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Variability of enzymatic systems in natural populations of *Anthyllis vulneraria* s. l. from three geographic regions of Poland. Part I. Ontogenetic variability of enzymatic systems in three woundwort populations during plant development

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Abstract

Analysis of variation in the four enzymatic systems of three populations of *Anthyllis vulneraria* was made. Different polymorphism of enzyme proteins in six terms of plant development was found by isoenzyme electrophoresis on polyacrylamide gel. Each population had a specific isoenzyme pattern and specific variability in the terms.

INTRODUCTION

Differentiation of approaches to taxons of *Anthyllis* genus by particular taxonomists clearly shows that this genus is characterized by high variability (Rothmaler, 1966; Hegi, 1964; Tutin et al., 1968). Jalas (1957) presented a hypothesis that this variability of woundwort may be explained by the fact that populations existing at present originate from one, large, hybrid swarm, which had developed in Europe after the last glacial period.

Recent studies (Łukaszewska et al., 1978) on the variability of 11 vegetative and 10 floral features showed that woundwort populations are characterized by high genetic specificity, related to particular regions of Poland. This observation has been supported by the results of analyses of phenol compounds, carried out for six populations originating from three geographical regions. At the same time significant polymorphism within populations was noted (Kalinowski, Bartkowiak, 1979).

In view of the above, additional studies were carried out in order to supplement the mentioned results with an analysis of variability of

enzymatic systems. In the first place, it was necessary to determine the stage of plant development, most suitable for comparative studies. Furthermore, it was necessary to obtain data on protein polymorphism within plant populations, and to determine its variability between particular populations.

In order to obtain as many data as possible on intra- and inter-population variability, four enzymatic systems, connected with different metabolitic processes were selected (malate dehydrogenase, esterases, acid phosphatases, and peroxidases). Rapid and precise method of determining the isoenzyme variability was used, i.e. electrophoresis on polyacrylamide gel (J o h n s o n, 1973).

Biometric methods were used for the interpretation of the results.

MATERIAL AND METHODS

1. Plant material

Three populations were selected for studies, originating from different geographic regions: Baltic Sea coast (white dune) — Chłopy (A), National Nature Reserve of Tatra Mountains — Kalatówki (B), and Wielkopolska Lowland — Rożnowo (C).

Seeds were collected from each wild population, and sown into flower-pots placed in a green house. Seedlings in the stage of seventh leaf were transferred to a cold storage room (about 4°C) for seven days, and then brought back to the green house.

Random sample of 30 plants was used for studies of enzyme systems. Three leaves were taken from each plant: the first one, the third one, and from the rosette. Analyses of enzymatic systems were carried out in six terms. First analysis was made on 7th day after plant transferr from cold storage room to the green house, and the last one — at the begining of plant blooming:

1st term — 5, 6. 11, 1974
2nd term — 18, 19. 12. 1974
3rd term — 29, 30. 01. 1975
4th term — 25, 26. 02. 1975
5th term — 2, 3. 04. 1975
6th term — 20, 21. 05. 1975

2. Biochemical methods

Leaf sample was homogenized in 4°C with an extraction buffer, weight ratio being 1:3. Composition of the buffer used was as follows:

0.1 M phosphoro-potassium buffer with pH 7.5, 0.1 M manganese chloride, 5% glycerine, and 10 mM mercaptoethanol, at extraction time of 20 min. After extraction whole sample was centrifuged at 15 000 r.p.m. The supernatant was transferred to gel pockets in the amount of 0.04 ml. Separation of proteins was made on 7.5% polyacrylamide plates, at current tension of 80-100 V (Kalinowski, Bartkowiak, 1975), and particular isoenzymes dyed by specific dyes.

Esterases and peroxidases were dyed according to the method by Almgard and Norman (1970), and malate dehydrogenase and acid phosphatases — according to the method by Sako and Stahmann (1972). In case of malate dehydrogenase amount of N-methylphenazine-metaphosphate used was doubled.

