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LIFE CYCLE OF HERBACEOUS PLANTS IN DISTURBED AND UNDISTURBED SITES OF OAK-LINDEN-HORNBEAM FOREST (*TILIO-CARPINETUM*)

ABSTRACT: In undisturbed sites not all genets of the species investigated completed their life cycles. During five years, only 5–18% of genets attained virginile phase. Disturbances in herb layer structure enhance chances of individuals to complete life cycle – in disturbed sites, from 0.4% to 57% of genets approached generative phase.
KEY WORDS: herb layer plants, development rate, survivorship, genet, deciduous forest

1. INTRODUCTION

Numerous authors are in the opinion that individuals of perennial herbaceous plants developed from seeds (genets) have little chances to survive the period from the seedling phase to the generative phase in herb layer of stabilised forest communities (Smirnova et al. 1976, Zaugolnova et al. 1988, Falińska 1990). Populations of majority plant species in herb layer maintain their abundance through vegetative reproduction (Uranov et al. 1977, Cook 1985, White 1985, Czarnecka 1986, Eriksson 1989). Hence, many authors have claimed that populations of forest perennials are continuously regenerating clones (Harbert 1961, Jones and Wilkins 1977). Other authors have suggested that individuals developed from seeds emerge in populations after local disturbances (i.e. destruction or injury of plant cover) and attain reproduction phase thus providing necessary genetical diversity (Eriksson 1989).

Individuals of perennial herbaceous plants are able to survive and reach successive ontogenetic phases through various life strategies at different develop-

mental stages (Grime 1979). In the seedling and juvenile phases, the strategy is directed towards survival, i.e. individuals are characterised by small sizes, small biomass increments, and simple architecture. Their chances to survive and successfully develop depend mostly on neighbouring plants. Competition and shading by mature plants reduce growth rate and delay progeny to reach successive developmental stages (Campbell et al. 1991). In populations of many plant species, individuals in juvenile phase create a reserve in a population (Grime 1987). Their survival and successful establishment is possible when a gap is formed in herb layer following death of a neighbour or in the case of the site disturbance. Grubb (1977) called such a gap a regeneration niche. The author has claimed that in dense communities, chances of a juvenile individual to survive and to develop afterwards depend on emergence of a regeneration niche in the closest vicinity of the individual.

The objectives of this work were to recognise life cycle of genets, especially their chances to attain reproduction phase in undisturbed herb layer of an oak-linden-hornbeam forest, and to determine changes in survivorship in successive ontogenetic phases when young genets grow in areas devoid of herb layer.

2. STUDY AREA AND METHODS

The studies were carried out in Białowieża Primeval Forest in 1979–1983. The area is best protected large forest complex in European lowland. The forest extends between 23°31‘ and 24°21‘ of eastern longitude and 52°29‘ and 52°57‘ of northern latitude. Observations were made in a permanent research area of Białowieża Geobotanical Station of Warsaw University in Białowieża National Park (Faliński 1966). In a patch of an oak-linden-hornbeam forest where herb layer structure was intact, 50 control plots (C) were delimited, each of an area of 1 m^2, in 3m × 4m grid. Nearby, 50 experimental plots (E) were established in the same spatial arrangement as the control plots, each of an area of 1m^2. In 1978, all plants together with below-ground parts were removed from the experimental plots without digging out the soil. The plots served to observe survivorship and development of genets growing without companion of mature plants.

In order to estimate genet numbers and survivorship at the control and experimental plots, seedlings of particular species emerging in the spring of successive seasons were counted by marking with plastic tubes and rings. During subsequent observations, numbers of live genets of particular species and their developmental phase were recorded of area 50m^2. The following developmental phases were distinguished after Smirnova et al. (1976): (1) seedling phase, (2) juvenile phase, (3) virginile phase, (4) generative phase. Observations started after snow cover was melted away, and were made every 5 days during spring, and every 10 days during summer and autumn – until the growing season ended.

Survivorship and development rates of genets of particular species were assessed for cohorts of seedlings emerged in 1979 for 5 years, in 1980 – for 4 years, in 1981 – for 3 years, and in 1982 – for 2 years.

3. RESULTS

3.1. LIFE CYCLE

Out of 26 perennial species in undisturbed herb layer of the oak-linden-hornbeam forest (the control plots), genets of 12 species attained juvenile phase (Table 1). Seedlings of the species emerged usually from the end of April to mid-June, and reached juvenile phase in September. Genets of *Hepatica nobilis* were the only ones reaching juvenile phase early in summer of the next year.

Perennial genets at the control plots approached virginile phase usually in third year of life, except *Viola riviniana V. reichenbachiana* reaching the phase in fourth, and *Hepatica nobilis* – in fifth year (Table 1).

