plots – seedlings of 48 species emerged in the experimental plots, whereas in the control plots – seedlings of only 25 species (Tables 3 and 4). Like in the control, seedlings of 10–30 species emerged in the experimental plots in the subsequent seasons.

In the year following the experimental herb layer removal (1979), seedlings of several species rarely reproducing generatively in oak-linden-hornbeam forests emerged, namely *Aegopodium podagraria* and *Carex pilosa.* Moreover, seedlings of species rare in that habitat emerged – *Rubus idaeus*, *Carex remota* massively, and *Cirsium palustre*, *Senecio* sp., *Polygonum* sp. – in a limited numbers (Table 4). In 1979, three times more tree seedlings emerged at the experimental than the control plots. The same was true for seedlings of herbaceous perennials, whereas the number of seedlings of annual plants at the experimental plots was three times smaller than that at the control.

In 1979, a considerable increase in seedling abundance of two species dominant in the herb layer of the oak-linden-

Table 4. Herbs seedling density per 1m^2 in the oak-linden-hornbeam forest. C – control plots, E – experimental plots, * – no data, frames denote statistically significant differences, values were rounded to 0.1 seedlings per m^2

Species		Year 1979	1980	1981	1982	1983	1984
Impatiens noli - tangere	C	30.2	62.4	49.2	27.5	8.3	5.6
	E	9.2	20.1	42.0	33.1	20.7	4.0
Oxalis acetosella	C	28.6	36.3	56.5	27.8	14.9	10.2
	E	20.4	35.2	60.9	31.0	28.0	4.5
Moehringia trinervia	C	6.0	4.7	5.0	5.7	4.3	1.5
	E	24.1	0.3	46.5	28.5	23.5	1.8
Urtica dioica	C	1.9	0.6	0.5	0.1	1.0	
	E	2.1	0.0	0.2	0.1	1.3	
Mycelis muralis	C	1.6	0.4	1.2	0.3	0.7	0.1
	E	0.5	0.2	1.9	1.3	1.0	
Hepatica nobilis	C	1.4	3.4	3.9	0.1	0.3	0.6
	E	0.2	0.2	0.2	0.0		
Sanicula europaea	C	0.9	0.1	0.1			
	E						
Viola riviniana	C	1.0	2.0	1.5	0.4	0.1	0.3
X *V. reichenbachiana*	E	2.3	1.0	0.4	0.0	0.4	0.1
Geranium robertianum	C	1.1	0.5	5.4	0.7	0.6	0.6
	E	0.0	0.0	0.1	0.0		0.0
Milium effusum	C	0.5	1.4	7.1	2.5	0.7	
	E	4.2	0.3	3.1	1.7	1.2	0.1
Galeopsis tetrahit	C	0.3	0.4	0.6		0.2	0.0
	E	0.4	0.2	0.4	0.1	0.4	0.04
Carex pilosa	C	0.2	0.1				
	E	4.3	1.6	0.1			
Anemone nemorosa	C	*	3.4	12.9	5.9	2.9	2.0
	E	2.7	5.4	5.9	3.5	1.3	1.1
Lamiastrum galeobdolon	C	0.1	0.2	2.8	0.3	0.3	0.7
	E	0.8	0.1	1.3	0.4	0.5	0.2
Rubus idaeus	C	0.1	0.0	0.1			
	E	53.2	0.3	0.2			
Ranunculus lanuginosus	C	0.1		0.8		0.0	
	E	0.2					
Cardamine amara	C	0.1	0	0.1	0	0	0
	E	0	0	0	0	0	0
Galium odoratum	C	0.1	0.4	0.1	0.0		
	E	0.1			0.0		
Stellaria holostea	C	0.0	0.6	0.0	0.6	0.1	0.1
	E			0.0			
Stellaria nemorum	C	0.0					
	E	0.1		0.0			
Circaea alpina	C		0.0				
	E			0.0			
Carex remota	C						
	E	10.3	0.4	0.3			
Carex digitata	C						
	E	3.1	0.3	0.0			
Aegopodium podagraria	C						
	E	0.2					
Luzula pilosa	C						
	E	0.2					
Taraxacum officinale	C			0.0			
	E	0.1		0.1			

Species which density were less than 0.1 seedlings per m^2 and were presnt only at experimental plots in 1979 year – *Cirsium rivulare, C. palustre, Galium palustre, Polygonum* sp., *Carex hirta, C. leporina, Senecio* sp., *Juncus* sp., *Calamagrostis arundinacea, Veronica officinalis, Aruncus silvester, Erigeron* sp., in 1979 and 1980 years – *Carex silvatica, Festuca gigantea*,in 1981 year – *Daphne mezereum, Chrysosplenium alternifolium.*