3. Statistical methods

For biometric analyses zymograms were prepared for the given enzyme system in particular population in the given term. In the next step synthetic and general zymograms were made. Synthetic zymograms embraced all bands found during all terms for particular enzyme systems, for each of the 30 plants originating from the given population. General zymograms embraced all bands found for given population during all terms. Hence, synthetic zymograms reflected qualitative and quantitative composition of bands in populations, whereas general zymograms — only the qualitative composition.

Variability noted in population in particular terms, and of synthetic zymograms, was expressed by polymorphism index, according to the following equation:

$$PI = \frac{1}{z} \sum_{i=1}^{z} q_i(1-q_i) \quad \text{(Marshall, Jain, 1969)}$$

where: z — number of bands found in the population, q_i — frequency of occurance of band in the population.

In order to define significance of differences between mean PI values in particular terms and populations, variance analysis was performed, whereas the significance of differences between two compared PI values was defined according to T. Tukey's test (Oktaba, 1972).

Inter-population variability was regarded both, with respect to the frequency of bands occurance in the population, and as regards their electrophoretic mobility. In order to define significance of differences between populations with respect to all enzymatic systems, chi-squared test for large samples was used (Elandt, 1964). Significance of differences between populations as regards particular enzymatic systems was defined chi-squared test for small samples (Nass, 1959).

RESULTS

Results of analyses concerning variability of particular enzymatic systems are presented below.

1. Malate dehydrogenase (MDH)

Different patterns of malate dehydrogenase were obtained in the six terms of analyses. In the population originating from Chłopy (A) some plants possessed band 0.19-c in the sixth term, and 0.25-e in the first term, whereas in the fourth term no activity was found on gel. Band 0.19-c in the population from Kalatówki (B) was found only in the fifth and sixth term. Lowland population — Rożnowo (C) possessed band 0.16-a in the fifth term, and 0.19-c only in the fourth term. Bands 0.17-b and 0.25-e were found in all populations in particular developmental periods, with the exception of Chłopy (A) population in the fourth term. In the third term a decrease of malate dehydrogenase activity was noted in all populations, as also in the fourth term in Chłopy (A) population, and in the sixth term in Rożnowo (C) population. Variability between particular terms is presented in Table 1 and Fig. 1.

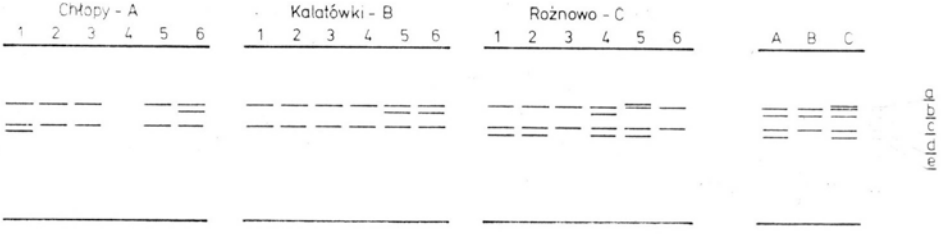

Fig. 1. Zymograms of qualitative variability of malate dehydrogenase between particular terms in the same population, and between populations.

Variability found in the three populations under study was different during plant development. Ranges of PI values were: 0.000-0.160 for Chłopy (A) population, 0.000-0.189 for Kalatówki (B) population, and 0.025-0.173 for Rożnowo (C) population. The lowest variability between particular populations was noted in the second term of analyses, and the highest one — in the fifth and sixth term. The highest differences of PI values between particular populations were observed in the first and the last term; the lowest — in the second and fifth term.

Variability of Kalatówki (B) and Rożnowo (C) populations in the third and fourth term was similar, being much higher than in Chłopy (A) population. Differences between mean PI values for particular terms, and mean PI for all terms were not significant. It should be, however, noted

Table 1

Frequency of malate dehydrogenase bands (in per cent) in the three populations in particular terms of analyses, and upon synthetic zymograms

Band	Chłopy — A						Kalatówki — B						Rożnowo — C						Synthetic zymogram		
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	A	B	C
0.16-a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0	0	30
0.17-b	13	100	7	0	20	87	63	100	60	3	100	89	100	100	67	100	100	100	100	100	100
0.19-c	0	0	0	0	0	13	0	0	0	0	64	37	0	0	0	23	0	0	13	76	23
0.23-d	100	100	100	0	20	40	100	100	100	27	68	68	100	96	100	100	40	20	100	100	100
0.25-e	10	0	0	0	0	0	0	0	0	0	0	0	87	100	0	30	60	0	10	0	100

