THE INFLUENCE OF SHOOT HARVESTING ON THE SIZE AND FECUNDITY OF *CONVALLARIA MAJALIS* L.

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ABSTRACT

The paper presents results concerning the size and fecundity of *Convallaria majalis* L. in populations both disturbed and undisturbed by shoot cutting. The subject of the investigations were coenopopulations of *Betulo-Quercetum*, *Fago-Quercetum*, *Melico-Fagetum*, *Stellario-Carpinetum* and *Tilio-Carpinetum*, in which, over a period of four consecutive years, *C. majalis* shoots were cut once a year.

In the undisturbed population the vegetative shoot is 22.2 ± 4.8 cm high, weighs 0.23 ± 0.16 g d.w., and most often has two leaves. The leaf lamina was 12.0 ± 2.5 cm long and 3.3 ± 1.1 cm wide. The largest shoots occur in the population in *Betulo-Quercetum*, and the smallest in the population in *Melico-Fagetum*.

The generative shoot is higher and has larger leaves than the vegetative shoot. The inflorescence most often consists of six flowers and is 21.3 ± 3.9 cm high and weighs 0.08 ± 0.03 g d.w. In the population in *Betulo-Quercetum* the inflorescence is the highest and has the greatest number of flowers.

Multiple raw material collection leads to the decrease of *C. majalis* shoot sizes. In the second year of the experiment the shoots were three times lighter.

Collection of raw material leads to a decrease in lily of the valley fecundity. After the second cut generative reproduction was halted and the influx of genets to the population was almost entirely eliminated.

KEY WORDS: *Convallaria majalis* L., medicinal plant, shoot size, fecundity, disturbances.

INTRODUCTION

A considerable part of Polish flora consists of commercial species, among which medicinal plants play an important role. Some of them are cultivated, while others are still obtained from natural habitats, e.g. *Frangula alnus*, *Convallaria majalis*, *Helichrysum arenarium* and *Asarum europaeum*. The collection of medicinal plants entails either cutting or digging them up; individuals are eliminated from the population or damaged by cutting of their leaves, shoots or flowers (Rumińska 1981). The population resources of these plants in Poland are controlled by administrative measures, the collection limits are estimated, moreover the biological and ecological effects of their collection on the exploited populations are usually unknown. Focusing only on the magnitude of collection may soon lead to an excessive overexploitation of medicinal plant resources in Poland and the impoverishment of the gene pool of some indigenous flora (Gawłowska 1984; Ławrynowicz and Olaczek 1988).

Convallaria majalis L. is a medicinal plant. In Poland it has for a long time been obtained from natural localities. The raw material used by the pharmaceutical industry consist of leaves and inflorescences which contain cardenolide

glycosides (Paris 1963), used for the treatment of cardiac insufficiency (Ożarowski 1983).

Obtaining *C. majalis* shoots as a raw material for the pharmaceutical industry is carried out on cultivation plots (plantations) and in natural populations by cutting the aboveground organs of this plant while it is in bloom. In neither instance is the raw material collected selectively; all the leaves and the inflorescence are removed from a fixed area (Grochowski 1976). In effect, cutting is the amputation of living parts of the organism, and it usually weakens its health and immunity against pathogens and competition pressure. *C. majalis* is not intensively grazed by large herbivores, as is the case with other plants in the groundcover of the forest ecosystems (Tolvanen et al. 1994). It may be inferred then, that the multiple amputation of shoots during the life of the plant, which has not been evolutionally adapted to being grazed by animals, has a negative impact and results in certain disturbances in demography, dynamics and population structure.

The aim of the research was to determine the type and direction of changes in the size of *Convallaria majalis* shoots and fecundity under conditions of long-term, simulated raw material collection for the pharmaceutical industry.

MATERIAL AND METHODS

The basic structural element of the *C. majalis* individual consists of the underground part (a rooted rhizome) and the aboveground one (leaves and inflorescence), further referred to as shoot. As such, the structural unit of an individual is the module (Harper 1977), i.e. a repeatable element in architecture of the individual.

The area of the coenopopulation is within the borders of the phytocoenosis (Rabotnov 1985). The name of the coenopopulation describes the plant community e.g. coenopopulation *C. majalis* in *Betulo-Quercetum roboris* (in short: coenopopulation in B-Q). All coenopopulations in the study area compose a regional population.

The field experiments were carried out from 1992 to 1997 in five coenopopulations of *C. majalis* located in northern Poland. Forest communities with numerous *C. majalis* coenopopulations were chosen for the investigations: *Betulo-Quercetum roboris* R. Tx. 1937, *Fago-Quercetum petraeae* R. Tx. 1955, *Melico-Fagetum* Lohm. ap. Seibert 1954, *Stellario-Carpinetum* Oberd. 1957 and *Tilio-Carpinetum* Tracz. 1962.

Forty plots with a total area of 400 m² were investigated. In the first year at every plant community four permanently marked experimental plots were set. Each of them was 16 m² (4 × 4 m), divided into 1 m squares, and was the basic plot. Additionally, four control plots (each 4 m²), located in the same aggregation of *C. majalis* as the experimental plot, were set in each plant community. Testing the size of the plot was carried out using the Greig-Smith grid scheme (1952) and the method introduced by Kwiatkowska and Symonides (1978).