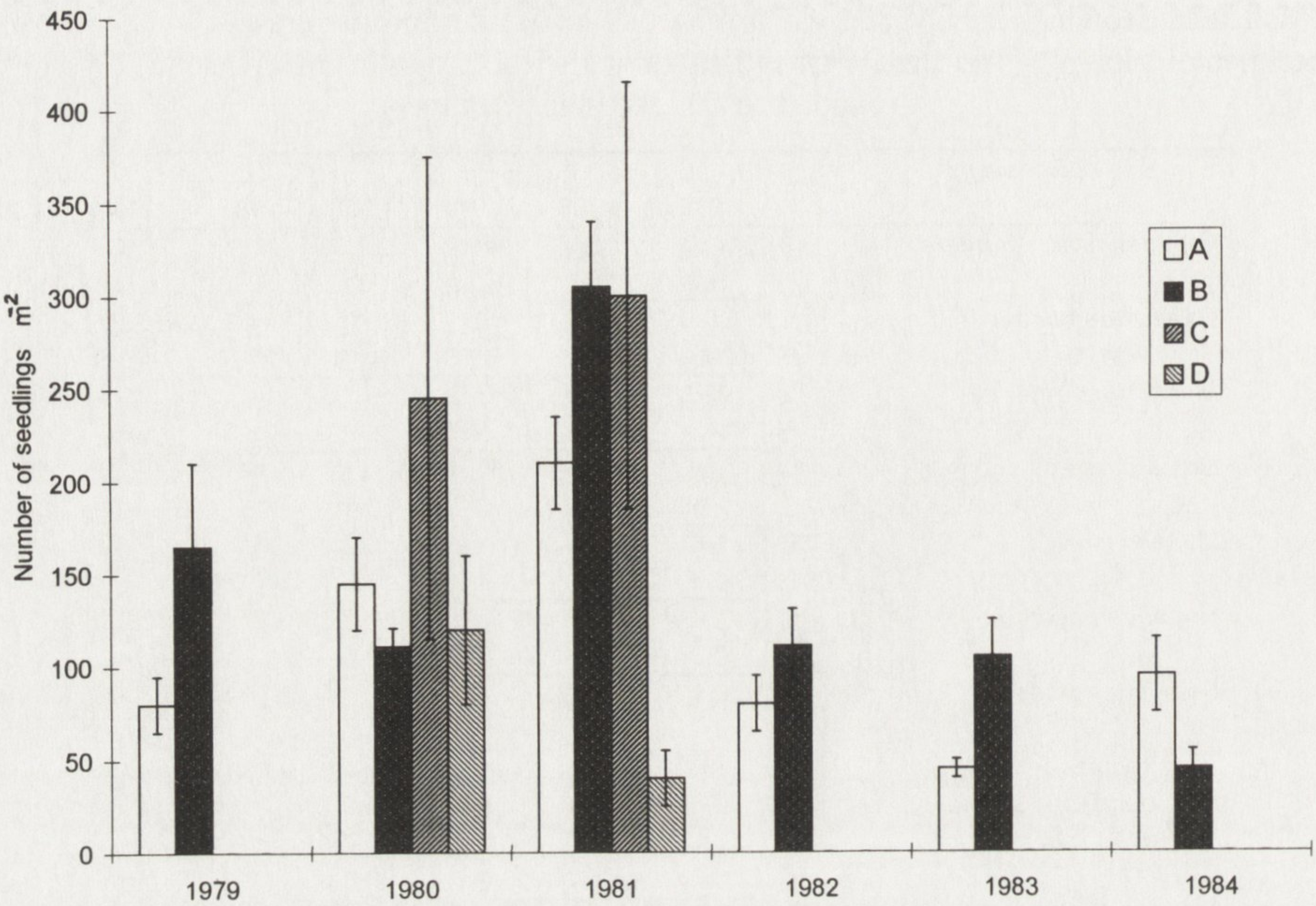

Fig. 3. Overall density of seedlings in an oak-linden-hornbeam forest of Białowieża National Park. Confidence intervals are indicated by vertical lines. A – control plots, B – experimental plots, C – hollows made by uprooted trees, D – plots in places of wild boar feeding

hornbeam forest – *Milium effusum* and *Lamiastrum galeobdolon* was noticed. Density of *M. effusum* seedlings at the experimental plots was 8 times higher than at the control, and that of *L. galeobdolon* – 4 times higher (Fig. 4). The differences were statistically significant. In the subsequent years, seedling density of the two species at the experimental plots was not different from that at the control ones. In populations of a few species – *Impatiens noli-tangere* and *Hepatica nobilis* – a significant decrease in number of their seedlings at the experimental plots was found in comparison with the control plots (Fig. 4).

