LIFE HISTORY VARIATION IN CIRSIUM PALUSTRE
AND ITS CONSEQUENCES FOR THE POPULATION DEMOGRAPHY
IN VEGETATION SUCCESSION

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ABSTRACT

The objective of the study was to describe the life-history pattern of the biennial species Cirsium palustre. It has been demonstrated that under optimum conditions in the greenhouse individuals live 1.5 to 2 years, in a mown meadow 2 to 3 years, and during the plant succession in abandoned meadows they prolong their life to several years. This is accompanied by a gradual decrease of C. palustre population size. A relationship between the life-history pattern differences during a plant succession and the population abundance dynamics has been found. Reproductive-phase age is correlated with the rosette size. In spite of the occurrence of many limiting factors during a succession (closed plant cover, shading by macroforbs, willows) C. palustre survives until the formation of forest communities. Its persistence is favoured by: protracted life history, attainment the reproductive phase at different ages (not only in the second year), formation of a permanent seed bank, airborne seeds and the emergence and survival of seedlings under the canopy of several-year old rosettes during a strong competition. The arresting of juvenile individuals under the rosettes for several years has been termed the "rosette mechanism". Cirsium palustre can be included among facultative biennials. In every conditions a proportion of individuals in a population attain the flowering phase in life year 2. During a succession the proportions of "triennial" and "quadriennial" forms, and at the terminal stage – of perennial monocarpic forms increase.

KEY WORDS: Cirsium palustre, biennial, life-history pattern, demography, size-dependence, succession.

INTRODUCTION

Among views on the life history of annual, biennial and perennial plant species there has been an opinion that the differences observed are of a continuum-related type (Harper 1977). This results from the fact that individuals of some annuals may live almost 2 years, e.g. Poa annua (Law et al. 1977; Law 1981), and individuals of species included among biennials may shorten their life to 1.5 years, e.g. Geranium robertianum (Falinski and Piroznikow 1983), or, like many other biennials, prolong it to several years (Holt 1972; Werner 1975; Symonides 1979; Gross and Werner 1982). On account of the considerable variation of their life cycles, some biennials are considered true biennials (Kelly 1985a, b), others facultative biennials (During et al. 1985, Kelly 1989a, b), or retarded biennials (Harper 1977), i.e. those of which the individuals do not attain the flowering phase in the second, but in the third or fourth growing season. The transient nature of this species group has often been emphasized, and it has been reported that, depending on the environmental conditions, biennials can complete their life cycle in a time period as long as that of the overwintering terophytes, and extend it to several growing seasons, resembling monocarpous perennials (Harper 1977; Werner 1975; Grubb 1977; Grime 1977; Hart 1977; Jong and Klinkhamer 1988; Gross 1980; Klemov and Raynal 1985; Kelly 1989a, b). Similar variation has been found in Cirsium palustre populations (Pons 1977; Ballegard and Warncke 1985a, b; Falinski 1989, 1991). It has often been reported that in heterogeneous habitats the life history of many species is significantly modified (Grubb et al. 1982; Lee and Hamrick 1983; Kelly 1989a, b). The increasing vegetation patchiness in abandoned meadows during the vegetation succession put forward the question whether or not and to what extent other species modify the life history of Cirsium palustre individuals.

In the present studies much attention has been given to follow the fate of C. palustre individuals in abandoned meadows, and especially to the relationship between the population dynamics and succession. Evidence has been sought after to indicate what C. palustre life strategy characteristics enable the species throughout the succession process to be present, from the initial to terminal stage.

The aim of this paper is to: 1) describe the pattern of life history of a biennial plant species in long-term studies, 2) assess the role of density and neighbours as factors causing differences in the life history pattern of C. palustre, 3) assess the relationship between the life cycle variation of C. palustre and the fate of populations during succession.
METHODS

Study area

The Reski Range is a 15 ha site unforested for 200 years, which is situated in the Narewka River valley close to the Białowieża National Park, in the middle of the Białowieża Primeval Forest (N 52°42'30", E 23°50'20").

The study was conducted between 1981 and 1995 in an abandoned meadow and constitutes a part of long-term study the demography of successional species, started in 1972 (Falińska 1985, 1991, 1995).

The patchiness of the vegetation of the Reski Range, caused by the abandonment of meadows in different time periods, made it possible to carry out investigations on the population dynamics of Cirsium palustre during the vegetation succession. At the beginning of the investigations the patches represented the various succession stages described in earlier studies (Falińska 1991).