Genets of majority perennials attained generative phase in sixth year, except genets of *Mycelis muralis* that started flowering in fourth or fifth year of life (Table 1).

In the disturbed sites, i.e. at the experimental plots, the genets reached juvenile phase 2 months earlier than those at the control plots. Virginile phase at the experimental plots was approached one year earlier than at the control, i.e. in second or third year of life, except *Hepatica nobilis*, reaching the phase in fourth year (Table 1).

Genets from two first cohorts (1979 and 1980) at the experimental plots attained generative phase in third or fourth year of life, with *Anemone nemorosa* reaching it in fourth year (Table 1). Genets of three species (*Hepatica nobilis, Rubus idaeus* and *Urtica dioica*) did not reach the phase during five years. As the plots were becoming overgrown by the plants, genet development slowed down (Figs. 1 and 2).

Table 1. The rate of ontogenetic development of genets (a year of attaining particular developmental phases) of selected species of herb layer in an oak-linden-hornbeam forest at the control (C) and experimental plots (E) in Białowieża National Park. j – juvenile phase, v – virginile phase, g – generative phase, * denotes that no genet attained a phase in the study period, n.d. – no data

No	Species	j		v		g	
		C	E	C	E	C	E
1.	*Mycelis muralis* (L.) Dum.	1	1	3	2	4-5	3
2.	*Lamiastrum galeobdolon* (L.) Ehrend.	1	1	3	3	*	4
3.	*Milium effusum* L.	1	1	3	2	*	3
4.	*Viola riviniana* Rchb. X *Viola reichenbachiana* Jord. ex Boreau	1	1	4	3	*	3-4
5.	*Stellaria holostea*	1	1	3	2	*	3
6.	*Urtica dioica* L.	1	1	*	3	*	*
7.	*Anemone nemorosa* L.	1	1	n. d.	3	n. d.	4-5
8.	*Oxalis acetosella* L.	1	1	n. d.	2	n. d.	3
9.	*Carex digitata* L.	1	1	*	2-3	*	4
10.	*Carex pilosa* Scop.	1	1	*	2	*	4
11.	*Hepatica nobilis* Schreb.	2	2	5	4	*	*
12.	*Rubus idaeus* L.	1	1		3		*
13.	*Carex remota* L.		1		2-3		3