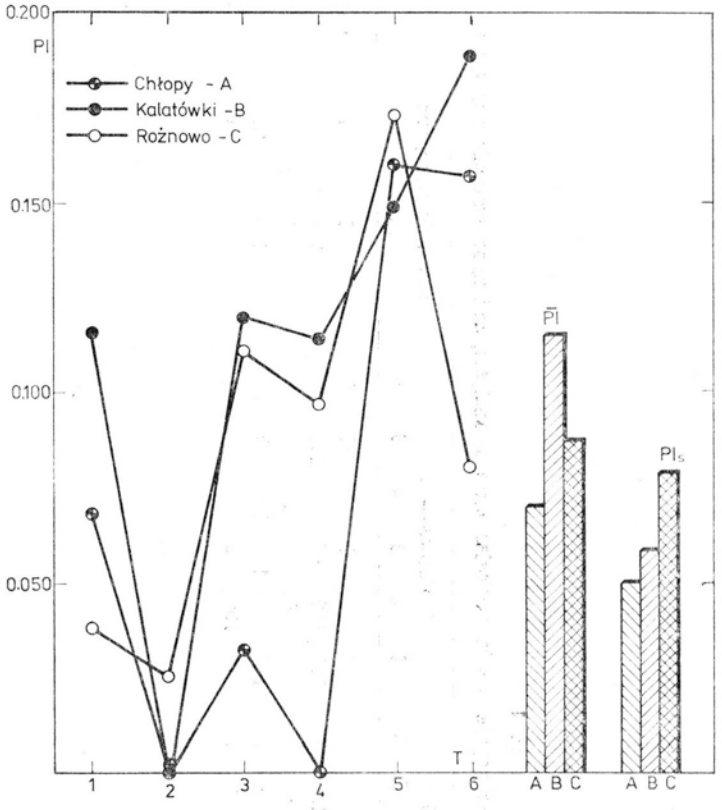

Fig. 2. Polymorphism index (PI) for successive terms (T), together with mean for a population ($\overline{PI}$), and for synthetic zymograms (PI_s) for malate dehydrogenase.

that Chłopy (A) population was characterized by a rather low variability compared to the other two populations.

Comparison of populations as regards malate dehydrogenase (from general zymogram — Fig. 1) showed that Chłopy (A) and Kalatówki (B) populations differed by two bands (0.16-a, 0.25-e), Chłopy (A) and Rożnowo (C) — by one band (0.16-a), and Kalatówki (B) and Rożnowo (C) — by two bands (0.16-a, 0.25-e). The three populations differed also as regards the frequency of occurance of particular bands (see Table 1).

Chi-squared test showed that the populations under study had different patterns of malate dehydrogenase:

$$\chi^2_{MDH} = 121.416 \qquad \chi^2_{0.05} = 15.507$$

2. Esterases (E)

Fig. 3 presents variability in three populations during plant development. In Chłopy (A) population bands 0.33-m and 0.40-r were

Table 2

Frequency of esterases bands (in per cent) in the three populations in particular terms of analyses, and upon synthetic zymograms