Natural disturbance

In hollows made by uprooted trees, seedlings of 16 species emerged in 1980, and in 1981 – seedlings of 18 species, whereas the respective numbers at the control plots were 26 and 29. Species composition of the seedlings was similar to that at the control plots (Table 5).

Overall density of seedlings in the hollows in 1980 was two times higher, and in 1981 – similar to that recorded for the control plots (Fig. 3). Beneath uprooted trees, seedlings of annual plants were more, and seedlings of trees and herbaceous perennials – less abundant than at the control plots. In 1980, seedlings of *Impatiens noli-tangere*, *Urtica dioica* and *Oxalis acetosella* occurred in greatest numbers (Table 5).

At the plots rooted about by wild boars, lower seedling densities and smaller species number were recorded when compare with the control plots (Fig. 3, Table 5). In 1981, the difference in seedling density between the two plot types was statistically significant. Great between-year variation was revealed in seedling density (Fig. 3). Species composition of seedlings in the plots considered was similar to that at the control. Seedling densities of trees and herbaceous perennials at the plots rooted about by wild boars were 2–4 times higher than those at

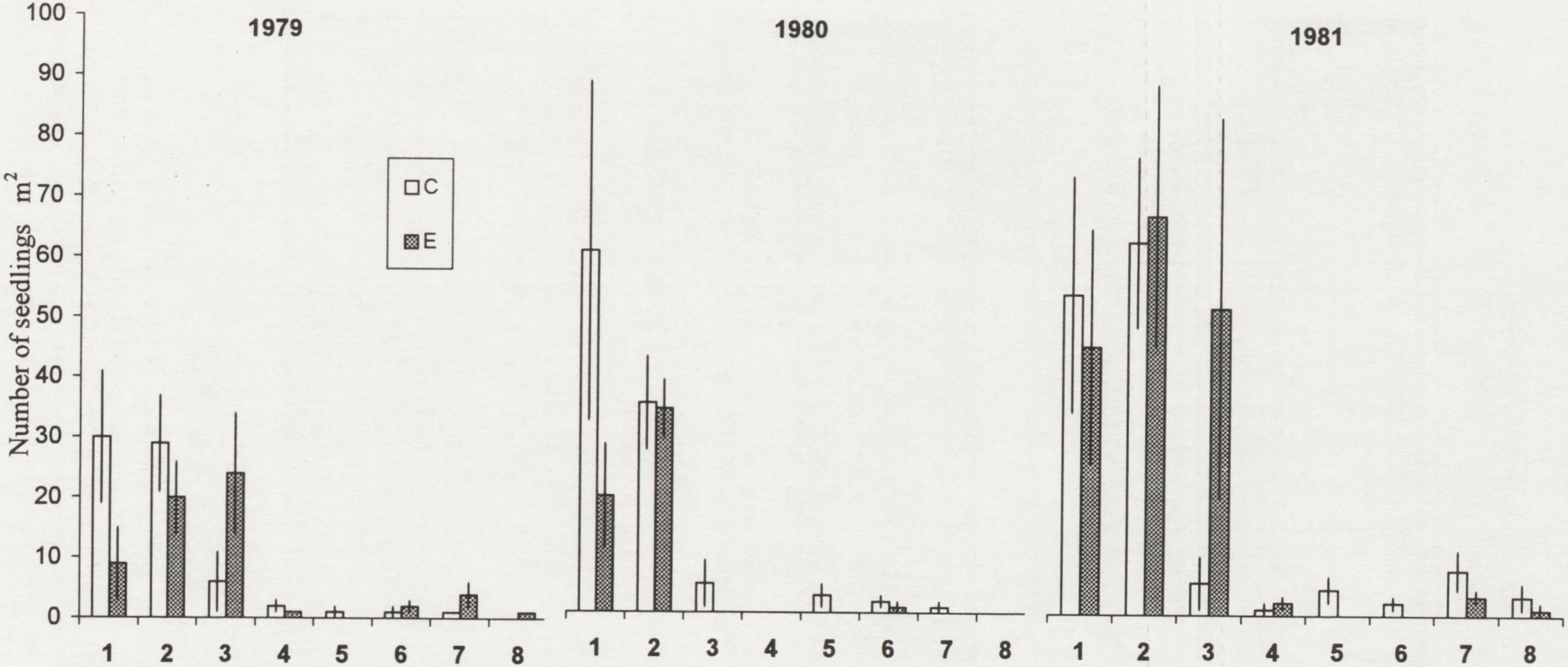

Fig. 4. Seedling densities per 1 m^2 of selected species of herb layer in an oak-linden-hornbeam forest of Białowieża National Park. Confidence intervals are indicated by vertical lines. 1 – *Impatiens noli-tangere*, 2 – *Oxalis acetosella*, 3 – *Moehringia trinervia*, 4 – *Mycelis muralis*, 5 – *Hepatica nobilis*, 6 – *Viola riviniana V. reichenbachiana*, 7 – *Milium effusum*, 8 – *Lamiastrum galeobdolon*. C – control plots, E – experimental plots

