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Production and germination of *Tussilago farfara* (L.) diaspores

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Abstract

In the paper the production of generative diaspores in *Tussilago farfara* (L.) was assessed in four different ecological systems. Also their morphological characteristics, as well as their germinability under natural and laboratory conditions were analysed, depending upon the age, density and size of diaspores, as well as sowing depth, substrate type and light conditions. The studies showed that diaspores: 1) were highly germinable under laboratory conditions; 2) did not germinate effectively under natural conditions; 3) were short-lived; 4) were tolerant to unfavourable habitat agents. *Tussilago farfara* was determined to exhibit high diaspore production only under conditions of suppresed interspecific competition.

Key words: *Tussilago farfara, diaspore production, achene shape and size, seed germinability, diaspore longevity*

INTRODUCTION

Pioneer plant species colonizing various biotopes with disturbed and unstable ecological structure are worth studying. In many papers biological properties of these species have been analysed, that enable them to colonize unfavourable habitats, but also make their survival there impossible for a longer time (e.g. Symonides 1974a, b, 1978a, b, Linhart 1976, Grime 1979, Schat 1983, Olivieri et al. 1983). The works mentioned above indicate that most pioneer plants reproduce only generatively. However, a few are capable also of vegetative propagation, though proportions of generative and vegetative offsprings in different developmental phases of pioneer populations are not known.

Among widespread expansive pioneer species there is *Tussilago farfara* L. It is capable of colonizing pioneer habitats, maybe because of a high production of anemochoric diaspores, their high germinability and low habitat requirements. It also can propagate vegetatively through rhizome fragmentation (Bakker 1960, Henson 1969, Sheldon 1971, Bostock 1976, 1978).

Generative reproduction prevails usually in a colonizing phase, whilst vegetative at later stages of population development. The latter ought to maintain a population even in a highly compact phytocoenose. However, it has been noticed that in some systems *T. farfara* is a constant phytocoenose component, whereas from others it retreats fairly rapidly. The reasons for both these events have not been fully elucidated.

The paper aims to assess the production of generative diaspores in various ecological systems, to analyse their morphological properties, as well as their germinability under natural and laboratory conditions. The effect of age, density and size of diaspores, that of the substrate type and its moisture, as well as the influence of light conditions and sowing depth upon germinability were studied.

The work constitutes a part of wider studies on reproductive strategy and tactics of this species.

METHODS

The field studies were conducted in 1982–1985 in Mazury, in environs of Nidzica, Four study areas, 2 × 25 m each, were located in an arable field (two), in a rafting site (one) and in a grassland (one). They were all divided into 50 1 m^2 plots. In an agrocoenose two studies areas were located 50 m apart, and one of them has not be cultivated since the beginning of an experiment. Table 1 contains a short characteristics of vegetation and soil conditions.

In successive growing seasons all fruiting shoots were counted in each plot, moreover in the vicinity of permanent areas heads were picked up from 20 shoots and in each infructescence all achenes were counted. Furthermore, the fraction of empty or damaged diaspores was determined and morphological characters of well developed diaspores, like achene length and width, pappus length, were analysed. The choise of well-developed colsfoot diaspores was not difficult due to their transparent seed coats. The measurements were conducted with the accuracy of 0.05 mm by means of a binocle.

Table 1

Description of study areas with *Tussilago farfara* in 1982

Study area	Agrocoenose	Old field	Rafting site	Grassland
Cover (%)	85	95	85	60
Species number	45	54	47	38
Dominants	*Fagopyrum sagitatum*	*Agropyron repens, Dactylis glomerata, Cirsium arvense*	*Festuca gigantea, Poa angustifolia, Ranunculus repens*	*Calamagrostis epigeios, Poa compressa, Torilis japonica*
Aspect	SE	SE	N	S
Slope	8.0	8.0	29.0	32.0
Soil type	heavy loam	hoavy loam	medium sand	coarse sand
pH in 1n KCl	7.3	7.5	7.1	7.3
Humus (%)	4.14	3.77	1.14	1.15
$CaCO_3$ (%)	29.89	35.88	0.90	0.33
Metal cations in 100 g soil:				
Ca^{+2}	106.79	108.49	16.35	14.47
Mg^{+2}	2.60	2.76	0.62	0.26
K^{+}	0.52	0.51	0.07	0.04
Na^{+}	0.84	0.84	0.15	0.18

Due to the lack of significant (at 5% error risk) differences between mean values of analysed properties of achenes collected from four study areas, in the further statistical elaboration a mixed diaspore sample was taken into account. Empirical frequency distributions of single properties were presented in histograms. Chi-square test for the goodness of fit was applied to compare them with the normal distribution (Oktaba 1966).

