EXPANSION OF *TUSSILAGO FARFARA* L. IN DISTURBED ENVIRONMENTS. III. SUCCESSFUL COLONIZATION AND THE PROPERTIES OF INDIVIDUALS

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ABSTRACT

The survival, seedling and juvenile growth rates and the effectiveness of development and renewal of individuals obtained from seeds and rhizomes were studied. The results showed that the success of *Tussilago farfara* L. in colonizing disturbed environments, after its seeds reach the site and germinate, is a function of several of the important traits of this species: 1) tolerance of seedlings and juveniles to a wide range of changeable external conditions, 2) fast growth and development of individuals, 3) a high degree of adaptability in reaching successive stages of development, 4) querilla type growth, 5) intense spreading and renewal of individuals of generative and vegetative origin, 6) high effectiveness of vegetative reproduction, 7) adaptable allocation of resources to above-, and underground shoots.

KEY WORDS: permanent colonization, seedling and juvenile survival, population dynamics, spreading and renewal of individuals, vegetative reproduction, biomass.

INTRODUCTION

The succes of colonization and permanent establishment in a disturbed environment is determined not only by the speed with which seeds reach sites suitable for germination and the high germination capacity of these seeds, but also by several biological properties which determine growth, development and reproduction of individuals under the prevailing external conditions, which are often changeable and frequently unfavorable (During et al. 1985, Rabinovitz and Rapp 1985, Grubb 1987, Mortimer 1987).

Taking into account the fact that disturbed environments differ vastly among each other in terms of the type, frequency and intensity of disturbances, it is obvious that their colonizers do not have a colonization strategy that would be common for this entire group. Expansive species of disturbed environments exhibit extraordinary and complex life strategies and adaptations to a wide range of changeable ecological conditions (Silvertown 1981, 1985, Olivieri et al. 1983, Symonides 1987, 1988, Peart 1989a). Their occurrence is escalating dramatically mainly due to increasing anthropopressure. One of the common and continually spreading species of disturbed environments is *Tussilago farfara* L. It is characterized by many traits that are typical for pioneering species, such as high fertility, light weight seeds, high germination capability and rate (Bakker 1960, Myerscough and Whitehead 1966, 1967, Sheldon and Burrows 1973, Namura-Ochalska 1987). These properties play an important role in the first stage of colonization but they do not fully explain the enormous expansion of this species in highly diversified, disturbed environments.

The aim of this study was to find an answer to the question, which *T. farfara* traits determine the success of colonization and expansion of the species in disturbed biotopes after the seeds reach these sites and germinate.

The range of this study included an evaluation of the survival of seedlings and juveniles depending on the density and depth of sowing, seed size, type of substrate and effectiveness of spreading and renewal of individuals obtained from seeds and rhizomes.

METHODS

The effects of depth and density of sowing, seed size and type of substrate on seedling survival and development of juveniles were examined under greenhouse conditions using 25x15x5 cm trays. The following experimental variants were taken into account:

a) four sowing densities - 20, 100, 200 and 500 seeds per tray,
b) four depths of sowing - 3, 2, 1 and 0 cm (surface sowing),
c) two seed sizes - small achenes (3.05 - 5.15 mm long and 0,25 - 0,35 mm wide) and large achenes (4.55 - 5.15 mm long and 0.50 - 0.60 mm wide) were sown separately and, in addition, small and large seeds were sown alternately,
d) six types of substrates - humus, sandy loam, clay loam, clay loam and sand (1:1) sand and gravel and sand.

In each experiment, with the exception of variant a, 100 seeds were sown and, except variant d, clay loam with sand was used as the substrate.

The number of individuals was counted every five days and their stage of development determined and described as belonging to one of the following stages: sprout, seedling, juvenile with the next pair of leaves developed. Studies on the growth and development of individuals obtained from rhizomes were carried out in a greenhouse, using 45x45x30 cm wooden crates. The following variants were taken into account:

a) three planting densities - 2, 10 and 20 seedlings and
b) three types of substrates - humus, sandy loam and sand.

The emergence and death of shoots were determined monthly from May to December.

The effectiveness of spreading and renewal of individuals obtained from rhizomes were studied on 0.25 m^2 plots in the experimental garden. The plots were isolated from each other by plastic foil placed at a depth of 0.3 meter. Four to five cm long fragments of rhizomes having only one node were buried on the plots in three density variants - 5, 15 and 45 per plot and three depth variants - 2, 10 and 30 cm, taking into account rhizomes of various ages - very young (white) and old (brown, woody). In addition to the variant in which density was analyzed, 15 rhizomes were used in the remaining variants and, with the exception of the variant in which different burying depths were used, the rhizomes were buried at a depth of 2 cm. After 12 months of the experiment the individuals were isolated, their shoots counted, then dried and their above-, and below-ground parts weighed.

Each variant of the experiment, both in the greenhouse as well as in the garden, was carried out in three replicates.

RESULTS

SURVIVAL AND DEVELOPMENT OF SEEDLINGS AND JUVENILES DEPENDING ON CONDITIONS OF GERMINATION AND GROWTH

a. Curves illustrating seedling and juvenile survival depending on the density of sowing indicate that their mortality rose along with increased seed density and equalled, starting from the lowest sowing density: 8, 33, 58 and 81%, respectively. The higher the sowing density, the sooner the seedlings began to die (Fig. 1).