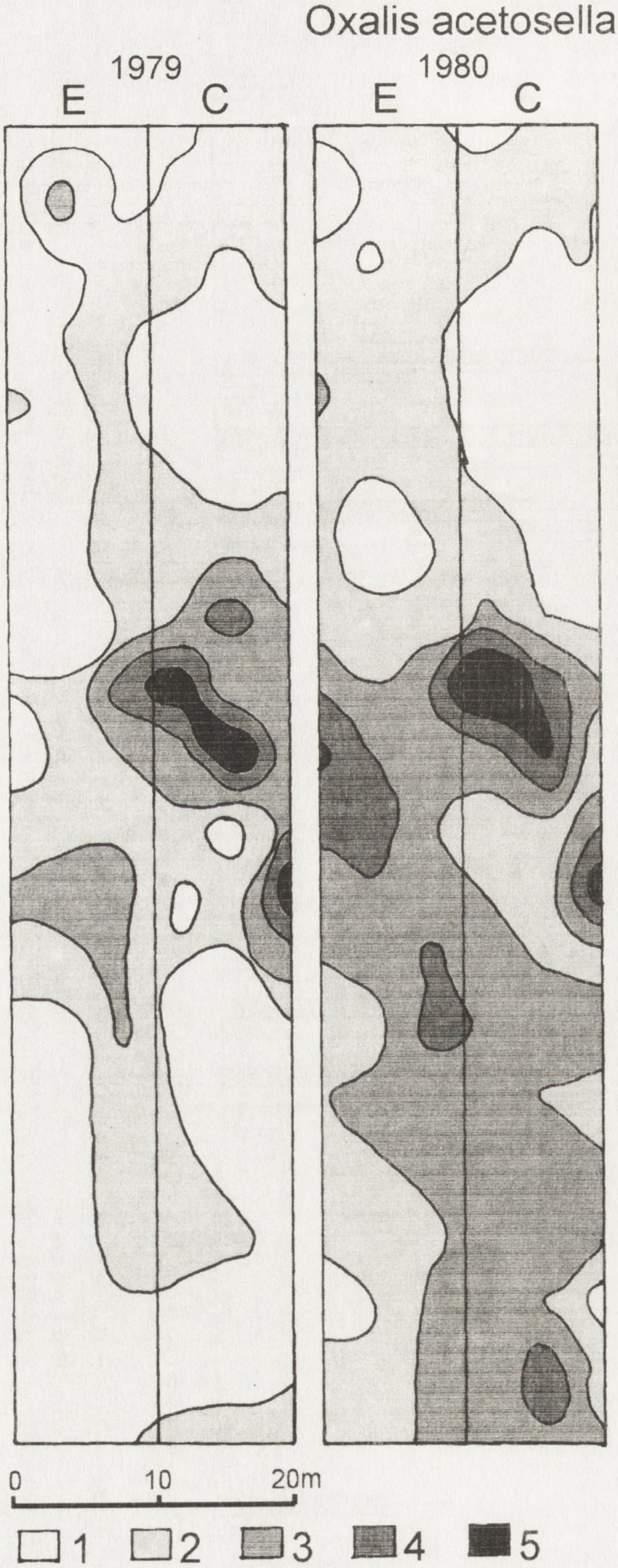

Fig. 5. Distribution of *Oxalis acetosella* seedlings of 2 000 m^2 (10m x 100m control + 10m x 100m experiment) in an oak-linden-hornbeam forest of Białowieża National Park. C – control plots, E – experimental plots, 1 – 1–20 seedlings per 1m^2, 2 – 21–40 seedlings per 1m^2, 3 – 41–60 seedlings per 1m^2, 4 – 61–80 seedlings per 1m^2, 5 – 81–100 seedlings per 1m^2

the control. The most abundant were seedlings of *Impatiens noli-tangere*, *Chrysosplenium alternifolium* and *Urtica dioica* (Table 5).