Band	Chłopy — A						Kalatówki — B						Rożnowo — C						Synthetic zymogram		
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	A	B	C
0.05-a	100	100	87	0	100	0	100	100	100	87	100	100	100	100	43	100	100	57	100	100	100
0.08-b	0	100	53	7	100	100	47	25	13	17	21	25	13	0	10	10	3	10	100	73	40
0.12-c	7	56	0	10	46	0	0	32	100	37	25	0	3	70	0	0	70	0	60	100	87
0.14-d	0	17	0	0	0	0	0	3	0	0	0	0	80	17	0	0	100	0	17	3	100
0.16-e	0	0	0	0	0	0	0	61	0	3	100	22	10	42	0	57	13	0	0	100	90
0.19-f	0	76	0	0	100	0	0	0	0	0	10	0	50	50	0	0	0	0	100	10	70
0.21-g	90	100	0	100	100	0	0	64	0	27	7	0	0	0	0	0	0	0	100	73	0
0.24-h	73	88	0	100	37	47	10	0	0	50	18	52	0	17	0	0	53	13	100	80	63
0.26-i	0	12	0	100	0	0	0	50	0	70	18	0	0	71	0	57	13	67	100	83	93
0.29-j	0	32	0	0	0	80	27	0	0	27	11	52	0	0	33	3	0	80	83	70	90
0.31-k	0	0	0	0	0	0	0	0	0	3	0	25	20	54	0	17	20	37	0	27	77
0.32-l	0	0	0	0	0	0	0	25	47	17	0	37	13	50	0	13	7	0	0	73	57
0.33-m	100	100	93	100	100	100	87	96	63	100	57	67	83	100	100	93	100	100	100	100	100
0.35-n	0	0	7	100	0	0	20	79	0	0	32	19	0	0	0	0	0	0	100	83	0
0.37-o	0	0	100	0	20	100	3	0	0	17	0	15	0	3	23	67	37	17	100	33	93
0.39-p	0	17	100	0	40	80	0	0	0	0	0	0	3	75	23	37	90	27	100	0	97
0.40-r	100	100	100	100	67	100	100	100	20	0	100	48	100	100	57	77	73	83	100	100	100
0.43-s	90	64	0	64	0	90	3	21	13	0	14	37	60	75	100	0	0	0	100	63	100
0.45-t	0	0	0	23	0	0	27	21	70	0	21	0	0	3	0	0	0	0	23	80	3
0.48-u	0	0	0	0	0	0	67	0	100	0	0	0	0	0	0	0	0	0	0	100	0

always found in successive developmental stages, whereas in Kalatówki (B) population — bands 0.05-a, 0.08-b, 0.33-m, and in Rożnowo (C) population — bands 0.05-a, 0.33-m, 0.39-p, and 0.40-r (acquired colour in all terms). The remaining bands occured with varying frequency in particular developmental stages. The poorest pattern of isoenzymes was noted in all populations in the third term, the richest — in the fifth term. Detail comparison of bands frequency in the six developmental stages is given in Table 2.

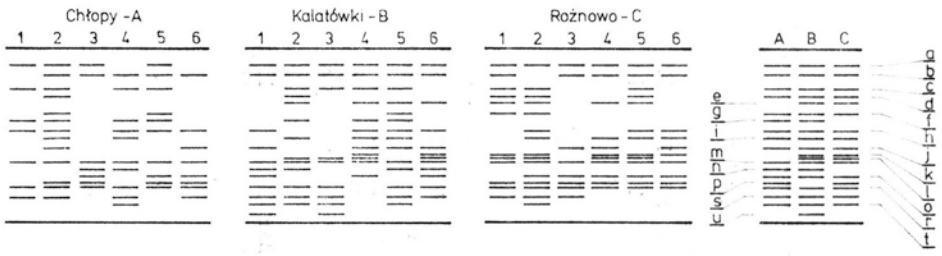

Fig. 3. Zymograms of qualitative variability of esterases between particular terms in the same population, and between populations.

Different variability was found in successive developmental stages of plant populations. Chłopy (A) population was most polymorphic in the second and fifth term, while Kalatówki (B) and Rożnowo (C) populations — in the sixth term. Variability within populations is presented in Fig. 4. Furthermore, Fig. 4 shows that as regards intra-population variability, the highest differences between populations were observed in the last term, whereas in the fifth term variability within populations was most similar. Variance analysis showed that PI differences for particular terms were insignificant, while average PI for populations was significantly different:

$$F_{calc.} = 20.99 \qquad F_{0.05} = 11.70$$

T. Tukey's test showed that Chłopy (A) population had significantly lower PI than the remaining two populations.

Populations under study differed by a lack, or frequency of occurance of particular esterases. Only in Kalatówki (B) population characteristic band (0.48-u) was found in the first and the third term. Furthermore, this population was characterized by high frequency of band 12-c, lack of 0.39-p, and low frequency of 0.19-f and 0.37-o. In Rożnowo (C) population band 0.14-d occured in 100%, band 0.31-k was characterized by high frequency, and there were no bands 0.21-g and 0.35-u. Chłopy (A) population was characterized by a lack of band 0.16-e.