The experimental plots were used to investigate the size and shape of shoots, as well as the results of cutting the shoots. Cutting the shoots of *C. majalis* was a simulation of collecting raw material for the pharmaceutical industry. The shoots were cut once a year while the plants were in bloom over a period of four consecutive years in all of the experimental plots. Each shoot was cut at ground surface. The aim of morphometric investigations was to determine the reaction of the plant to a diversity of phytocoenotic-biotope conditions in areas of the particular coenopopulations, and to determine the reactions to disturbances caused by the annual cutting of shoots. The samples were collected from the experimental and control plots when the lily of the valley was blooming. A total of about 2,700 shoots were collected. After desiccation, the length, width and area of the leaf lamina were measured, along with the height of the shoot and the inflorescence and its weight. Leaf width was determined to within 1 mm, leaf length, shoot and inflorescence height were measured to within 0.5 cm, and dry weight (d. w.) to within 0.01 g. The shoot habitus was determined based on the number of leaves. The reaction of the plants to cutting of the aboveground organs was determined on the basis of biometric measurements of 3,600 shoots. Fecundity was determined on the basis of 750 generative shoots from disturbed and undisturbed populations. The number of flowers and fruits per shoot and seeds in ripe fruits were recorded.

Statistical processing entailed computation the arithmetic mean ($\bar{X}$), standard deviation (S.D.), median (Me), modal (Mo), and the variability coefficient according to the following formula: $CV = S.D. \cdot \bar{X}^{-1}$.

For each feature a histogram was determined with the distribution function of the normal distribution, and normal distribution asymmetry analysis was done, taking into consideration skewness (Sk) and kurtosis (Kr). The compliance of the empiric feature distribution with the normal distribution was verified using the χ^2 test (Okta 1980; Łomnicki 1995).

The significance of the differences between the features was done using the variance analysis method (ANOVA) and additionally with the t-Student test (Okta 1980). The hypothesis regarding the significance of differences between the arithmetic means and the significance of correlations and regressions were tested using the variance analysis method and the F coefficient. The statistical considerations were done at an error risk level of $\alpha = 0.05$ (Okta 1980).

RESULTS

Size and fecundity in the undisturbed population

In the regional population, regarded as the comparative, the vegetative shoot is 22.2 ± 4.8 cm high, weighs 0.23 ± 0.16 g d.w. and usually has two leaves (1.7 ± 0.5). The leaf lamina is 12.0 ± 2.5 cm long and 3.3 ± 1.1 cm wide. The variability of shoots, expressed through the dry mass weight, is high in the population ($CV = 0.69$; Table 1), which probably results from the high morphologic plasticity of *C. majalis* and the diversity of phytocoenotic-biotope conditions, especially edaphic ones (Kosiński 1996).

All the features which determine the size of the shoot, i.e. height and weight, as well as, width and length of the leaf lamina, show a positive correlation, with the highest values of the correlation between the leaf area and its width ($r = 0.96$). The leaf area is positively dependent on the shoot mass ($r = 0.88$) and leaf length ($r = 0.89$).

The generative shoot is 28.3 ± 4.9 cm high, weighs 0.47 ± 0.17 g d.w., and it almost always has two leaves (2.0 ± 0.2) which are 13.5 ± 2.5 cm long and 3.7 ± 0.9 cm wide. The inflorescence most often consists of six flowers (6.4 ± 1.3), is 21.3 ± 3.9 cm high, and weighs 0.08 ± 0.03 g d.w. (Table 2). The inflorescence is the least variable part of the plant, e.g. the variability coefficient of the number of flowers is only $CV = 0.20$. The generative shoot is higher ($p < 0.001$) and it has larger leaves ($p < 0.001$) in comparison with the vegetative shoot. Furthermore, it is characterized by greater stability (Table 2) which confirms the thesis that generative features are more stable than somatic features.

The fecundity of an individual with an iterative scheme of architecture depends on the number of generative shoots, among other factors. In the regional population, fruit is produced by every third flower (35.6%), thus there are only a few fruits in infructescence (2.1 ± 1.1 ; Table 3). The stability of this feature is low ($CV = 0.53$) which may indicate a significant influence of environmental and intrapopulation conditions on fecundity. Most often there is one seed in a fruit ($Mo = 1$; 3.6 ± 2.2), and in the entire infructescence there are three seeds (7.8 ± 5.7 , $Mo = 3$). The distribution of the number of fruits per shoot is more right skewed than in the case of flowers ($Sk = 1.01$ versus $Sk = 0.14$), since often only one fruit is created from many flowers (Fig. 1). The distribution of the number of seeds in the infructescence reveals that it is of one mode type and it

TABLE 1. Features of vegetative shoots in control (contr.) and experimental (exp.) plots after three shoot cuts.