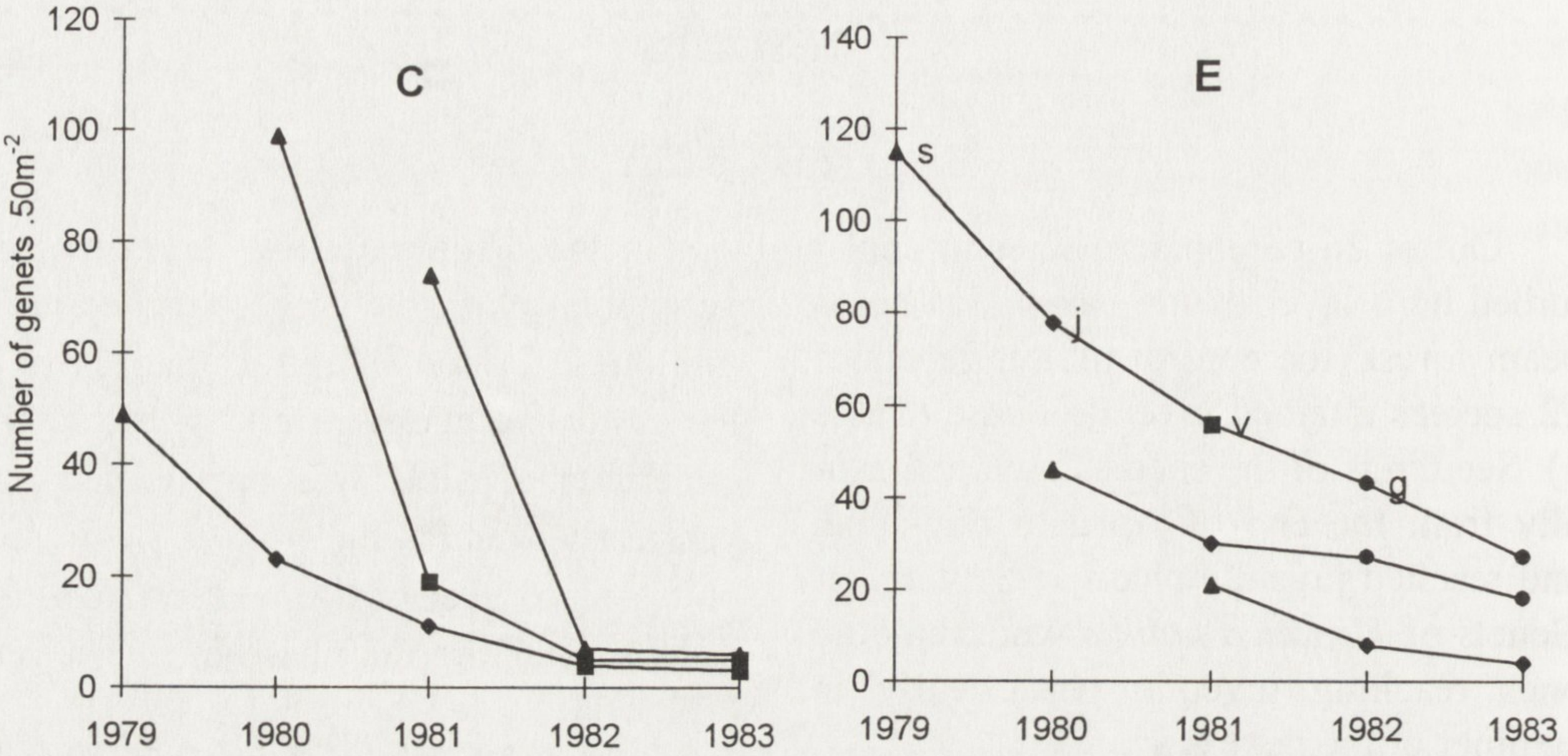

Fig. 1. Changes in abundance per 50 m^2 of *Viola riviniana* x *V. reichenbachiana* genets in an oak-linden-hornbeam forest of Białowieża National Park. C – control plots, E – experimental plots, s – seedling phase, j – juvenile phase, v – virginile phase, g – generative phase