Chłopy (A) differed from Kalatówki (B) population by five bands (0.16-e, 0.31-k, 0.32-l, 0.39-p, 0.48-u), and from Rożnowo (C) popula-

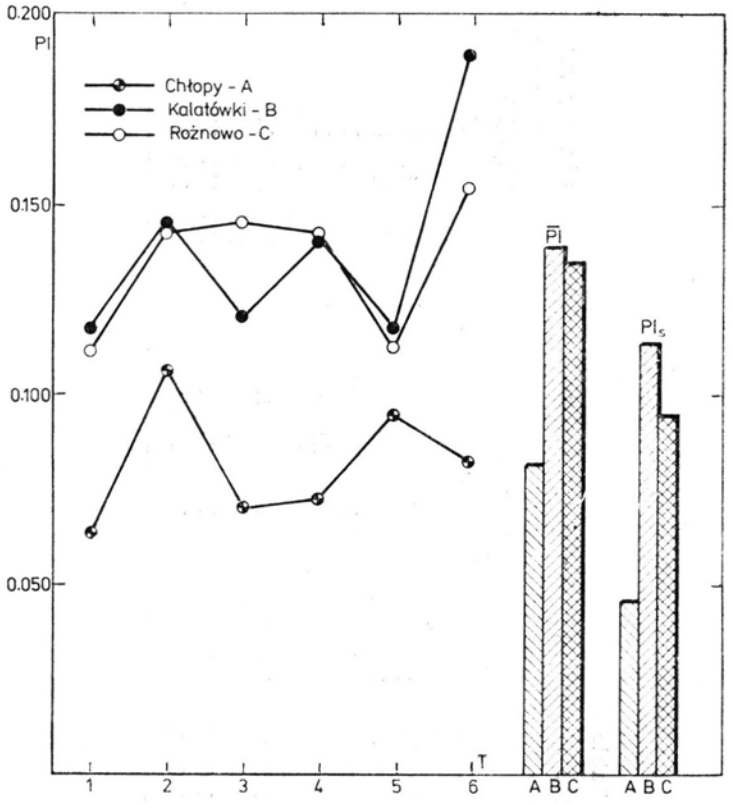

Fig. 4. Polymorphism index (PI) for successive terms (T), together with mean for a population ($\overline{PI}$), and for synthetic zymograms (PI_s) for esterases.

tion — also by five bands (0.16-c, 0.21g, 0.31-k, 0,32-l, 0.35-n). Kalatówki (B) differed from Rożnowo (C) population by four bands (0.21-g, 0.35-n, 0.39-p, 0.48-u).

Chi-squared test showed that these populations possessed specific esterase spectra:

$$\chi^2_E = 119.098 \qquad \chi^2_{0.05} = 43.773$$

3. Acid phosphatases (PH)

As regards acid phosphatases, variability in the three populations is presented in Fig. 5 and Table 3. In the six stages of plant development only band 0.21-g was always present; the remaining ones occured with different frequency. Attention should be given to lowered activity of acid phosphatases in the third term in population from Kalatówki (B) and Rożnowo (C). In Chłopy (A) population lowered activity of PH was observed in the third and the fourth term. Two final developmental

Table 3

Frequency of acid phosphatases bands (in per cent) in the three populations in particular terms of analyses, and upon synthetic zymograms

Band	Chłopy — A						Kalatówki — B						Rożnowo — C						Synthetic zymogram		
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	A	B	C
0.04-a	0	0	0	0	60	100	0	0	0	0	0	0	0	100	0	83	87	83	100	0	100
0.08-b	0	0	0	0	0	0	10	0	0	0	0	0	100	0	0	23	7	17	0	10	100
0.10-c	100	60	0	0	100	100	100	0	0	0	15	47	100	92	0	0	30	93	100	100	100
0.13-d	0	0	0	0	0	0	43	0	0	53	37	0	0	67	0	100	33	27	0	70	100
0.15-e	57	0	0	0	73	0	90	71	0	100	44	47	83	75	0	10	27	60	90	100	100
0.19-f	0	100	0	0	30	100	0	3	0	0	89	0	83	0	0	0	13	0	100	89	83
0.21-g	100	100	100	100	100	100	97	100	100	97	100	90	100	100	100	100	100	100	100	100	100
0.23-h	0	0	0	0	0	100	0	0	0	0	0	0	0	0	0	0	0	0	100	0	0
0.30-i	0	12	27	0	100	100	0	0	0	100	100	30	0	3	0	100	50	57	100	100	100
0.34-j	0	0	0	0	100	100	0	0	0	90	100	23	0	7	0	100	13	57	100	100	100