Four patches were chosen to represent the range of variability within the vegetation. Patch (a), floristically rich, grass-dominated with Cirsium palustre, Geum rivale, Ranunculus acris, Lychnis flos-cuculi, Myosotis scorpioides – meadows unknown for 5 years (initial stage); patch (b), floristically rich dominated by macroforbs, such as Lysimachia vulgaris, Lythrum salicaria, Cirsium rivulare and Cirsium palustre – meadows unknown for 10 years (temporary stage); patch (c) dominated by Carex acutiformis, with small clumps of C. palustre within sedge aggregates and patch (d), dominated by willows – meadows unknown for 15 years (terminal stage, early phase).

A control area (designated as 0) was set up in a meadow abandoned in 1981, i.e. when researches on the growth of C. palustre population from the initial phase to the formation of willow scrub (initial phase of the terminal stage) were started. As indicated by earlier studies, this process lasts about 15 years.

Two 25 m² plots were selected in each patch: one (a₁, b₁, c₁, d₁) was used for detailed long-term observations, while the other (a₂, b₂, c₂, d₂) was used for experiments. Plots were subdivided into 1 m x 1 m subplots.

Field studies

In each growing season in 1981-1994 observation was conducted in 25 m² plots located in patches of meadows fallow different time periods (5, 10, 15 years). Seedlings, rosettes, flowering individuals and fruiting individuals were counted at 5-7 day intervals. The data obtained were used for the assessment the variation in abundance and population age structure during succession. The rosette diameter of the generative shoots was measured in flowering and nonflowering individuals. The aim was to establish the relationship between the rosette size and the getting the generative phase by individuals growing among various neighbours, i.e., grasses (plot a), macroforbs (plot b), sedge (plot c) and willows (plot d).

The stages of life cycles was observed in the greenhouse and in the field. During the growing season of 1981 and 1984, seedlings found in 25 m² plots were labelled: control (0) – cohort 1; dominated by grasses (a) – cohort 2; macroforbs (b) – cohort 3; sedge (c) – cohort 4 and willows (d) – cohort 5 were labelled. Individual growth was observed for several growing seasons, depending on the life span of the individuals of particular cohorts. In the flowering period the rosette diameters and shoot height measured, and the fruits produced by particular individuals counted.

Greenhouse experiment

Similar studies on of the life cycle of individuals of 3 cohorts (1981, 1984, 1992) was carried out in the greenhouse. Seedlings of the first cohort developed from 960 seeds planted in the greenhouse in 32.05 m² plots, 30 seeds in each, in the autumn of 1981. The second cohort (1984) developed from seeds produced by greenhouse individuals in 1984. The aim of the observation of the individual life history in the greenhouse and in the field was to estimate the duration and pattern of individual life history of Cirsium palustre under various conditions. Also, in the greenhouse an experiment was carried out on the effect of density on the individual growth and life-history pattern. In 1989 seedlings were planted there in 0.25 m² plots at three density rates: 1, 2, 4, each in 10 replicate plots. Observations were continued from 1989 to 1991. In 1992 a total of 12000 seedlings emerged in 32.05 m² plots in greenhouse. Their life history was observed in 1992-1995, and the data have been used in an analysis of the effect of density on the growth and life history of the rosettes (cohort 3).

Field experiment

In three meadow patches dominated by grasses (plots a₁), macroforbs (b₁) and sedge (c₁) the plant cover was removed from ten 1 m² plots. Emerged seedlings were counted during the subsequent three growing seasons. The plots were weeded and only C. palustre individuals were left. Analogous observation on the emergence of seedlings was conducted in every patch of 10 plots from which the plant cover had not been removed (a₁, b₁, c₁); they served as control plots.

Seed bank

Soil samples for seed bank analyses were taken twice: in autumn (September) 1989, after the termination of fruiting, and in spring (April) 1990, before the beginning of the vegetation growth. In 25 m² plots (a₂, b₂, c₂) 50 samples (2 from each 1 m²) of the size of 100 cm³ were taken. C. palustre seeds were picked out from them in the laboratory. 10 soil monoliths of the size of 0.25 m², collected near the experimental plots, were placed in trays in the greenhouse. Seedling emergence was subsequently monitored every 2-3 days for 12 months.