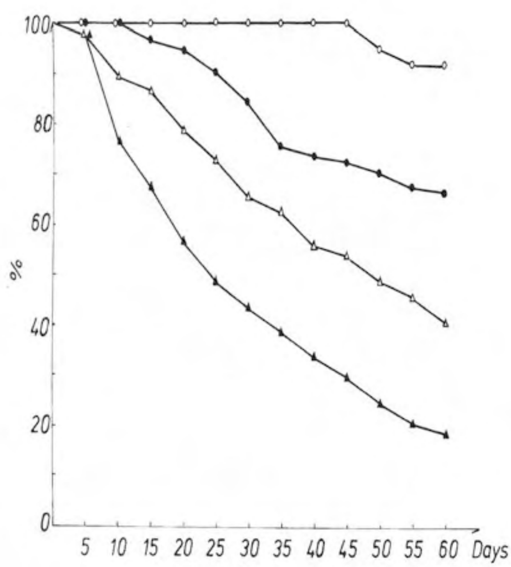

Fig. 1. Survival of individuals depending on sowing density. 100% - seed density

Increasing the sowing density also delayed the development of the seedlings. However, with time and increased mortality of the seedlings and fall in the population density, the development of the surviving individuals accelerated (Fig. 2).

b. The experiment revealed a dramatic fall in the number of survivors as the, sowing depth increased; in contrast with the surface sowing variant, in which 100% emergence of seedlings was observed, at depths of 1 and 2 cm the mortality was 50 and 88% of the sown seeds, respectively (Fig. 3).

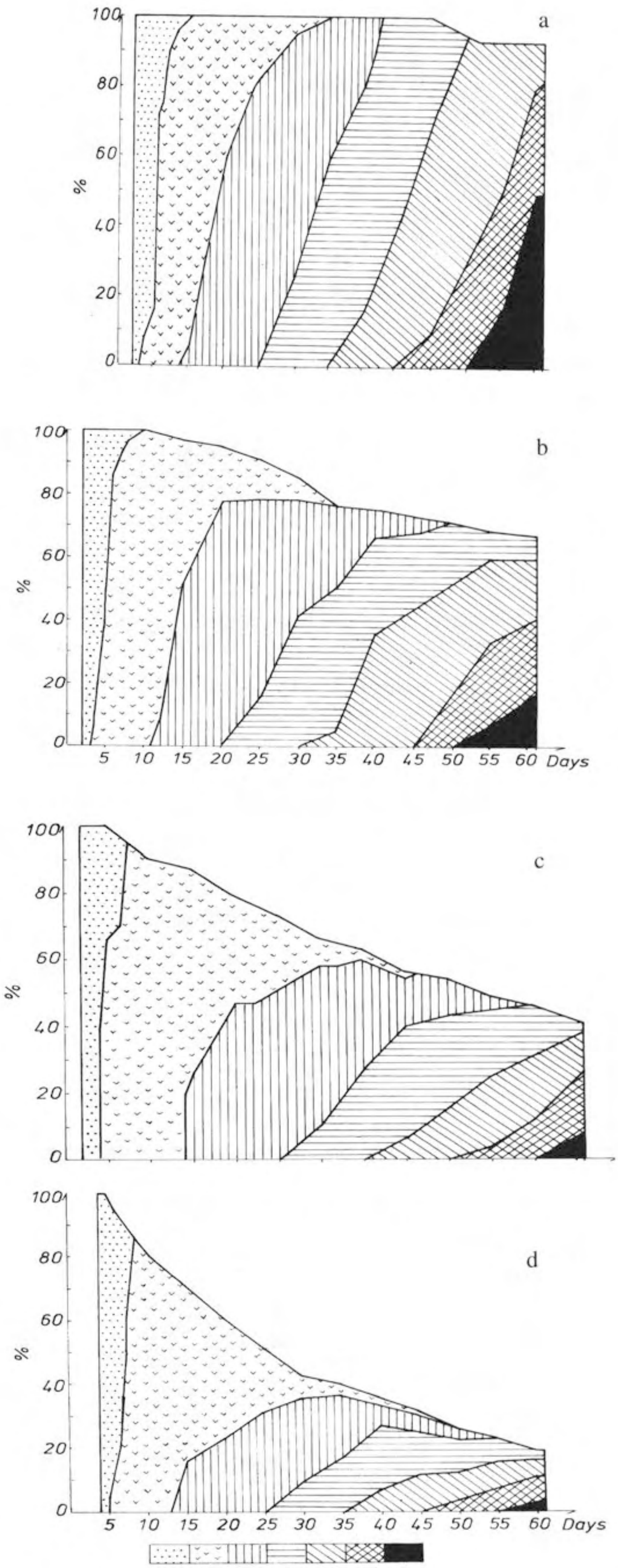

Fig. 2. Survival curves and developmental rates of individuals depending on sowing density: 20 (a), 100 (b), 200 (c) and 500 (d) seeds per tray. Stages of development: sprout (1). seedling (2), individual with: first (3), second (4), third (5), fourth (6) and fifth (7) pair of leaves