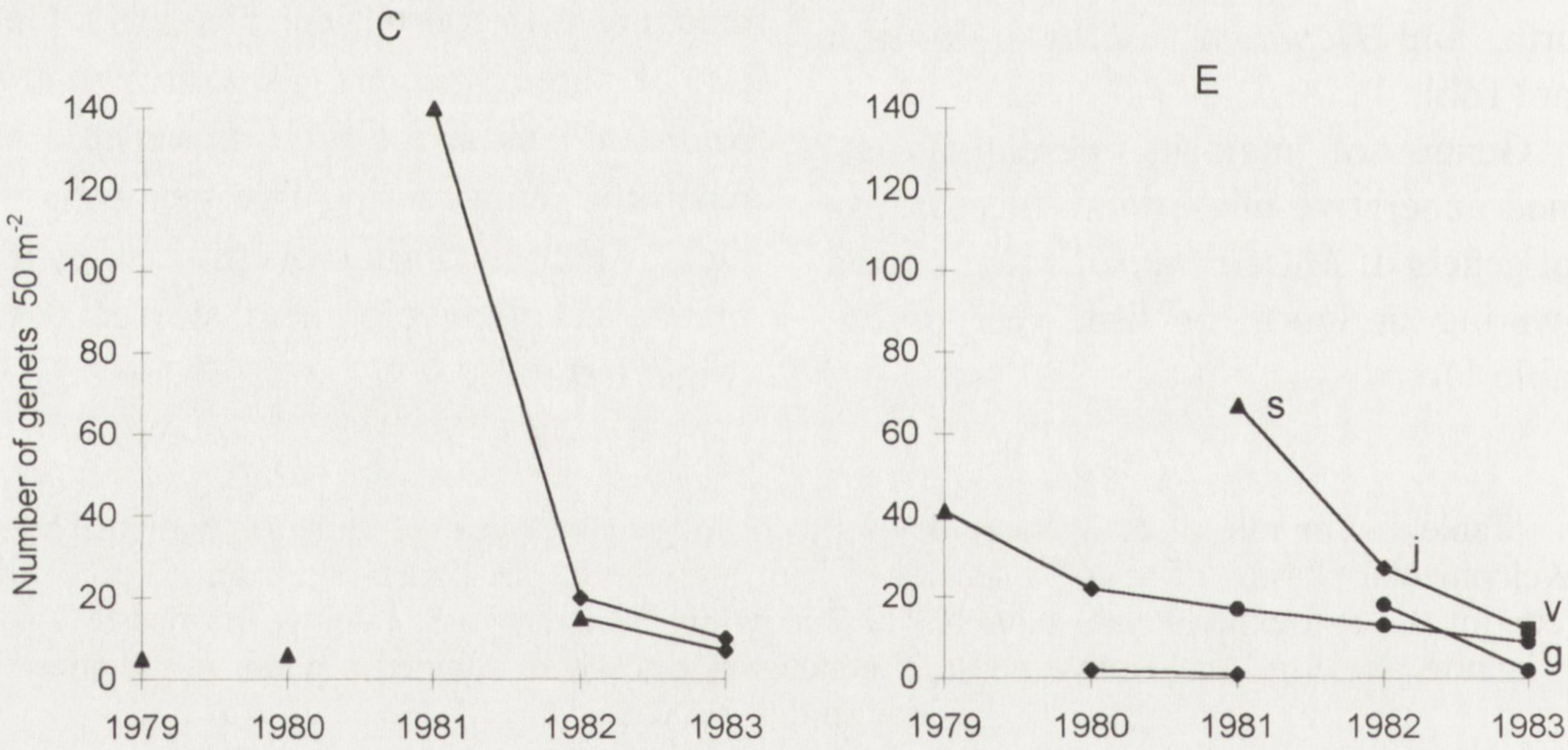

Fig. 2. Changes in abundance per 50 m^2 of *Lamiastrum galeobdolon* genets in an oak-linden-hornbeam forest of Białowieża National Park. See Fig. 1 for symbol description

3.2. SURVIVORSHIP

In undisturbed herb layer (the control plots), from 10% to 69% of perennial seedlings survived attaining juvenile phase (Table 2). Considering survivorship, the species examined may be subdivided into two groups: (1) when 1/3–1/2 of seedling cohort approached juvenile phase (*Milium effusum, Mycelis muralis, Viola riviniana V. reichenbachiana*), (2) when 1/3–1/4 of seedling cohort attained the age of juvenile phase (*Hepatica nobilis, Urtica dioica, Stellaria holostea*). In some years, no seedling attained juvenile phase, e.g. in population of *Stellaria holostea* in 1979 and 1981 (Table 2). Abundance of such cohorts was exceptionally low (from 1 to 8 seedlings per 50 m^2). Majority genets remained in juvenile phase to third or fourth year of life.

Table 2. Abundance per 50 m^2 and survivorship of genet cohorts of selected species of herb layer in an oak-linden-hornbeam forest of Białowieża National Park. C – control plots, E – experimental plots, * denotes that no genet attained a phase in the study period, n.d. – no data

Species	Year	Cohort abundance		Juvenile phase %		Virginile phase %		Generative phase %	
		C	E	C	E	C	E	C	E
Mycelis muralis	1979	85	26	32	81	7	23	1	57
	1980	22	8	55	88	18	62	15	36
	1981	56	93	49	43	*	35		16
Milium effusum	1979	26	211	31	31	0	25	*	10
	1980	69	16	54	94	12	63	*	13
	1981	354	157	47	57	9	19	*	*
Viola riviniana X *V. reichenbachiana*	1979	49	115	69	81	8	49	*	12
	1980	99	46	47	74	5	57	*	2
	1981	74	21	34	62	*	19		*
Hepatica nobilis	1979	69	12	20	42	10	33	*	*
	1980	163	10	26	40	*	30		*
	1981	196	11	31	64	*	0		*
Lamiastrum galeobdolon	1979	7	41	0	83	0	39	*	12
	1980	10	2	10	50	0	0		
	1981	140	67	53	52	9	18		*
Stellaria holostea	1979	1	41	0	76	0	22		2
	1980	31	7	29	71	6	29	*	29
	1981	1	1	0	0	0	0		
Urtica dioica	1979	96	103	33	46	0	4	0	*
	1980	29	1	31	0	0	0		
	1981	27	9	22	0	0	0		
Anemone nemorosa	1979	n.d.	137	n.d.	70	n.d.	49	n.d.	1
	1980	168	272	n.d.	87	n.d.	57	n.d.	0.4
	1981	164	294	n.d.	57	n.d.	23	n.d.	*
Carex digitata	1979	0	154		78		34		6
	1980	0	14		93		64		14
	1981	0	1		100		*		
Carex pilosa	1979	8	216	0	52		32		0.5
	1980	6	82	0	72		39		1
	1981	0	4		50		25		*
Carex remota	1979	0	517		95		65		16
	1980	0	18		67		17		*
	1981	0	17		65		35		*

Virginile phase was reached by 5–18% of seedling cohorts (Table 2). The greatest chances to attain the phase in undisturbed parts of the oak-linden-hornbeam forest had genets of *Mycelis muralis* (18%) and *Milium effusum* (12% of the cohort). In some cohorts, no genet attained virginile phase, e.g. *Urtica dioica* that emerged in 1979–1981, *Lamiastrum galeobdolon* from 1979 and 1980, and *Milium effusum* from 1979.