RESULTS

Density

During a 15-year period the density of C. palustre in different meadow patches changed significantly. In a patch, in which after the cessation of mowing C. palustre density was low (1.6 ± 0.9 m²), a threefold density increase was found 4 years later. A high density level persisted for another 4 years and then dropped. 15 years after the cessation of mowing the density of C. palustre was similar to that in the initial period (Fig. 1a), i.e., in the year of abandonment. In a patch where on the cessation of mowing C. palustre density was equal to 4.8/m² density changes during the subsequent 5 years were small, whereas the density dropped gradually (Fig. 1b).

The distribution of individuals, in relation to the length of time elapsed from the cessation of mowing, also differed. The highest aggregation was found on willow-scrub edges, that is, 15 years after meadow abandonment, and during the formation of macroforb communities, i.e., 5 years after it (Fig. 2).

A comparison of C. palustre density in plots in which various other species prevailed, revealed the highest C. palustre...
density in grass and macroforb aggregations, and the lowest in sedge and willow assemblages, the differences being statistically significant (P<0.05) (Table 1).

Density and rosette size

The results of greenhouse experiment indicate that the optimum area for rosette growth and flowering-shoot production is 0.25 m² (Table 2). In 0.25 m² experimental plots, each holding a single individual, the rosette diameter of individuals varied between 30 and 40 cm, and 90% of them flowered in the second year of their life. In plots of the same size holding 4 individuals each the rosette diameter was almost a half smaller, ranging from 17 to 24 cm (the differences being statistically significant - P<0.05), and only 30% of them flowered in life year 2.

Immediately after the cessation of mowing there usually grew 1 or 2 individuals in each of the 0.25 m² plots. In a meadow fallow for 9 years as large a proportion as 70% of individuals formed assemblages of 2 to 4 in each of the 0.25 m² plots (Fig. 3).

The effect of density on the survival to flowering was studied in the most numerous greenhouse cohort. In autumn 1992 a total of 12113 seedlings were found, their density being 2785 ± 117.025 m². A total of 988 (x = 35.3 ± 4.4) survived until the rosette stage, and 182 (x = 7.6 ± 1.9) until the generative phase. In 32 plots the density varied considerably. Rosette size was negatively correlated with density, the flowering phase to be positively correlated with the rosette size, and the number of fruits with the shoot height (Table 3, 4).

Neighbours and the rosette size

The largest C. palustre rosettes (31.3 ± 7.1 cm) were found in plots with grasses domination, and the smallest (17.4 ± 4.0 cm) in willow aggregations. The differences were statistically significant (P<0.05). In macroforb aggregations and on willow aggregation edges rosettes of similar size were found (24.1 ± 3.2 cm and 25.2 ± 4.5 cm, respectively), although the density of C. palustre in the macroforb aggregations was three times as high as around the willow aggregations (P<0.01). In plots, in which C. acutiformis and necromass dominated, the rosettes were much smaller and of similar size (Table 1)

Variable effect of other plant species on the C. palustre individual life-history pattern and growth has been confirmed by removal experiment. Most significant rosette-size differences followed the removal of the sedges and macrofors, and less significant differences occurred after the removal of the grasses. Flowering and nonflowering rosettes in the experimental and in the control plots differed in their size (Table 5).

<table>
<thead>
<tr>
<th>TABLE 1.</th>
<th>Influence of neighbours on density and rosette size in Cirsium palustre.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type of patch</td>
<td>No. of subplots per m²</td>
</tr>
<tr>
<td>grasses (a)</td>
<td>18</td>
</tr>
<tr>
<td>macrofors (b)</td>
<td>9</td>
</tr>
<tr>
<td>sedges (c)</td>
<td>14</td>
</tr>
<tr>
<td>willows: in patch (d1)</td>
<td>9</td>
</tr>
<tr>
<td>in edge (d2)</td>
<td>8</td>
</tr>
<tr>
<td>necromass (e)</td>
<td>12</td>
</tr>
</tbody>
</table>

* - P < 0.05; ** - P < 0.01; N.S. - not significant.
Table 2. The effect of rosette diameter on flowering of *Cirsium palustre* (greenhouse experiment).

<table>
<thead>
<tr>
<th>No of individuals per 0.25m²</th>
<th>No. of subplots per 0.25m²</th>
<th>No. of rosettes</th>
<th>Rosette diameter (x ± SD) (cm)</th>
<th>No. of flowering individuals</th>
<th>Frequency flowering individuals (%)</th>
<th>Height of shoot (x ± SD) (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>10</td>
<td>10</td>
<td>34.8 ± 5.6 *</td>
<td>9</td>
<td>90</td>
<td>139.7 ± 20.6 *</td>
</tr>
<tr>
<td>2</td>
<td>10</td>
<td>20</td>
<td>25.6 ± 7.3 *</td>
<td>12</td>
<td>60</td>
<td>116.9 ± 7.5 *</td>
</tr>
<tr>
<td>4</td>
<td>10</td>
<td>40</td>
<td>20.6 ± 3.0 *</td>
<td>10</td>
<td>25</td>
<td>102.2 ± 5.6 *</td>
</tr>
</tbody>
</table>

* - P < 0.05

Table 3. Density, survival and flowering of *Cirsium palustre* in greenhouse (1992-1995).