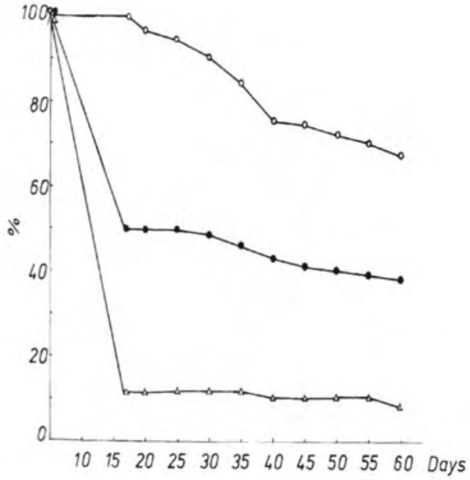

Fig. 3. Survival of individuals depending on sowing depth. 100% - total number of seeds

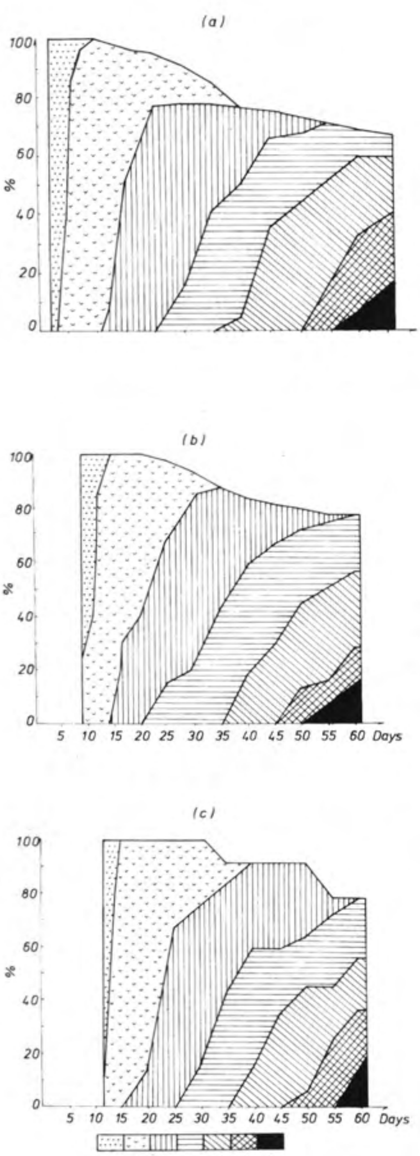

Fig. 4. Survival curves and developmental rates of individuals at sowing depths of: 0 cm (a), 1 cm (2) and 2 cm (3). Stages of development: sprout (1), seedling (2), individual with: first (3), second (4), third (5), fourth (6) and fifth (7) pair of leaves

The increased depth of sowing was responsible mainly for the high death rate of sprouts. Increased sowing depth did not, however, affect the further development of the surviving individuals and, after two months of the experiment, in all of its variants the individuals had reached a comparable morphological and developmental stage (Fig. 4).

c. The results of this experiment point to a significant difference in survival of individuals depending on the size of the seed from which they developed; the lowest death rate (29%) was found for plants deriving from only large seeds, whereas an almost two-fold higher rate was observed in the variant which took into account only small seeds (Fig. 5).

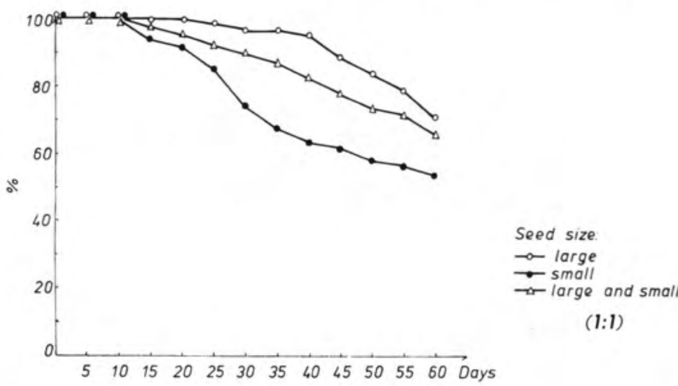

Fig. 5. Survival of individuals depending on seed size. 100% - total number of seeds

Particulary large differences in the survival of individuals were found in the variant in which large and small seeds were used. During the two-month duration of the experiment almost all of the individuals which came from the large seeds survived, while only 45% of those from small seeds survived (Fig. 6).

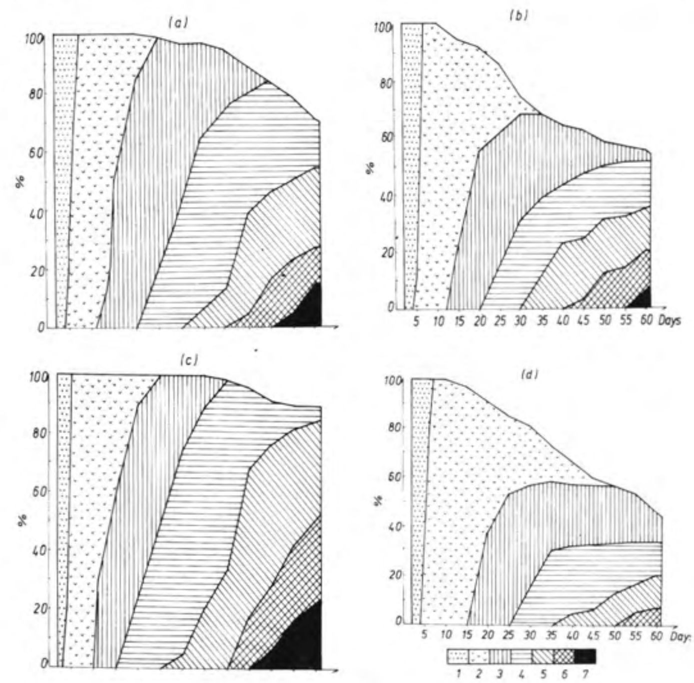

Fig. 6. Survival curves developmental rates of individuals depending on seed size: large, only large seeds sown (a), small, only small seeds sown (b), large, mixed, alternating sowing (c), small, mixed alternating sowing (d). Stages of development: sprout (1), seedling (2), individual with: first (3), second (4), third (5), fourth (6) and fifth (7) pair of leaves

