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# Recession of *Tussilago farfara* (L.) population from the agrocoenose as a result of cultivation abandonment. I The effect of fallowing on population dynamics

ANNA NAMURA-OCHALSKA

Department of Phytosociology and Plant Ecology, Institute of Botany, Warsaw University,
Al. Ujazdowskie 4, 00-478 Warsaw, Poland

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## Abstract

The paper evaluates the effect of fallowing on seasonal and multiyear dynamics, as well as on the spatial structure of *Tussilago farfara* population. In four years turfing and rapid increase in the size of grass populations — those of *Agropyron repens* (L.) PB. and *Dactylis glomerata* caused the elimination of *Tussilago farfara* population. The studies have showed that a decrease in the population size resulted from hampering of both vegetative and generative reproduction. The interspecific competition for available space seems to be a crucial factor limiting emergence of new shoots. In the agrocoenose big population size of *Tussilago farfara* remained throughout the studies.

*Key words: Tussilago farfara, fallowing, population dynamics, spatial structure of a population, species biomass and cover*

## INTRODUCTION

Population establishment under worsening environmental conditions depends upon biotope-phytocoenotic relations. In species capable of vegetative and generative reproduction unfavourable effect of their environment leads rather to limitation of plant reproduction than to an increase in its death risk (Harper and Ogden 1970, Stebbins 1971, Werner 1972, 1977, Kays and Harper 1974, Kawano 1975, Turkington and Harper 1979a, Trathan 1983 and others).

It is commonly known that populations of the same species in different ecological systems show considerable differentiation both in generative and vegetative reproduction (Falińska 1969a, b, 1970, 1977, 1979a, b, c, 1981, McArthur and Conell 1971, Watts 1974, Andel and Vera 1977, Bostock 1980). From many studies it can be inferred that phytocoenotic factors, mainly interspecific competition for environmental resources, play an important role in the realization of reproductive potential (Zarzycki 1965a, b, Baskin and Baskin 1979, Werner 1980, Law 1981). Again they mostly determine the importance of one or the other reproductive mode in population regeneration. Usually, the fraction of vegetative as related to that of generative offspring grows with an increase in vegetation cover. In very compact communities the factor of interspecific competition may lead to the inhibition of reproductive processes and to the elimination even of expansive species – dominants at early successional stages and in loose communities (Zarzycki 1968, Bazzaz 1969, 1975, Grime 1979, Barkham 1980). This problem forms the subject of a present paper. The work aims at the explanation of causes and an analysis of the course of regression of *Tussilago farfara* population from arable fields recently abandoned. The studies comprise: 1) four-years' and seasonal changes in size and spatial structure of the population, 2) the rate of emergence and death of shoots in successive growing seasons, and 3) changes in the species composition of communities, as well as in quantitative relations between individual species in successive years of fallowing. The data studied were related to those obtained in the analysis of the same properties of *Tussilago farfara* population in adjacent arable field, so under similar soil and climate. It has enabled to determine unequivocally the effect of biocoenotic factors on the dynamics and structure of a population of the species studied.

The work is a part of wider studies on the biology of *Tussilago farfara* in various ecological systems (Namura-Ochalska 1987).

## SUBJECT AND METHODS OF THE STUDY

*Tussilago farfara* reproduces both vegetatively and generatively. In a growing season it flowers in early spring before leaf development. It exhibits rapid sequence of phenological phases: flowering, fruit maturation, and germination. Achenes are nondormant. Radicle and cotyledons form already in 24 hours after sowing. The further growth results in the formation of adventitious roots, leaves and rhizomes (Fig. 1). Under favourable conditions vegetative propagation takes place already in the first growing season – rhizomes give new leafed shoots. Primordia of generative shoots form in autumn, but they grow further as late as early spring when generative shoots with flower heads develop.

Field studies were conducted in 1982-1985 in the Mazury, in the neighbourhood of Nidzica. In an arable field where *Tussilago* was a dominant weed two 2 × 25 m study areas were located 50 m apart. They were divided into 200 0.25 $m^2$ plots. One of the areas was fallowed. A short characteristics of soil and vegetation in successive years of studies are given in Tables 1 and 2.

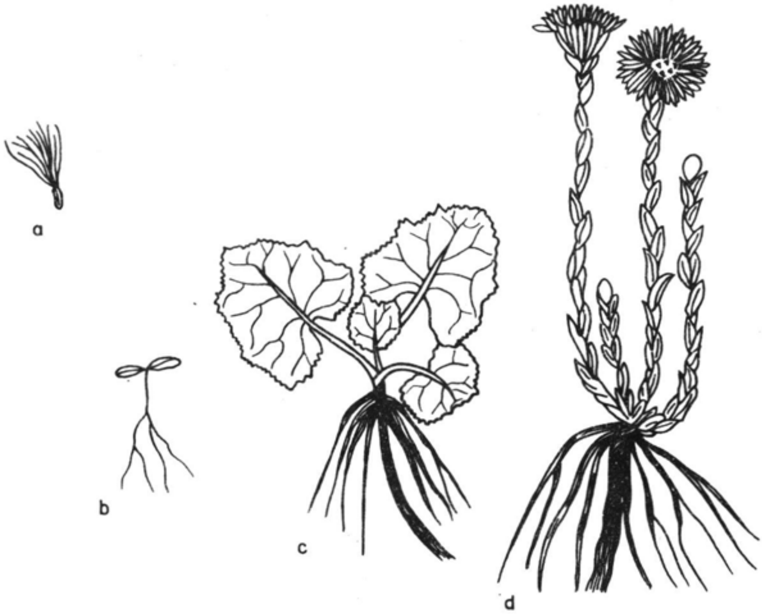

Fig. 1 *Tussilago farfara* – developmental phases: a – achene, b – seedling, c – leafed vegetative shoot, d – generative shoots with flower heads

