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## DEMOGRAPHY OF *ANEMONE NEMOROSA* L. IN DRY-SITE DECIDUOUS FOREST (TILIO-CARPINETUM) IN THE BIAŁOWIEŻA FOREST

**ABSTRACT:** Studies were performed in a patch of oak-hornbeam forest *Tilio-Carpinetum typicum* in the Białowieża Forest, in the years 1980–1989.

In the *Anemone nemorosa* population the density modifies the architecture of individuals, whereas it does not influence their development rate.

Intensive feeding of wild boars is the most important factor regulating the dynamics and structure of the *A. nemorosa* population.

The effectiveness of generative reproduction is very differentiated in the consecutive years. The effectiveness of this reproduction is very high, as compared with other populations of this species, but the proportion of individuals of vegetative origin in the population is very low. Rejuvenation of the population takes place primarily by way of vegetative reproduction, the effectiveness of which is comparable with that of other perennial species populations. Generative reproduction is more intensive and more effective at sites of higher population density, and vegetative reproduction – at sites of lower density.

**KEY WORDS:** generative reproduction, vegetative reproduction, development rate of individuals, architecture of individuals.

### 1. INTRODUCTION

Studies of plant demography are focused on generative reproduction. Vegetative reproduction has been investigated only in plants that develop vegetative diaspores.

*Anemone nemorosa* is a perennial plant of the polycormonal type of growth. In spring, this species is dominant in the floor vegetation of European deciduous

forests. Every year *A. nemorosa* develops leaves (lasting ca. 2 months) and flower shoots from buds on perennial rhizomes (Łukasiewicz 1962). It reproduces vegetatively, without diaspore formation but by way of rhizome disintegration (Ziman 1985). This species has been the object demographic studies from the standpoint of generative reproduction (Tumidajowicz 1977, Trela-Sawicka 1975, Canullo 1985, 1988), population structure, exchange rate of individuals (Tumidajowicz 1975, Canullo 1985, Shirreff and Bell 1984) and population dynamics in succession (Faliński and Canullo 1985, Canullo 1988), as well as of the biology of this species (Łukasiewicz 1962, Ziman 1985).

The present studies were aimed at:

- (1) the description of the ontogenetic development of *A. nemorosa* individuals derived from rhizome disintegration or from seeds;
- (2) the determination of the effectiveness of the vegetative and generative reproduction;
- (3) the description of population structure;
- (4) the determination of the differentiation of population structure and reproduction effectiveness as a function of population density.

## 2. METHODS

Studies were carried out in a patch of dry-site deciduous forest *Tilio-Carpinetum* Tracz. 1962 typicum in the Białowieża Forest, in the Roadside Reserve, section 319. Observations were taken in 31 square test plots (each of a 0.25 m<sup>2</sup> area) distributed every 2 m along three lines distant from each other by 10 m.

In the years 1980–1984, at the time of maximal flowering of *A. nemorosa*, the degree of cover of this plant and of other species of forest floor vegetation, the number of generative shoots, number of leaves and number of seedlings were recorded for each test plot.

For evaluation of the numbers of individuals, in autumn of 1984 all *A. nemorosa* rhizomes were dug out from the test plots. Each self-dependently rooted rhizome with one or more apical buds that developed one or more overground leaves or a generative shoot were regarded as an individual (Fig. 1). For each test plot the rhizomes were divided into 2 groups: damaged and undamaged, and were counted. In the case of the undamaged rhizomes, their following characters were analyzed:

- rhizome length (exact to 0.1 cm);
- number of branches;
- number of annual-increment segments in the longest rhizome fragment;
- number of living annual-increment segments on branches;
- consecutive no. of the annual-increment segment on which the branch was present;

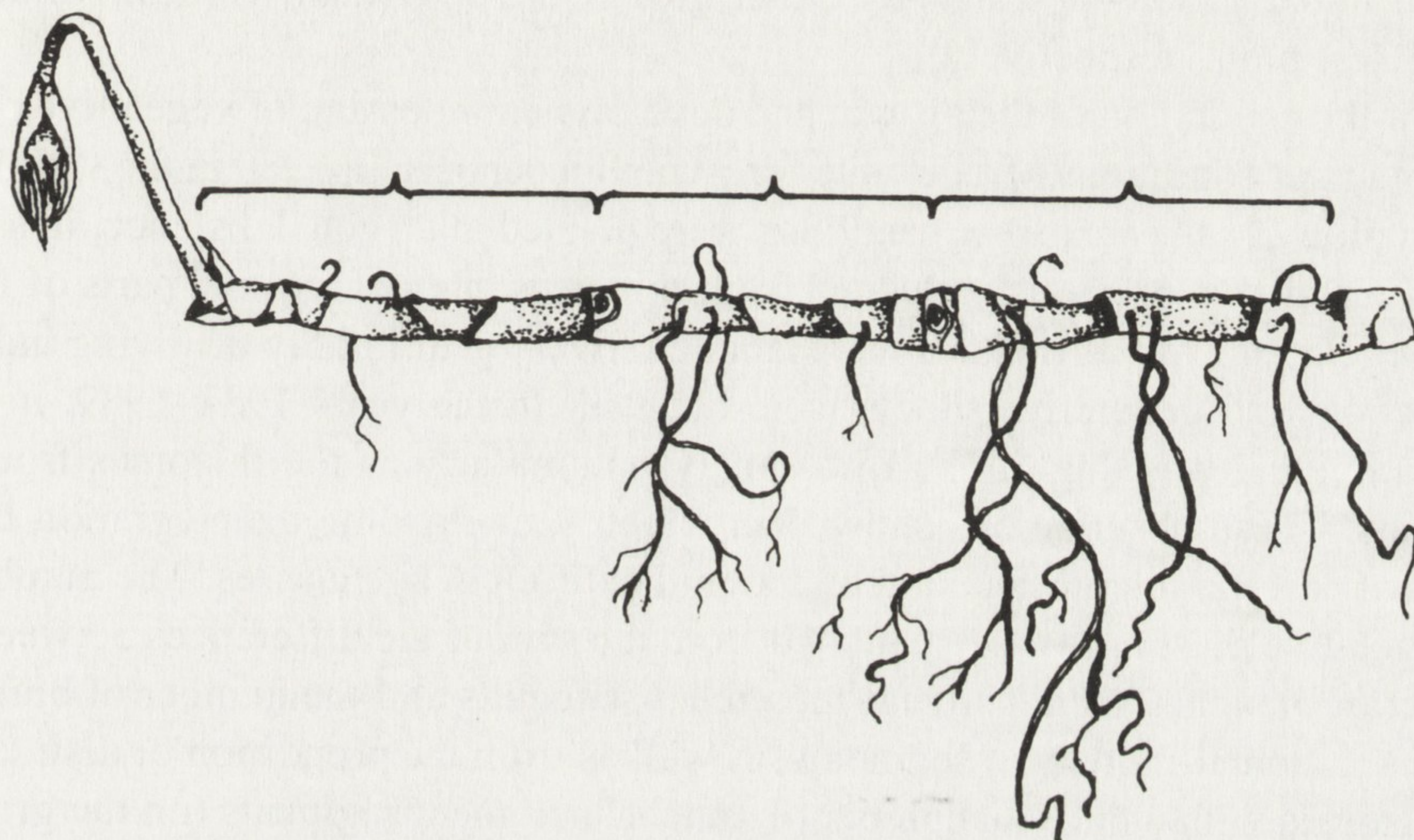


Fig. 1. Morphology of *Anemone nemorosa* rhizome.  
Annual-increment segments are denoted by braces

– presence or absence of primary root and tuberiform annual-increment segments pointing to rhizome origin from a seedling.

Subsequently the rhizomes were dried at 80° C to constant weight and weighed.

On the grounds of the individual's architecture, number of annual-increment segments and proportion of the length of the living to the dead part of rhizome, individuals were classified into the following developmental phases:

(1) juvenile phase – not branched rhizomes containing most often up to three annual-increment segments;

(2) virginal and generative phase together – either not branched rhizomes containing more than four annual-increment segments, or branched rhizomes without a dead part, or else rhizomes with a dead part of a length not exceeding 1/2 of the length of the living part;

(3) subsenile phase – rhizomes with dead part length amounting to 1/2–1/3 of the living part length;

(4) senile phase – rhizomes with dead part length exceeding 2/3 of the living part length.