Population:		Regional					<i>Betulo-Quercetum</i>					<i>Fago-Quercetum</i>				
Feature		n	$\bar{X} \pm \text{S.D.}$	min.-max.	Me	CV	n	$\bar{X} \pm \text{S.D.}$	min.-max.	Me	CV	n	$\bar{X} \pm \text{S.D.}$	min.-max.	Me	CV
Leaf length [mm]	(contr.)	2870	120.0 $\pm$ 25.0	50-214	119.0	0.21	541	135.2 $\pm$ 27.7	56-214	135.0	0.21	480	119.1 $\pm$ 23.3	50-190	120.0	0.20
	(exp.)	690	76.7 $\pm$ 19.7	15-150	75.0	0.26	123	85.2 $\pm$ 23.1	37-135	85.0	0.27	121	65.5 $\pm$ 16.7	30-110	65.0	0.26
Leaf width [mm]	(contr.)	2870	33.2 $\pm$ 10.7	9-78	32.0	0.32	541	37.7 $\pm$ 12.3	10-74	37.0	0.33	480	30.1 $\pm$ 8.9	10-70	29.0	0.30
	(exp.)	690	19.7 $\pm$ 7.0	4-45	19.5	0.36	123	22.4 $\pm$ 9.3	7-45	21.0	0.42	121	17.1 $\pm$ 6.0	7-32	17.0	0.37
Shoot height [mm]	(contr.)	1683	221.9 $\pm$ 47.8	79-395	221.0	0.22	300	238.2 $\pm$ 52.7	110-395	241.0	0.22	294	223.3 $\pm$ 45.2	79-365	225.0	0.20
	(exp.)	591	131.7 $\pm$ 35.8	45-240	130.0	0.27	102	147.4 $\pm$ 38.1	65-225	147.5	0.26	119	135.3 $\pm$ 38.5	55-240	130.0	0.29
Shoot weight [g d. w.]	(contr.)	1683	0.23 $\pm$ 0.16	0.02-1.19	0.19	0.69	300	0.33 $\pm$ 0.21	0.03-1.19	0.31	0.63	294	0.19 $\pm$ 0.11	0.02-0.65	0.16	0.61
	(exp.)	591	0.06 $\pm$ 0.04	0.01-0.23	0.05	0.67	102	0.07 $\pm$ 0.04	0.01-0.18	0.07	0.57	119	0.05 $\pm$ 0.03	0.01-0.15	0.04	0.60
Number of leaves	(contr.)	1683	1.7 $\pm$ 0.5	1-3	2.0	0.29	300	1.8 $\pm$ 0.4	1-3	2.0	0.22	294	1.6 $\pm$ 0.5	1-2	2.0	0.29
	(exp.)	591	1.2 $\pm$ 0.4	1-2	1.0	0.33	102	1.2 $\pm$ 0.4	1-2	1.0	0.33	119	1.0 $\pm$ 0.1	1-2	1.0	0.10

		<i>Melico-Fagetum</i>					<i>Stellario-Carpinetum</i>					<i>Tilio-Carpinetum</i>				
Feature		n	$\bar{X} \pm \text{S.D.}$	min.-max.	Me	CV	n	$\bar{X} \pm \text{S.D.}$	min.-max.	Me	CV	n	$\bar{X} \pm \text{S.D.}$	min.-max.	Me	CV
Leaf length [mm]	(contr.)	757	108.8 $\pm$ 21.5	50-195	109.0	0.20	615	120.1 $\pm$ 20.4	60-214	120.0	0.17	477	121.1 $\pm$ 24.5	55-198	116.0	0.20
	(exp.)	142	71.0 $\pm$ 16.4	34-110	72.0	0.23	144	85.5 $\pm$ 17.6	45-150	85.0	0.21	160	75.7 $\pm$ 17.4	15-120	75.0	0.22
Leaf width [mm]	(contr.)	757	28.4 $\pm$ 7.5	10-57	28.0	0.27	615	33.6 $\pm$ 8.2	9-62	33.0	0.25	477	38.2 $\pm$ 13.0	11-78	36.0	0.34
	(exp.)	142	17.6 $\pm$ 5.7	4-32	18.0	0.33	144	21.5 $\pm$ 6.3	7-45	21.0	0.27	160	19.6 $\pm$ 6.3	4-39	20.0	0.30
Shoot height [mm]	(contr.)	429	198.5 $\pm$ 39.8	85-301	200.0	0.20	359	229.3 $\pm$ 43.7	110-380	230.0	0.19	301	228.8 $\pm$ 48.4	110-363	225.0	0.21
	(exp.)	130	107.3 $\pm$ 24.8	52-165	106.0	0.23	119	140.9 $\pm$ 30.3	75-215	140.0	0.21	120	132.1 $\pm$ 33.1	45-210	125.0	0.25
Shoot weight [g d. w.]	(contr.)	429	0.16 $\pm$ 0.09	0.02-0.55	0.15	0.56	359	0.24 $\pm$ 0.13	0.02-0.80	0.22	0.55	301	0.24 $\pm$ 0.17	0.02-1.03	0.19	0.70
	(exp.)	130	0.04 $\pm$ 0.02	0.01-0.12	0.04	0.50	119	0.07 $\pm$ 0.03	0.02-0.18	0.07	0.43	120	0.07 $\pm$ 0.05	0.01-0.23	0.05	0.71
Number of leaves	(contr.)	429	1.8 $\pm$ 0.4	1-3	2.0	0.24	359	1.7 $\pm$ 0.5	1-2	2.0	0.27	301	1.6 $\pm$ 0.5	1-3	2.0	0.31
	(exp.)	142	1.1 $\pm$ 0.3	1-2	1.0	0.27	119	1.3 $\pm$ 0.5	1-2	1.0	0.39	120	1.3 $\pm$ 0.2	1-2	1.0	0.15

TABLE 2. Features of generative shoots.

