EXPANSION OF *TUSSILAGO FARFARA* L. IN DISTURBED ENVIRONMENTS. I. POPULATION RENEWAL UNDER CONDITIONS OF PLANT COVER DESTRUCTION.

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ABSTRACT

The effectiveness of renewal of a *Tussilago farfara* L. population after destruction of the plant cover was studied. This process proceeded at a very intense rate mainly due to querilla type vegetative growth. In its successive years the renewing population was characterized by: 1) a dynamic spurt in the number of individuals in the first year after destruction, attaining a maximum the following year; 2) a complete lack of generative shoots in the first year; 3) high mortality of seedlings; 4) change in spatial structure; 5) increased differentiation in the way individual plants spread. Seven-year studies have shown that even drastic disturbances in the environment did not eliminate *T. farfara*, moreover, complete destruction of the plant cover created favourable conditions for population renewal.

KEY WORDS: population dynamics, seasonal changes in population density, spatial structure, clonal growth.

INTRODUCTION

Intensifying synanthropization of vegetation and the need to reclaim degraded biotopes using spontaneous colonizers have, most distinctly in recent years, drawn the attention of ecologists to the species of disturbed environments (Sebens and Thorne 1985, Gray et al. 1987, Symonides 1988, Cornelius 1990a, 1990b, Cornelius and Faensen-Thiebes 1990). The constant rise in the number and diversity of disturbed habitats creates ever new practically unlimited possibilities for constant expansion of these species. Regardless of the wide diversity of the environments disrupted by man, the most common occurrence is the conspicuous (mainly above-ground) disappearance of plant populations on them. The most important factor, then, in the permanent establishment of a species in a disturbed environment is its ability to renew its population in the period between disruptions.

The manner and effectiveness of renewal depend mainly on the biology of the given species (Cook 1985, Falińska 1989a, 1989b, 1991, Peart 1989a, 1989b, 1989c) as well as on the type and intensity of the disturbances (Bazzaz 1983, Mack and Pyke 1984, Begon et al. 1986).

From the evolutionary point of view, the ability to renew both from seeds found in the soil and from dormant nodes that survived the disturbance seems to be one of the adaptations allowing individuals to survive and function in disturbed environments (Armstrong 1982, Mortimer 1987).

A widely occurring species common to disturbed environments, which has two effective ways of reproduction, is the common coltsfoot. *Tussilago farfara* L. It is characterized by clonal growth and polycorm structure of individuals. Its following traits are worthy of noting (Fig. 1).

- a) a double life cycle – annual for shoots and perennial for the genet,
- b) the ability of each individual to undergo two extremely different forms of clonal growth – phalanx and querilla growth,
- c) morphological and functional shoot dimorphism,
- d) temporal separation of the vegetative and generative stages.

Fig. 1. Diagram of the *Tussilago farfara* development cycle. Stages of development: seed (s), seedling (se), juvenile (j1 - j2), vegetative (w), generative (g1-g3). Seed-derived individuals in the vegetative stage of development (w/g), rhizome-derived individuals in the vegetative stage of development (w/w). Rhizomes are marked with thick lines.

The purpose of this study was to analyze *T. farfara* population renewal under conditions of destruction of the vegetation cover.

The seven-year period of study encompassed an evaluation of changes in:

- a) population dynamics over a period of several years,
- b) seasonal population size,
- c) seedling and juvenile survival,
- d) spatial structure of the population,
- e) structure of individuals.

TABLE 1. Species cover on the rafting site in successive study years.