Table 5. Seedling density per $1m^2$ in hollows made by uprooted trees and in places rooted about in the oak-linden-hornbeam forests of Białowieża National Park

Species	Beneath uprooted trees		At plots rooted about by wild boars	
	1980	1981	1980	1981
HERBS				
Impatiens noli-tangere	157.2	98.8	56.2	
Urtica dioica	36.0	25.3	7.1	2.8
Oxalis acetosella	20.8	32.2	3.4	1.3
Geranium robertianum	6.4	9.2	3.6	0.7
Anemone nemorosa	6.0	1.6		
Viola sp.	2.0	2.0		0.2
Mycelis muralis	1.6	2.4		
Milium effusum	1.6			0.4
Lamiastrum galeobdolon	1.2	5.9	0.9	
Carex pilosa		0.1		
Alium ursinum		0.4		
Geum urbanum		0.4		
Hepatica nobilis	0.8			
Rubus idaeus	0.4	0.4	0.7	
Circaea lutetiana	0.4	2.0	0.6	
Ranunculus lanuginosus	0.4	2.8	7.4	1.1
Stellaria nemorum	0.4		0.7	0.5
Moehringia trinervia		9.6		1.5
Chrysosplenium alternifolium			35.4	10.9
Cardamine amara			1.6	2.9
Aegopodium podagraria			0.2	
Pulmonaria obscura			0.2	
Taraxacum officinale			0.2	
Lapsana communis				0.2
TREES				
Carpinus betulus	6.0	10.0	3.3	1.8
Acer platanoides	2.8		0.4	
Tilia cordata		0.8		
Picea abies		35.4		4.9
Fraxinus excelsior			3.3	0.4

3.3. DYNAMICS OF SEEDLING ABUNDANCE

In the herb layer of the oak-linden-hornbeam forest, seedlings of each species began to emerge at the control plots in the last week of April or early in May. Until mid-May, the seedling number wad increasing rapidly. Seedling abundance approached a peak at the end of May or beginning of June (Fig. 6). In June and July, the seedling emerged sporadically.

Seedlings of majority species lost their cotyledons and approached the juvenile phase towards the end of the growing season. Seedlings of *Hepatica nobilis* and *Sanicula europaea* were the only species approaching their juvenile phase the next spring. Until the end of the season, approximately 10% of seedlings survived (Fig. 6). Seedling survival rate of majority of the perennials amounted to 50%,