Population:		Regional					<i>Betulo-Quercetum</i>					<i>Fago-Quercetum</i>				
Feature		n	$\bar{X} \pm S.D.$	min.-max.	Me	CV	n	$\bar{X} \pm S.D.$	min.-max.	Me	CV	n	$\bar{X} \pm S.D.$	min.-max.	Me	CV
Leaf length	[mm]	627	134.7 ± 25.4	75-215	130.0	0.19	237	137.0 ± 26.9	75-215	135.0	0.20	230	133.7 ± 25.0	80-210	130.0	0.19
Leaf width	[mm]	627	37.4 ± 8.8	17-70	36.0	0.24	237	39.3 ± 8.9	21-62	39.0	0.23	230	35.7 ± 9.0	17-70	35.0	0.25
Shoot height	[mm]	320	282.6 ± 48.9	140-435	285.0	0.17	120	273.5 ± 56.8	170-435	270.0	0.21	120	291.8 ± 39.3	190-370	295.0	0.13
Inflorescence height	[mm]	320	212.8 ± 39.2	115-320	210.0	0.18	120	223.0 ± 38.1	145-320	220.0	0.17	120	211.2 ± 35.3	115-300	215.0	0.17
Number of flowers		320	6.4 ± 1.3	3-10	6.0	0.20	120	6.8 ± 1.1	4-10	7	0.16	120	6.2 ± 1.3	3-9	6.0	0.21
Inflorescence weight	[g d. w.]	320	0.08 ± 0.03	0.02-0.17	0.08	0.37	120	0.09 ± 0.03	0.03-0.17	0.09	0.32	120	0.08 ± 0.02	0.02-0.13	0.08	0.30
Shoot weight	[g d. w.]	320	0.47 ± 0.17	0.15-0.97	0.46	0.35	120	0.52 ± 0.18	0.19-0.97	0.53	0.35	120	0.43 ± 0.15	0.15-0.84	0.42	0.34
Number of leaves		320	2.0 ± 0.2	1-3	2.0	0.10	120	2.0 ± 0.2	1-3	2.0	0.10	120	1.9 ± 0.3	1-2	2.0	0.16

		<i>Melico-Fagetum</i>					<i>Stellario-Carpinetum</i>					<i>Tilio-Carpinetum</i>				
Feature		n	$\bar{X} \pm S.D.$	min.-max.	Me	CV	n	$\bar{X} \pm S.D.$	min.-max.	Me	CV	n	$\bar{X} \pm S.D.$	min.-max.	Me	CV
Leaf length	[mm]	32	128.8 ± 13.7	95-160	130.0	0.11	66	116.9 ± 17.6	90-160	115.0	0.15	62	129.4 ± 19.8	95-195	130.0	0.15
Leaf width	[mm]	32	41.8 ± 9.1	27-57	45.0	0.22	66	32.7 ± 8.1	11-54	32.0	0.25	62	36.1 ± 5.5	27-50	35.0	0.15
Shoot height	[mm]	16	255.0 ± 28.8	205-305	260.0	0.11	33	247.1 ± 36.7	190-345	245.0	0.15	31	282.4 ± 43.9	140-365	285.0	0.16
Inflorescence height	[mm]	16	156.6 ± 27.5	115-220	157.5	0.18	33	166.2 ± 29.4	105-230	160.0	0.18	31	179.7 ± 39.3	125-295	180.0	0.22
Number of flowers		16	5.9 ± 1.2	3-8	6.0	0.20	33	5.5 ± 0.8	4-7	6.0	0.15	31	5.4 ± 1.0	4-8	5.0	0.19
Inflorescence weight	[g d. w.]	16	0.06 ± 0.01	0.03-0.08	0.06	0.16	33	0.06 ± 0.02	0.03-0.09	0.05	0.25	31	0.04 ± 0.01	0.02-0.07	0.04	0.32
Shoot weight	[g d. w.]	16	0.45 ± 0.10	0.23-0.61	0.46	0.22	33	0.35 ± 0.13	0.17-0.68	0.33	0.36	31	0.41 ± 0.11	0.23-0.62	0.41	0.27
Number of leaves		16	2.0 ± 0.0	2-2	2	0	33	2.0 ± 0.0	2-2	2.0	0	31	2.0 ± 0.0	2-2	2.0	0.00

TABLE 3. Lily of the valley fecundity.

Population:	Regional					<i>Betulo-Quercetum</i>				
Feature (number)	n	$\bar{X} \pm S.D.$	min.-max.	Mo	CV	n	$\bar{X} \pm S.D.$	min.-max.	Mo	CV
Flowers/shoot	330	5.9 ± 1.3	1-11	5	0.22	100	6.1 ± 1.1	4-9	6	0.18
Fruits/shoot	330	2.1 ± 1.1	1-7	1	0.52	100	2.5 ± 1.4	1-7	2	0.56
Seeds/shoot	330	7.8 ± 5.7	0-33	3	0.73	100	9.6 ± 6.9	1-31	3	0.72
Seeds/fruit	705	3.6 ± 2.2	0-13	1	0.69	246	3.9 ± 2.9	0-13	1	0.74

Population:	<i>Fago-Quercetum</i>					<i>Tilio-Carpinetum</i>				
Feature (number)	n	$\bar{X} \pm S.D.$	min.-max.	Mo	CV	n	$\bar{X} \pm S.D.$	min.-max.	Mo	CV
Flowers/shoot	130	5.3 ± 1.0	1-8	5	0.19	100	6.6 ± 1.4	4-11	7	0.21
Fruits/shoot	130	2.1 ± 1.0	1-5	2	0.48	100	1.8 ± 1.0	1-5	1	0.54
Seeds/shoot	130	6.9 ± 4.7	1-33	4	0.68	100	7.2 ± 5.4	0-23	2	0.74
Seeds/fruit	276	3.3 ± 2.3	0-12	1	0.70	183	3.9 ± 2.2	1-10	2	0.56

is positively skewed (Fig. 2). The positive skewness of the distribution of features which describe fecundity proves their strong modification by intrapopulation, phytocoenotic or biotope features. Fecundity is highly dependent on shoot weight ($r = 0.58$).