<table>
<thead>
<tr>
<th>Year of life</th>
<th>Survival (Total)</th>
<th>Life stage</th>
<th>Rosette diameter</th>
<th>Density per 0.25 m²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year of life</td>
<td>n</td>
<td>%</td>
<td>seedlings</td>
<td>rosettes</td>
</tr>
<tr>
<td>0</td>
<td>12113</td>
<td>12113</td>
<td>1018</td>
<td>806</td>
</tr>
<tr>
<td>1</td>
<td>1018</td>
<td>9</td>
<td>806</td>
<td>49</td>
</tr>
<tr>
<td>2</td>
<td>988</td>
<td>97</td>
<td>49</td>
<td>35</td>
</tr>
<tr>
<td>3</td>
<td>84</td>
<td>9</td>
<td>0</td>
<td>35</td>
</tr>
<tr>
<td>4</td>
<td>13</td>
<td>15</td>
<td>0</td>
<td>13</td>
</tr>
</tbody>
</table>

Fig. 2. *C. palustre* individual areas (rosette diameter) and their distribution in relation to the time of meadow abandoning. Black dots in circles denote flowering individuals (fragments of a 25 m² plot).
experiments where flowering was positively correlated with the rosette size ($r = 0.40$, $P<0.05$), and rosette size was negatively correlated with the density ($r = -0.38$, $P<0.05$) (Table 3).

**Seedling abundance dynamics**

*C. palustre* seedlings appeared from April till October. Most of them emerged in June and July, both in the laboratory and under natural conditions (Figs 6, 7). However, at all succession stages most seedlings appeared in the first growing season following the removal of the vegetation cover. In the subsequent years, after the vegetation cover had regenerated, the number of seedlings was at a rule a half lower. Differences in the abundance of seedlings between the early succession stage (meadow) and the later one (willow scrub) persisted for three years.

The largest number of *C. palustre* seedlings emerged in the early and in the transition stages of succession, i.e. in plots in which grasses (plot a1) and macroforbs (plot b1) dominated (Fig. 6).

**Effect of the plant cover on seedling emergence**

The experiment on the effect of the plant cover on seedling emergence indicated that the removal of plants (by cutting – simulated mowing) was in all followed by increased numbers seedlings: 10 fold in plots "a" and "b" and 5 fold in plot "c". This regularity has been confirmed by the greenhouse experiments, where seedlings emerged on soil monoliths taken from various patches (Fig. 7).

**Seed bank**

In spring, the largest supply of *C. palustre* seed ($5.0 \pm 1.5/m^2$) in the soil was found in a site at an early succession stage and a 50% lower one in later succession stage sites, i.e. in macroforbs ($3.0 \pm 0.6$, $P<0.05$) and in willow scrub ($2.1 \pm 1.0$, $P=0.01$) (Table 7).

Only in sites of succession-stage III were significant differences revealed by comparing the seed supplies in autumn and spring: in the willow scrub the autumn seed bank was twice as large as the spring one ($P<0.05$) (Table 6). Seed bank calculation per $1 m^2$ and comparison with the seedling density in the same plots after uncovering the soil showed that at all succession stages only 5-10% of seeds from the bank developed into seedlings (Table 8).

**Differences in life-history patterns**

In abandoned meadows *C. palustre* individuals as a rule prolong their life to 3 or 4, seldom 5 or 6 years. Diagramatic life-table of the three cohorts studied show differences in the individual flowering age and life span in relation to the habitat conditions. With advancing succession the individual life span is extended and flowering is retarded (Fig. 8). Individuals found in a mown meadow patch (plot 0) lived the shortest time, usually 2 or 3 years. In the periods of macro-

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**Fig. 3. Changes in *C. palustre* density during succession: Phases: 0 – at cessation of mowing; I – after 5 years; II – after 10 years; III – after 15 years, around willow aggregations in meadows; IV – after 20 years on the edges of willow scrub.**

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**Rosette size and the flowering of individuals**