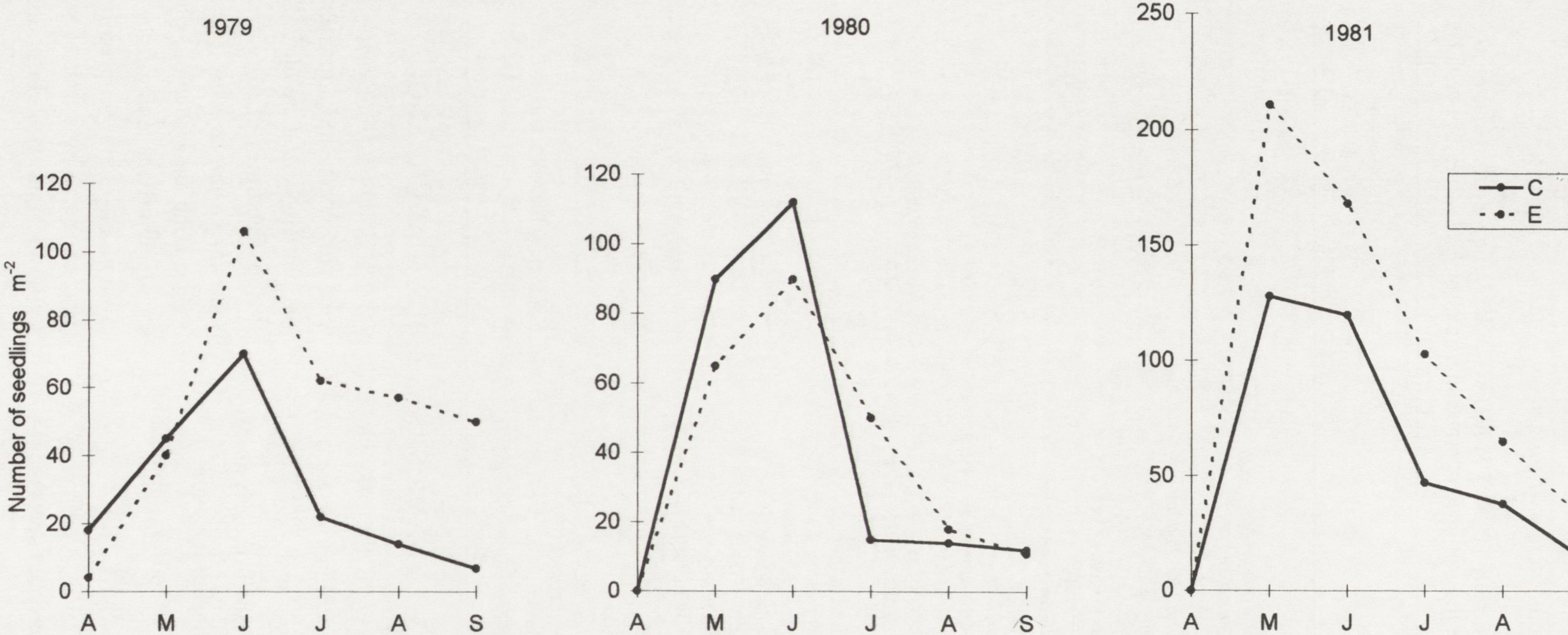

Fig. 6. Seasonal dynamics of seedling abundance in an oak-linden-hornbeam forest of Białowieża National Park. C – control plots, E – experimental plots

except some of the seasons when it was higher, e.g. 73% of the seedlings of *Milium effusum* survived until the end of September 1982, and 63% – in population of *Lamiastrum galeobdolon*. From 22% to 33% of *Urtica dioica* and *Stellaria holostea* seedlings survived until the end of the season.

Seedling survival rate at the experimental plots amounted to about 60% (Fig. 6). During first three years of the experiment, seedling survival rates of majority of the perennials ranged from 42% to 81%. Seedling survival rates of *Stellaria holostea*, *Lamiastrum galeobdolon* and *Mycelis muralis* increased most when compare with the control plots.

3.4. SEED GERMINATION AND DEVELOPMENT OF SEEDLINGS

Germinating power and developmental ability of seedlings meant as percentage of seeds transforming into seedlings was highly variable in populations of the community considered, being the highest – 20–30% – for *Oxalis acetosella* and *Hepatica nobilis*, slightly lower – between ten and twenty per cent – for *Anemone nemorosa*, *Lamiastrum galeobdolon* and *Stellaria holostea* (Table 2). The lowest ability of seeds to develop seedlings (less than 5%) was characteristic of *Sanicula europaea*, *Galium odoratum* and *Ranunculus lanuginosus* (Table 2). The ability of particular species to form seedlings from the seeds displayed great year-to-year variability. Some species produced more seedlings in 1981, whereas some others – in 1982 (Table 2).

After the experimental herb removal, the germinating power of seeds increased in some populations when compare with the control plots. This group consisted of *Anemone nemorosa* in 1980, *Lamiastrum galeobdolon* and *Stellaria holostea* in 1982, and *Mycelis muralis* in 1981, whereas in the remaining years the germination power was smaller than that recorded at the control (Table 2). In other species populations occurring in the experimental plots, e.g. *Oxalis acetosella*, *Galium odoratum*, the chances of seeds to produce seedlings did not change. Still other species from the experimental plots did not produce seedlings at all. This referred to the species of low frequency in the herb layer considered, namely *Lathyrus vernus*, *Sanicula europaea* and *Ranunculus lanuginosus*.

4. DISCUSSION

A compact layer of herbaceous plants in an oak-linden-hornbeam forest restricts seedling emergence of majority perennials and trees. Seedlings of some species have not emerged at all until gaps are formed in the plant cover providing conditions necessary for seed germination and seedling development. A local disturbance of herb layer exerts completely different influence on seedling emergence of annual plants (mainly *Impatiens noli-tangere*). Much fewer seedlings of annuals have emerged in sites where plants had been removed than in a compact herb layer. Experiments performed in Białowieża National Park consisting in herb layer removal from a riverside forest showed that a considerably greater number of *Impatiens noli-tangere* seedlings emerged after herb removal than at the control plots (Falencka 1983). Importance of plant cover for seedling emergence depends on physiological requirements of the seedlings and site conditions. In drier sites, plants that require much air humidity to develop will grow better when plant cover is compact, which reduces the risk of being shrivelled up in comparison with bare ground. In more humid sites bare ground is, in turn, more suitable as more light is available, which stimulates the plant development. Similar factors were involved where close neighbourhood of other plants favoured seedling emergence of *Spergula vernalis* on inland dunes near Toruń (Symonides 1974, 1979) or biennial grass *Aristida longiseta* in Texas (Flower 1988). However, seedling emergence of the plants having their ecological optimum in oak-hornbeam forests is inhibited by the presence of plant cover. Removal of the plant cover followed by creation of gaps resulted in emergence of numerous seedlings of species rare in the oak-linden-hornbeam forest but abundantly represented in seed bank of the forests, e.g. *Rubus idaeus* and *Carex remota* (Pirożnikow 1983), and species rarely reproducing generatively, e.g. *Aegopodium podagraria* and *Carex pilosa*. The experimental herb layer removal released space free from plants, the space being similar to regeneration niche formed after death of single individuals. According to Grubb (1977), a chance of seedling to emerge in such places increases due to locally reduced competition from the side of mature plants. Other studies have indicated that the chances of seedlings to emerge in dense communities increase after removal of plants (Flower 1988, Czarnecka 1995, Brzosko in press).