In spring of 1985 50 individuals being in the generative phase were dug out and analyzed similarly as the material treated in 1984. This allowed for singling out in each age class in group (2) the individuals being in the virginal and generative phase. Age structure of the population was described on the basis of the proportion of individuals in the developmental phases singled out.

For evaluation of the differences in size structure, developmental phases and rhizome architecture as a function of population density, the test plots were

divided into 2 groups of a density either greater or lower than its mean value (13 and 18 test plots, respectively).

For the estimation of the growth and development rates and of vegetative reproduction under conditions of a dry-site forest phytocoenosis, in 1980 in the vicinity of the test plots 200 *A. nemorosa* seedlings were planted at an equal distance, in a 1 m<sup>2</sup> experimental area previously cleaned from rhizomes and overground parts of forest floor vegetation. All individuals were labelled. Every year in May the living individuals, leaves and generative shoots were counted. In the years 1984–1989, in June each individual was dug out and was analyzed similarly as the rhizomes from the test plots. These observations showed in which year rhizome disintegration began and what part the rhizomes disintegrated in the different age classes. The number of the vegetative diaspores was calculated from the sum of the differences between the number of branches with  $n$  annual-increment segments and the number of branches with  $n + 1$  annual-increment segments, as well as from the proportion of disintegrating rhizomes with a definite number of annual-increment segments (on the grounds of 9-year observations of the individuals planted in the experimental area in 1980).

For the determination of the production of generative diaspores, every year at the beginning of June 100 generative shoots were collected and achenes were counted.

The effectiveness of the generative reproduction was assessed from the proportion of the fruits achenes production level per 1 m<sup>2</sup> to the number of seedlings per 1 m<sup>2</sup> in the next season.

The effectiveness of the vegetative reproduction was evaluated from the proportion of the number of vegetative diaspores (with a definite number of annual-increment segments to the number of disintegration-derived individuals, in the following age classes).

For evaluation of the effect of the parental plants on seedling recruitment, in 1985 the seedling numbers were determined at 31 test plots from which in autumn of 1984 *A. nemorosa* individuals have been dug out, and at 31 vicinal plots set up in forest floor vegetation with an intact structure.

From the series of the quantitative characters, their distributions were obtained and their mean values and standard errors were calculated. The significance of the differences between means was evaluated by analysis of variance, at  $p \leq 0.05$ . Coefficients of Spearman's correlation between characters were calculated.

### 3. RESULTS

#### 3.1. THE DEVELOPMENT AND ARCHITECTURE OF INDIVIDUALS

The development of *Anemone nemorosa* individuals depends on their origin, as there are developmental differences between the individuals derived from rhizome disintegration and those originating from seeds. Vegetative reproduction proceeds

by way of falling away of branches from the rhizome, and of disintegration of the not branched rhizome parts. The development of individuals derived from rhizome disintegration begins, irrespective from which part of the rhizome the fragment has originated, either in the juvenile phase (if the rhizome has 1–3 living annual-increment segments, and the dead part of rhizome is shorter than 1/2 of rhizome), or in the virginal phase (if the rhizome has 1–3 living annual-increment segments and has at least one branch, or if it has 4–11 living annual-increment segments and the dead parts of rhizome are either absent or their length does not exceed 1/2 of rhizome length). The longest and most viable rhizomes being in the virginal phase may as early as in the next season attain the generative phase that lasts from 4 to 14 years of age (Fig. 2). The differences in the mean number of living annual-increments segments between groups of individuals being in different phases were in the major part of cases significant; these differences were insignificant only between the groups of juvenile and senile individuals and the groups of subsenile and virginal individuals.

In all developmental phases the individuals displayed very high variation in length. Individuals in the generative phase exhibited the greatest mean length (12 cm), and those in the subsenile phase – a 8-cm length. Individuals in the senile and virginal phase were characterized by a similar mean length (5 and 6 cm, respectively) (Fig. 3). The differences in the mean length between the major part of phases were significant.

After 4 years of age some rhizomes disintegrated and fragments of rhizomes initiated, in dependence on the number of the annual-increment segments and architecture, the development of new individuals in the juvenile or virginal phase. In the case

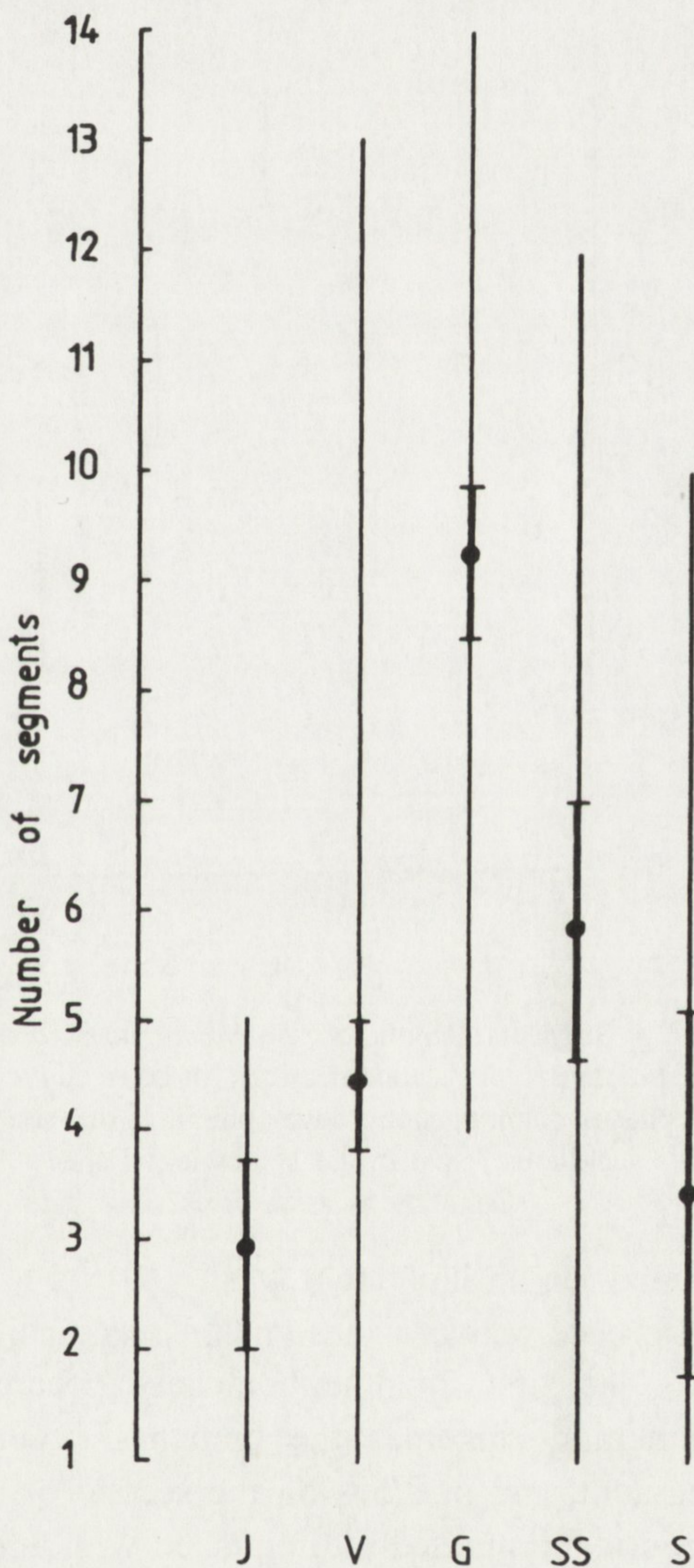


Fig. 2 Mean number of annual-increment segments (with standard error and dispersion range) in *Anemone nemorosa* polycormones being in different developmental phases J – juvenile phase, V – virginal phase, G – generative phase, SS – subsenile phase, S – senile phase