The rosettes of flowering individuals were as a rule larger than those of non-flowering individuals, even if the age of the individuals compared was the same (Table 6). Only 10% of individuals with rosette diameter below 20 cm produced flowering shoots, 75% of those with rosettes of size class 20-40 cm, and 90-100% of those above 40 cm (Fig. 4). Shoot height was also correlated with the rosette size ($r = 0.69$, $P<0.01$) (Fig. 5). This has been confirmed by greenhouse ex-

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**Table 4. The effect of rosette diameter on size and fruiting of individuals under different density condition (in greenhouse).**

<table>
<thead>
<tr>
<th>Type of density</th>
<th>Density per 0.25 m²</th>
<th>Rosette diameter (cm)</th>
<th>Height shoot (cm)</th>
<th>No. of fruits</th>
</tr>
</thead>
<tbody>
<tr>
<td>law</td>
<td>1.6 ± 0.7</td>
<td>31.3 ± 7.1</td>
<td>199.6 ± 20.5</td>
<td>69.2 ± 15.9</td>
</tr>
<tr>
<td>medium</td>
<td>3.6 ± 1.9</td>
<td>24.1 ± 3.8</td>
<td>160.2 ± 13.9</td>
<td>48.4 ± 5.7</td>
</tr>
<tr>
<td>high</td>
<td>5.6 ± 2.3</td>
<td>20.5 ± 5.2</td>
<td>136.8 ± 1.8</td>
<td>40.7 ± 6.8</td>
</tr>
</tbody>
</table>

* - $P<0.05$; ** - $P<0.01$; N.S. - not significant.
forb and scrub formation individuals extended their life to 4 or 5, sporadically 6 years.

Under experimental conditions (in the greenhouse and in a meadow) most individuals (60%) complete a full life cycle within 1.5 and 2 less often 3 years (Fig. 9). 20% of the individuals of greenhouse C. palustre cohorts flowered in the first, and 78% in the second years of their life. The remainder of the individuals died at the rosette stage (Fig. 9a).

Individuals of the cohort in a control plot 0 lived 2 or 3 years; 55% flowered in the second, and 25% in the third year of their life. Only 2 rosettes survived till life year 4 (Fig. 9b).

Individuals of the cohort in patch dominated by grasses lived 2 to 4 years. 30% of them flowered in the second, 20 in the fourth year (Table 6).

Individuals of the cohort in a patch dominated by macroforbs and willows lived 3 to 6 years. 22% of them flowered in the third, 18% in the fourth, 10% in the fifth, and 5% in the sixth year. Other individuals died at the rosette stage (Fig. 9c).

In both cohorts the seedling stage sustained the highest mortality. 7-13% of seedlings attained the juvenile (settled seedling) stage, 53-87% of the juvenile individuals attained the rosette stage (vegetative), 52-77% of the rosettes of either cohort produced flowering shoots (in the greenhouse – 78%).

Change in size of Cirsium palustre population

Cessation of mowing (patch 0) was immediately followed by a population-abundance increase which continued for 5 years. During the subsequent 10 years the population abundance decreased gradually (Fig. 10). In a meadow patch follow 5 years a density of 103 individuals per 25 m² was found at the beginning of the study. Four years later a gradual abundance decrease began. In a patch where mowing had been ceased 10 years earlier 20 individuals per 25 m² were recorded. In that population the abundance variations were of the fluctuation type. A comparison of the population-size variations during succession indicates that a successions progress is followed by a population-abundance regression (Fig. 10). If during the first 5-6 years following their abandonment meadows are inhabited by sedges, then population regression starts in the 9th or 10th year of population growth, preceded by the failure of the rosette-stage individuals to attain the flowering phase.

The highest abundance has been recorded for the transition stage of succession, in the period of macroform growth, and the lowest for willow scrub, i.e., meadows not mown for 15 years (Fig. 11).

DISCUSSION

As indicated by the data from the present studies, especially those from the experiments, Cirsium palustre can be included among facultative biennials, because a proportion of individuals of every cohort flowered in the second year of their life. If the limiting factors are eliminated, their proportion may come up to 40-70%, e.g. in the greenhouse and mown meadow (Fig. 9). As large a proportion as 20% of the individuals in the greenhouse flowered in life year 1, and 70% in year 2, the remainder of them died at the rosette stage in life years 2 or 3. Other investigators also found that under optimum conditions some C. palustre individuals flowered in the first or second year of their life (Pons and During 1987). The flowering-limiting and retarding factors in Cirsium palustre, as for other biennials, are: the vegetative cover, competition
TABLE 5. The relationship between rosette size and flowering in experimental plots (removal of plants) and control plots (without cutting of plants) in three patches in abandoned meadow. Data collected from 10 m² plots in patch.