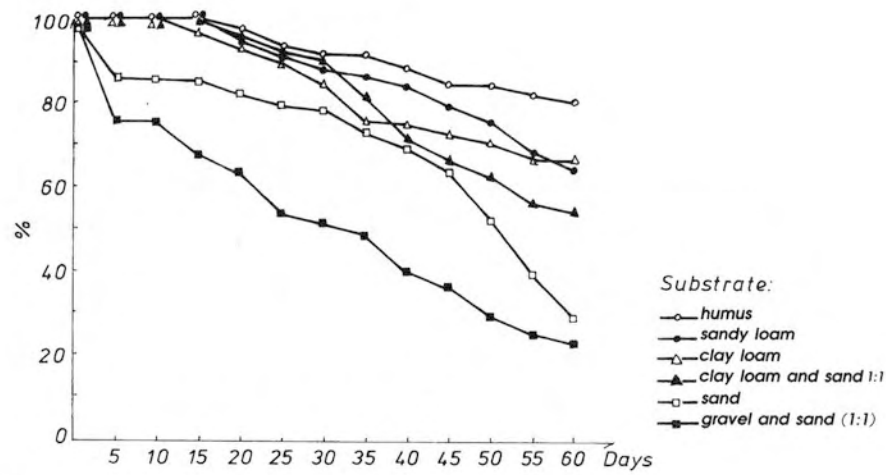

Fig. 7. Survival of individuals depending on type of substrate. 100% - total number of seeds

At the end of the experiment, with the exception of the individuals which had grown from the small seeds in the variant with the mixture of large and small seeds, in all of the remaining variants the individuals had reached the stage with five pairs of leaves. Their percentage was greatest however, when they had grown from large seeds and grew neighboring those from the small seeds.

d. The type of substrate had a large effect on survival and mortality; 80% survival was found in the trays containing humus, over 60% on sandy loam and clay loam while only 21-23% on sand and gravel with sand, where a high mortality rate was already noticeable at seed germination and during seedling growth (Fig. 7).

The substrates which were not favorable to seedling survival were also not beneficial for the rate of development of the survivors; after two months only those individuals which grew on humus and loam had reached the five pairs of leaves stage (Fig. 8).