During five years, genets of only one species, namely *Mycelis muralis*, attained generative phase at the control plots. From 1% to 15% of seedling cohorts reached the phase (Table 2).

In disturbed sites (the experimental plots), seedling survivorship of majority species until they reached juvenile phase was higher by 13–49% in comparison with the control plots. *Milium effusum* seedlings from 1979 were the only whose survivorship at the experimental plots was the same as at the control. Juvenile phase at the experimental plots was attained even by 90% of seedlings of certain cohorts (*Carex digitata, C. remota, Milium effusum*). Some cohorts of seedlings at the experimental plots died before they reached juvenile phase (*Urtica dioica* from 1980 and 1981, and *Stellaria holostea* from 1981).

As the plots were becoming overgrown by the plants, differences in survivorship of the seedling cohorts up to juvenile phase decreased between the control and experimental plots. In the third year after herb layer removal from the experimental plots, survivorship between the seedling and juvenile phase in populations of *Mycelis muralis* and *Lamiastrum galeobdolon* was slightly lower than at the control plots (Table 2). In sites devoid of plants, no inhibition of genet development at the stage of juvenile phase was observed. However, the phenomenon only comprised cohorts colonising newly disturbed sites. In 1979, plants occupied on average 10% of the area of the experimental plots, in 1980 – 20%, whereas in 1981 and 1982 – 40%. Since 1981, when herb layer coverage at the experimental plots reached 40%, the plants initiated a strategy of waiting in the juvenile phase, i.e. slowed down their development at this stage, likewise in undisturbed areas where plant coverage in successive years ranged from 60% to 70%.

Per cent of seedling cohorts in populations of the examined species attaining virginile phase at the experimental plots ranged from 4% to 65% (Table 2). The highest survivorship at this stage of development was characteristic of *Carex remota* genets. In disturbed sites, genets survivorship to virginile phase was higher by 9–52% than that in undisturbed plots. Survivorship at this stage at the experimental plots increased to the highest degree in the case of *Mycelis muralis, Milium effusum* and *Viola riviniana V. reichenbachiana* (Fig. 1). Cohorts of genets from 1981 (fourth year of plot overgrowing) were characterised by considerably lower survivorship until virginile phase than the cohorts from 1979 and 1980 (by 7–44%). The most distinct decrease in survivorship was found for genets of *Milium effusum, Viola riviniana V. reichenbachiana* and *Anemone nemorosa* (Table 2).

At the experimental plots, no decrease in genets survivorship of majority populations was observed between juvenile and virginile phase, except populations of *Urtica dioica* and *Carex remota* where the decrease amounted to 21–67%.

In disturbed fragments of the oak-linden-hornbeam forest (the experimental plots) even genets of species typical of the forest type, whose seedlings usually

die in undisturbed sites, attained generative phase in three-four years. At the experimental plots, from 0.4% to 57% of genets reached generative phase (Table 2). The highest survivorship at this stage was characteristic of genets of *Mycelis muralis* and *Stellaria holostea*. In disturbed sites of an area of 50 m^2, generative phase was attained by 1–83 genets belonging to consecutive cohorts. The most abundant flowering genets originated from those seedling cohorts that emerged at the experimental plots first. In population of *Carex remota* the generative phase was attained by 83 genets per 50 m^2, in *Milium effusum* – 21 genets 50 m^{-2}, in *Mycelis muralis* – 15 genets 50 m^{-2}, in *Viola riviniana* x *V. reichenbachiana* – 14 genets 50 m^{-2}, in *Carex digitata* – 9 genets 50 m^{-2}, and in every remaining species – 1 genet per 50 m^2. Of the cohorts from 1980 at the experimental plots, generative phase was attained by 1–2 genets (Fig. 3).

In populations of majority perennials of the disturbed as well as undisturbed sites, chances of genets to survive to the next season increased with genets age. *Hepatica nobilis* and *Viola riviniana V. reichenbachiana* were the only populations where survivorship of older individuals was not higher than that of younger ones.