Correlation coefficients between achene width and length, as well as between achene and pappus lengths were computed. To verify the hypothesis on the lack of correlation between the analysed characters t-test was used (Oktaba 1966).

To assess diaspore germinability depending upon their age, as well as substrate moisture and light conditions 3 replicates of 100 diaspores each were sown on filter paper in Petri dishes. They were a mixed sample of diaspores from all four study areas. Only undamaged, full-quality diaspores were sown uniformly with the same distances in and between rows. Petri dishes were kept either under normal light conditions (16 h light, 8 h darkness), or in darkness.

The effect of substrate moisture on the germination was analysed in 5 treatments: filter paper saturated with water in 100, 50, 30 and 10% respectively, as well as immersed in 2 mm of water. Germs were calculated every 24 h. Germination rate was estimated from Pieper coefficient (Grzesiuk and Kulka 1981). To assess diaspore longevity the experiment was repeated each month from May (just after dissemination) to October (loss of germination capacity). Diaspores were stored in plastic, closed containers.

Further experiments were conducted in trays, 25 × 15 × 5 cm each. The effect of sowing depth, substrate type and diaspore density upon germinability were then assessed. Following treatments were applied:

a) sowing depth of 3, 2, 1 and 0 cm (surface sowing);
b) 7 substrates: filter paper, humus, vegetable soil, 1:1 mixture of sand and loam, loamy soil, sand, 1:1 mixture of sand and gravel;
c) diversified diaspore size: small (3.05–6.65 mm long and 0.25–0.36 mm wide) and big (4.55–5.15 mm long and 0.50–0.60 mm wide) diaspore were shown separately and alternatively together;
d) 4 density treatments: 20, 100, 200 and 500 diaspores per tray.

Each treatment was threefold replicated at the same, except the last experiment, sowing density as in Petri dishes. In experiments a, c and d arable heavy loam was applied.

Diaspore germinability under natural conditions was estimated from the seedling number in plots in successive years and from the diaspore production established earlier.

RESULTS

DIASPORE PRODUCTION UNDER NATURAL CONDITIONS

The results indicated big differences in diaspore production both between and within populations in single years (Fig. 1).

The highest diaspore number (23 308 1 m^{-2}) was found in 1985 in a population in the rafting site. On the other hand, very low diaspore production, less than 500 diaspores per 1 m^2 occured in 1984–1985 in the old field and in the grassland, as well as in 1984 in the rafting site.

Temporal changes in diaspore production were of dual nature, either irregular fluctuations (agrocoenose and rafting site) or directional changes (old field and grassland). In the latter case there was a significant decrease in the number of produced diaspores from year to year till the generative reproduction was, in practice, stopped. For four study years there was 51-fold decrease in the old field and 22-fold decrease in the grassland.