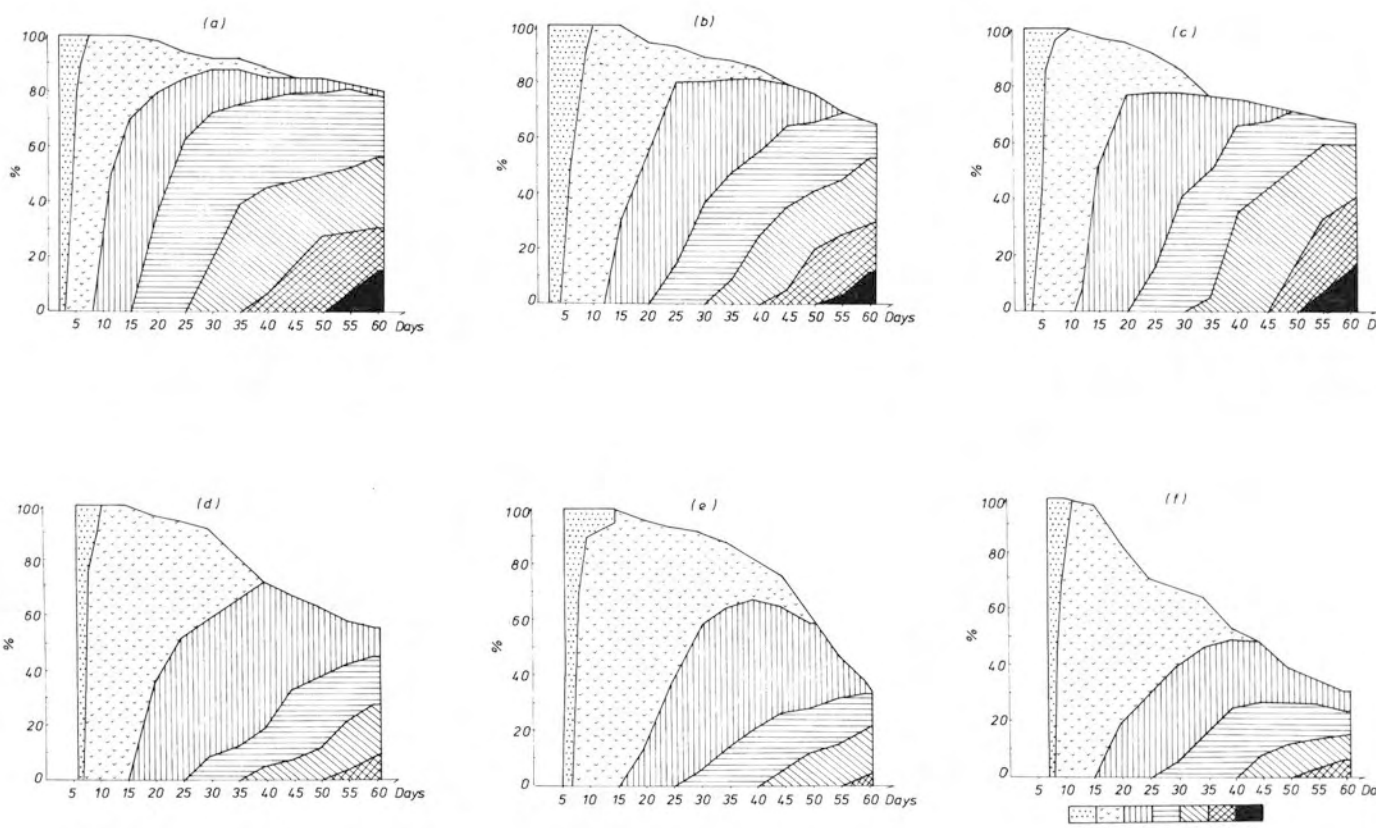

Fig. 8. Survival curves and developmental rates of individuals growing on: humus (a), sandy loam (b), clay loam (c), clay loam and sand (d), sand (e) and gravel and sand (f)

Stages of development: sprout (1), seedling (2), individual with: first (3), second (4), third (5), fourth (6) and fifth (7) pair of leaves

In the remaining experimental variants clear retardation of development of young plants was observed, although in none of them was it completely arrested.

THE EFFECTIVENESS OF SPREADING OF INDIVIDUALS DEPENDING ON SEEDLING DENSITY AND TYPE OF SUBSTRATE

a. The results of the experiment showed that the individuals growing under the least crowded conditions spread the most; in the variant with 2 and 10 seedlings, the number of shoots kept increasing throughout the experiment (Fig. 9).

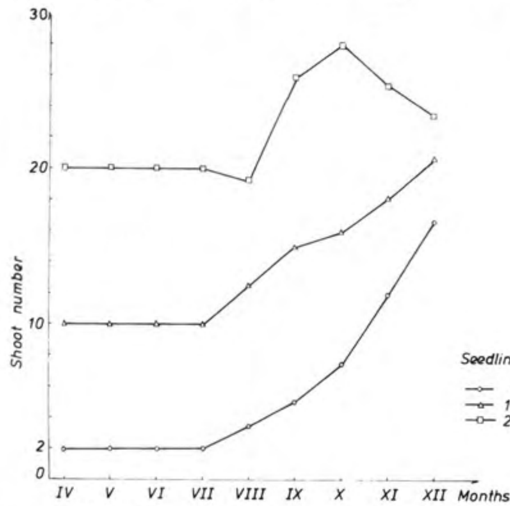

Fig. 9. Seasonal changes in vegetative shoot number in relation to initial seedling density

In the variant with the highest initial density, the shape of the curve reflecting seasonal changes in shoot number was different; it showed rising density till October, then a fall. Regardless of the initial seedling density and changes in number throughout the year, the number of vegetative shoots significantly equalized in December. The ten-fold differences in initial seedling density fell to only 1.4 at the conclusion of the experiment.

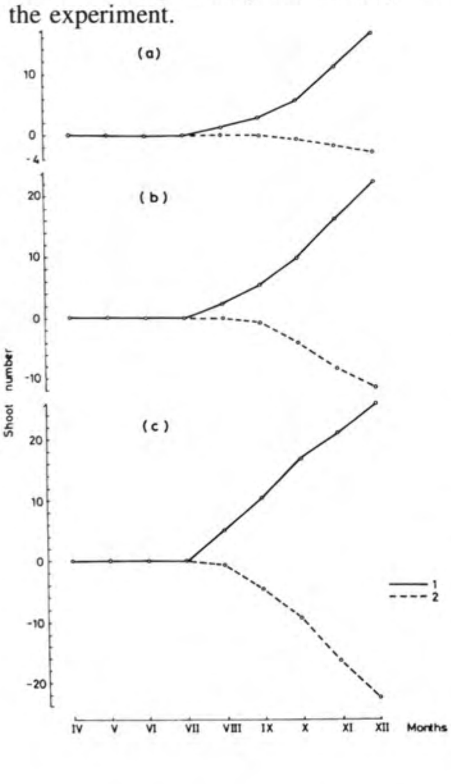

Fig. 10. Cumulated emergence (1) and cumulated death (2) of vegetative shoots dependings on initial seedling density. Initial density: 2 (a), 10 (b) and 20 (c) seedlings per crate

The observed dynamics of shoot number were the combined result of their emergence and dying, which intensified as the initial seedling density increased (Fig. 10). New shoots began to appear at the beninning of August in all of the experimental variants. During the subsequent five months the greatest emergence of shoots occurred in the variant with highest seedling density. The process of dying off of the shoots, with the exception of the variant with the lowest initial density, occurred with the same intensity as their appearance (Fig. 10). Earlier dying of the shoots was seen when the initial number of individuals was higher.

b. The curves illustrating the seasonal changes in vegetative shoot number indicate that the type of substrate influences seasonal changes in density which result from the dynamics of shoot appearance and death. The highest number of shoots was found on the substrates rich in nutrients, the lowest on sand (Fig. 11).