Species	1982	'83	'84	'85	'86	'87	'88
<i>Tussilago farfara</i> L.	3	+	4	5	3	2	3
<i>Cirsium arvense</i> (L.) Scop.	2	+	2	2	1	2	2
<i>Torilis japonica</i> (Houtt.) DC.	2	+	2	1	1	1	1
<i>Poa angustifolia</i> L.	2	+	2	1	1	1	1
<i>Calamagrostis epigejos</i> (L.) Roth.	2	-	1	2	3	2	2
<i>Arrhenatherum eliatum</i> (L.) Beauv. ex J. and C. Presl	2	-	1	2	2	2	2
<i>Festuca gigantea</i> (L.) Vill.	2	-	1	1	2	1	2
<i>Holcus lanatus</i> L.	2	-	1	1	2	1	1
<i>Ranunculus repens</i> L.	2	-	1	1	1	1	1
<i>Equisetum sylvaticum</i> L.	1	+	2	2	2	1	1
<i>Deschampsia caespitosa</i> (L.) Beauv.	1	-	1	1	2	2	2
<i>Taraxacum officinale</i> Weber	1	+	1	1	1	1	1
<i>Cerastium vulgatum</i> L.	1	-	1	1	1	1	1
<i>Arenaria serpyllifolia</i> L.	1	1	1	1	1	+	+
<i>Anemone ranunculoides</i> L.	1	1	1	1	1	+	+
<i>Poa trivialis</i> L.	1	-	1	1	+	+	1
<i>Agrostis stolonifera</i> L.	1	-	1	1	+	1	+
<i>Stellaria media</i> (L.) Vill.	+	-	1	1	+	+	+
<i>Rumex acetosella</i> L.	+	-	1	1	+	+	+
<i>Dryopteris filix-mas</i> (L.) Schott	+	-	+	+	+	+	+
<i>Anemone nemorosa</i> L.	+	-	+	1	+	1	1
<i>Cardamine pratensis</i> L.	+	-	+	+	+	+	+
<i>Rubus caesius</i> L.	+	-	+	+	+	+	+
<i>Potentilla reptans</i> L.	+	-	+	1	+	+	+
<i>Fragaria vesca</i> L.	+	-	+	+	+	+	+
<i>Veronica chamaedrys</i> L.	+	-	+	+	+	+	+
<i>Galium molugo</i> L.	+	-	+	+	+	+	+
<i>Erigeron canadensis</i> L.	+	-	+	+	+	+	+
<i>Cirsium vulgare</i> (Savi) Ten.	+	-	+	+	+	+	+
<i>Lapsana communis</i> L.	+	-	+	+	+	+	+
<i>Luzula pilosa</i> (L.) Willd.	+	-	-	+	+	+	+
<i>Trifolium repens</i> L.	+	-	+	+	+	+	r
<i>Epilobium montanum</i> L.	+	-	+	+	-	+	+
<i>Convolvulus arvensis</i> L.	+	-	+	+	-	+	-
<i>Veronica officinalis</i> L.	+	-	+	+	+	-	-
<i>Ranunculus acris</i> L.	+	-	-	+	+	-	-
<i>Prunella montana</i> Lej.	+	-	-	+	+	-	-
<i>Linaria vulgaris</i> Miller	+	-	+	+	-	-	-
<i>Leontodon autumnalis</i> L.	+	-	+	+	-	-	-
<i>Mycelis muralis</i> (L.) Dumort.	+	-	-	+	+	-	-
<i>Lolium perenne</i> L.	+	-	-	+	+	-	-
<i>Carex hirta</i> L.	+	-	-	-	+	+	-
<i>Artemisia vulgaris</i> L.	+	-	-	-	+	-	-
<i>Hieracium murorum</i> L.	+	-	+	-	-	-	-
<i>Galeopsis tetrahit</i> L.	+	-	+	-	-	-	-
<i>Achillea millefolium</i> L.	+	-	-	-	-	-	-
<i>Majanthemum biofolium</i> (L.) F.W.Schm.	+	-	-	-	-	-	-
<i>Capsella bursa-pastoris</i> (L.) Medicus	-	-	1	1	+	+	+
<i>Urtica dioica</i> L.	-	-	+	+	+	+	+
<i>Viola riviniana</i> Reichenb.	-	-	-	+	+	+	+
<i>Ajuga reptans</i> L.	-	-	-	+	+	+	+
<i>Scutellaria galericulata</i> L.	-	-	-	+	+	-	+
<i>Galium aparine</i> L.	-	-	-	+	+	-	+
<i>Gnaphalium sylvaticum</i> L.	-	-	-	+	+	-	+
<i>Stachys sylvatica</i> L.	-	-	-	-	+	-	+
<i>Geum urbanum</i> L.	-	-	-	-	+	-	+
<i>Calamintha acinos</i> (L.) Clairv.	-	-	-	-	+	-	+
<i>Senecio vernalis</i> Waldst and Kit.	-	-	-	-	+	-	+
<i>Vicia cracca</i> L.	-	-	-	+	-	-	+
<i>Senecio vulgaris</i> L.	-	-	-	-	+	-	-
<i>Artemisia campestris</i> L.	-	-	-	-	-	-	+