Each year, from April till October in the fallow, and from May till August in the agrocoenose, in each plot all generative and vegetative colsfoot shoots were counted. Also all basic statistical characteristics were calculated, namely, mean density, standard deviation and coefficient of variation. The method of interval estimation at 5% error risk was applied to find whether differences in mean density values were significant. On the grounds of the shoot number

Table 1

Soil characteristics in study areas*

| Properties | Mean values |
|---|---|
| pH in $H_2O$ | 7.8 |
| pH in KCl | 7.4 |
| Humus content (%) | 4.0 |
| $CaCO_3$ content (%) | 32.9 |
| Carbon content (%) | 2.1 |
| Metal cation content**: $Ca^{+2}$ | 107.6 |
| $Mg^{+2}$ | 2.7 |
| $K^{+}$ | 0.5 |
| $Na^{+}$ | 0.8 |
| Total metal cation content S** | 112.8 |
| Hydrolytic acidity $H_h$** | 5.1 |
| Exchange capacity of soil T** | 117.9 |
| Degree of soil exchange saturation with bases $V_s$** | 95.7 |

* Due to insignificant differences in soil properties between study areas only mean values are given.

** In $m \cdot e \cdot 100g^{-1}$ soil.

Table 2

Species cover in the study areas with *Tussilago farfara* in successive study years

| Species | Fallow | | | | Agrocoenose | | | |
|---|---|---|---|---|---|---|---|---|
| | 1982 | 1983 | 1984 | 1985 | 1982 | 1983 | 1984 | 1985 |
| *Agropyron repens* (L.) PB. | 4 | 4 | 4 | 3 | 2 | 2 | 1 | 1 |
| *Tussilago farfara* L. | 4 | 3 | 2 | + | 4 | 4 | 3 | 4 |
| *Dactylis glomerata* L. | 2 | 2 | 3 | 5 | 1 | 1 | 1 | 1 |
| *Cirsium arvense* (L.) Scop. | 2 | 2 | 1 | 1 | 2 | 1 | 2 | 1 |
| *Taraxacum officinale* Weber. | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| *Trifolium repens* L. | 1 | 1 | 1 | 1 | + | + | + | + |
| *Medicago lupulina* L. | 1 | 1 | 1 | + | + | 1 | 1 | 1 |
| *Sinapis arvensis* L. | 1 | 1 | 1 | + | 1 | + | 1 | 1 |
| *Vicia cracca* L. | 1 | 1 | 1 | + | 1 | + | 1 | 1 |
| *Euphorbia helioscopia* L. | 1 | 1 | + | + | 1 | 1 | + | 1 |
| *Galium aparine* L. | 1 | 1 | + | + | + | + | + | 1 |
| *Equisetum arvense* L. | 1 | + | + | + | + | 1 | + | + |
| *Sonchus arvensis* L. | 1 | + | + | + | 1 | 1 | 1 | + |
| *Poa pratensis* L. | 1 | + | + | + | + | + | 1 | + |
| *Stachys palustris* L. | 1 | + | + | + | 1 | 1 | 1 | 1 |
| *Chenopodium album* L. | + | + | + | + | 1 | 2 | 1 | 1 |
| *Stellaria media* L. | + | + | + | + | + | 1 | + | + |
| *Silene alba* (Miller) E. H. L. | + | + | + | + | + | + | + | + |
| *Camelina sativa* (L.) Crantz. | + | + | + | + | + | + | + | + |
| *Viola arvensis* Murray. | + | + | + | + | + | + | + | + |
| *Buglossoides arvensis* (L.) I. M. | + | + | + | + | + | 1 | + | 1 |
| *Lapsana communis* L. | + | + | + | + | 1 | 1 | + | 1 |
| *Agrostis stolonifera* L. | + | + | + | + | + | + | + | + |
| *Myosotis arvensis* (L.) Hill. | + | + | + | r | + | + | + | + |
| *Artemisia vulgaris* L. | 1 | + | + | – | + | + | 1 | + |
| *Fagopyrum esculentum* Moench, Meth. | + | + | + | – | 5 | + | + | + |
| *Cerastium vulgatum* L. | + | + | + | – | + | + | + | + |
| *Consolida regalis* S. F. Gray. | + | + | + | – | + | + | + | + |
| *Fumaria officinalis* L. | + | + | + | – | + | + | + | + |
| *Plantago arenaria* Walds. Kit. | + | + | + | – | + | + | 1 | + |
| *Polygonum aviculare* L. | + | + | – | – | – | + | r | – |
| *Arenaria serpyllifolia* L. | + | + | – | – | + | + | + | + |
| *Ranunculus repens* L. | + | + | – | – | – | – | + | + |
| *Neslia paniculata* (L.) Desv. | + | + | – | – | 1 | + | 1 | 1 |
| *Trifolium pratense* L. | + | + | – | – | – | – | + | + |
| *Anagalis arvensis* L. | + | + | – | – | + | + | + | + |
| *Mentha arvensis* L. | + | + | – | – | – | + | + | + |
| *Veronica arvensis* L. | + | + | – | – | + | + | + | + |
| *Galium mollugo* L. | + | + | – | – | – | – | – | – |
| *Setaria viridis* (L). Beauv. | + | + | – | – | – | + | r | – |
| *Convolvulus arvensis* L. | – | + | r | – | + | + | + | + |
| *Veronica triphyllos* L. | + | – | + | – | + | + | – | + |
| *Rumex acetosella* L. | + | – | + | – | – | – | + | r |
| *Capsella bursa-pastoris* (L.) Medicus | + | r | – | – | – | – | – | – |
| *Erisimum cheiranthoides* L. | + | – | – | – | + | + | – | + |
| *Potentilla anserina* L. | + | – | – | – | + | + | + | – |
| *Galeopsis tetrahit* L. | + | – | – | – | + | + | + | + |
| *Conyza canadensis* (L.) Cronq. | + | – | – | – | – | – | – | – |
| *Leucathemum vulgare* Lam. | + | – | – | – | – | – | – | – |
| *Avena sativa* L. | – | + | – | – | – | 5 | 5 | 5 |
| *Linaria minor* L. | – | + | – | – | + | + | + | – |
| *Anchusa arvensis* (L.) Bieb. | – | – | + | – | – | – | + | r |