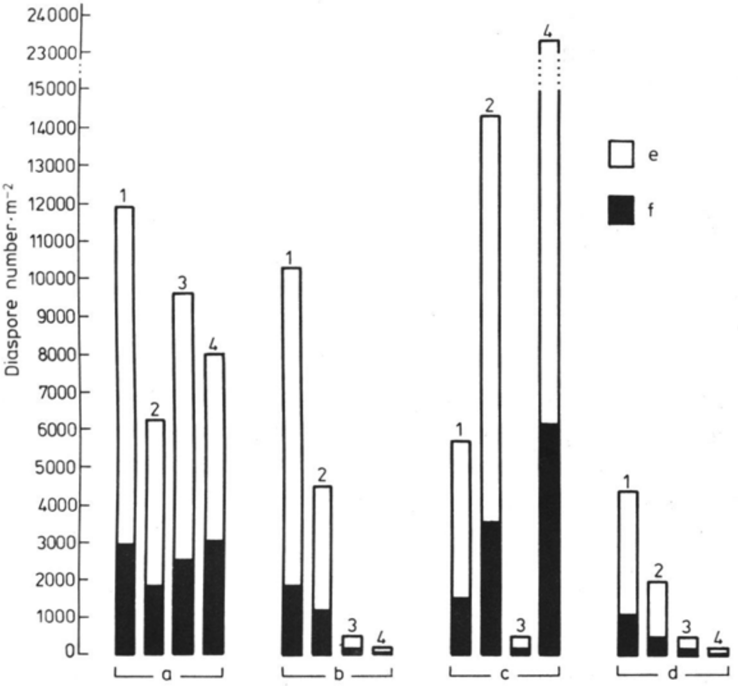

Fig. 1. Generative diaspore production in four successive years (1–4), a — agrocoenose, b — old field, c — rafting site, e — fraction of diaspores capable of germination, f — fraction of empty diaspores

Both direction and amplitude of the changes in the diaspore production from year to year were similar in extremely different ecological systems like old field and grassland. It indicated more significant influence of phytocoenotic conditions than soil properties.

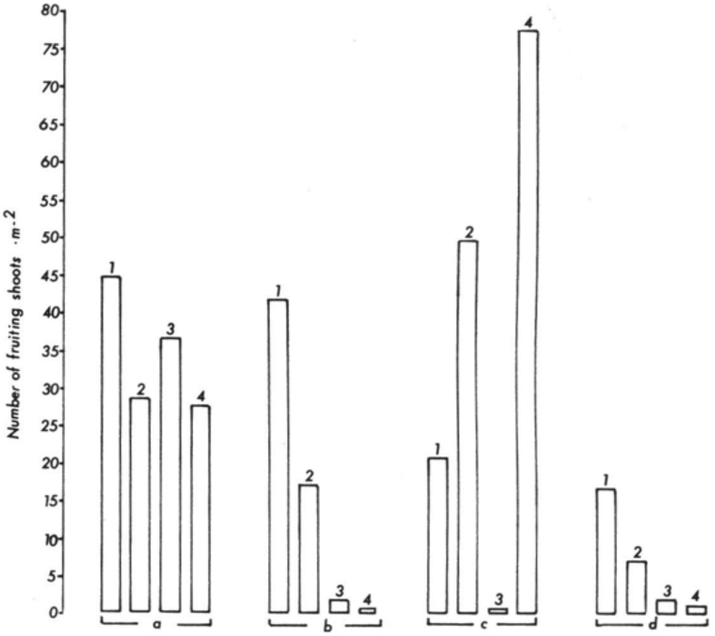

Fig. 2. Fruiting shoot density in four successive years (1–4), a-d as in Fig. 1

The number of produced diaspores was always a function of the density of fruiting shoots (Fig. 2) governed mostly by phytocoenotic conditions.

In each population, irrespective of growing season and diaspore production, more or less one fourth of total diaspore were empty.

DIASPORE MORPHOLOGY

The studies showed that variability of diaspore morphology was fairly low, as the coefficient of variation did not exceed 14%. Empirical frequency distributions fitted the normal distribution (achene and pappus lengths) or were close to it (achene width) (Fig. 3).

At the interval values taken into account the highest frequency characterized the fraction of achenes 3.95–4.25 mm long and 0.45–0.50 mm wide, with pappus 11.50–12.50 mm long. Mean achene length equaled 4.00 ± 0.42 mm its mean width — 0.43 ± 0.06 mm. Pappus was threefold longer than an achene (12.11 ± 0.99 mm). Like achene dimensions also their shape was only

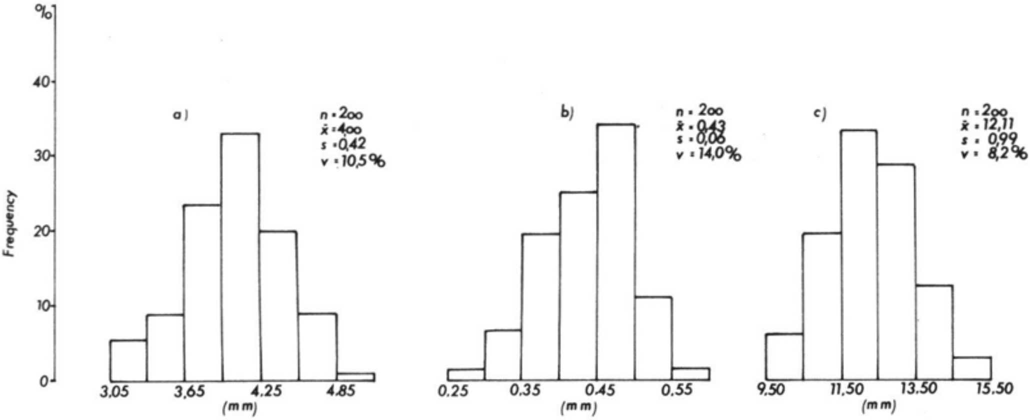

Fig. 3. Frequency distributions of achene length (a), achene width (b), pappus length (c) in a mixed sample from all four study areas