Earlier studies on the biology and ecology of *T. farfara* have shown that its population remains relatively steady under conditions of regularly recurring disturbances on fields under systematic culture and that its population rapidly regresses after the disturbances cease when the field is laid fallow (Namura-Ochalska 1988, 1989).

METHODS

The study was conducted from 1982 to 1988 in the Mazury Lake District near Nidzica. A permanent plot 2 x 25m, divided into 200 plots, each with an area of 0,25 m² was delineated on a rafting site at Lake Zręczno.

Over the seven-year period of the study the rafting site was used twice, which in 1983 completely ripped of the vegetation layer, while in 1987 the plant cover was destroyed by 50%.

Each year, the numbers of generative and vegetative shoots were counted on each plot in April and July, respectively. These data served as the basis for evaluating the long-term population dynamics of the species. Due to the difficulties in isolating multishooted individuals a single shoot was considered to be a unit of population.

In order to analyze the seasonal population size and spatial structure of the renewing population after total destruction of its above-ground parts in 1984, 48 plots were delineated in a systematic way, spacing 16 plots every 5 meters. The new shoots and seedlings were counted and marked every month from March to October. This procedure was continued until the population was destroyed again, i.e., over a period of three successive years.

In the last year of the study in August, 10 individuals were removed from densely and loosely soded plots. The shoots were counted and the total lengths of the rhizomes per individual were measured.

All of the accompanying species were listed every year at the height of the growing season and their cover was assessed according to the Braun-Blanquet scale (Table 1).

The soil characteristics of the studied area are presented in Table 2.

TABLE 2. Soil properties in study area.

Properties	Mean values
Mechanical group	coarse sandy soil
pH in H ₂ O	7,7
pH in KCL	7,1
Humus content (%)	1,1
Carbon content (%)	0,6
CaCO ₃ content (%)	0,9
Metal cation content *	C ^{a+2} 16,4
	Mg ⁺² 0,6
	K ⁺¹ 0,1
	Na ⁺¹ 0,2
Total metal cation content S*	17,2
Hydrolytic acidity H _h *	3,0
Exchange capacity of soil T*	20,2
Degree of soil exchange saturation with bases V _s (%)	85,1

* Metal cations in 100 g soil

RESULTS

POPULATION DYNAMICS

The population dynamics of *T. farfara* over the seven year period of study were characterized by dramatic changes in number from year to year (Fig. 2).

The dynamic of population renewal after complete destruction of the plant cover were especially interesting. Vegetative shoots began to grow vigorously as early as the next year after destruction. Population density at that time doubled in comparison with the period preceding the use of the rafting site. The population reached its peak density (over 30 vegetative shoots per surface unit) in the second year after destruction, whereas in the next season it declined sharply to the state preceding the catastrophe (Fig. 2).

Fig. 2. Changes in the density of vegetative (1) and generative (2) shoots.

An increase in population number was also noted after the second disaster, although the density of the vegetative shoots was markedly lower this time.

Although emergence of generative shoots after total destruction of the above-ground plant parts was not noted until the second year of renewal of the rafting site, their number was, similarly as that of the vegetative shoots, very high. The highest

Fig. 3. Seasonal changes in population number in successive years after destructions of plant cover.

mean density of the generative shoots was found in the third year of renewal, after which their number dropped radically (Fig. 2).