seasonal and multiyear population dynamics was assessed. Different study period on study and control sites was caused by agronomical practices in the arable field.

In the further analysis in both study areas 48 plots were demarced systematically (16 plots every 5 meters). Each month in each plot newly emerged shoots were labelled and mapped, while those which died were counted. The data enabled to follow the rate of shoot emergence and death in a growing season.

In full growing season, each year, the cover of all species accompanying *Tussilago farfara* in both areas were assessed. In the end of the studies (in August) in 48 plots chosen earlier above-ground shoots of all species were cut, then dried and weighed. In the analysis of dry weight distribution in both areas only species with their biomass equaled at least 5% of the total biomass were taken into account.

## RESULTS

### CHANGES IN POPULATION SIZE OF *T. FARFARA* IN FOUR-YEARS' CYCLE

Cultivation abandonment resulted in almost total elimination of *Tussilago* population. The cover of a population in the fallow, as related to that in the arable field was in successive years: 84.2%, 71.0%, 22.2% and 7.1%, respectively (Fig. 2). In four years of the study density of vegetative shoots in the fallow decreased over 45 times: from 15.0 ± 7.6 in the first season to 0.3 ± 0.8 0.25 $m^{-2}$ in the last study year (Fig.3). A decrease in the number of vegetative shoots is accompanied by 60-fold diminution of the fraction of flowering shoots.

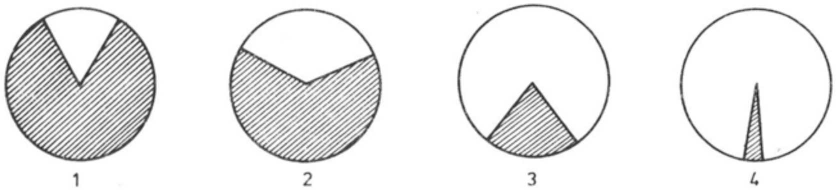

Fig. 2. The size of *Tussilago farfara* population in the fallow as related to the agrocoenose. 100% — population size of *Tussilago farfara* in the agrocoenose, dark sector — population size of *Tussilago farfara* after cultivation abandonment

In the agrocoenose in four growing seasons both increase and decrease in shoot density were noted, it was higher in 1982 and 1984, amounting to 18.8 ± 6.4 and 7.9 ± 7.5 for vegetative phase, and 11.5 ± 6.3 and 9.2 ± 3.9 for generative phase.

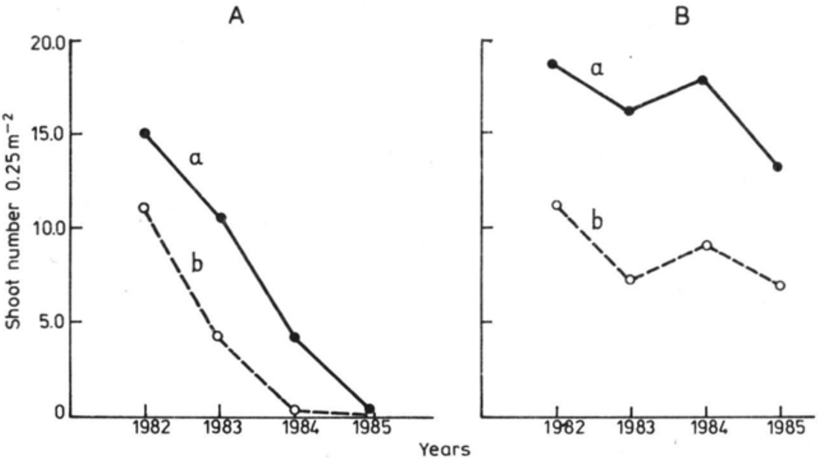

Fig. 3. Changes in population size of *Tussilago farfara* in the fallow (A) and in the agrocoenose (B) in four study years: a — vegetative shoots, b — generative shoots