slightly variable, which was confirmed in positive values of correlation coefficient between achene length and width (r = 0.42), as well as between achene and pappus lengths (r = 0.31).

DIASPORE GERMINATION UNDER LABORATORY CONDITIONS

Diaspore germinability depending on age

Coltsfoot diaspores were highly germinable just after their maturation, but in a few months after dissemination they lost their viability (Fig. 4).

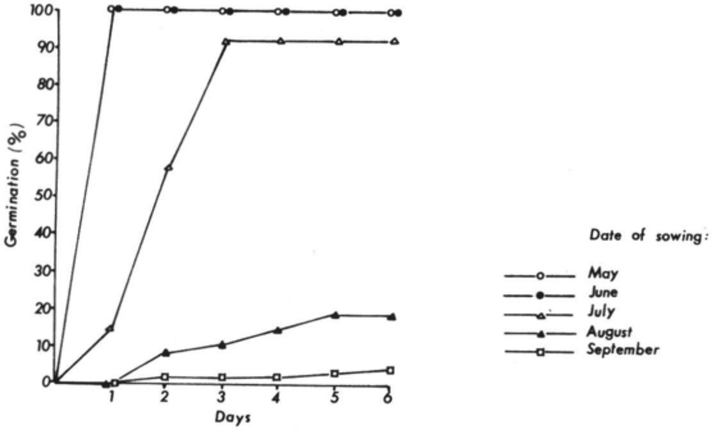

Fig. 4. The effect of diaspore age on their germinability

It was determined that diaspores sown on a filter paper in May and June germinated in 100% already in 24 h. In July their germinability slightly decreased (to 92.0%) and germination process lasted to 3 days.

Rapid decrease in diaspore germinability, synchronic with diminished germination rate took place in August. Then Pieper coefficient increased to 78.7 h. In September only 4.7% diaspore germinated in as long as 144 h (6 days). Diaspores lost their viability in 5 months after maturation. In October not even one germ developed.

Diaspore germinability depending on substrate moisture and light conditions

The results of studies on the effect of substrate moisture on diaspore germinability indicated that diaspores were tolerant of excess of water, but very susceptible to its shortage (Fig. 5). Both diaspores immersed in water and those lying on a filter paper saturated in 100 or 50% germinated already in 24 h. The decrease in substrate moisture resulted mostly in the reduction of germination rate. Hence, on 30%-saturated filter paper, though all diaspores germinated, the germination period lengthened to 5 days. On 10% saturated filter paper germination capacity rapidly diminished to 22.7%, the first germs appeared as late as on the second day, the last on the sixth day. Mean germination time of a single diaspore was as long as 3 days.

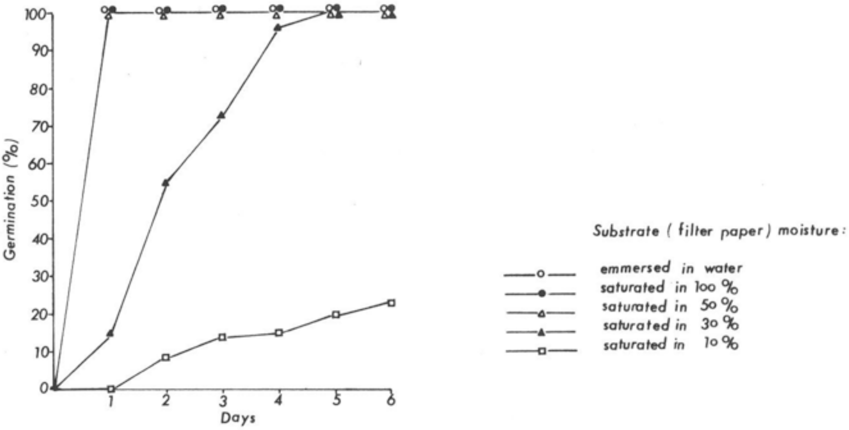

Fig. 5. The effect of substrate moisture on diaspore germinability

The studies showed that even total lack of light adversely affected neither germination capacity, nor its rate at the sufficient substrate moisture.