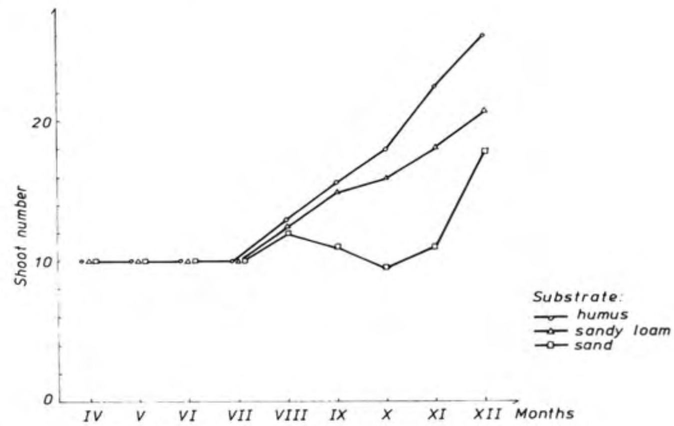

Fig. 11. Seasonal changes in the number of vegetative shoots depending on type of substrate

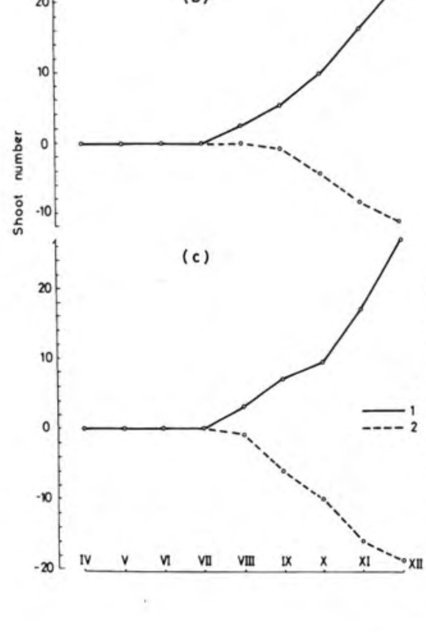

Fig. 12. Cumulated emergence (1) and cumulated death (2) of vegetative shoots depending on type of substrate.
Type of substrate:
humus (a)
sandy loam (b)
sand (c)

In those variants in which humus and loam were used as substrate, the pattern of change in the number of shoots was similar. After a four-month period of stabilization, constant emergence of shoots occurred, more intensely on the humus.

The higher number of shoots on the humus than in the other experimental variants was mainly the result of their low mortality (Fig. 12). The lowest density on sand in the entire period of observation was the effect of their intense dying which occurred concomitantly with the emergence of new shoots. The substrate mainly affected therefore the rate of shoot death.

THE EFFECTIVENESS OF EMERGENCE AND SPREADING OF RHIZOME–DERIVED INDIVIDUALS DEPENDING ON THEIR DENSITY

The results obtained in this experiment show that the emergence of individuals obtained from rhizome fragments is very effective. Even those small fragments of rhizomes which have only one node give rise to above-ground shoots and develop underground organs (Fig. 13).

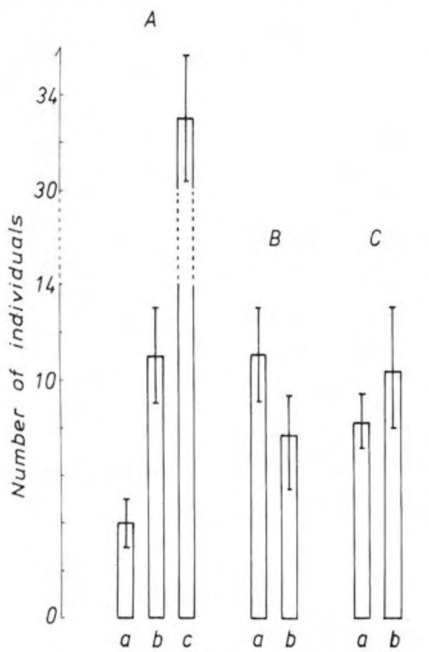

Fig. 13. Effectiveness of emergence of rhizome-derived individuals depending on the density of rhizome fragments (A), their position (B) and age (C).
Density of rhizome fractions: 5 (a), 15 (b) and 45 (c) on an area of 0,25 m^2;
depth of rhizome burying: 2 cm (a), 10 cm (b) and 30 cm - no individuals;
age of rhizome: young (a) and old (b)

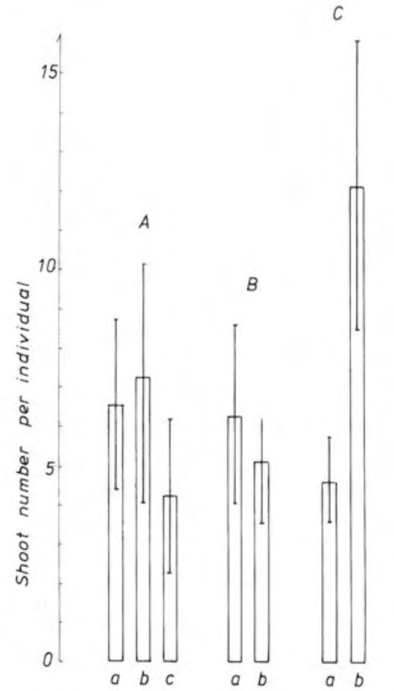

Fig.14. The mean number of above-ground shoots of a rhizome-derived individual depending on the density of rhizome fragments (A), their position (B) and age (C).
Density of rhizome fraction: 5 (a), 15 (b) and 45 (c) on an area of 0,25 m^2; depth of rhizome burying: 2 cm (a), 10 cm (b); age of rhizome: young (a) and old (b)