### SEASONAL CHANGES IN POPULATION SIZE OF *T. FARFARA*

In both study areas significant differences both in the course of seasonal dynamics and mean density were found (Fig. 4). In the begining of growing season (March, begining of April) a population was represented only by

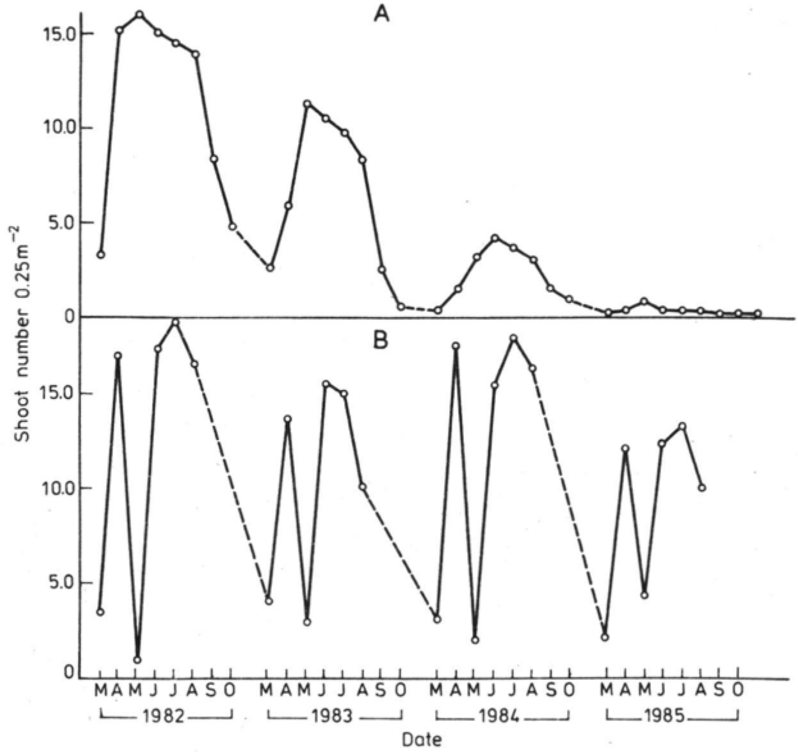

Fig. 4. Seasonal population dynamics of *Tussilago farfara* in the fallow (A), and in the agrocoenose (B)

generative shoots which number depended upon the number and size of vegetative shoots of a previous year. In spring (April, May) also vegetative shoots emerged besides flowering shoots. Further changes in population size during growing season depended upon the emergence and death of vegetative shoots.

In each year the curves of population dynamics in the fallow were characterized by a rapid increase and decrease only in the initial and final period of a growing season. Rapid development of generative shoots enabled to reach the maximun already in spring. Gradual changes in population size in the full of growing season are governed by continuous emergence of vegetative shoots, first accompanied by the process of elimination of generative shoots, whereas a decrease in shoot number in autumn is caused by intense death of all vegetative shoots.

In the agrocoenose life cycle of *T. farfara* is disturbed by agronomical practices. They damage the population in spring (ploughing) and summer (harvest). Hence, the curve of population dynamics is bimodal, with spring and

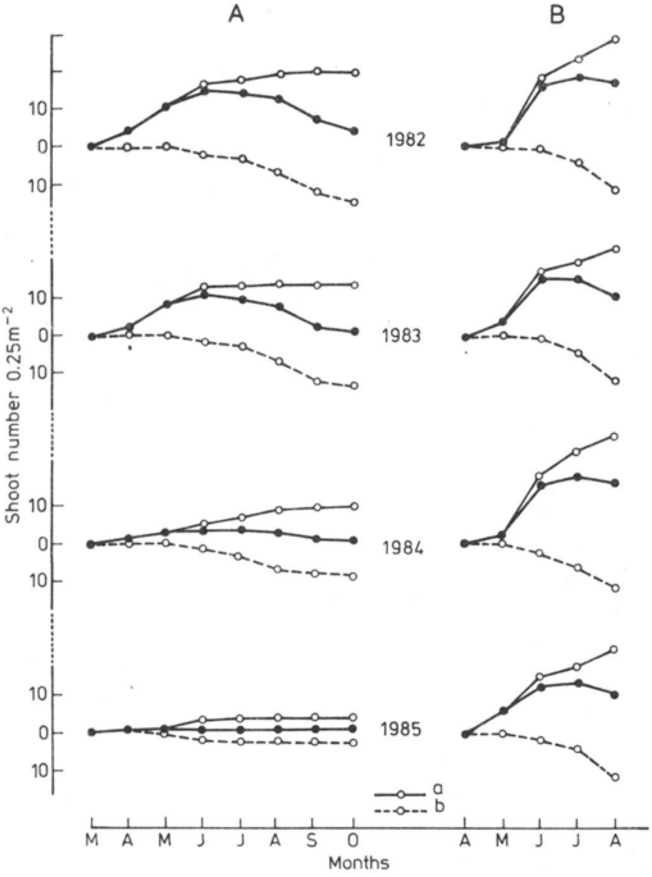

Fig. 5. Seasonal rate of emergence and death of *Tussilago* vegetative shoots in the fallow (A) and in the agrocoenose (B) in four successive years: a — cumulative propagation of vegetative shoots, b — cumulative death of vegetative shoots