Diaspore germinability depending upon sowing depth

The increase in sowing depth significantly decreased germination capacity and caused late seedling emergence (Fig. 6). At surface sowing diaspores were highly germinable, already on the second day 100% of diaspores germinated. 1 cm sowing depth resulted in 50% decrease in germination capacity, furthermore, the first seedlings emerged on the fifth day, germination peak took place on the eighth day and the process terminated on the ninth day after sowing. Mean germination time of a single diaspore was fourfold longer (Pieper coefficient — 7.35 days).

Only 11.2% of diaspores sown at 2 cm depth germinated, further delay in their emergence was found. The first seedlings appeared as late as a weak after sowing, the last — on the twelveth day. Hence, compared to surface sowing, germination capacity decreased tenfold while its rate fivefold (Pieper coefficient — 9.90 days). Among diaspores sown deeper none germinated.

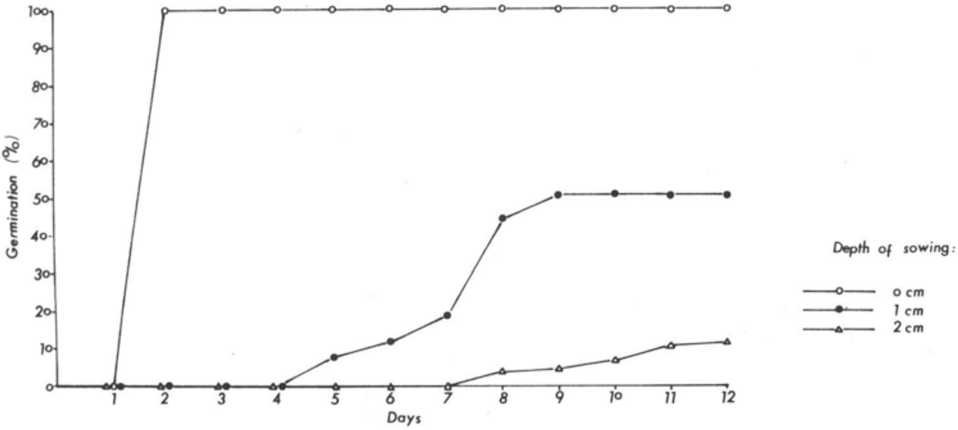

Fig. 6. The effect of sowing depth on diaspore germinability

The effect of substrate type on diaspore germinability

The results of the studies indicated that *T. farfara* diaspores could germinate on various substrates, their germinability depended upon the substrate type (Fig. 7).

In four substrate treatments 100% diaspores germinated, on filter paper in one day, whereas in humus, vegetable soil and sand-loam mixture in two days. Germination on loamy soil, sand and sand-gravel mixture was markedly less intensive. Irrespective of substrate type most germs emerged already on the second day after sowing, but their germination capacity decreased to 91.5%, 86.7% and 76.3% respectively and Pieper coefficient value increased to 2.34, 2.67 and 3.38 days, respectively.

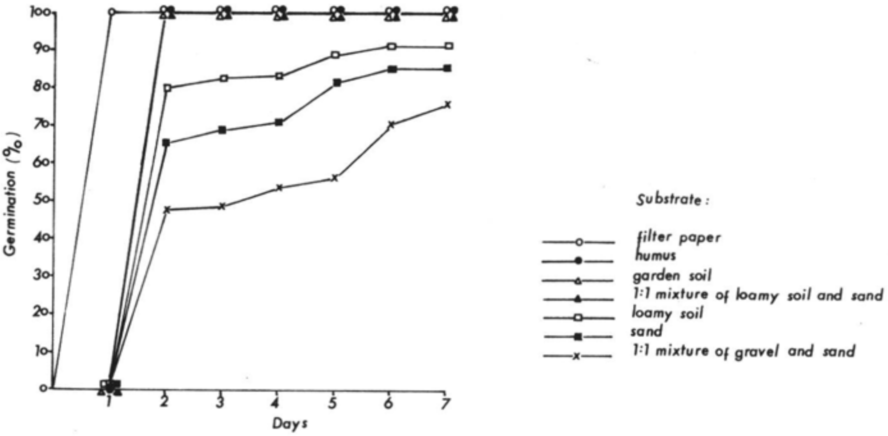

Fig. 7. The effect of substrate type on diaspore germinability

Diaspore germinability depending upon their size and density

Diaspore size affected neither their germination capacity nor their germination rate. The studies showed that both small and big diaspores, sown in the same or separate trays germinated in 100% in merely two days.