In the coenopopulation in *Betulo-Quercetum* the vegetative shoot is the largest and it usually consists of two leaves (1.8 ± 0.4), and the leaf lamina is 13.5 ± 2.8 cm long and 3.8 ± 1.2 cm wide (Table 1). The plant reaches a height of

23.8 ± 5.3 cm and weighs 0.33 ± 0.21 g d.w. The majority of shoots (78.7%) have two leaves, but in the regional population there are a few less (70.5%). The fraction of shoots with three leaves is the highest in this coenopopulation. The leaf length is the least variable feature ($CV = 0.21$), while the most flexible feature is shoot weight ($CV = 0.63$). The shoot is higher and heavier ($p < 0.001$) than the one that occurs in the regional population (Fig. 3).

Fig. 1. Number of fruits in infructescence in control plots.

Fig. 2. Number of seeds in infructescence in control plots.

Fig. 3. Shoot height (A) and weight (B) and leaf width (C) in control plots.
— min.-max., □ — S.D., · — $\bar{X}$, Reg. — regional population, B-Q, M-F, F-Q, T-C, S-C — coenopopulation, see methods.

The average number of generative shoots is $13.8 \pm 3.7\%$. They almost always consist of two leaves (2.0 ± 0.2), its inflorescence is 22.3 ± 3.8 cm high, and it usually has seven flowers (6.8 ± 1.1 , Table 2). The variability of the number of flowers is, in this case, the lowest ($CV = 0.16$). The generative shoot in the B-Q is heavier than the one in the regional population, but the leaf lamina is of a similar height and size, although, its inflorescence is higher and it has more flowers ($p < 0.01$).

There are 2.5 ± 1.4 fruits in the infructescence, and they are created by almost every second flower (40.3%, see Table 3). One fruit has an average of 3.9 ± 2.9 seeds, but in the entire infructescence there are from several to over a dozen seeds (9.6 ± 6.9). The distribution of the number of fruits reveals that most often there are two fruits, i.e. two times more than in the regional population ($p < 0.01$).

In the coenopopulation in *Fago-Quercetum* the vegetative shoot is 22.3 ± 4.5 cm high and weighs 0.19 ± 0.11 g d.w. The leaf lamina is 11.9 ± 2.3 cm long, but it varies between 3.0 ± 0.9 cm (Table 1). The shoot is smaller, lighter and it has narrower leaves than that growing in the B-Q (Fig. 3). Over a half of shoots (62.6%) have one leaf, which is a specific feature of this coenopopulation. In general, however, they are as equally as high, but lighter than in the regional population ($p < 0.001$). They are also lighter than those which occur in the coenopopulations in S-C and T-C ($p < 0.001$). This may be connected with poorer illumination (in F-Q 9.5% of light, in B-Q 25%, while in S-C 35%).

The generative shoot reaches a height of 29.2 ± 3.9 cm and weighs 0.43 ± 0.15 g d.w., including the inflorescence at 0.08 ± 0.02 g d.w., and its size does not vary from that of the regional population. There are three times fewer blooming and fructifying shoots than in B-Q ($5.3 \pm 5.1\%$ versus $13.8 \pm 3.7\%$). There are also less flowers in the inflorescence (6.2 ± 1.3 versus 6.8 ± 1.1 ; $p < 0.01$; Table 2) and fruits (2.2 ± 1.0 , versus 2.5 ± 1.4 ; Table 3), although, they have a similar number of seeds (3.3 ± 2.3 , versus 3.9 ± 2.9 in B-Q).

In the coenopopulation in *Melico-Fagetum* the vegetative shoot reaches a height of 19.9 ± 4.0 cm, its average weight is 0.16 ± 0.09 g d.w. and it usually has two leaves (75.4% of the shoots have two leaves). The leaf lamina is 10.9 ± 2.2 cm long and 2.8 ± 0.8 cm wide (Table 1). The shoot is smaller and lighter and its leaf lamina is smaller than that from the regional population ($p < 0.001$) and in the coenopopulations in B-Q and F-Q (Fig. 3). The distribution of shoot weight is less skewed than in the regional population and in the B-Q and F-Q populations. This is due to the fact that these populations are less diverse, probably because of little pressure from competitors, which are not numerous in the *Melico-Fagetum* groundcover. About 2% of shoots bloom and fructify, thus, in comparison with other coenopopulations, these are the least numerous. It must be emphasized that fruits are created sporadically, so the only effective reproduction means in this coenopopulation is vegetative.