stages were characterized by higher activity of isoenzymes of acid phosphatases, this being expressed by colouration of higher number of bands upon gel.

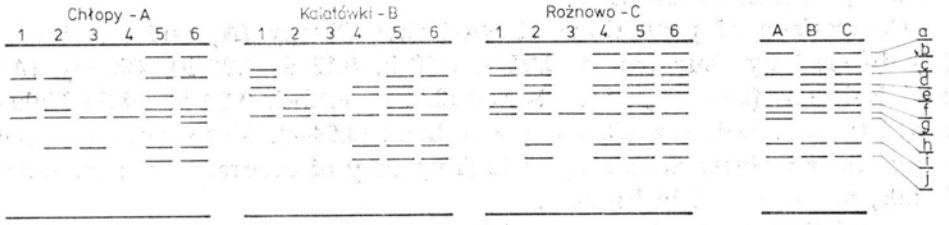

Fig. 5. Zymograms of qualitative variability of acid phosphatases between particular terms in the same population, and between populations.

Variability (PI) within populations in the six terms is presented in Fig. 6. As it is seen, Kalatówki (B) and Rożnowo (C) populations were least variable in the third term, whereas Chłopy (A) — in the fourth and sixth term (PI = 0.000). With respect to polymorphism index, the highest differences between populations were noted in the first and last term, the least — in the second term.

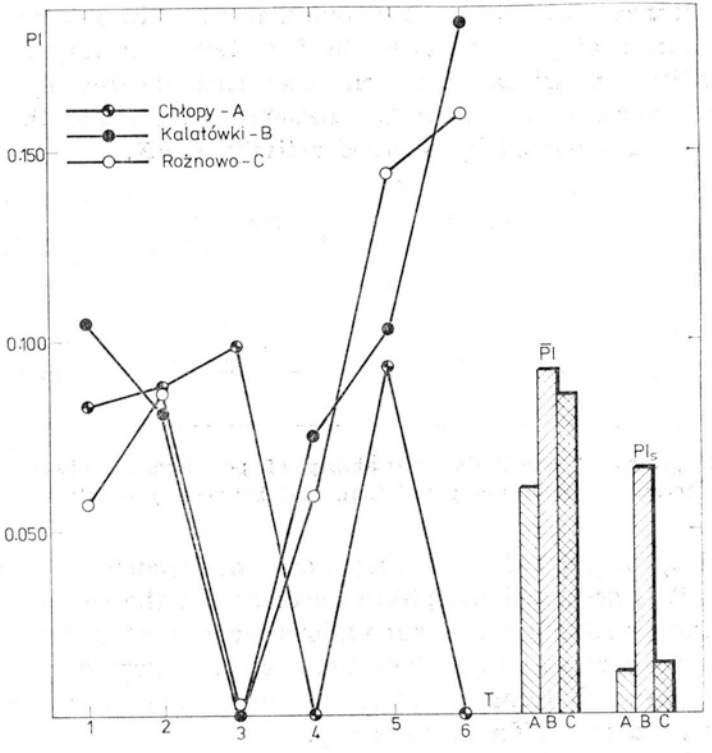

Fig. 6. Polymorphism index (PI) for successive terms (T), together with mean for a population ($\overline{PI}$), and for synthetic zymograms (PI_S) for acid phosphatases.

Kalatówki (B) population was the most variable one, as reflected by PI_s values for the synthetic zymogram, as well as average $\overline{PI}$ from the six terms. PI values for particular terms and populations did not show significant differences.