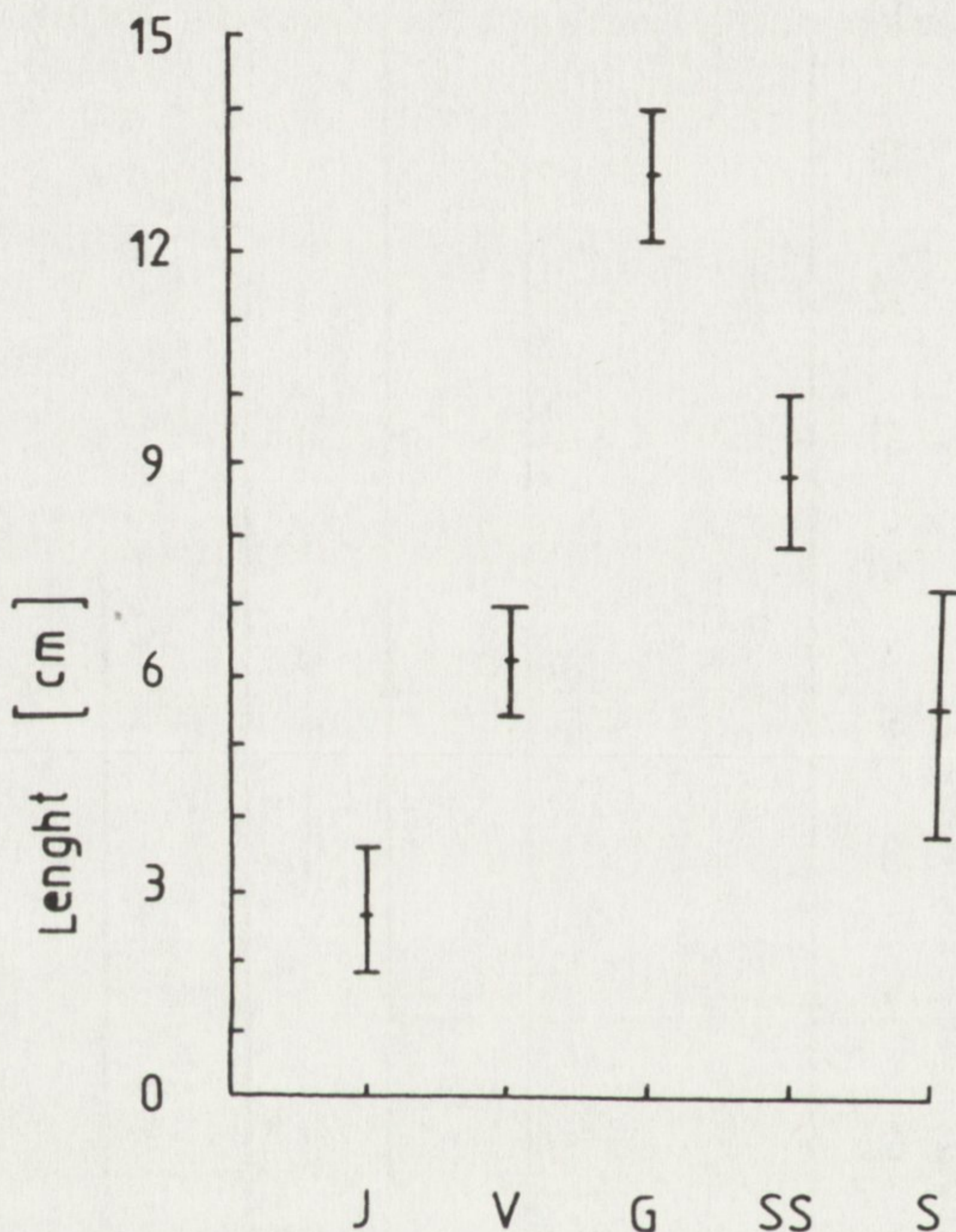


Fig. 3. Mean length of *Anemone nemorosa* rhizomes (with standard error) in consecutive phases of ontogenetic development in dry-site deciduous forest in the Białowieża Forest. Denotations as in Fig. 2

of rhizomes that continued to develop without disintegration, after 5 years of age the oldest rhizome parts began to die away. Some rhizomes having a dead part disintegrated; the anterior part of rhizome initiated the development of an individual in the juvenile or virginal phase, and the posterior one – its development in the subsenile or senile phase, in dependence on the proportion of the living to the dead part length. Individuals in the senile and subsenile phase failed to become rejuvenated; the annual increments of rhizomes were smaller than the dying – caused losses, this leading to death of the individual.

In the disintegration – derived rhizomes the mean annual length increment was 1.4 cm. The magnitude of the annual length increment increased with the individual's age. In the test plots with population density smaller than the mean one; the mean

annual length increment was by 3 mm longer than in the remaining test plots; the difference between these means was insignificant.

The first rhizome branches appeared after 4 years of age. In 1/3 of the branching rhizomes the branches occurred on the youngest annual-increment segment, and in 2/5 – on the second or third segment. The probability of branch occurrence gradually diminished with age of the annual-increment segment. Most often the branch remained on the rhizome for only one year. The percentages of branches that remained on the rhizome for two and three years were 16 and 7%, respectively. The probability of lasting on the rhizome for further years dropped so that among 1623 branches only one remained there for 13 years. Most frequently the rhizome branches fell off. When a 1-year old segment fell off, the probability of its being "recruited" to the population was low and amounted to 34% (i.e. it equalled the proportion, in the population, of 1-year old individuals derived from rhizome disintegration).

Among individuals in the younger age classes, more than a half were represented by not branched rhizomes, but from the fourth year of age there occurred more branched than not branched rhizomes. On the other hand, nearly all 15–20 years old individuals developed rhizome branches. In the test plots with population

density exceeding the mean one, in all age classes the number of rhizome branches was 1.5–3 times higher, as compared with the remaining test plots.

Seed-derived individuals reached in the 2nd year of age the juvenile phase that lasted until the 4th or 5th year of age, when they attained the virginal phase. In the 5th year of age some individuals began to flower. The generative phase lasted until the end of the observation period, i.e. until the 11th year of age (Fig. 4).