Density of sown diaspores had a slight effect upon the course of germination process. At density of 500 diaspores per a tray germination capacity decreased to 95.3% and the process lasted four days (Fig. 8). However, it is worth stressing that 80% of germs emerged on the second day, thus Pieper coefficient value increased only 12 m.

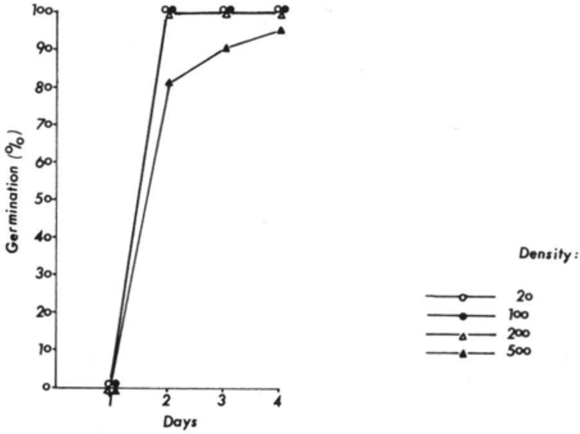

Fig. 8. The effect of diaspore density (per a tray) on their germinability

In all other density treatments diaspores germinated in 100% in the first two days.

DIASPORE GERMINATION UNDER NATURAL CONDITIONS

Diaspore germination under natural conditions significantly differed from that in laboratory. It was indicated both by low germination effectivity and high variability of seedling density (within a single study area in successive years, as well as between study areas) (Fig. 9). From the diaspore production value in the studied areas and from the seedling number it may be inferred that as little as 0.5% diaspores germinated.

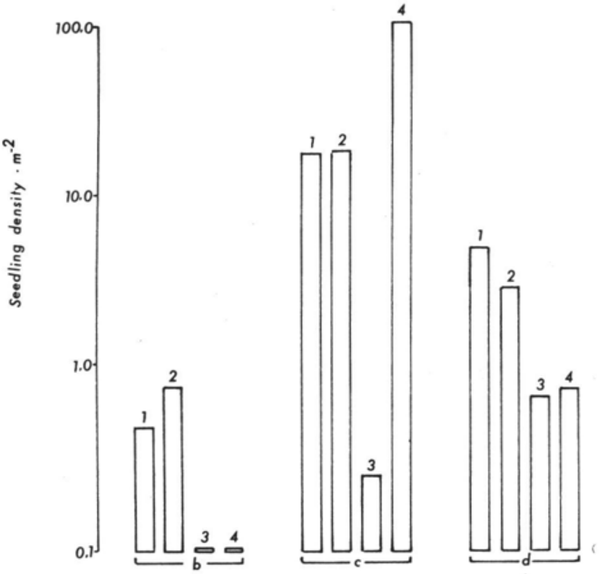

Fig. 9. Seedling density in four successive study years (1–4), b-d as in Fig. 1

The highest seedling number (over 100 m^{-2}), corresponding to the highest diaspore production occurred in 1985 in the rafting site. Also the highest variation in seedling density was found there. In the last two years in the old field no seedlings appeared, which was associated with the decrease in the number of produced diaspores.

However, seedling number was not always governed by diaspore production. Thus, in the old field and in the grassland, even in years with high diaspore production, not more than a few seedlings emerged in 1 m^2. The lack of correlation between diaspore production and seedling density indicated that these were environmental factors which controled diaspore germination under natural conditions.

DISCUSSION

The studies have showed that *T. farfara* exhibits many properties characteristic of r-species like high, though variable in years, diaspore production, anemochory, high germination capacity and rate, and germinating diaspores tolerant to unfavourable habitat conditions, coupled with low competitive ability. All these properties are typical of expansive pioneer species (Harper 1967, Harper and Odgen 1970, MacArthur 1972, Gaines et al. 1974, Abrahamson 1975, McNaughton 1975, Kawano and Nagai 1975, Hickman 1975, Bostock and Benton 1979).