summer maximum. The density of *Tussilago* shoots in the agrocoenose was high for the whole study period irrespective of the course of dynamics curve.

The results of the studies showed that in the agrocoenose the rate of the turnover of vegetative shoots was much higher than that in the fallow (Fig. 5). In successive years there were 8, 9, 13 and 19 shoots more per 0.25 $m^2$ in the agrocoenose than in the fallow. Contrary to uncultivated area, where most shoots appeared in May and June, the effectivity of vegetative propagation in the agrocoenose was high throghout the whole life period of plant above-ground parts. The process of shoot elimination began in two analysed areas at the same time, but it was more intense in the agrocoenose.

## CHANGES IN SPATIAL STRUCTURE OF *TUSSILAGO FARFARA* POPULATION

With a decrease in population density in successive years of fallowing the mode of shoot distribution in space also changed (Fig. 6). In the first study year in 200 0.25 $m^2$ plots 100% frequency was found. Shoot density distribution was similar to the normal distribution. With the fallowing the fraction of plots with the lowest density values and those with no shoots increased exponentially whereas the number of plots with the highest density values decreased. In four-year-old fallow plots with no shoots were as many as 85%, while in the remaining 15% at most five shoots grew. In the analysed plots no significant correlation was found between density of vegetative shoots in successive years, correlation coefficients amounted to $-0.02$, $-0.07$, $+0.10$, $+0.03$, respectively.

The interpolation maps of population density indicated that throughout the studies there was a mosaic of shoot aggregations and thinnings (Fig. 7). With the fallow colonization by *Dactylis glomerata* (L.) and *Agropyron repens* (L.) PB. the aggregation number and size, as well as the area they occupied decreased. Such results indicate close relationship between shoot distribution and the size of available space. The process of elimination of *T. farfara* shoots took place firstly in sites highly turfed.

## QUALITATIVE AND QUANTITATIVE CHANGES IN COMMUNITY STRUCTURES AFTER CULTIVATION ABANDONMENT

The recession of Tussilago population after cultivation abandonment was caused by still more pronounced presence of grasses, *D. glomerata* and *A. repens.* For four study years in the fallow the process of replacement of dominants took place (Fig. 8). In the first year of fallowing, although the proportion of *Agropyron* increased, colsfoot still dominated. In the next two years a rise in *Agropyron* cover was accompanied by a decrease in that of *Tussilago.* Also *D. glomerata* population size gradually increased, its expansion led to almost entire colonization of the fallow in the fourth year of fallowing. Again during the studies in this area over seventy times diminution of *Tussilago* biomass was noted, being in the last growing season only 0.5% of the total species biomass.