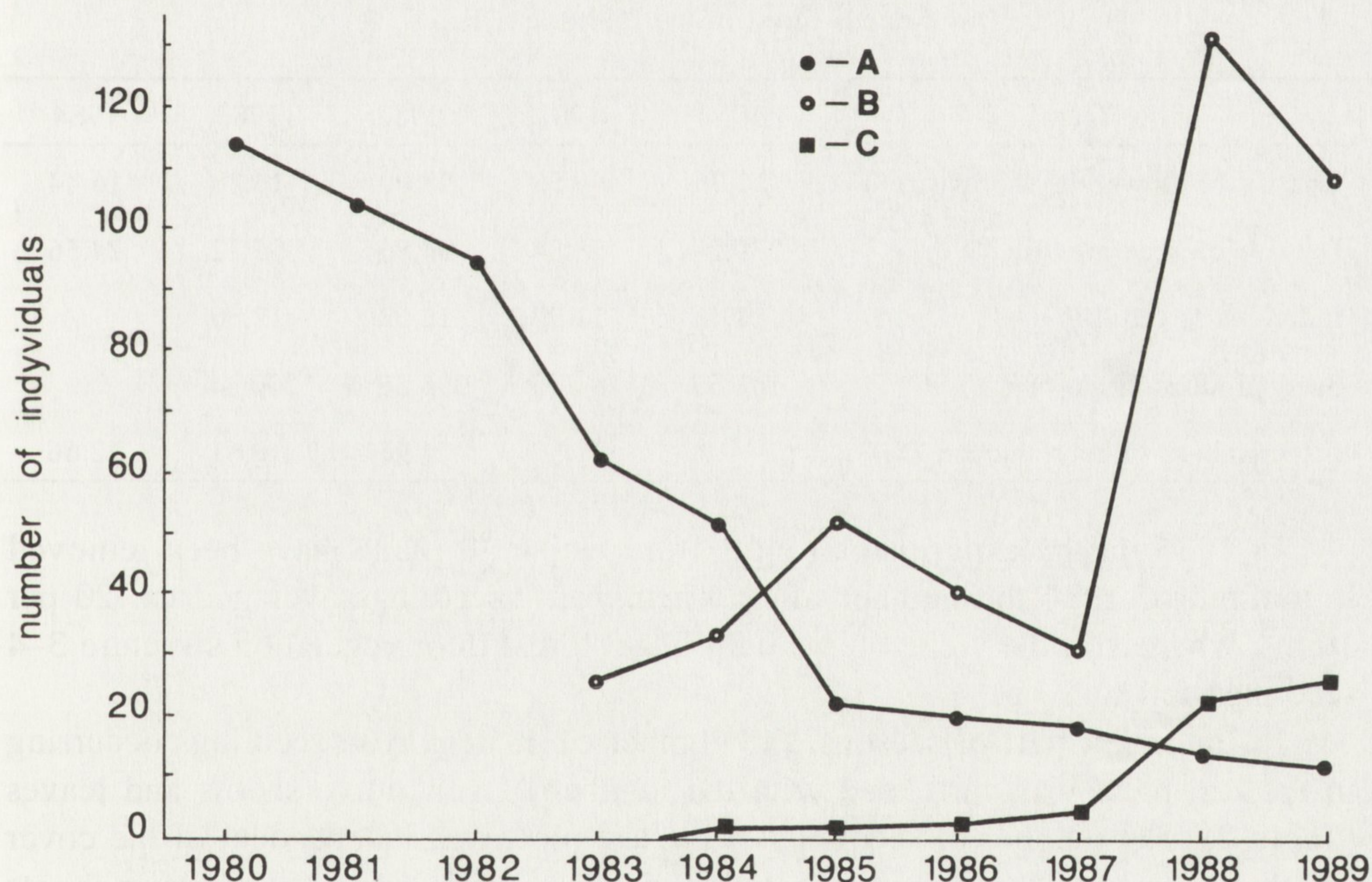


Fig. 4. Dynamics of the numbers of *Anemone nemorosa* individuals in the field experiment. A – individuals that continue growth without disintegration, B – individuals formed as a result of rhizome disintegration, C – individuals in the generative phase

Until the 7th year of age 34% of rhizomes disintegrated, and until the 11th year of age 5% of individuals remained as a whole. Individuals resulting from disintegration were in the juvenile or in the virginal or else in the generative phase. In the seed-derived individuals the annual length increment during the first 3 years of age was 0.1–0.3 cm, and between 4–11 years of age – 4.3 cm (on the average, 1.9 cm).

### 3.2. THE EFFECTIVENESS OF GENERATIVE AND VEGETATIVE REPRODUCTION

Individuals derived from seeds and from rhizome disintegration were recruited to the *A. nemorosa* population. Every year 3–22% of all overground elements of the population undertook generative reproduction. Also every year

their density changed – from ca. 11 to 66 shoots per  $m^2$  (Table 1). "Individual" fertility (number of fruits per 1 flowering shoot) changed only slightly from year to year, and amounted to ca. 12 achenes per 1 shoot. The production of generative diaspores remained within the range of 142–785 per  $1 m^2$ . The effectiveness of generative reproduction fluctuated between 5–42% (Table 1).

Table 1. The effectiveness of generative reproduction in *A. nemorosa* population in dry-site deciduous forest in the Białowieża Forest

Year	1980	1981	1982	1983	1984
Density of flowering shoots ( $m^{-2}$ )	11.36	65.56	28.00	16.28	16.44
Density of seedlings ( $m^{-2}$ )	239.2	58.84	38.86	35.72	24.56
Individual's fertility	12.46	11.97	12.02	12.30	
Seed production ( $m^{-2}$ )	141.55	784.75	336.56	200.24	
Effectiveness of reproduction (%)	–	41.57	4.95	10.61	12.66

In 1985, in the experimental plots from which all plants have been removed in autumn of 1984 the number of *A. nemorosa* seedlings averaged ca. 20 per  $10 m^2$ , whereas in the vicinal plots with intact forest floor vegetation structure 3–4 seedlings fell to  $10 m^2$ .

In the major part of seasons, the number of *A. nemorosa* seedlings occurring in the test plots was correlated with the number of generative shoots and leaves (Table 2). The number of seedlings in the test plots was independent of the cover of other species of forest floor vegetation, whereas the number of flowering shoots

Table 2. Values of coefficients of Spearman correlation between selected characters of *Anemone nemorosa* population at 31 test plots ( $0.25 m^2$  each) in consecutive vegetation seasons

Characters	1980	1981	1982	1983	1984
Number of seedlings vs. number of flowering shoots	0.5569*	0.3310	0.4111*	0.2839	0.4413*
Cover of forest floor vegetation layer vs. number of seedlings	0.3653	0.3550	0.1629	0.3316	0.5561*
Number of shoots flowering in the previous season vs. number of seedlings			0.4130*	0.5401*	0.3801*
Cover of forest floor vegetation layer vs. number of flowering shoots	0.3651	0.7289*	0.3694	0.4461*	0.6415*

\* significant correlation.



was correlated negatively with the cover of these species (Table 2). The number of seedlings was the greater, the higher the number of the generative shoots in the previous season. Seedling density was greatest in the year in which the densities of the generative shoots and leaves were lowest.

Among the seedlings that occurred in spring of 1984, ca. 3% survived until autumn (Table 3). The survival of seedlings and attainment of the consecutive developmental phases did not depend on the density of the seedling cohort (Table 3). Individuals that originated from seedlings accounted for 1.58% of the population, whereas the remaining individuals were derived from vegetative diaspores.

Among 310 undamaged rhizomes per 1 m<sup>2</sup>, every year ca. 74 rhizomes disintegrated on the not branched fragments, this giving 148 diaspores capable of developing into new individuals (Table 4).

The investigated *A. nemorosa* population contained 101 damaged rhizomes per 1 m<sup>2</sup>. Among 323 vegetative diaspores, 101 formed new individuals; thus, the effectiveness of the vegetative reproduction was 31.27%. At the test plots with

Table 3. The survival of *Anemone nemorosa* individuals that developed from seedlings until autumn of 1984 in dry-site deciduous forest in the Białowieża Forest

Year	Seedling density × 10 m <sup>-2</sup>	Density of individuals derived the cohort in 1984 × 10 m <sup>-2</sup>	Survival (%)
1980	2392.0	4.0	0.17
1981	584.4	5.3	0.91
1982	388.6	5.3	1.36
1983	357.2	9.3	2.60
1984	245.6	6.7	2.73

Table 4. Production of vegetative diaspores on rhizome branches per 1 m<sup>2</sup> in *Anemone nemorosa* population in dry-site deciduous forest in the Białowieża Forest

Age of branches (years)	Number of branches	% of branches surviving until next year	Number of branches falling off from rhizomes
1	174.88	16.09	146.74
2	28.14	46.19	15.14
3	13.00	53.84	6.00
4	7.00	55.10	3.14
5	3.86	59.25	1.57
6	2.29	50.00	1.14
7	1.14	25.00	0.86
Σ *	230.31	*	174.59

*A. nemorosa* population density smaller than the mean one, the effectiveness of the vegetative reproduction was by 8% higher, as compared with the test plots with a density exceeding the mean one.

### 3.3. AGE STRUCTURE

Among *A. nemorosa* individuals, the proportion of rhizomes of the virginal phase was highest (Fig. 5). Individuals being in the juvenile and generative phase occurred in similar proportions. The participation of the senile and subsenile individuals was lowest (Fig. 5).