In the coenopopulation in *Stellario-Carpinetum* the vegetative shoot weighs 0.24 ± 0.13 g d.w. and is 22.9 ± 4.4 cm high, while the width of the leaf lamina is 3.4 ± 0.8 cm, and its length oscillates around 12.0 ± 2.0 cm (Table 1). These shoots are as high as in the B-Q ($p < 0.05$), but they are lighter ($p < 0.001$; Fig. 3). The generative shoot is 24.7

± 3.7 cm high and it weighs 0.35 ± 0.13 g d.w. The inflorescence consists of 5.5 ± 0.8 flowers, i.e. fewer than in B-Q and F-Q (Table 2). In the S-C there are $4.6 \pm 5.5\%$ blooming shoots, i.e. three times less than in the B-Q (13.8%), but over two times more than in the M-F (1.9%).

In the coenopopulation in *Tilio-Carpinetum* the vegetative shoot weighs 0.24 ± 0.17 g d.w. and is 22.9 ± 4.8 cm high, and is similar to that confirmed in the S-C (Table 1). The leaf lamina is 12.1 ± 2.5 cm long and it is 3.8 ± 1.3 cm wide; this last feature is significantly different for both coenopopulations, in S-C and T-C ($p < 0.01$). The shoots are similar in height to those in F-Q and B-Q, but statistically they are significantly lighter than in the B-Q (Fig. 3). The generative shoot grows to a height of 28.2 ± 4.4 cm and weighs 0.4 ± 0.1 g d.w. There are 5.4 ± 1.0 flowers in the inflorescence (Table 2), i.e. fewer than in the B-Q and F-Q ($p < 0.001$). Fruits are created in every fourth flower (26.6%), and there is only 1.8 ± 1.0 fruit in every infructescence (Table 3), and each of them has 4.0 ± 2.3 seeds. The distribution of the number of fruits in the infructescence reveals that most often there is only one fruit; this means that the fecundity in the T-C is similar to the M-F, and it is considerably lower than in the B-Q. There are $3.9 \pm 5.1\%$ shoots which bloom and fructify, i.e. fewer than in the B-Q (13.8%), F-Q (5.3%) and S-C (4.6%), but twice as many as in the M-F (1.9%).

Size and fecundity in the disturbed population

Regional population

Vegetative shoot: In the first stage of the experiment, i.e. after cutting the lily of the valley, the vegetative shoots weighed 0.09 ± 0.07 g ($Me = 0.07$ g), and they were almost three times lighter than those in the undisturbed population. As a result of a one-time cut in the plots, the average newly-created vegetative shoot was 0.14 g lighter the following year. The difference between these shoots and the ones from the control plots is statistically significant ($p < 0.001$). Such a significant decrease in the biomass of particular shoots is the basic reason for the crop's rapid decrease the year after the first lily of the valley cut. In the second and the third years of the experiment the decrease of the vegetative shoot biomass was not high, and it was statistically unimportant, amounting to 0.02 and 0.01 g/shoot, respectively. As a result of subsequent disturbances, the shoot weight distribution was becoming more right skewed, i.e. the number of lighter shoots was increasing in the population, mainly due to the fact that their habitus was changing. In the undisturbed population they mainly had two leaves, sometimes even three leaves, however, after the third cut the majority of vegetative shoots had only one leaf, the lamina was 30% smaller and was often located lower on the shoot. The vegetative shoots, growing after the third disturbance, were four times lighter, almost two times lower and had significantly smaller assimilation areas (Table 1).

Generative shoot: The reactions of blooming and fructifying shoots to the analyzed form of disturbances are more evident than in the case of vegetative shoots. One year after the first cut statistically significant differences were apparent for every feature. The inflorescence was lower, lighter and it had fewer flowers (4.9 ± 1.1 versus 6.4 ± 1.3 ; $p < 0.001$) than in the undisturbed population (Fig. 4). These changes indicate a significant decrease in fecundity, even after the first interference (Fig. 5). The lily of the valley in the plots

Fig. 4. Height of inflorescence in experimental (A) and control (B) plots. n_1 , n_2 – number of inflorescences in plots: n_1 – experimental, n_2 – control.

Fig. 5. Number of flowers in inflorescence in control (o) and experimental plots after 1 and 2 shoot cuts.

basically stopped blooming after the second disturbance (Fig. 6); the few generative shoots were dispersed and often had a deformed inflorescence. Thus, it can be assumed that even after a single interference the influx of genets to the population is basically eliminated.

Fig. 6. Number of flowers in control (o) and experimental plots after 1, 2 and 3 shoot cuts.

The coenopopulation in Betulo-Quercetum

Vegetative shoot: In this coenopopulation, characterized by the most shapely shoots, the arithmetic mean of their weight before the experiment was almost two times higher than after the first, three times after the second and five times higher after the third interference. The decrease in shoot biomass after the first disturbance was slightly lower than in other coenopopulations, probably due to their greater

Fig. 7. Shoot weight in control (o) and experimental plots after 1, 2 and 3 shoot cuts.

abundance. After the third disturbance, the shoot weight was similar to that in other coenopopulations (Fig. 7).

Fewer and fewer three-leaved shoots occurred in the subsequent years of the experiment, although the decrease in their numbers was slow. A year after the first disturbance the number of three-leaved shoots remained the same, after the second their number decreased by 10%, but after the third their number was 90% lower.