Uprooted trees locally destroy plant cover and cause the upper soil layer and litter to be moved elsewhere. The hollows made by uprooted trees are supplied with rain water, which allows soil moisture to be maintained for a longer time. Such places are almost devoid of seed banks, and emerging seedlings originate from seed rain. This reduces both species diversity and seedling abundance of perennials and trees in comparison with the control plots. Herb layer regeneration proceeds here gradually. In the beginning, annual plants appear, mainly *Impatiens noli-tangere* and short-lived perennials such as *Oxalis acetosella*, as well as *Urtica dioica*. The two former species are able to colonise such places through autochory. Seedlings of *Urtica dioica* emerge here presumably from seeds brought by roe-deers and red deers together with excreta of the animals. This is because the animals often use hollows made by uprooted trees as dens. Then the hollows are gradually colonised by other plant species, mainly by *Lamiastrum galeobdolon, Stellaria holostea* and *Majanthemum bifolium*, through vegetative reproduction. A similar pattern of colonisation of small gaps formed by single windthrow trees has been reported by Moore and Vancant (1986) for deciduous forests of North America. During the first and second year after a tree falls down, annuals predominate in the gaps, and then – after five to seven years – perennials.

According to Faliński (1986), disturbances resulting from wild boar feeding create numerous sites safe for seed germination because destruction of plants constituting herb layer and mixing upper soil layers accelerates decomposition of organic matter of destroyed plants, litter and wild boar faeces. However, this type of disturbances does not promote rapid herb layer regeneration, mainly due to recurrent plant destruction by wild boar feeding.

Disturbed fragments of the deciduous forest regenerate relatively slowly due to low plant reproductiveness and limited seed dispersion. Plant reproductiveness in the oak-linden-hornbeam forest is limited by a low frequency of individuals in generative phase. In populations of majority perennials occurring in this community, fraction of reproducing individuals does not exceed a few per cent. A greater fraction of individuals in generative phase (20–30%) is characteristic of short-lived perennials, e.g. *Oxalis acetosella,* biennials, and species characterised by a very low fecundity, e.g. *Galium odoratum*. Site disturbances create new places safe for seed germination, but the rate of regeneration depends on seed bank abundance. If a disturbance does not destroy the seed bank, numerous seedlings will already emerge during the next growing season. In contrast, if the seed bank is destroyed, regeneration will proceed slowly, because majority perennials typical of herb layer of oak-linden-hornbeam forests does not disperse seeds for long distances. This is testified by very sharply outlined clumps of seedlings around maternal plants in populations of many species examined, e.g. *Hepatica nobilis, Milium effusum*, which results from the fact that heavy seeds, having no special adaptations to disperse, fall down in the close vicinity of maternal plant. Some authors have claimed that subsequent generations of plants characterised by a strong competitive ability and highly specialised genotypes occupy fixed ecological niches owing to the above described type of seed dispersal (Levin 1981, Begon and Mortimer 1989, Eriksson 1992, Brzosko in press).

Components of herb layer in the oak-linden-hornbeam forest are adapted to strong competition through considerable germinating power and ability to develop seedlings. In populations of species playing the essential role in herb layer forming, from less than twenty to thirty per cent of seeds produce seedlings, whereas in populations of less important species – only several per cent. The field experiment revealed seed germination and successful development of seedlings of many plant species to be inhibited by mature individuals of the same as well as other species. Seed chances to develop into seedlings depend on diaspore properties (their size, germinating power, germination biology) and conditions the diaspores get into (soil fertility and moisture, litter thickness, presence of other plant species) (Flower 1988, Falińska 1990, Tumidajowicz 1995, Kwiatkowska 1996). It could be expected that in case of species of similar biology growing under unified conditions of a mixed deciduous forest seedlings should be produced by similar per cent of seeds. There were, however, great differences among populations of species investigated. The group of species having the greatest chances to produce seedlings from the seeds included mainly species reproducing generatively as well as vegetatively. In populations of two perennial species characterised by low frequency in the herb layer examined and generative type of reproduction, namely *Ranunculus lanuginosus* and *Sanicula europaea*, very small per cent of seeds developed seedlings. Thus, although the plants could not become dominants, their populations could be maintained and reproduce every year during the period of 17 years (Faliński 1986).