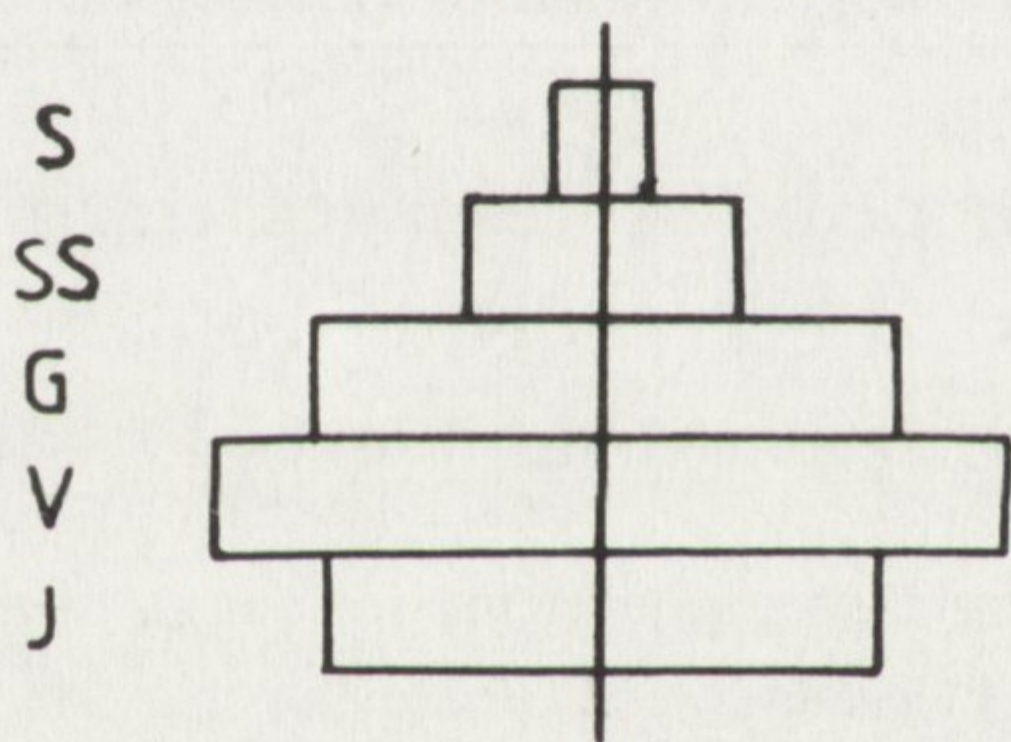


Fig. 5. Age structure of polycormones in the *Anemone nemorosa* population in dry-site deciduous forest in the Białowieża Forest  
Denotations as in Fig. 2

Test plots of an *A. nemorosa* population density either greater or lower than its mean value did not differ significantly in the mean age structure.

In 1980 in the *A. nemorosa* population the participation of seedlings was highest. Generative shoots accounted for 4% of the *A. nemorosa* overground units (Fig. 6). In the consecutive vegetation seasons the proportions of the overground shoots and leaves changed (Fig. 6). In the years 1981–1984 the percentage of seedlings fluctuated between 13–19%, that of leaves – between 59–79%, and that of the generative shoots – between 8–22%.

### 3.4. SIZE STRUCTURE

In the *A. nemorosa* population the mean rhizome length was 6.7 cm. The length of the best developed rhizome, together with branches, was 58.5 cm. In the population, the proportion of 2–4 cm long rhizomes was highest; they accounted for 1/4 of all rhizomes. Rhizomes longer than 8 cm represented 1/3 of the population (Fig. 7).

The sum of rhizome length per 1 m<sup>2</sup> remained within the range of 4.5–78.5 m. It averaged ca. 26 m per 1 m<sup>2</sup>. Most frequently the rhizome length per 1 m<sup>2</sup> amounted to 20–30 m.

One third of the rhizomes (29%) was damaged. Among the undamaged rhizomes, one half was branched. The major part of the branched rhizomes (65%) had one branch. The best developed rhizome had 11 branches. The predominant part of rhizomes formed only branches of the I order; 16% of individuals produced branches of the II and III order.

Among the branched rhizomes, those of a 4–6 cm length were most frequent. Rhizomes longer than 16 cm accounted for 11% of their total number.

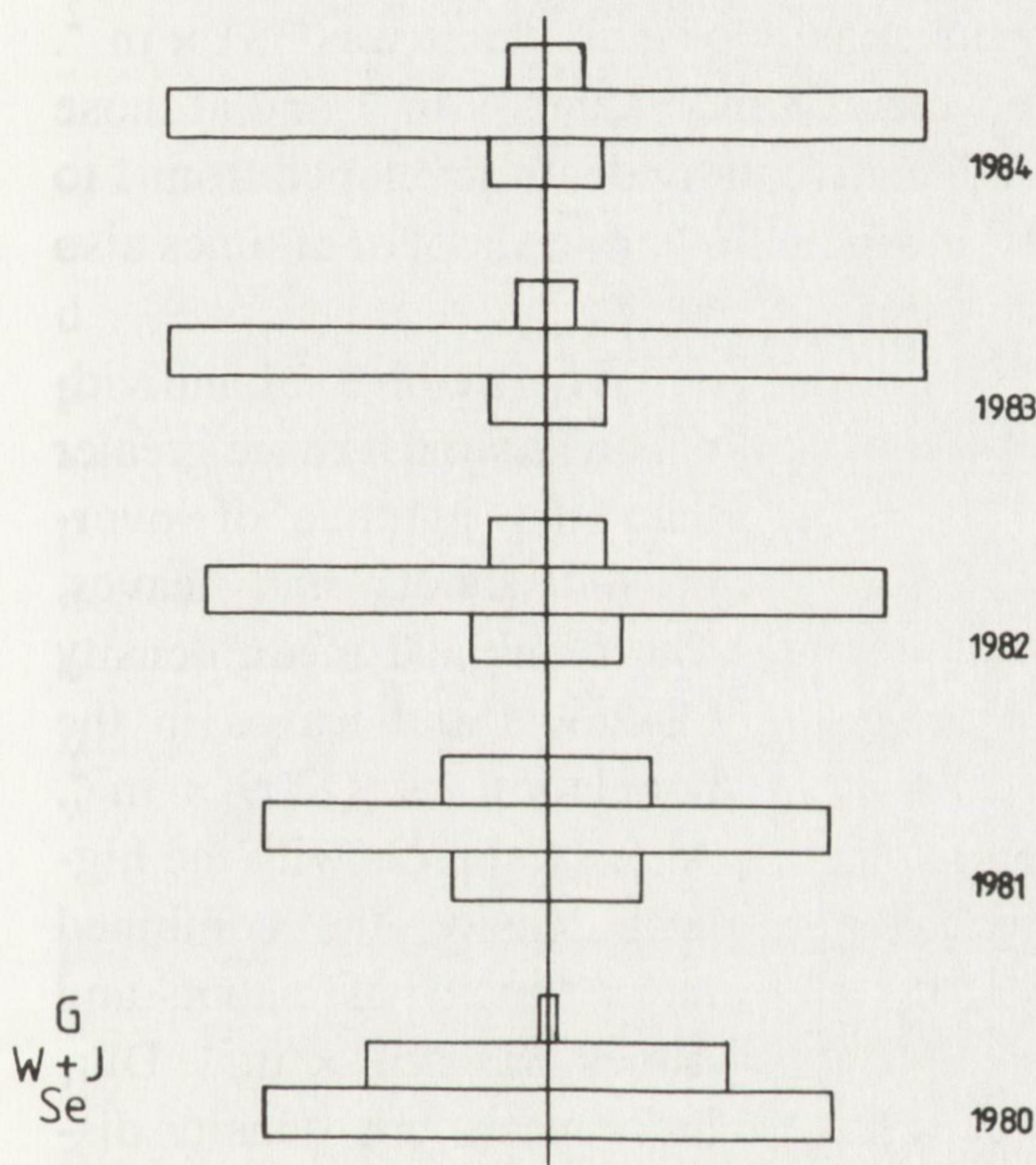


Fig. 6. Developmental phases structure of overground morphological elements of *Anemone nemorosa* in dry-site deciduous forest in the Białowieża Forest. G – generative shoots, W + J – leaves, Se – seedlings