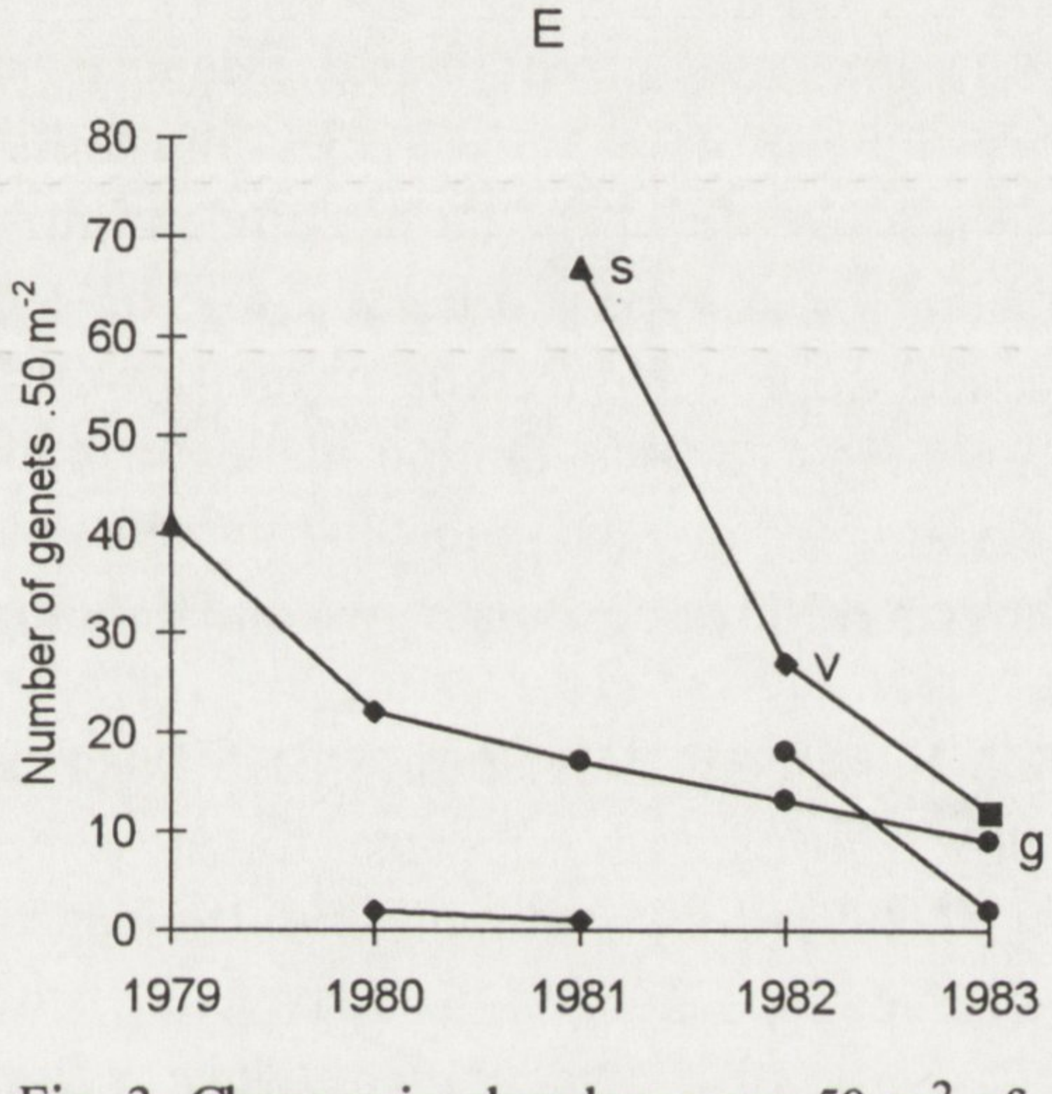

Fig. 3. Changes in abundance per 50 m^2 of *Carex digitata* genets at the experimental plots in an oak-linden-hornbeam forest of Białowieża National Park. Symbol description – Fig. 1

4. DISCUSSION

In dense forest communities rarely individuals developing from seeds attain virginile phase. Before genets approach generative phase, they increase in size, multiply number of shoots and produce vegetative diaspores. Individuals formed from buds or vegetative diaspores are much more advanced in development than those formed from seeds, although their age may be the same. Chances of plants developed from vegetative diaspores or buds to survive and develop fast are thus much greater (Uranov et al. 1977, Kawano et al. 1987, Falińska 1990).

The data presented in this work suggest that in populations of majority herb layer species of the oak-linden-hornbeam forest type not all individuals developed from seeds die before attaining generative phase. Inhibition of genet's development for 3–4 years allows an individual to "wait" for some free space in a dense herb cover, called by Grubb (1977) a regeneration niche. Young individuals have no favourable conditions to live until they reach the height of herbaceous

plant canopy, and their growth and development carry on very slowly. When a regeneration niche appears, growth rate of an individual is possible to increase, and the plant architecture may become more complicated due to greater accessibility to resources (Grubb 1977). When plants attain virginile phase, they are very likely to reach generative phase. Because in populations of some species in undisturbed herb layer of the oak-linden-hornbeam forest type, from 5% to 18% of genets approach virginile phase, I would conclude that regeneration niches in such places are not rare, and thus some seedlings have chances to survive and develop afterwards.