Comparison of populations showed that Chłopy (A) and Kalatówki (B) differed by four bands (0.04-a, 0.08-b, 0.13-d, 0.23-h), Chłopy (A) and Rożnowo (C) — by three bands (0.08-b, 0.13-d, 0.23-h) while Kalatówki (B) and Rożnowo (C) — by one band (0.04-a). Moreover, the three populations differed with respect to frequency of occurance of particular bands, as presented in Table 3.

Populations were characterized by specific patterns of acid phosphatases:

$$\chi^2_{PH}=119.084 \qquad \chi^2_{0.05}=28.869$$

4. Peroxidases (PX)

Qualitative variability between particular terms is demonstrated in Fig. 7, and differences in band frequency are given in Table 4. In Chłopy (A) population the highest number of bands was found in the first two terms. Kalatówki (B) population was characterized by the largest spectrum of peroxidases in the first term, contrary to Rożnowo (C) population, in which this term was characterized by the least number of bands. In the three populations under study the two last terms were characterized by lowered activity of PX.

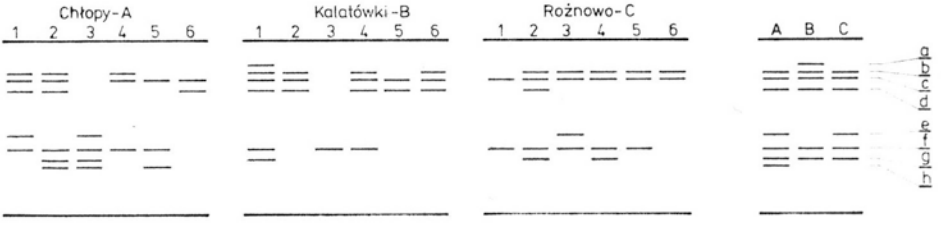

Fig. 7. Zymograms of qualitative variability of peroxidases between particular terms in the same population, and between populations.

Variability in populations during plant development is presented in Fig. 8. As it is seen, polymorphism decreased in the second and third term. In the remaining terms populations were more variable, and the differences with respect to PI between particular populations were the highest in the sixth term. PI values between terms, and mean PI for populations, did not differ significantly.

Qualitative comparison between populations showed that Chłopy (A) and Kalatówki (B) differed by three bands (0.08-a, 0.28-e, 0.35-g),

Table 4

Frequency of peroxidases bands (in per cent) in the three populations in particular terms of analyses, and upon synthetic zymograms

Band	Chłopy — A						Kalatówki — B						Rożnowo — C						Synthetic zymogram		
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6	A	B	C
0.08-a	0	0	0	0	0	0	13	0	0	0	0	0	0	0	0	0	0	0	0	13	0
0.10-b	67	100	0	27	0	0	47	100	0	27	0	33	0	8	17	100	23	17	100	100	100
0.12-c	93	96	0	100	100	100	70	89	0	83	100	33	30	100	7	43	100	100	100	100	100
0.15-d	30	90	0	0	0	30	60	93	0	23	100	23	0	80	0	0	0	0	90	100	80
0.28-e	27	0	100	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	100	0	3
0.32-f	100	3	100	60	3	0	83	0	100	27	0	0	100	25	100	83	57	0	100	100	100
0.35-g	0	3	3	0	0	0	23	0	0	0	0	0	0	8	0	3	0	0	7	23	10
0.37-h	0	3	10	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0