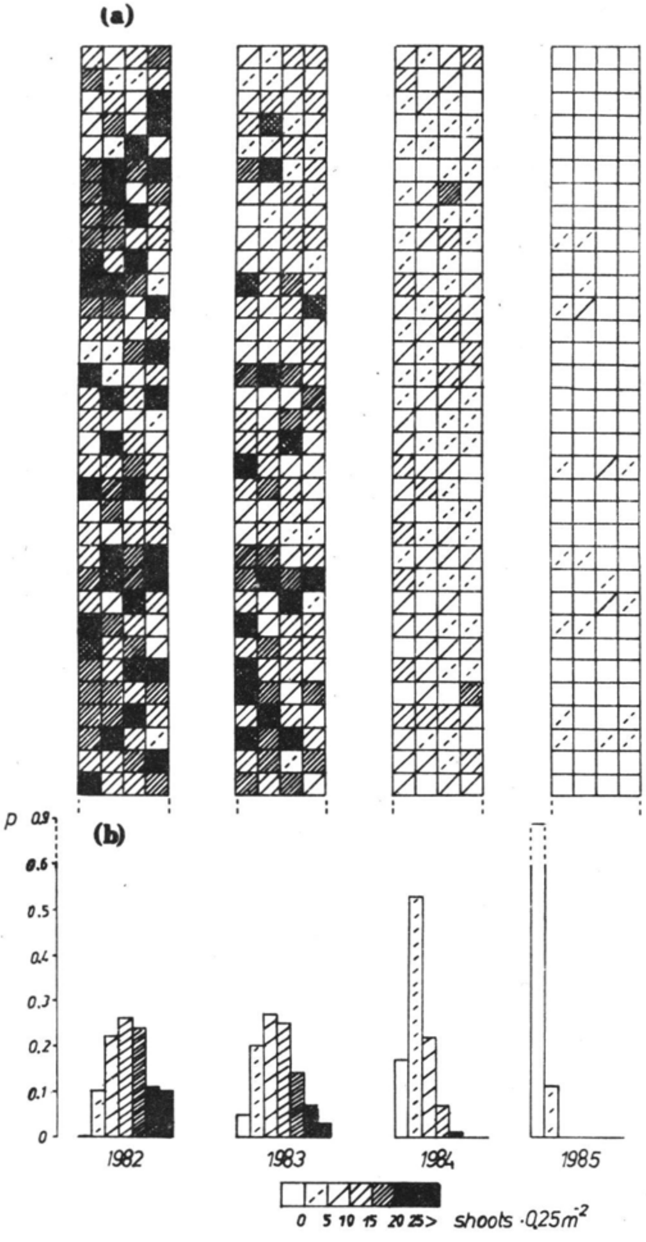

Fig. 6. Cartogram (a) and frequency distribution (b) of density of *Tussilago* shoots per 0.25 m$^2$

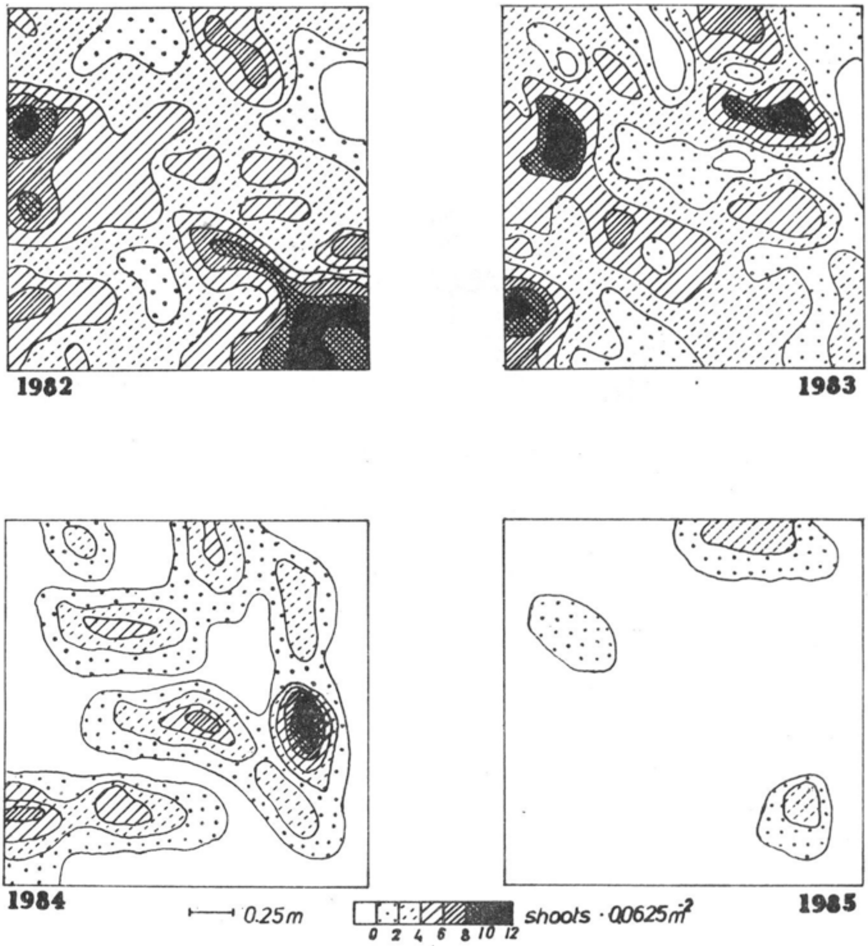

Fig. 7. Decrease in the size of *Tussilago farfara* population and change in its spatial structure in successive years of fallowing