For plants constituting herb layer of the oak-linden-hornbeam forest type, 1%–2% of full sunlight is sufficient to survive, especially in the first year of life (Puchalski and Prusinkiewicz 1990). These studies have confirmed opinions of authors working on development of perennials that an individual living in a stabilised community attains virginile phase, starts to produce plagiotropic shoots and reproduce after at least 4 years (Łukasiewicz 1976, Gatsuk et al. 1980, Falińska 1982, Czarnecka 1995, Tumidajowicz 1995). Majority of juvenile individuals constitutes a reserve of a population (so called bank of juvenile individuals) expecting favourable sites for their development to appear (Connel and Slatyer 1977, Grime 1987). In stabilised communities, an expression "replacement of individuals in a population" should preferably be used instead of "increase in number of individuals", because a greater number of progeny does not mean that more individuals than usually will attain reproductive phase. The results presented seem to testify that regardless of magnitude of seedling production, a similar number of individuals attain mature vegetative phase every year. Number of young genets joining a population every year is very small in relation to the number of mature individuals (Pirożnikow 1992). It is interesting that number of young genets attaining virginile phase does not depend on population abundance nor longevity of the complete life cycle of individuals. Although the virginile phase in undisturbed areas is attained by several to more than ten individuals per 50 m^2 every year, considering frequency of generative phase in ontogenetic development of majority perennials examined, not only a chance to introduce single individuals developed from seeds and able to crossing into a population exists, but also replacement of all or a part of maternal individuals attaining senile phase is possible. The chance is considerably greater when individuals are able to reproduce vegetatively and to expand themselves. Firstly, maternal individuals may continue their lives through increase in size and vegetative reproduction, which causes generative phase to last much longer than 3–4 years. Secondly, young individuals developed from seeds, after they had attained virginile phase, may produce a greater number of generative shoots through increase in size and vegetative reproduction. In the case of two species, namely *Anemone nemorosa* and *Oxalis acetosella*, investigation of live genet fate in undisturbed herb layer was impossible. Rapid increase of plants in size after reaching virginile phase is a reason of overlapping acreages of neighbouring individuals, which makes impossible to ascribe above-ground shoots to a given genet without injuring the plants. Populations of *Anemone nemorosa* produce seeds very abundantly, and seedlings are produced every year. Although the rate of individual development is very slow, not all genets die be-

fore attaining generative phase. An analysis of rhizomes of that species indicates that in undisturbed sites of the oak-linden-hornbeam forest, 2–3% of genets attain generative phase in sixth or seventh year of life (Pirożnikow 1994). In disturbed sites (at the experimental plots), genets of *A. nemorosa* attain the phase two years earlier.

In stabilised communities of deciduous forests, site disturbances occur as a result of windthrow trees or feeding of large mammals (Faliński 1986). Trees falling down together with roots uncover soil of an area of a few to more than ten square meters. In those areas seedlings and vegetative diaspores emerge rapidly. Young individuals devoid of neighbours grow and develop fast. In the bare areas made by windthrow trees a chance appears to attain reproduction phase even by progeny of those species whose genets die in the first year of life in herb layer with typical structure. This mainly relates to species uncommon to herb layer of the oak-linden-hornbeam forest type, such as *Carex remota* or *Rubus idaeus*. Sites devoid of herb layer may sometimes occupy from 12% to 15% of the area of a natural oak-linden-hornbeam forest of Białowieża National Park (Faliński 1976). Hence, the chances to complete life cycle by genets of plants colonising hollows made by uprooted trees are fairly great. An attention should be paid to a sedge, *Carex pilosa*, a species common to oak-linden-hornbeam forests of Białowieża Primeval Forest. Genets of the species rarely emerge in undisturbed herb layer, but complete their life cycle in disturbed sites colonising such sites for a long time and reproducing vegetatively by subsequent generations. Smirnova's studies (1987) revealed that genets of that species in deciduous forests near Moscow flower in sixth or seventh year of life, i.e. two or three years later than at the experimental plots in Białowieża Primeval Forest.

Second source of natural disturbances in an oak-linden-hornbeam forest may be feeding of large mammals, particularly wild boars. Feeding wild boars destroy herb layer to a high degree. Area of places intensively rooted about by wild boars may occupy as much as 30% of forest floor (Faliński 1986). Rooting does not increase chances of genets to attain generative phase, because animals usually revisit several times a year the feeding places, and destroy young, weakly rooted plants. Considering the number of genets attaining maturity – generative or virginile phase – during five years of the studies, the plant populations may be subdivided into two groups:

(1) Plant populations whose genets attain virginile or generative phase when living in undisturbed sites: a) number of genets surviving may replace all maternal plants when those will reach senile phase; this group consists of perennials characterised by exclusively generative propagation (*Viola riviniana V. reichenbachiana*, *Hepatica nobilis*, *Mycelis muralis*), b) generative phase is attained by genets replacing only a part of maternal plants, while residual plants are being replaced by individuals developed from vegetative diaspores or buds. This group includes species reproducing generatively as well as vegetatively (*Milium effusum, Stellaria holostea, Lamiastrum galeobdolon*).