Generative shoot: In subsequent stages of the experiment the generative shoot became smaller, lighter and more deformed and it had fewer flowers. The number of generative shoots in the population after the second interference was very low, at about 1%.

The coenopopulation in Fago-Quercetum

Vegetative shoot: The year after the first cut the vegetative shoots were over two times lighter (0.08 ± 0.06 g), after the second they were three times lighter (0.06 ± 0.04 g), and after the third they were four times lighter (0.05 ± 0.03 g; Fig. 7). One reaction of the plant to this kind of disturbance was a reduction in the number of leaves on the shoot. In the control plots, shoots with one or two leaves were equally numerous, while after the first disturbance every third shoot had two leaves and after the second cut almost all the shoots had one leaf. As the number of leaves decreased to one, and three-leaved shoots became two leaved, a simultaneous and significant decrease in size of the leaf lamina was observed, which was two times smaller than in the control plots after the third cut (Table 1).

Generative shoot: Inflorescence modifications in the coenopopulation in F-Q were similar to those in other populations and occurred at the same stage of the experiment, e.g. after the first disturbance when the inflorescence became smaller, lighter and it had fewer flowers (it decreased from 6.2 ± 1.3 to 4.8 ± 0.9 ; $p < 0.001$). Moreover, after the second disturbance the fraction of blooming shoots decreased to 0.5%, i.e. the level at which potential recruitment of genets does not play an important role in population reproduction. The main effect of such a reaction to this type of disturbance is a decrease in the assimilation area and lily of the valley fecundity, and the almost complete extinction of generative reproduction after the second harvest.

The coenopopulation in Melico-Fagetum

The vegetative shoots growing in experimental plots a year after the first harvest were over two times lighter (0.07

± 0.04 g), and after the third harvest they were four times lighter (0.04 ± 0.02 g) and were the lightest (Fig. 7).

Before the experiment, the proportion of shoots with one and two leaves was as 1:1; after subsequent cuts, there was a greater number of shoots with one leaf. After the third harvest, shoots with one leaf dominated in the population. Its leaves were smaller and the entire shoot was characterized by advanced miniaturization. After the second harvest the vegetative shoots from M-F, which in the control plots varied in size from those of F-Q, became so much like them that there was no longer a statistically significant difference between them. The rate and type of changes are similar here as with shoots from other coenopopulations (Table 1).

Generative shoots did not appear in the experimental plots after the second disturbance (Fig. 5).

The coenopopulation in Stellario-Carpinetum

Vegetative shoots: After the first harvest the vegetative shoot weighs 0.24 ± 0.13 g d.w. and its height is 22.9 ± 4.4 cm, while the width of the leaf lamina is 3.4 ± 0.8 cm, and is 12.0 ± 2.0 cm long (Table 1). After the first harvest, the growing shoot is 2.5 times lighter (0.10 ± 0.06 g d.w.), after the second harvest its weight decreases only slightly, and after the third harvest its weight stabilizes at a level of 0.07 ± 0.03 g (Fig. 7). After the third interference the assimilation area of the leaves decreases in comparison with the state prior to the experiment, the leaf length decreases from 12.0 ± 2.0 to 8.6 ± 1.8 cm, and the width from 3.4 ± 0.8 to 2.2 ± 0.6 cm. The number of leaves on the shoot also decreases (from two, more rarely three, to almost only one) and the shoot height decreases almost two times (from 22.9 ± 4.4 to 14.1 ± 3.0 cm; Table 1). The changes within the assimilation area occur in accordance with the same scheme as in other coenopopulations.

Generative shoot: After the first harvest, inflorescence is one third lower, two times lighter and it has fewer flowers (decrease from 6.4 ± 1.3 to 4.3 ± 1.3 ; $p < 0.001$; Fig. 5). Also the fraction of these shoots in the population is then three times lower and amounts to 1.4%. No generative shoots were found in the experimental plots after the third disturbance (Fig. 6).

The coenopopulation in Tilio-Carpinetum

After the first harvest the vegetative shoots are almost three times lighter (0.09 ± 0.06 g d.w.; Fig. 7) and they have clearly smaller assimilation areas, thus they react to disturbances similarly to the way which is described for other coenopopulations.

After the first harvest, the generative shoots were by a third lower (20 ± 2.8 cm), two times lighter (0.2 ± 0.04 g d.w.), three times less numerous (1.3%) and they had fewer flowers (Fig. 5). Flowers after the second harvest were sporadic, and they were non-existent after the third harvest (Fig. 6).

The basic result of this form of disturbance in the T-C, which was similar to that in other coenopopulations, was the decrease in shoot size and fecundity and a clear modification of their habitus involving the reduction of the number of leaves and their assimilation areas. Moreover, after the first harvest almost all generative shoots had already disappeared. It must be emphasized that both in the T-C and other coenopopulations, the morphologic reactions of

shoots that regenerated after a subsequent harvest always did so in accordance with the same scheme, they did not have any specific features and the rate of their changes from year to year was similar everywhere.