High diaspore production in populations occurs under conditions of supressed interspecific competition, caused, in the analysed ecological systems, by man. In the course of the studies the population in the rafting site has exhibited the biggest diaspore number (23 000 1 m^{-2}) due to previous elimination of other species pressure (destruction of vegetation by log tipping). Also high diaspore production (12 000–6250 diaspores 1 m^{-2}) occurs in the agrocoenose, owing to agronomical techniques that limit the development of natural vegetation.

In *T. farfara* diaspore production has been also highly variable both between and within populations. It depends upon the body of biotope-phytosociological and weather conditions in single years. In the old field and grassland in the course of the studies a considerable decrease in diaspore production has been observed, maybe due to sod formation. In the rafting site and in agrocoenose, thus in man-utilized areas, irregular fluctuations took place. Variable seed production in a single species has been also found in stabilized phytocoenoses (Falińska 1977, 1978, Pirożnikow 1983).

Irrespective of production value and the nature of its changes in a many-years' cycle the number of produced diaspores has been always a function of fruiting shoots. The number of the latter is not directly associated with a biotope quality (soil type, slope and aspect). Populations growing in the same (agrocoenose, old field), or similar (rafting site, grassland) habitat conditions differ both in shoot density and in the nature of its variability. Thus, an interspecific competition plays a major role.

Apart from high diaspore production also their high anemochoric dispersibility over long distances enables *T. farfara* to colonize new areas. Elongated and provided with pappus achenes are easily disseminated even at gentle wind breeze. At wind speed up to 3.05 cm m^{-1} dissemination range may attain 4.45 km h^{-1} (Sheldon and Burrows 1973). However, most diaspores are carried only for several hundreds meters from a fruiting individual (Bakker 1960). Hence, the colonization of far habitats depends, to a large extent, upon germination rate and capacity.

The studies have showed that under laboratory conditions colsfoot diaspores may germinate in one day in 100%, but their high germinability is maintained only for a few months. It is worth noting that short dispore longevity in this species has been also found by Bakker (1960), as well as Myerscough and Whitehead (1966). Fruiting timing (April, May) plays a crucial role, as it enables diaspores to disseminate before full growing season.

High diaspore tolerance to unfavourable biotope conditions, typical of most pioneer species (Klemow and Raynal 1983, Mack and Pyke 1984), increases the chance to colonize successfully bare or disturbed habitats. It is essential because of short longevity of non-dormant, in fact, diaspores.

From the conducted studies it may be inferred that colsfoot diaspores, irrespective of their size, germinate over a wide range of abiotic factors variation. They germinate in 100% both in light and darkness on various substrates, at various sowing density, even totally emerged in water. However, diaspores do not tolerate too dry substrate and too deep sowing. Water shortage at germination results in the rapid decrease in germinability. Whereas, too deep sowing, though does not inhibit germination, makes the germ growth difficult due to small amounts of nutrients stored in seeds.

Under natural conditions both colonization of new sites and increase in a population size of *T. farfara* are restricted by phytocoenotic agents. Colsfoot, like most pioneer species, is a week competitor (Werner 1975, Symonides 1979a, b, c, 1985, Grime 1979). With the increase in a competition both density of generative shoots and diaspore production rapidly decrease, followed by reduced seedling density. Such events have been encountered in the old field and in the grassland where invasion of grasses with well-developed root systems, such as *Agropyron repens* (L.) P. B., *Dactylis glomerata* L., *Festuca gigantea* (L.) Vill., *Poa angustifolia* L., *Calamagrostis epigeios* (L.) Roth., *Agrostis alba* L., has resulted in 50-fold (in the old field) and 20-fold (in the grassland) reduction of diaspore production, as well as decrease in seedling number.

However, seedling number in the analysed populations is not directly associated with diaspore production. The results obtained suggest that it may be mostly determined by the degree of vegetation cover. Phytocoenotic conditions limit space available to diaspores and govern mortality of week-competitive seedlings (Zarzycki 1964, Begon et al. 1986). Thus, elimination of interspecific competition results in the increase in seedling density. Neverthless, in spite of high diaspore production, even then only 0.5% germinate under natural conditions.

The results elucidate why *T. farfara* is capable of rapid colonization of pioneer or disturbed habitats.