SEASONAL CHANGES IN POPULATION NUMBER

Curves showing the changes in the number of individuals in the renewing population reveal that distinct differences both in the course and in mean densities occurred only between the first and two successive years of covering the rafting site (Fig. 3).

Fig. 4. Survival of seedling and juvenile forms. 100% = total number at beginning of growing season.

These differences were caused mainly by the lack of generative shoots and merely sporadic emergence of seedlings in the first year after total destruction of the above-ground plant cover. Due to this, the seasonal changes in population number in 1984 reflected mainly the emergence and death of vegetative shoots.

The population dynamics of the second and third year after destruction were similar and showed a clearly defined peak in numbers occurring in May which was related to the large number of seedlings which appeared and then died off. Survival curves show that at this time the death rate of seedlings and juveniles was about 90% (Fig. 4).

The seasonal population spurt began in March with the appearance of generative shoots. The vegetative shoots, similarly as in the previous year, appeared in April and their number kept increasing in May concomitantly with the death of generative shoots. The drop in population number during the final period of vegetation was caused mainly by the death of vegetative shoots.

Fig. 5. Cartograms of shoot density(a) and distribution of its values(b)

CHANGES IN THE SPATIAL STRUCTURE OF THE RENEWING POPULATION

Significant changes in the spatial structure of the renewing population accompanied changes in population number in the successive years of renewal (Fig. 5). Cartograms of vegetative shoot density and density distribution indicate that the largest fraction of plots having the highest densities and the smallest fraction with the lowest densities were observed in the second year of renewal of the rafting site. In that year the density on the experimental sites achieved its maximal value which exceeded 60 vegetative shoots per surface unit (0,25m²) along with the concomitant greatest degree of scattering of the number of shoots on individual plots. The fact that along with plots having dozens of shoots there were some with only a few shoots indicates that the population had a clump structure. Regardless of the changes in spatial structure, a 100% frequency was found each year on the 0,25m² plots.

THE EFFECT OF REGENERATION OF THE RAFTING SITE COVER ON THE STRUCTURE OF INDIVIDUALS

In the third year of population renewal at the height of the vegetative season on the renewing rafting site, large variations were found in the clonal growth rate and manner of spreading of individuals, which led to sharp differences among the polycorms in terms of their structure, i.e. the number of above-ground shoots, total rhizome length and their branching system (cf. Figs. 6 and 7). The most sizable individuals grew on sodless sites (Fig. 6).

Fig. 6 Structural diagram of an individual under conditions of loose sodding.

TABLE 3. Structure of *Tussilago farfara* individuals according to degree of sodding.

Loosely sodded plots				Densely sodded plots		
Successive individual	Above-ground shoot number	Rhizome number	Total rhizome length (m)	Above-ground shoot number	Rhizome number	Total rhizome length (m)
1	7	12	3,7	1	5	1,0
2	4	8	1,3	1	4	0,9
3	16	25	4,2	4	6	1,5
4	11	29	3,8	2	4	0,6
5	6	7	1,0	1	3	0,5
6	21	26	5,6	3	6	1,1
7	17	24	5,0	2	5	1,3
8	15	11	1,8	2	4	1,5
9	21	21	4,7	3	6	1,1
10	18	19	2,0	4	5	1,7
$\bar{x}$	13,6	18,2	3,3	2,3	4,8	1,1
s	6,2	8,1	1,6	1,2	1,0	0,4
V(%)	45,8	44,3	49,7	50,4	21,5	33,7

Explanations: $\bar{x}$ – mean value, s – standard deviation, V – coefficient of variation

All of them were built of numerous shoots although they were characterized by a high degree of dispersion in terms of the analyzed traits (Table 3).

Individual polycormones were thus composed of 4-21 shoots with total rhizome lengths from 1 to over 5.5 meters.

In contrast, the individuals growing on densely sodded plots were comprised of only 1-4 shoots with few rhizomes (Fig. 7).