DISCUSSION

The size of individuals of the same age depends, among others, on habitation conditions, (Andrzejewska and Falińska 1983). In the *C. majalis* population this feature is very changeable and mainly dependent on phytocoenotic-biotope conditions. According to Weiner and Thomas (1986), the size of individuals depends also on pressure from competitors, herbivores, pathogens and other environmental influences. The present investigations indicate that fecundity, similarly to cardenolide levels (see Kosiński 1996, 1998), depends not on the size of the polycormones, but rather on the abundance of their modules. Confirmation of this comes from the results obtained from the coenopopulation in *Betulo-Quercetum*. In this case, the module reactions are similar to those of the entire plant with one-shoot architecture (Leverich and Lewin 1979, Solbrig 1981, Watkinson et al. 1983, Watkinson and White 1985, Szmeja 1987a, b, 1994).

C. majalis reproduces generatively and vegetatively, but, as is the case with many other perennials, mainly vegetative reproduction is significant (Harper 1977; Falińska 1979, 1985, 1991; Pirożnikow 1983; Szmeja 1987a, b, 1994; Czarnicka 1996). According to Ponert (1980), lily of the valley is a self-pollinating plant. This kind of reproduction is enhanced by the plant's hanging flowers and loose pollen, which easily falls onto the pistil's stigma from the anthers that are positioned on short filaments (Hegi 1909). The author observed that the flowers are open, thus they may also be allogamous. When the anthers break, they are quite often visited by insects, mainly small coleoptera from the Nitidulidae, Byturidae, Staphylinidae and Cantharidae families, as well as by bumble bees (*Bombus* sp.). It cannot be ruled out that there are allogamous flowers alongside autogamous flowers within the inflorescence (Eriksson 1999). The number of flowers pollinated in this way is unknown.

There are many similarities between animal grazing on a plant and cutting it; in both cases the aboveground organs, principally the leaves and the inflorescence, are eliminated (Haeggström 1990, Malkamäki and Haeggström 1997). *C. majalis* contains toxic substances from the amino acid and glycoside groups (Harborne 1997). According to Haeggström (1990), these glycosides are not toxic for domestic cattle. There are also probably not toxic for deer (*Capreolus capreolus*) as they have been observed grazing lily of the valley on many occasions.

Grazing damages plants and changes their habitus and vitality. The effects of grazing depends, among others, on the plant's life cycle (Falińska 1996). *C. majalis* tolerates selective grazing by wild animals, however, intensive sheep and cattle pasturing leads to a decrease in size and weight of shoots the following year (Malkamäki and Haeggström 1997). As a result of defoliation, *C. majalis* rhizomes supply a lower level of assimilation products, produce fewer and smaller leaves, and generative shoots which have less flowers and fruits. A similar reaction is

seen in other clonal plants, such as *Trientalis europaea* (Piqueras 1999). Probably, this leads to significant physiological disturbances, including difficulties in transferring metabolites. This type of reaction was also confirmed in *Lolium perenne* individuals which had been grazed (Mars-hall and Sagar 1968).

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WPLYW POZYSKIWANIA PĘDÓW
NA WIELKOŚĆ I PŁODNOŚĆ *CONVALLARIA MAJALIS* L.

STRESZCZENIE

Przedstawiono wielkość i płodność *Convallaria majalis* L. w populacji zaburzanej i nie zaburzanej wycinaniem pędów. Przedmiotem badań były cenopopulacje w *Betulo-Quercetum*, *Fago-Quercetum*, *Melico-Fagetum*, *Stellario-Carpinetum* i *Tilio-Carpinetum*, w których raz w roku, przez cztery kolejne lata ścinano pędy *C. majalis*.

W populacji nie zaburzanej pęd wegetatywny ma wysokość $22,2 \pm 4,8$ cm, ciężar $0,23 \pm 0,16$ g s.m. i składa się przeważnie z dwóch liści. Błazka liściowa ma długość $12,0 \pm 2,5$ cm i szerokość $3,3 \pm 1,1$ cm. Najmniej zmienną cechą jest długość liścia, natomiast najbardziej plastyczną – ciężar pędu. Największe pędy występują w cenopopulacji w *Betulo-Quercetum*, a najmniejsze – w *Melico-Fagetum*.

Pęd generatywny, w porównaniu z wegetatywnym, jest wyższy i ma większe liście. Kwiatostan składa się przeważnie z sześciu kwiatów, ma wysokość $21,3 \pm 3,9$ cm i ciężar $0,08 \pm 0,03$ g s.m. Kwiatostan jest pod względem cech ilościowych najmniej zmienną częścią rośliny. Dojrzały owoc powstaje tylko z co trzeciego kwiatu, jest w nim najczęściej tylko jedno nasiono, a w całym owocostanie przeważnie trzy. W cenopopulacji w *Betulo-Quercetum* kwiatostan jest najwyższy i ma najwięcej kwiatów. Płodność konwalii jest tu wyższa niż w pozostałych cenopopulacjach.

Wielokrotny zbiór surowca prowadzi do spadku wielkości pędów *C. majalis*. W drugim roku eksperymentu pędy nadziemne były trzykrotnie lżejsze. W czwartym roku pędy maturalne były czterokrotnie lżejsze, prawie dwukrotnie niższe i miały mniejszą powierzchnię asymilacyjną.

Zbiór surowca prowadzi do spadku płodności konwalii. Po pierwszym wycięciu pędów nastąpiła redukcja liczby kwiatów, a po drugim zahamowanie reprodukcji generatywnej i niemal całkowite wyeliminowanie dopływu genotów do populacji.

SŁOWA KLUCZOWE: *Convallaria majalis* L., roślina lecznicza, wielkość pędów, płodność, zaburzenia.