The effect of biotope and phytocoenotic conditions upon the further development of individuals, their vegetative propagation, as well relation between generative and vegetative reproduction will be discussed in the next paper.

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Produkcja i kiełkowanie diaspor Tussilago farfara (*L.*)

Streszczenie

Praca jest częścią szerszych studiów nad strategią i taktyką reprodukcyjną *Tussilago farfara* L. Celem badań zaprezentowanych w niniejszej pracy była ocena produkcji generatywnych diaspor w różnych układach ekologicznych oraz zdolności i szybkości kiełkowania w warunkach naturalnych i laboratoryjnych. Zbadano wpływ wieku, zagęszczenia i wielkości diaspor, głębokości siewu, wilgotności i rodzaju podłoża a także warunków świetlnych na zdolność i szybkość kiełkowania.

Badania terenowe przeprowadzono w latach 1982–1985 na Mazurach w okolicach Nidzicy. Powierzchnie badawcze o rozmiarach 2 × 25 m wyznaczono na polu uprawnym, na odłogu, na bindudze i murawie. Zwięzłą charakterystykę roślinności i warunków glebowych zawiera tabela 1. Na podstawie zagęszczenia pędów owocujących i liczby niełupek w owocostanie oszacowano produkcję diaspor. Zdolność i szybkość kiełkowania w warunkach laboratoryjnych

badano wysiewając po 100 diaspor w 3 powtórzeniach. Uwzględniono następujące układy eksperymentalne:

a. Różny wiek diaspor — wysiewając diaspory 1-miesięczne, 2-miesięczne, 3-miesięczne, 4-miesięczne, 5-miesięczne i 6-miesięczne.
b. 4 Warianty zagęszczenia — 20, 100, 200 i 500 diaspor.
c. Zróżnicowany rozmiar diaspor.
d. Głębokość siewu równą 3 cm, 2 cm, 1 cm i 0 cm.
e. 5 Wariantów wilgotności podłoża — 100%, 50%, 30%, 10% oraz przy całkowitym zanurzeniu diaspor w wodzie.
f. 7 Rodzajów podłoża — bibułę, próchnicę, glebę kompostową, gliniastą, gliniastą wymieszaną z piaskiem, piasek, żwir wymieszany z piaskiem.
g. Naturalne warunki świetlne (16 godzin na świetle i 8 godzin w ciemności) i całkowitą ciemność.

Kiełkowanie w warunkach naturalnych oceniono na podstawie liczby siewek oraz oszacowanej produkcji diaspor.

Stwierdzono między innymi: 1) bardzo dużą produkcję diaspor w warunkach osłabionej konkurencji międzygatunkowej (do 23 000 na 1 m^2) i gwałtowny spadek tej produkcji na powierzchniach z silnie zwartą pokrywą roślinną (rys. 1); 2) zależność między liczbą wytworzonych diaspor a zagęszczeniem pędów owocujących (rys. 2); 3) mało zmienny rozmiar i kształt niełupek (rys. 3); 4) bardzo duża zdolność i szybkość kiełkowania w warunkach laboratoryjnych (100% w ciągu 24 godzin) a równocześnie całkowitą utratę zdolności kiełkowania w ciągu zaledwie kilku miesięcy (rys. 4); 5) dużą tolerancję kiełkujących diaspor na niekorzystne czynniki siedliskowe; diaspory niezależnie od ich wielkości kiełkowały zarówno na świetle, jak i w ciemności, na różnych podłożach, przy różnej gęstości siewu, w warunkach nawet całkowitego zanurzenia w wodzie (rys. 7 i 8); 6) brak tolerancji diaspor jedynie na nadmiernie suche podłoże i zbyt dużą głębokość siewu (rys. 5 i 6); 7) małą efektywność kiełkowania w warunkach naturalnych, uwarunkowaną przede wszystkim stosunkami fitocenotycznymi limitującymi przestrzeń dostępną dla diaspor, jak również decydującymi o śmiertelności słabych konkurencyjnie siewek (rys. 9).

Reasumując, duża produkcja diaspor, ich anemochoryczne rozsiewanie, duża zdolność i szybkość kiełkowania oraz duża tolerancja kiełkujących diaspor na niekorzystne warunki siedliskowe wyjaśniają zdolność szybkiej kolonizacji przez *T. farfara* pionierskich lub zaburzonych biotopów.