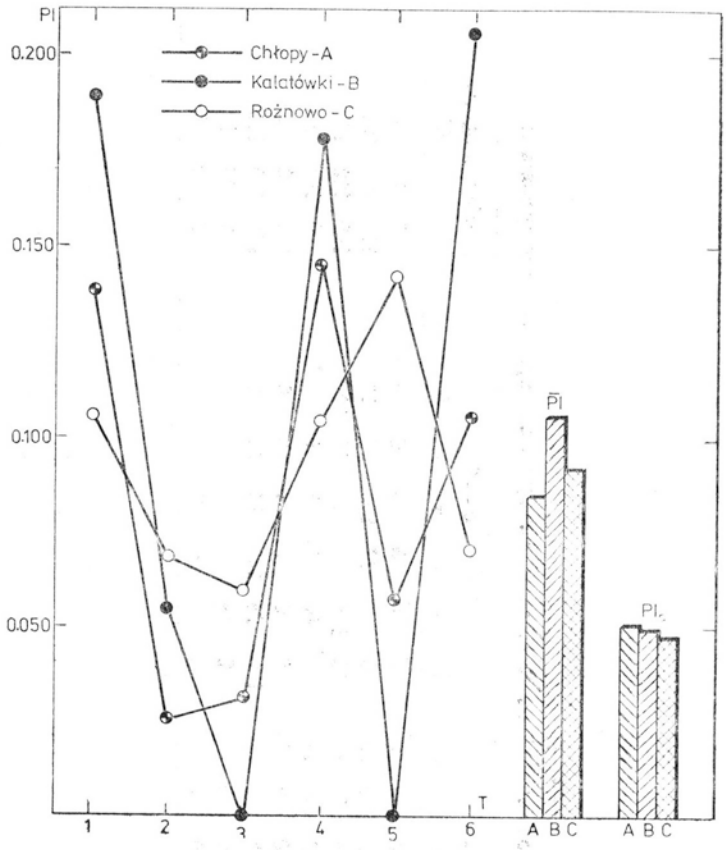

Fig. 8. Polymorphism index (PI) for successive terms (T), together with mean for a population ($\bar{PI}$), and for synthetic zymograms (PI_s) for peroxidases.

Chłopy (A) and Rożnowo (C) — by one band (0.37-h), and Kalatówki (B) and Rożnowo (C) — by two bands (0.08-a, 0.28-e).

Similary as for previous enzymatic pattern, it was shown that the populations possessed characteristic spectra:

$$\chi^2_{PX} = 126.351 \qquad \chi^2_{0.05} = 24.996$$

DISCUSSION

Analyses of enzymatic patterns in the three populations of woundwort, originating from different geographic regions of Poland, showed that there exists qualitative variability during plant development. In successive terms various enzymatic patterns were observed in the same plant individuals. This fact should be connected with different enzymatic activity, characteristic for particular stages of plant development. As it is supposed, this activity is determined genetically since the plants

developed in similar conditions. Similary, it was found in *Festucca* (Nelson et al., 1975) that characteristic enzymatic activity in six populations was determined genetically. Appearance of differences during plant development can be explained by differences in the genetic structure (seeds were sown at the same time, and culture conditions were similar). Abbot (1975) pointed out that differences between morphological features during the development of *Senecio vulgaris* seeds had a genetic background.

In the second and third term (January, February) lower activity of enzymes was observed. It is possible that this results from lower light intensity and shorter day connected with particular stages of plant development.

The main scope of this work was to define the most characteristic stage of plant development, suitable for comparative studies. The results point to the fact that in order to obtain full picture of the variability of enzymatic proteins in woundwort populations, it is necessary to characterize them in particular developmental stages (terms). Terms of analyses should fall into first stages of development or shortly before blooming since at these terms the highest number of informations is obtained at the highest variability.

Furthermore, an attempt was made to initially determine variability between populations from different geographic regions of Poland. The results showed that the populations under study are different, as proved by chi-squared test for large samples:

$$\chi^2_{\text{enz. pattern}} = 117.908 \qquad \chi^2_{0.05} = 12.592$$

Any more detail analysis of the inter-population variability was not possible due to low number of populations. In order to obtain full picture of variability between populations it would be necessary to study more populations, as presented in the second part of this paper.

This work was undertaken within the frames of branch problem 09.7-3.2.2.

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Zmienność układów enzymatycznych w naturalnych populacjach Anthyllis vulneraria s.l. z trzech regionów geograficznych Polski. Cz. I. Zmienność układów enzymatycznych w trzech populacjach przelotu w czasie rozwoju roślin

Streszczenie

W czasie rozwoju roślin trzech populacji *Anthyllis vulneraria* z trzech regionów geograficznych Polski obserwowano zmienność białek enzymatycznych, a w populacjach różny polimorfizm. Każda z badanych populacji miała charakterystyczne spektrum rozdzielonych układów enzymatycznych.