Fig. 7. Structural diagram of an individual under conditions of dense sodding

Significant differences in the manner of rhizome branching were seen depending on the degree of sodding of the plot. Intense development and branching were found only on plots with no sod. There numerous lateral shoots appeared at a depth of up to 0.3 meters. On those plots where grasses dominated, lateral rhizomes appeared much deeper, i.e. below the level of root growth of the dominant species (cf. Figs. 6 and 7).

CHANGES IN VEGETATION ON THE RAFTING SITE DURING THE SEVEN-YEAR PERIOD OF OBSERVATION.

Renewed use and then abandonment of the rafting site mainly caused dramatic quantitative changes in the dominant species (Fig. 8). The types of species occurring changed much less over the successive years. Of the 47 species registered at the start of the study, 70% survived until 1988, with both the retreating species and the new colonizers not achieving significant coverage in any of the studied years (Table 1).

Complete destruction of the vegetation cover in 1983 caused a sudden drop in grass density and an abrupt increase in *T. farfara* coverage, up to 70% of the surface in the second year after the catastrophe. However, in the third year of renewal of the rafting site plant cover, *T. farfara* lost its position as the absolutely dominant species in favour of the grass population. Coverage by *Calamagrostis epigejos*, *Deschampsia caespitosa*, *Arrhenatherum elatius*, *Holcus lanatus* and *Festuca gigantea* increased dramatically.

Due to the second destruction of the plant cover in 1987, the total plant coverage dropped to 50%. On those plots completely

devoid of plants or only slightly covered, vegetative *T. farfara* ramets appeared abundantly in the next year. Overall, however, *T. farfara* coverage was decidedly more sparse than after total destruction of the plant cover.

The expansion of grasses on the regenerating rafting site also caused a significant change in the vertical structure of the plant cover. A two-layered community was formed with the upper layer composed of grasses reaching a height of 1 meter.

Fig. 8 Changes in major species cover of the rafting site. Species: *Tussilago farfara* (1), *Calamagrostis epigejos* (2), *Deschampsia caespitosa* (3), *Arrhenatherum elatius* (4), *Holcus lanatus* (5), *Poa angustifolia* (6), *Festuca gigantea* (7), *Equisetum sylvaticum* (8), *Ranunculus repens* (9), *Torilis japonica* (10), *Cirsium arvense* (11).

DISCUSSION

Destruction of the plant cover creates good conditions for renewal of *T. farfara* populations. The removal of vegetation which left the ground completely bare, with absolutely no potential competitors and with improved lighting conditions was a favourable change of environmental factors for *T. farfara*. Effective colonization by *T. farfara* of areas devoid of other plants has already been noticed by Bakker (1960), Myerscough and Whitehead (1967), Krzaklewski (1979).

From among the biological properties of a species which enable the intense renewal of an individual after its above-ground parts have been destroyed, the most important are its large number and high activity of dormant buds and high clonal growth rate. The removal of the vegetation cover probably stimulated the activity of the lateral buds, similarly as in the case of other clonal species after disintegration of polycorms (Grime 1979, Abrahamson 1980, Silvertown 1987, Davies and Evans 1990).

Analysis of the developmental biology of *T. farfara* reveals its very interesting characteristic ability to undergo two diametrically different types of clonal growth: querilla and phalanx growth. However, intense querilla type growth plays the major role in population renewal. Due to this type of growth the massive appearance of vegetative shoots is possible as early as

the year of rafting site renewal. Many authors consider this type of individual growth to be the most expansive way of taking over an area and using its nutritional resources, which becomes particularly evident in disturbed environments (Callaghan 1980, Duke 1985, Jackson et al. 1985).

The continuity of querilla type clonal growth makes population renewal completely independent of generative reproduction and is a significant adaptation of a species to relatively constant occurrence in disturbed environments. In such environments, inflorescences are frequently destroyed before seeds can mature, which also occurred on the studied area in spring. In turn, the use of the rafting site in autumn destroyed the newly forming generative shoots which were beginning to appear at this time, thus their total lack in the first year after the disturbance.

Arresting the development of the generative shoots probably had a favourable effect on the growth rate of rhizomes. The storage materials earmarked for the development of inflorescences lacking chlorophyll could be used for the growth of rhizomes and appearance of new vegetative shoots.