(2) Plant populations whose almost all genets die before reaching generative phase when living in undisturbed sites. Life cycle of such species is only completed in disturbed sites. This group consists of species reproducing mostly vegetatively (*Carex pilosa, C. digitata, Urtica dioica*).

Spatial variability of seed production, seed bank and number of individuals require representativeness of samples to be discussed. Former studies performed within International Biological Programme have revealed that variability in seed production is represented by 48 plots, each of 1 m^2 in area. Since the range of variability in density and distribution of seedlings was similar to that measured previously, it can be assumed that areas of 50 m^2 or 100 m^2 may also give reliable results. Although all species occurring in the plots were taken into consideration, survivorship could only be assessed for sufficiently abundant populations. In order to examine survivorship of genets of species low in number and frequency of individuals, studies should be made on areas much larger than 100 m^2.

5. CONCLUSIONS

1. In undisturbed fragments of an oak-linden-hornbeam forest, dense plant cover reduces survivorship as well as the rate of genet development (Tables 1 and 2). Majority genets die at the stage of seedling or in juvenile phase.

2. In the sites where herb layer was disturbed (at the experimental plots), the rate of genet development was found to be accelerated in comparison with the control plots (Tables 1 and 2).

3. Perennials constituting herb layer in the oak-linden-hornbeam forest type belong to two groups: (1) species whose genets complete their life cycle in undisturbed sites and replace all dying individuals, e.g. *Mycelis muralis, Hepatica nobilis* (Fig. 1), (2) species whose almost all genets in undisturbed sites die before attaining reproduction phase – completing life cycle is possible in disturbed sites, e.g. *Carex pilosa, C. digitata, Urtica dioica* (Fig. 3).

4. As the experimental plots were becoming overgrown, the differences in survivorship of seedling cohorts until juvenile and virginile phase between the experimental and control plots decreased (Table 2).

6. SUMMARY

The objective of this work was to recognise life cycle of perennial genets in a stabilised community of an oak-linden-hornbeam forest (*Tilio-Carpinetum*), especially to evaluate chances to attain reproduction phase in undisturbed herb layer, as well as changes in survivorship of genets in successive developmental phases in sites devoid of herb layer.

The investigations of genet survivorship were performed in Białowieża National Park in 1979–1983. The study area consisted of 50 control plots, each of an area 1 m^2, in undisturbed sites and 50 experimental plots of the same areas of 1 m^2, from where herb layer was removed in 1978. There were 12 species included into the studies. These were the species most frequently occurring in the form of genets in the herb layer of the forest examined.

In undisturbed herb layer, genets of the species examined attained virginile phase in third, fourth or fifth year of life, whereas in disturbed sites (at the experimental plots) – one year earlier (Table 1). In the disturbed sites, genets belonging to two first cohorts (from 1979 and 1980) attained generative phase in third or fourth year of life (Table 1).

In the disturbed herb layer, from 5% to 18% of seedling cohorts attained virginile phase, while in the disturbed sites – from 4% to 65% (Table 2). In the disturbed sites, generative phase was attained by 0.4–57% of

genets (Table 2). As the experimental plots were becoming overgrown, survivorship of genets declined (Figs 1–3). The greatest differences in genet survivorship between undisturbed and disturbed herb layer were characteristic of *Mycelis muralis, Milium effusum* and *Viola riviniana V. reichenbachiana* populations (Fig. 1).

In undisturbed herb layer, virginile phase is attained by several to more than ten genets per 50 m^2, hence, a real chance exists for individuals developed from seeds to join the population. Herb layer disturbance enhance chances of genets to attain the phase. In populations of *Viola riviniana V. reichenbachiana*, *Hepatica nobilis* and *Mycelis muralis*, replacement of individuals takes place exclusively through individuals developed from seeds. In populations of other species, e.g. *Milium effusum, Stellaria holostea, Lamiastrum galeobdolon*, generative phase is attained by such a number of genets that some of individuals leaving a population may only be replaced by the genets. In populations of certain species growing in undisturbed herb layer all genets die, and life cycle is completed in disturbed sites only, e.g. *Carex pilosa, C. digitata, Urtica dioica.*

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