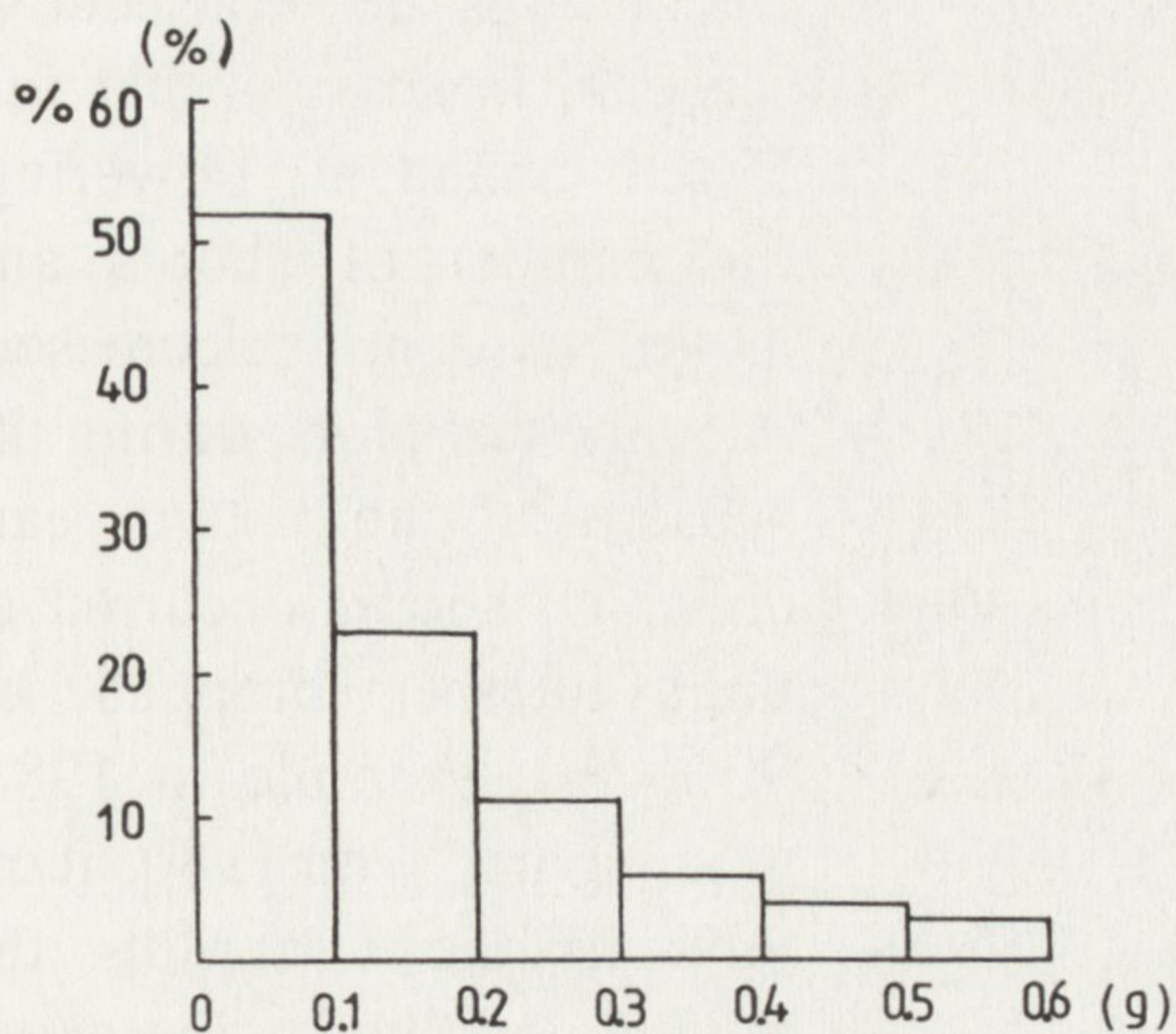


Fig. 8. Distribution of dry weight of *Anemone nemorosa* rhizome in dry-site deciduous forest in the Białowieża Forest

being up to 0.1 g (Fig. 8). Mean dry weight of an *A. nemorosa* individual at different test plots ( $0.25 \text{ m}^2$ ) was the greater, the higher the density of shoots and leaves.

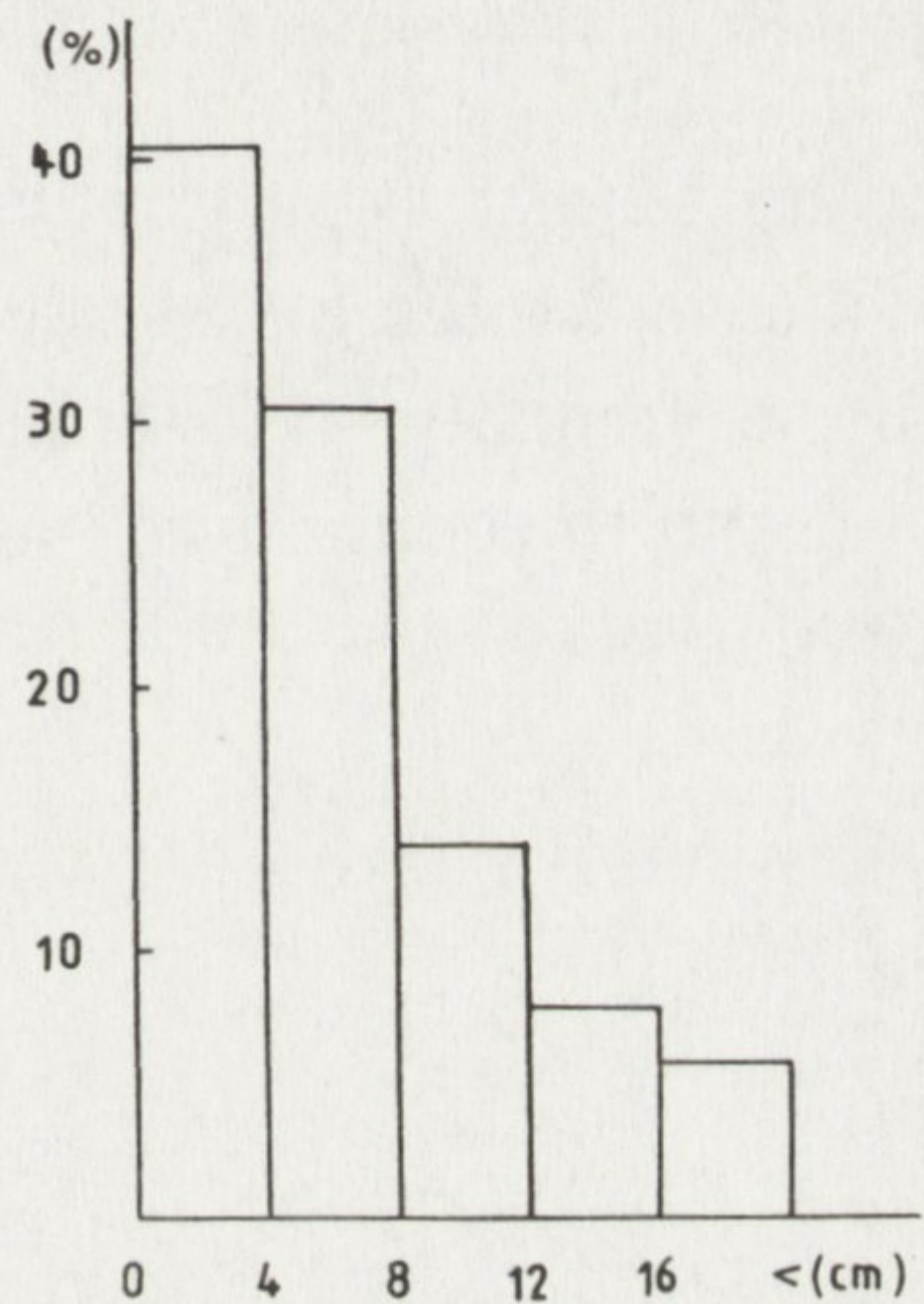


Fig. 7. Distribution of *Anemone nemorosa* rhizome length in dry-site deciduous forest in the Białowieża Forest

Not branched rhizomes were much shorter than the branched ones. More than a half of the not branched rhizomes did exceed the length of 4 cm. One rhizome out of 100 not branched rhizomes was longer than 16 cm.

The mean rhizome length was closely similar at both – the test plots with mean population density exceeding or being smaller than the mean one. On the other hand, there was a difference in the proportion of the branched rhizomes; namely, in the test plots with population density exceeding the mean one there grew more (by 14%) branched rhizomes than in the other test plots.

In the *A. nemorosa* population the individual dry weight was very differentiated and fluctuated between 0.006–0.912 g. Mean dry weight was 0.140 g. In the population somewhat more than a half of the individuals displayed dry weight

## 3.5. DENSITY

In the *A. nemorosa* population the mean density of individuals was  $381 \times \text{m}^{-2}$ . At the sites with the lowest density there were  $108 \text{ individuals} \times \text{m}^{-2}$ , and at those with highest density –  $1020 \text{ indiv.} \times \text{m}^{-2}$ . Vegetative individuals developed from 1 to 6 leaves, and the generative ones – usually a single flowering shoot or at times also 1–4 leaves.