Other competitive adaptation is high survival rate of seedlings towards the end of a growing season. Grubb (1977) has claimed that in communities with dense plant cover, seedlings have poor chances to win a competition with mature individuals. Hence, the greatest chances to succeed are provided by precedence in colonising those fragments of the site where other plants have been removed from due to a disturbance or death of an individual, called after G r u b b (1977) a regeneration niche. The greatest number of regeneration niches is formed after winter, so that seedling emergence is restricted to two – three weeks of the growing season.

5. CONCLUSIONS

1. Gap formation in herb layer following experimental removal of plants resulted in doubled seedling number in the next year, when compare with the control plots. Seedling density at the experimental plots amounted to 162 indiv. m^{-2}, whereas at the control plots – to 82 indiv. m^{-2}. Seedlings of two times more species emerged at the experimental plots in comparison with the control plots.

2. At the experimental plots seedlings of species rare in herb layer of the oak-linden-hornbeam forest, e.g. *Rubus idaeus, Carex remota* emerged numerously (Tables 3 and 4).

3. Survival rate of the seedlings till the end of the growing season amounted to 10% in populations of majority perennials. Survival rate increased at the experimental plots by 10–40%.

4. Species number of seedlings emerging in hollows made by uprooted trees was reduced by half in comparison with the control plots. Density of the seedlings was two times higher in one year, whereas in the second year – similar (Fig. 3).

5. Seedling density and species number at the plots frequently visited by wild boars were lower than at the control plots (Fig. 3).

6. In populations of species dominant in herb layer of the oak-linden-hornbeam forest from 5% to 30% of seeds produced seedlings (Table 2). At the experimental plots, per cent of seeds producing seedlings increased in some populations, e.g. *Anemone nemorosa, Lamiastrum galeobdolon, Stellaria holostea* (Table 2).

7. In populations of some species, clumps of seedlings emerged every year in the same places (Fig. 5).

6. SUMMARY

This study aimed at determining densities and survival rates of seedlings of herbaceous plants in undisturbed herb layer of an oak-linden-hornbeam forest and in natural and experimentally formed gaps. The following hypotheses have been put forward: (1) dense plant cover reduces germination and development of seedlings, (2) gap formation in herb layer stimulates seedling emergence and enhances their chances to survive, (3) density and species diversity of seedlings depend on gap type, (4) in undisturbed herb layer locality of sites safe for seed germination changes every year.

The investigations were performed in Białowieża National Park in 1978–1984. Four plot types were included: (1) control, (2) in herb layer disturbed experimentally through plant removal, (3) in hollows made by uprooted trees, (4) in places of wild boar feeding (Fig. 1). All seedlings of herbaceous plants in the plots were scored and marked. In order to estimate per cent of seeds producing seedlings in populations of 11 plant spe-

cies of different reproduction types, plant fertility and densities of generative shoots were determined in 1979–1982.

From among 31 species of herbaceous plants occurring in the herb layer (Table 1), seedlings of 24 species emerged in the plots during the period of six years. Seedling densities in particular years ranged from 43 to 238 per m^2 (Fig. 3). In populations of species dominant in the herb layer, sites safe for seed germination did not change their localities for 3 years (Fig. 5). In populations of subdominants locality of safe sites depended on presence of generative shoots in the previous season.

In the gaps made experimentally in the herb layer (at the experimental plots) seedling densities and species number of the seedlings were doubled in the year following herb layer removal (1979) (Fig. 3, Table 3 and 4). In the next seasons, seedling densities and species numbers were similar to those recorded at the control plots. Seedling densities in populations of *Impatiens noli-tangere* and *Hepatica nobilis* was significantly lower at the experimental than the control plots (Fig. 4). Seedlings emerging in hollows made by uprooted trees and in places of wild boar feeding belonged to a smaller number of species than those found at the control plots, but species composition of the seedlings was similar (Table 5). In one season, seedling density in hollows made by uprooted trees was two times higher, while in the second season – similar to that at the control plots. The respective values at the plots of wild boar feeding were lower (Fig. 3).

At the control plots, about 10% of seedlings survived till the end of the growing season, whereas at the experimental plots – about 60% (Fig. 6). Every year, from 3% to 30% of shoots of the plant population examined approached generative reproduction phase (Fig. 2). At the control plots from 5% to 30% of seeds produced seedlings (Table 2). At the experimental plots, per cent of seeds developing into seedlings increased in certain populations only.

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