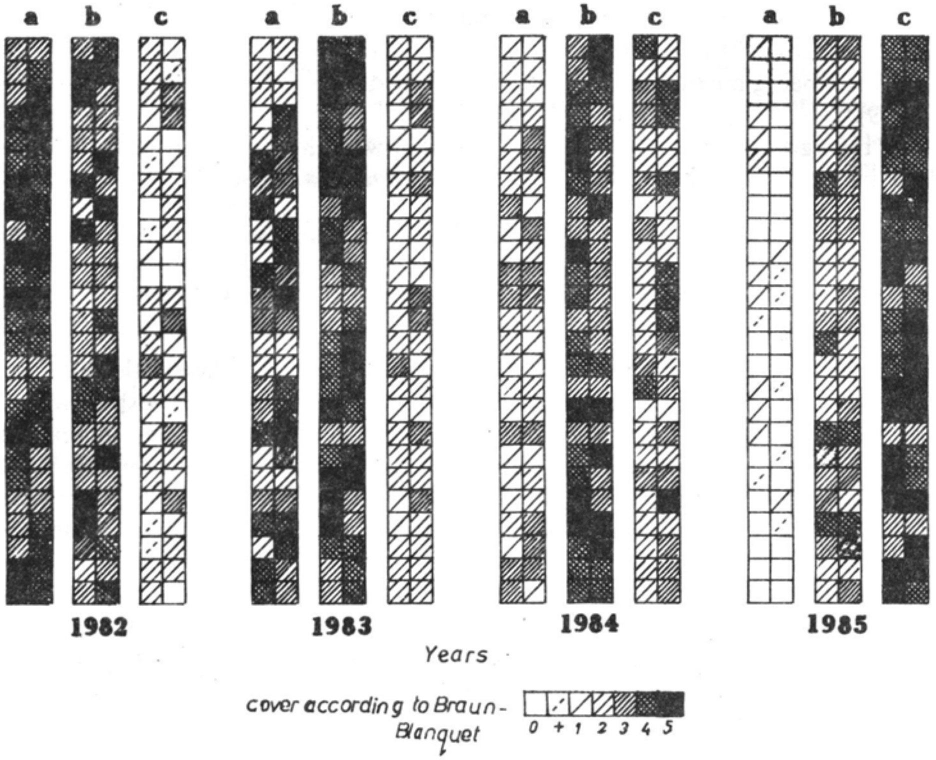

Fig. 8. Changes in cover of three dominant species: a — *Tussilago farfara*, b — *Agropyron repens*, c — *Dactylis glomerata*

An increase in the cover of *D. glomerata* and *A. repens* was also accompanied by a decrease in the number and proportions of other phytocoenose components (Table 2). From among 52 species noted in the fallow throughout the studies only 24 remained till the last study year.

The changes in vegetation structure caused by four-years' overgrowing of

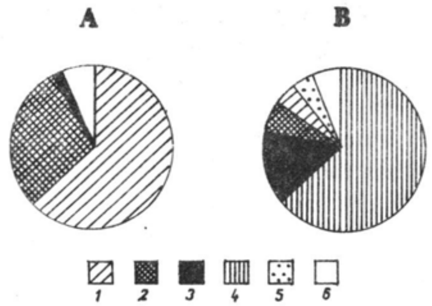

Fig. 9. Species biomass percentage in the four-year-old fallow (A), and in the agrocoenose (B). 1 — *Dactylis glomerata*, 2 — *Agropyron repens*, 3 — *Tussilago farfara*, 4 — *Avena sativa*, 5 — *Cirsium arvense*, 6 — species with their biomass not exceeding 5% of the total biomass

old field led to the formation of the phytocoenose where merely two species accounted for 90% of the total biomass, the percentage of dominant, *D. glomerata*, being more than 60%, while that of subdominant (*A. repens*) – 30% (Fig. 9).

In the agrocoenose *T. farfara* is a dominant weed in each growing season. In 1985 its proportion in the total species biomass was 14.5%.

## DISCUSSION

The results of the studies indicate rapid change in phytocoenotic relations after the cultivation abandonment which has been caused by the expansion of two grass species: *Agropyron repens* and *Dactylis glomerata*. Increasing proportion of both grasses gave, already in the first growing season 100 % of their cover and resulted in the turfing of the area growing bigger each year which affected unfavourably *Tussilago farfara* population. Because of undergoing changes the latter was eliminated merely in four years of fallowing, even though in the agrocoenose it was still a dominant weed.

The establishment of a population under changing phytocoenotical conditions depends mainly on biology of co-habiting species, especially on their growth form (Cahn and Harper 1976, Werner 1976, 1980, Harper 1981, Trathan 1983, Harper 1986). A decrease in the shoot density of *T. farfara* in the first year after cultivation abandonment was caused mostly by an increase in *Agropyron* cover, which formed in a top soil layer compact stolon mat. The four-year-old fallow was in turn occupied by *D. glomerata*. This grass possesses a strong root system which together with tussock form of growth determines its high competitive ability (Ralski 1965, Kreuz et al. 1970). *T. farfara* exhibits rapid rhizome growth but their proportion in the soil unit volume is small. The species with such a mode of growth show tendency to occupy space quickly, but also to retreat fast under the stress of later colonizers (Lieth 1960, Werner 1976, Harper 1977, 1981). Hence, it might be concluded that the competition for available space takes place mainly below the ground. Fine and fragile *Tussilago* rhizomes are not able to grow through a dense and thick layer of stolons and root systems of dominant grasses. So root competition is a crucial agent in the recession of *T. farfara* population. It is worth noting that in the analysed fallow also mechanical damage of *Tussilago* rhizomes caused by *Agropyron* stolons was found.

The results suggest that the retreat of colsfoot population results from the lack of available space also on the ground. The space necessary for the functioning of a population decreases due to increasing turfing of the fallow. The size of the available area affects both shoot density and spatial structure of *T. farfara* population. Similar response to an increase in interspecific competition was found in many species, annuals, biennials and perennials (Symonides 1974, 1979a, b, c, 1986, Falińska 1977, 1979a, b, c, 1981, Turkington and Harper 1979a, b, Gross 1980, Werner 1980).

Effective propagation of *Tussilago* shoots in the fallow may be successful only before the full development of dominant grass species. Hence close relation was found between shoot density and the size of available space.

No correlation was found between colsfoot vegetative shoot density in plots in successive study years. The occurrence of large, compact aggregations of *Tussilago* in one year does not guarantee the emergence of new shoots in the next growing season.