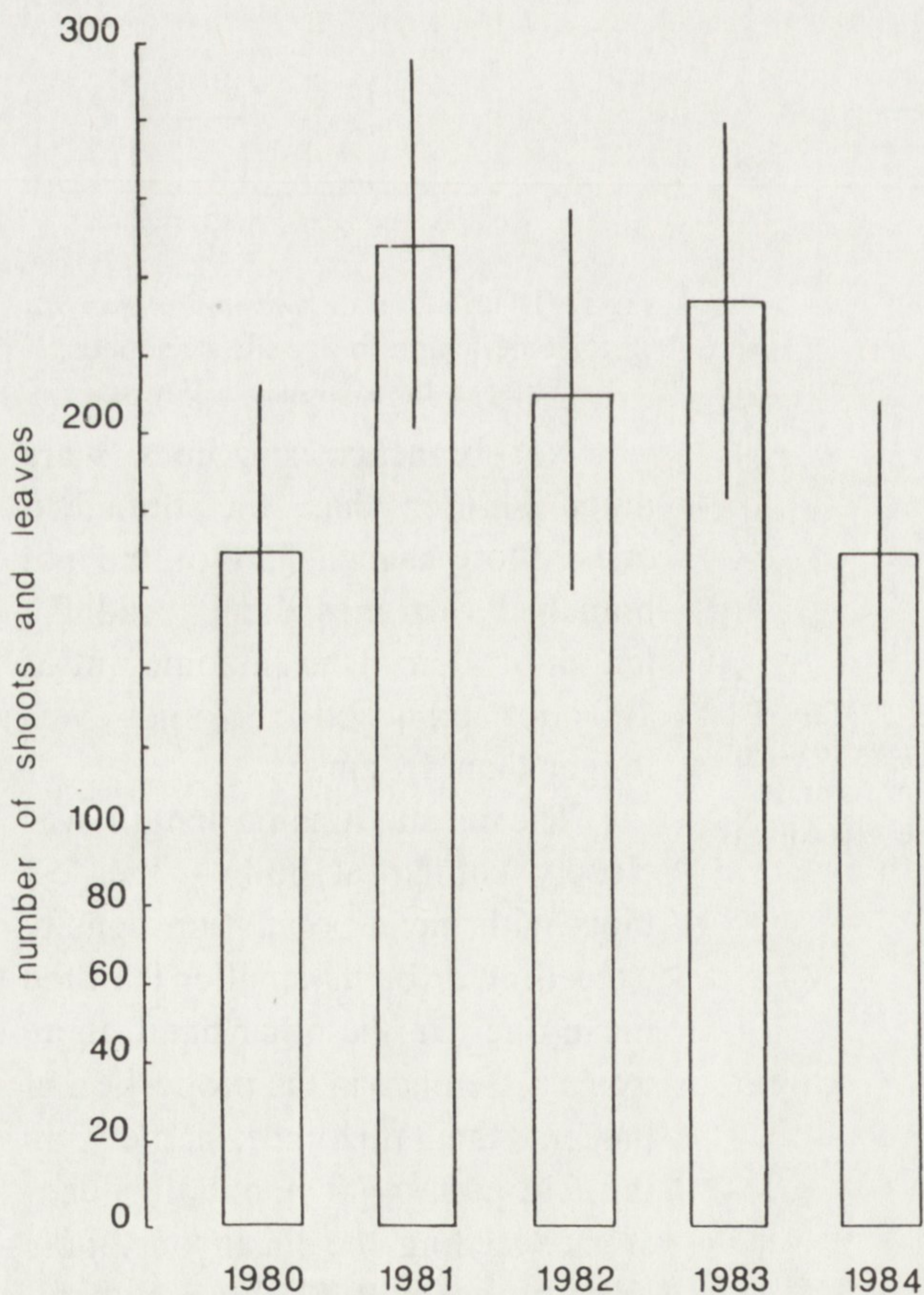


Fig. 9. Density (with confidence intervals) of *Anemone nemorosa* overground elements in dry-site deciduous forest in the Białowieża Forest

The number of individuals was almost twice greater than the number of overground shoots and leaves. The combined mean density of shoots and leaves in the population was  $209 \times \text{m}^{-2}$ . At the test plots with the highest density, the combined mean density of shoots and leaves was  $552 \times \text{m}^{-2}$ . During 5 years this density displayed only small changes and fluctuated from  $170 \times \text{m}^{-2}$  to  $250 \times \text{m}^{-2}$  (Fig. 9).

The number of shoots and leaves at the different test plots exhibited very great fluctuations in consecutive seasons. In seasons that followed abundant flowering, the number of shoots and leaves evidently decreased. At some test plots, during the subsequent one or two years either no shoots occurred or their number dropped by 90%. For example in 1981, as compared with 1980, at ca. 70% of the test plots the number of shoots increased and at the other test plots it dropped; in 1982 at 30% of the test plots the number of shoots rose, and at the other ones it decreased. In other seasons the number of test plots with a reduced number of shoots and that of test plots with an increased number of shoots were similar.

#### 4. DISCUSSION

The differentiation of plant density in the population areage creates differences in the developmental conditions and longevity of individuals. According to many authors, the greater the individual areage, the better the development of individuals; in the case of annual plants, these circumstances also promote complicated architecture and enhance the fertility (Wilkoń-Michalska 1976, Symonides 1974, Falencka 1983). As far as perennial herbaceous plants are concerned, the size of individual areage influences, likewise, their architecture. Namely, the greater the areage, the more overground shoots are produced by an individual; this improves its biomass increment, as well as its reproductive capability and competitiveness, as compared with one-shoot individuals (Falińska 1985, 1990).

The density of leaves and generative shoots in the *Anemone nemorosa* population examined in the present studies is very similar to that found for a Tilio-Carpinetum patch in the Białowieża National Park (Pirożnikow 1991). In Southern Poland, population density of *A. nemorosa* in Tilio-Carpinetum patches is 2–6 times higher (Tumidajowicz 1975, 1977).

*A. nemorosa* individuals form definitely more rhizome branches in the population areage regions where the population density exceeds the mean one. The intensity of intraspecies competition modifies only the architecture of individuals and reproduction, whereas it causes no differences in rhizome length and dry weight of individual. In the population examined, similarly as in forest populations of *A. nemorosa* described by other authors, a half of individuals has branched rhizomes, and the other half – not branched ones, whereas in meadows vicinal to forests the proportion of branched rhizomes is much higher (Tumidajowicz 1975, Schirreff and Bell 1984, Faliński and Canullo 1985). As the present state of knowledge, there are no grounds to explain this regularity.

In the examined *A. nemorosa* population the mean length of rhizome is by 2–5 cm smaller, as compared with another dry-site deciduous forest patch in the Białowieża Forest (Faliński and Canullo 1985), and with dry-site deciduous forests in Southern Poland (Tumidajowicz 1975) or England (Schirreff and Bell 1984). This may be due to very frequent feeding of wild boars in the examined patches and to the duration of the vegetation season of *A. nemorosa*; this is testified to by the 1.5–2.5 times smaller length of the annual-increment segments, as compared with other regions (Tumidajowicz 1975, Schirreff and Bell 1984). Probably both above factors are responsible for the fact that the mean rhizome biomass is smaller in the examined *A. nemorosa* population than in other populations of this species (Tumidajowicz 1975, Faliński and Canullo 1985). The present findings confirm the occurrence of a negative

correlation between the biomass of individuals and population density, as reported for *A. nemorosa* by Aulak (1976).

In the investigated dry-site forest patch there occur, apart from *A. nemorosa*, early-spring geophytes: *Corydalis solida* and *Ixopyrum thalictroides*. Both of them are, however, subdominants and cannot be regarded as competitors of *A. nemorosa*. Other perennials that are components of forest floor vegetation attain a vegetation maximum only in June (Falińska 1973) and thus cannot compete with *A. nemorosa*.