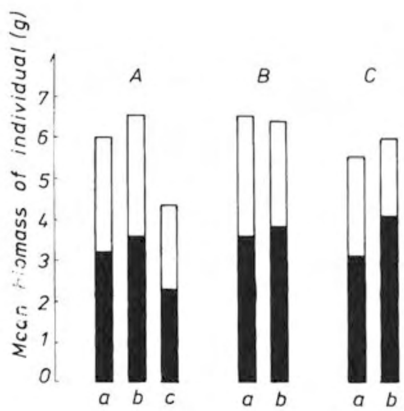

Fig.15. Proportion of above-ground (light columns) and underground (dark columns) biomass of rhizome-derived individuals depending on the density of rhizome fragments (A), their position (B) and age (C).
Density of rhizome fractions: 5 (a), 15 (b) and 45 (c) on an area of 0,25 m^2, depth of rhizome burying: 2 cm (a), 10 cm (b) and 30 cm - no individuals, age of rhizome: young (a) and old (b)

From the three factors taken into account in this study, only excessive depth at which the rhizome fragments were buried limited the emergence of shoots. With increasing depth the percentage of rhizomes which produced new shoots cleary decreased. Not one shoot emerged from the one-node shoot fragments which were buried at a depth of 30 cm.

In all of the experimental variants, the individuals derived from rhizome fragments already began to spread intensely in the first year of growth (Fig. 14). The greatest differences in the number of emerging shoots occurred among the individuals from rhizomes of different ages. The individuals which arose from the older rhizomes grew almost three times more shoots than those from the very young rhizomes.

The high spreading effectiveness of individuals of vegetative descent seen in the first year after emergence is also indicated by the high biomass of their above-, and below-ground parts found in almost all of the experimental combinations, with the biomass of the rhizomes always being greater than of the above-ground parts (Fig. 15). Only the individuals from the rhizome fragments sown at the highest density had a relatively low biomass; low effectiveness of above-ground shoot emergence was also found in this variant (cf. Figs. 14 and 15).

DISCUSSION

Detailed analysis of the development of *T. farfara* individuals under differentiated biotopic and phytocenotic conditions points to several of their biological traits which are characteristic for typical colonizers, such as tolerance of seedlings and juveniles to a wide range of variable environmental conditions, fast rate of individual growth starting from the sprout, their versatile growth and development (Gross 1980, Law 1981, Gray et al. 1987 and literature cited therein). These properties play a major role mainly in the initial phases of colonization of disturbed environments enabling the individuals to survive under changeable biotopic and phytocenotic conditions. Even under conditions of limited resources, e.g. high overpopulation, the seedlings showed a 20% survival rate, similarly about 30% of juveniles survived on an extremely deficient substrate such as sand or gravel and sand. Taking into account the great fertility of individuals (see Namura-Ochalska 1987), this survival rate can assure the start of successful colonization.

The high adaptability of growth and development of juveniles, confirmed in this series of experiments, enables them to make fuller use of available resources, thus increasing their chance of survival under unfavourable conditions (Łomnicki 1988, Shipley and Keddy 1988, Shipley et al. 1989). The rate of development of *T. farfara* seedlings is also, as shown in this study, to a certain extent a function of seed size, but the differences among juveniles are mainly due to secondary causes, as has been shown for other species as well (Falencka 1983, Gross 1984, Mithen et al. 1984, Hutchings 1986, Shipley and Parent 1991).

The results of these experiments indicate that only sowing too deeply, due to the small amount of storage materials in the seed, prevents the seedling from emerging above ground. On unstable ground, a frequent feature of disturbed biotopes, intense burying of *T. farfara* seeds may be a factor limiting colonization. Taking into account, however, the numerous adaptations of seedlings and juveniles to growth and development in disturbed environments, the survival of even a few seedlings provides a chance for successful colonization.

Successful colonization, according to most authors, is based not only on the survival of individuals after the seeds reach the site and germinate, but mainly on the emergence and development of a new population, where the appearance of new individuals can take place through both generative as well as vegetative reproduction (Rabinowitz and Rapp 1985, Gray et al. 1987 and literature cited therein, Grime et al. 1988 and literature cited therein, Peart 1989 a,b). In *T. farfara*, the chance of effectively colonizing disturbed biotopes is notably improved by the rapid achievement by the individuals' ability to spread and renew; the experiments carried out in the greenhouse showed that the rhizomes begin to develop after only two months and that the above-ground shoots begin to multiply after three months. Polycorms, which are much less sensitive to environmental conditions than single-stemmed individuals, develop as the result of both of these processes (Cook 1985 and literature cited therein, Falińska 1989a,b, 1991, Cain 1990). The increase in the number of shoots due to spreading and renewal of individuals, as shown in these experiments, was very intense primarily under conditions of low population density. This permits *T. farfara* to quickly gain control over the area and, due to the large size of its leaves, the invasion of other pioneer species is hindered by limitation of free space and light. These studies have also demonstrated the ideal adaptation of *T. farfara* to effective renewal even on such extremely barren soils as sand and sandy gravel. The spreading of polycorms on infertile soils and in very dense populations is often considered to be an adaptation mechanism which prevents depletion of the environment's resources and allows the plant to "move" looking for more favorable conditions for growth and development (Meijden and Waals-Kooi 1979, Noble et al. 1979, Harper 1986 and literature cited therein, Slade and Hutchings 1987).