Compact vegetation cover in the fallow also results in an absence of generative reproduction, in spite of high diaspore germinability (Namura-Ochalska 1987). With no space for their germination diaspores die in four months after dissemination. Seedlings, which appear occasionally under the conditions of strong competition are eliminated before they are able to form leaves and rhizomes. It should be noted that also a decrease in diaspore production takes place with the fallowing, owing to decreasing in years density of generative shoots.

However, the obtained results suggest that the competition for light plays only indirect role. Shading of *T. farfara* shoots by 1 m high grass layer, alhough probably affects unfavourably their development, does not directly cause increased shoot mortality shortly after the cultivation abandonment. Such statement seems to be supported by a successful development of *Tussilago* in the agrocoenose. Shading of colsfoot shoots by cultivated plants does not significantly decrease their density. The population abundance in the arable field remains high throughout the studies.

From the studies it may be inferred that a decrease in the density of both vegetative and generative shoots of *Tussilago* in the fallow is caused by the inhibition of both reproduction modes. At the annual growth cycle of above-ground parts and fairly rapid rhizome dying, the hampering of the emergence of new shoots inevitably leads to the death of individuals, and in consequence to the regression of the population.

Summing-up, the studies on the recession of *Tussilago farfara* population from the agrocoenose after cultivation abandonment have showed that interspecific competition is a crucial agent which inhibits both vegetative and generative reproduction, which agrees with the results obtained by Bakker (1960), and Krylova and Kaporova (1983). It should be stressed that intensity of interspecific competition increases under favourable habitat conditions; in poorer habitats the process of species replacement would last probably much longer (cf. Zarzycki 1965a, b, Ågren and Fagerström 1980, Werner 1980).

The studies have also showed that the proportions of other phytocoenose components are strongly limited due to the turfing increasing in years. The number of species in four-year-old fallow is halved compared to the agrocoenose, while the proportion of *D. glomerata* is as high as 60% and that of *A. repens* – 30% of the total biomass.

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# *Wycofywanie się populacji Tussilago farfara (L.) z agrocenozy jako wynik zaprzestania uprawy. I. Wpływ ugorowania na dynamikę populacji*

## Streszczenie

Praca jest częścią szerszych studiów poświęconych wycofywaniu się populacji *T. farfara* L. z agrocenozy po zaprzestaniu uprawy. Celem badań było wyjaśnienie przyczyn i zbadanie przebiegu procesu eliminacji podbiału. Zakres badań obejmował analizę czteroletnich i sezonowych zmian liczebności i struktury przestrzennej populacji, szybkości pojawu i wymierania pędów oraz zmian składu gatunkowego i stosunków ilościowych w kolejnych latach badań. Badania prowadzono w latach 1982-1985 na Mazurach w okolicach Nidzicy. Na polu uprawnym założono dwie powierzchnie badawcze, każda o rozmiarach 2 × 25 metrów, przy czym jedną z nich zaprzestano uprawiać. Powierzchnie podzielono na 200 stałych poletek badawczych. Zwięzłą charakterystykę warunków glebowych oraz spis roślinności w kolejnych latach badań zawierają tabele 1 i 2. Najistotniejsze fazy rozwoju osobników *T. farfara* ilustruje rys. 1. Na podstawie zagęszczenia pędów *T. farfara* oceniono wieloletnią i sezonową dynamikę liczebności populacji. Szczegółowa rejestracja pędów umożliwiła natomiast prześledzenie tempa ich pojawu i wymierania.

W celu analizy zmian stosunków fitocenotycznych, oszacowano w pełni sezonu wegetacyjnego pokrywanie wszystkich gatunków. Badania wykazały: 1) spadek zagęszczenia zarówno wegetatywnych, jak i generatywnych pędów *T. farfara* w kolejnych latach po zaprzestaniu uprawy (rys. 2 i 3); przy czym jego intensywność rośnie w miarę ugorowania (rys. 4); 2) nie stwierdzono wpływu śmiertelności pędów na proces wycofywania się populacji *T. farfara* z ugoru (rys. 5); 3) nie stwierdzono korelacji między zagęszczeniami pędów w kolejnych sezonach wegetacyjnych (rys. 6); 4) ścisłą zależność zarówno zagęszczenia pędów, jak i ich struktury przestrzennej od wielkości dostępnej powierzchni, gwałtownie malejącej wskutek wzrostu pokrywania *Dactylis glomerata* L. i *Agropyron repens* (L.) PB. (rys. 7 i 8); 5) całkowitą zmianę stosunków ilościowych w fitocenozie po czterech latach ugorowania, w wyniku której udział *D. glomerata* wyniósł aż 60%, a *A. repens* – 30% całkowitej biomasy (rys. 9).

Reasumując, badania wykazały, że bezpośrednią przyczyną wycofywania się populacji *T. farfara* jest zahamowanie obu typów reprodukcji spowodowane gwałtownym wzrostem konkurencji międzygatunkowej. Pierwszoplanową rolę wydaje się odgrywać konkurencja korzeniowa o wolną przestrzeń pod powierzchnią gleby.