At sites with *A. nemorosa* population density exceeding the mean one, the proportion of flowering shoots is higher, inversely as in the major part of other perennials studied (Falińska 1990, Zaugulnova et al. 1988). At sites of more abundant development of the *A. nemorosa* population there are more seedlings than at other sites; this suggests that under conditions of stabilized ecosystems the *A. nemorosa* population density does not exceed the optimal one. This is confirmed by an absence of any greater differences in the individual development rate between sites with a higher or lower population density. A similar relationship between *A. nemorosa* shoot and leaf density, on the one hand, and seedling recruitment has been found in Central Italy by Canullo (1988) and by Symonides (1979) in the *Corynephorus canescens* population. Usually seed semination is concentrated round the parental plants (Harper 1977). Despite the abundance of seeds and the highest density of the seed bank in the vicinity of the generative individuals, in most perennials studied seedling recruitment is lower near these individuals than at a certain distance from them (Harper 1977). According to many authors, the individual's success in the sense of taking roots by the seedling and its further development may be promoted by local perturbances (Harper 1977, Grime 1979). In the case of *A. nemorosa*, feeding of wild boars may create favourable conditions for seedling development. In studies of a dry-site deciduous forest in the Białowieża National Park, Faliński has shown that during 7 years on a 7.2-ha area the major part of sites underwent 2–7 times perturbances caused by wild boars (Faliński 1986). According to this author, feeding of wild boards in dry-site deciduous forests may be the decisive factor that influences the structure and dynamics of geophyte populations.

The very slight effectiveness of generative reproduction is characteristic of many perennial plants, particularly in stabilized ecosystems (Zarzycki 1968, Tumidajowicz 1977, Pirożnikow 1983, Falińska 1990). In the examined *A. nemorosa* population the effectiveness of the generative reproduction is fairly high (5–42%), whereas in dry-site deciduous forests in Southern Poland it amounts at most to 2% (Tumidajowicz 1977). Nevertheless, generative reproduction plays a minimal role in the rejuvenation of the population, because the major part of seedlings "lose" in the competition with vegetative diaspores. In perennial plants of the polycormonal type of growth the annual recruitment, to the

population, of several or 10–20 individuals that have developed from seedlings is sufficient for maintaining genetic diversity (Eriksson 1989).

In the reproduction of *A. nemorosa*, similarly as of very many plants adapted to intensive competition, vegetative reproduction plays a much more significant role than the generative one. *A. nemorosa* reproduces vegetatively in two ways: (1) by falling away of the youngest branches of rhizomes, (2) by disintegration of the longer fragments of rhizomes. In the case of reproduction of type (1), the progeny individuals start from the juvenile phase, with a biomass exceeding that of a 3 years old juvenile individual derived from a seedling. In reproduction of type (2) no deep rejuvenation occurs, and the individual starts from the virginal or generative phase, but without the "ballast" of the dying-away rhizome ending. As the annual length increments of rhizome are relatively small (most often – up to 3.5 cm), this type of reproduction does not allow for occupying a new areage distant from the parental individual. However, in deciduous forests the high frequency of feeding of wild boars (Faliński 1986) causes translocation of the rhizomes in space. Probably this factor is decisive of the considerable variation in the density of the overground shoots from season to season in some particular test plots, whereas the mean population density fails to change drastically.

In the major part of the *A. nemorosa* populations studied by other authors, the density of leaves and generative shoots has been reported to exceed 1.2–1.5 times that of rhizomes (Canullo 1985, Tumidajowicz 1975). According to the present results, in 1984 every second rhizome, on the average, developed a leaf or a generative shoot. Zaugulnova et al. (1988) have shown that the fluctuations in the density of *A. nemorosa* leaves and vegetative shoots in the consecutive vegetation seasons were related to activation of the rejuvenating buds on rhizomes, and not to mortality of the whole individuals. In my opinion, *A. nemorosa* rhizomes that during feeding of wild boars have been dug underground to a depth exceeding 5–10 cm do not activate their buds, and do so only after translocation of rhizomes closer to soil surface. Under adverse growth conditions, many perennial plants have been found to stop temporarily the formation of overground shoots and leaves (Rabotnov 1985). In such plants the number of the annual-increment segment fails to be an exact measure of the individual's calendar age (Zaugulnova et al. 1988, Falińska 1990).

The effectiveness of *A. nemorosa* vegetative reproduction, estimated at 30–40% (in dependence on population density), is similar to that of other species of perennials that reproduce by way of rhizome disintegration, e.g. species of the genus *Carex* (Noble et al. 1979) or *Potentilla anserina* (Eriksson 1986). The fact that the effectiveness of the vegetative reproduction is by 8% higher at sites with lower population density, as observed in the present studies, has been recorded by many authors (cit. Falińska 1990).

## 5. SUMMARY

Objectives of the present studies were: (1) to examine the ontogenetic development of *Anemone nemorosa* individuals derived from seeds and from rhizome disintegration; (2) to determine the effectiveness of the generative and vegetative reproduction; (3) to describe the population structure; (4) to determine the degree of differentiation of population structure and reproduction effectiveness as a function of population density.

Observations and field experiments were performed in a dry-site deciduous forest patch in the Roadside Reserve in the Białowieża Forest, in the years 1980–1989. The development rate of individuals depends on their origin; namely, the individuals derived from rhizome disintegration start from the juvenile or virginal phase, in dependence on the number of living annual-increment segments. The generative phase lasts from 4 to 14 years of age, but individuals being in this phase do not every year form flowering shoots. Each year between 5–42% of seeds are transformed into seedlings. In the year in which the number of flowering individuals was smallest, seedling density was highest. The effectiveness of the generative reproduction of the examined *A. nemorosa* population is very high, as compared with other populations of this species, but the proportion of individuals of generative origin in the population is very low.

Rhizome disintegration may occur after 4 years of age. The probability of disintegration rises with the individual's age. Not all rhizome fragments initiate the development of new individuals; the effectiveness of the vegetative reproduction is estimated at 31%. Intensive feeding of wild boars, that causes breaking or translocation or else loss of rhizomes from the population is the most important factor regulating population dynamics and structure.

In the *A. nemorosa* population examined, mean density of individuals amounts to  $381 \times m^{-2}$ , and at the sites with the highest density – to  $1020 \times m^{-2}$ . Population density modifies the architecture of individuals (its rise leads to an increase in the number of branches), whereas it does not influence the development rate of individuals, age structure and size of the population.

## 6. POLISH SUMMARY

Celem niniejszej pracy było (1) zbadanie rozwoju ontogenetycznego osobników *Anemone nemorosa* pochodzących z nasion oraz z rozpadu kłączy, (2) określenie efektywności reprodukcji generatywnej i wegetatywnej, (3) opis struktury populacji, (4) określenie stopnia zróżnicowania struktury populacji oraz efektywności reprodukcji w zależności od zagęszczenia.

Obserwacje i eksperymenty terenowe prowadzono w latach 1980–1989 w płacie grądu w Rezerwacie Przyszosowym. Tempo rozwoju osobników zależy od pochodzenia: osobniki pochodzące z rozpadu kłączy startują od fazy juvenilnej lub wirginilnej w zależności od liczby żywych członów przyrostu rocznego. Faza generatywna trwa od 4 do 14 roku życia, ale osobniki w tej fazie rozwoju nie wykształcają co roku pędów kwiatowych. Każdego roku od 5 do 42% nasion przekształca się w siewki. Największe zagęszczenie siewek zaobserwowano w roku, w którym zakwitło najmniej osobników. W porównaniu do innych populacji tego gatunku, efektywność reprodukcji generatywnej jest bardzo wysoka, lecz osobniki pochodzenia generatywnego mają bardzo niewielki udział w populacji.

Rozpad kłączy może nastąpić po zakończeniu czwartego roku życia. Prawdopodobieństwo rozpadu wzrasta z wiekiem osobnika. Nie wszystkie fragmenty kłączy inicjują rozwój nowych osobników: efektywność reprodukcji wegetatywnej w badanej populacji oszacowano na 31%. Najważniejszym czynnikiem regulującym dynamikę i strukturę populacji badanego gatunku jest intensywne żerowanie dzików, które powoduje pękanie i przemieszczanie kłączy oraz ubywanie ich z populacji.

W badanej populacji średnie zagęszczenie osobników *A. nemorosa* wynosi  $381 \times m^{-2}$ , w miejscach o największym zagęszczeniu znaleziono  $1020$  osobników  $\times m^{-2}$ . Zagęszczenie



modyfikuje architekturę osobników (wzrost jej wpływa na zwiększenie liczby rozgałęzień), nie wpływa natomiast na tempo rozwoju osobników, strukturę wieku i wielkość populacji.

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