The study has shown that the actual effectiveness of emergence of vegetative shoots during the year is significantly higher than would seem just on the basis of their number. Concomitantly with the emergence of new shoots, other shoots die, which occurs most intensely in very dense populations and on poor soil. In this respect, *T. farfara* resembles many other species with querilla type growth (Marks and Prince 1981, Bartlett and Noble 1985, Harper et al. 1986). The relatively high mortality of the shoots under the experimental conditions may have been due to the small dimensions of the trays and thus of excessive limitation of space. The localization of most of the shoots near the tray walls may also be attributed to this factor.

Successful colonization and establishment under conditions of constant disturbances increases the high effectiveness of vegetative reproduction. Individuals can develop even from small rhizome fragments containing only one node, and this regardless of their age and density, under a rather wide range of depths at which the parent rhizome is buried.

Due to the intensive clonal growth from activated dormant buds, individuals of vegetative descent are characterized by effective renewal and spreading, regardless of the density, age and position of the rhizomes. This trait in combination with querilla type growth permits *T. farfara* to rapidly colonize the free area after the plant cover has been destroyed, which has been found for many clonal species (Harper 1986, Hutchings and Bradbury 1986, Bernard 1990, Falińska 1991).

An important adaptation of *T. farfara* to colonizing disturbed biotopes is the plasticity of its allocation of resources to above-ground and underground shoots. The greater proportion of rhizomes and roots in the total biomass of an individual than of above-ground shoots increases the effectiveness of absorption of water along with mineral salts and accumulation of storage materials (Slade and Hutchings 1987, Shipley 1989, Schmid and Bazzaz 1990).

The experiments have shown that successful colonization and persistence in disturbed environments is possible due to the mixed strategy of *T. farfara*. Several of its traits, such as the abundant production of very light seeds (see Namura-Ochalska 1987), anemochoria, high germination capacity and velocity, are characteristic for "spender" type species, others, such as effective vegetetative growth, well-developed system of underground organs, characterize "saver" type species according to the classification presented by During (During et al. 1985). According to the complex classification by Grime (1979), *T. farfara* can be classified as having at least three types of reproductive strategies: 1) anemochoric dissemination, 2) seasonal renewal through seeds and vegetative reproduction, 3) vegetative expansion.

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EKSPANSJA PODBIAŁU POSPOLITEGO *TUSSILAGO FARFARA* L. W ŚRODOWISKACH ZABURZONYCH. III. SUKCES KOLONIZACYJNY A WŁAŚCIWOŚCI OSOBNIKÓW

STRESZCZENIE

Pionierskie właściwości *T. farfara* nie wyjaśniają w pełni zaskakującej wręcz zdolności kolonizacji i trwałego zasiedlania zaburzonych środowisk, po uprzednim zniszczeniu roślinności.

Celem pracy poza szczegółową analizą przebiegu cyklu życiowego w zróżnicowanych warunkach biotopowo-fitocenotycznych było odpowiedzenie na pytanie, które cechy gatunku umożliwiają skuteczną kolonizację i trwałe zasiedlenie zakłóconych biotopów, po dotarciu i wykiełkowaniu nasion w warunkach nagiego podłoża.

Badania wykazały między innymi: 1) dużą tolerancję siewek na warunki zewnętrzne - mogą one rosnąć i rozwijać się w szerokim zakresie zmienności gęstości siewu, z nasion wysianych powierzchniowo i zasypanych, jedynie zbyt duża głębokość siewu uniemożliwia pojaw siewek, niezależnie od wielkości nasion, z których pochodzą, na różnym, nawet skrajnie ubogim podłożu, 2) plastyczne tempo rozwoju osobnikow juwenilnych w zależności od czynnikow środowiska, przy czym w warunkach ograniczonych zasobów następuje opóźnienie w osiąganiu kolejnych faz rozwojowych; 3) szybkie w ontogenezie rozrastanie się osobnikow; pojaw nowych pędów wegetatywnych następuje już w czwartym miesiącu licząc od daty wysiewu, niezależnie od zagęszczenia siewek (rys. 9 i 10), oraz rodzaju podłoża dużą efektywność rozmnażania wegetatywnego z fragmentów kłączy, przy czym osobniki mogą się rozwijać nawet z małych odcinków, zawierających tylko jeden węzeł, intensywne rozrastanie i odnawianie się osobników pochodzenia wegetatywnego, niezależnie od uwzględnionego zakresu zagęszczenia kłączy, ich wieku i położenia, wysoką choć zmienną wartość nadziemnej i podziemnej biomasy,przy czym biomasa kłączy była zawsze większa niż biomasa pędów nadziemnych. Cechy te po osiągnięciu fazy wkraczania i kiełkowania nasion zapewniają *T. farfara* sukces kolonizacji nagiego podłoża w zróżnicowanych środowiskach zaburzonych.

SŁOWA KLUCZOWE: trwała kolonizacja, przeżywalność siewek i osobników juwenilnych, dynamika populacji, rozprzestrzenianie się i odnowa osobników, reprodukcja wegetatywna, biomasa