In spite of the large number of generative shoots and the high number of produced seeds found in the successive years of this study and the significant emergence of seedlings, especially in the second and third year of the study, their survival rate was very low. Only a few lasted to the end of growth season and were able to develop rhizomes. The part played by individuals developed from generative shoots is, however, very important since it is well known that intense vegetative growth and massive appearance of shoots leads to a depletion of genetic stock and creates favourable conditions for the development of pathological individuals (Harper 1986). When the vegetative shoots were very dense, especially in the first and second years of regeneration of the rafting site vegetation cover, *T. farfara* leaves were heavily attacked by the fungus, *Coleosporium tussilaginis*, while *Lepidoptera* larvae attacked inside the shoots.

There is no doubt that one of the conditions permitting intense regeneration of the *T. farfara* population was the significantly slower rate of regeneration of such grasses occurring on the rafting site as: *Deschampsia caespitosa*, *Arrhenatherum elatius*, *Holcus lanatus*, *Festuca gigantea*. With the exception of the last grass, these grasses do not develop rhizomes and due to their low set branching nodes they do not react favourably to low cutting and grazing (Hegi 1954, Falkowski 1982). Tearing off the vegetation cover resulted in destruction of their branching nodes and death of their root systems, which in effect led to favourable conditions for renewal of the *T. farfara* population.

The increasing degree of sodding of the surface as the plant cover regenerated began to crowd the area above and below the soil surface and distinctly restricted clonal growth, most notably, querilla type growth. This is indicated by the drop in the number of vegetative shoots and their clump-like distribution which became evident in the third year after destruction of the plant cover. It was also found that increased sodding affected the structure of *T. farfara* polycorms by limiting both the number of above-ground shoots as well as the number and manner of branching of rhizomes. The fact that rhizomes which are located near highly developed root systems of grasses can grow deeper and that their few lateral branches grow only out of those nodes which are situated below the layer in which the subterranean organs of other species develop, increases the persistence of *T. farfara* on sites where the plant cover is dense. This is undoubtedly an energetically expensive adaptation and when the area is densely sodded the population regresses rapidly (cf. Namura-Ochalska 1988, 1989).

Studies over a period of seven years have shown that even drastic disturbances in the environment do not eliminate *T. farfara* populations, moreover, they are a necessary condition for these populations to survive and expand. Intense clonal growth occurs on sites where the plant cover has been destroyed. In result of this the vegetative shoots which develop permit *T. farfara* to quickly dominate the free space. The generative shoots in turn make it possible to colonize new, degraded biotopes.

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EKSPANSJA PODBIAŁU POSPOLITEGO *TUSSILAGO FARFARA* L. W ŚRODOWISKACH ZABURZONYCH. I. ODNAWIANIE SIĘ POPULACJI W WARUNKACH NISZCZENIA POKRYWY ROŚLINNEJ

STRESZCZENIE

W pracy oceniono efektywność odnawiania się populacji *Tussilago farfara* L. po zniszczeniu pokrywy roślinnej. Proces ten zachodzi gwałtownie głównie dzięki wzrostowi wegetatywnemu typu „querilla”. Odnawiającą się populację charakteryzuje w kolejnych latach między innymi: 1/ gwałtowny wzrost liczebności już w pierwszym roku po zniszczeniu, z maksimum w roku następnym; 2/ całkowity brak pędów generatywnych w pierwszym roku; 3/ wysoka śmiertelność siewek; 4/ zmiana struktury przestrzennej; wzrost różnicowania w sposobie rozrastania się osobników. Siedmioletnie badania wskazują, że nawet drastyczne zaburzenia środowiska nie powodują eliminacji *T. farfara*, co więcej, całkowite zniszczenie pokrywy roślinnej stwarza dogodne warunki odnawiania się populacji.

SŁOWA KLUCZOWE: dynamika liczebności, sezonowe zmiany zagęszczenia, struktura przestrzenna, wzrost klonalny.