<table>
<thead>
<tr>
<th>Type of patch</th>
<th>Phase</th>
<th>Control</th>
<th>Removal</th>
<th>Control versus removal P</th>
</tr>
</thead>
<tbody>
<tr>
<td>dominated by grasses</td>
<td>non-flowering</td>
<td>20.5 ± 1.0</td>
<td>*</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>flowering</td>
<td>31.3 ± 7.1</td>
<td>*</td>
<td>N.S.</td>
</tr>
<tr>
<td>dominated by macroforbs</td>
<td>non-flowering</td>
<td>21.0 ± 2.0</td>
<td>**</td>
<td>N.S.</td>
</tr>
<tr>
<td></td>
<td>flowering</td>
<td>24.08 ± 3.2</td>
<td></td>
<td>*</td>
</tr>
<tr>
<td>dominated by sedges</td>
<td>non-flowering</td>
<td>16.3 ± 1.5</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>flowering</td>
<td>25.9 ± 8.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* - P < 0.05; ** - P < 0.01; N.S. - not significant.


<table>
<thead>
<tr>
<th>Year</th>
<th>Year of life</th>
<th>Survival of individuals</th>
<th>Survival from seedlings to rosettes</th>
<th>Flowering</th>
<th>Survival to flowering from:</th>
<th>Rosette diameter (cm)</th>
<th>Heigt of shoot</th>
<th>No. of fruits/in individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>%</td>
<td>seedlings</td>
<td>rosettes</td>
<td>n</td>
<td>%</td>
<td>%</td>
<td>%</td>
</tr>
<tr>
<td>1981</td>
<td>1</td>
<td>202</td>
<td>101</td>
<td>50</td>
<td></td>
<td></td>
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<tr>
<td>1982</td>
<td>2</td>
<td>64</td>
<td>63</td>
<td>45</td>
<td>19</td>
<td>30</td>
<td>9</td>
<td>30</td>
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<tr>
<td>1983</td>
<td>3</td>
<td>45</td>
<td>30</td>
<td>22</td>
<td>23</td>
<td>50</td>
<td>11</td>
<td>36</td>
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<tr>
<td>1984</td>
<td>4</td>
<td>15</td>
<td>30</td>
<td>2</td>
<td>12</td>
<td>90</td>
<td>6</td>
<td>20</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>202</td>
<td>101</td>
<td>54</td>
<td>26</td>
<td>50</td>
<td></td>
<td></td>
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</tbody>
</table>


<table>
<thead>
<tr>
<th>Succession phases</th>
<th>Date of sample</th>
<th>No. of samples with seeds 100 cm²</th>
<th>Frequency n=50/100 cm² (%)</th>
<th>No. of seeds (total)</th>
<th>No. of seeds per 100 cm² x ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1981 Autumn</td>
<td>24</td>
<td>48</td>
<td>107</td>
<td>4.8 ± 1.6 N.S.</td>
</tr>
<tr>
<td></td>
<td>1982 Spring</td>
<td>31</td>
<td>62</td>
<td>156</td>
<td>5.0 ± 1.5 *</td>
</tr>
<tr>
<td>II</td>
<td>1981 Autumn</td>
<td>31</td>
<td>62</td>
<td>99</td>
<td>3.2 ± 0.9 N.S.</td>
</tr>
<tr>
<td></td>
<td>1982 Spring</td>
<td>29</td>
<td>58</td>
<td>86</td>
<td>3.0 ± 0.6 *</td>
</tr>
<tr>
<td>III</td>
<td>1981 Autumn</td>
<td>30</td>
<td>60</td>
<td>132</td>
<td>4.3 ± 1.9 **</td>
</tr>
<tr>
<td></td>
<td>1982 Spring</td>
<td>25</td>
<td>50</td>
<td>52</td>
<td>2.1 ± 1.0</td>
</tr>
</tbody>
</table>

* - P<0.05; ** - P<0.01; N.S. - not significant.
TABLE 8. Relationship between seed bank and emergence of seedlings of *Cirsium palustre* in patches dominated by various species. Seed bank was assessed in March before the beginning of vegetation growth in the meadows; seedlings were counted in May and June 1989.

<table>
<thead>
<tr>
<th>Succession phases</th>
<th>Density of seeds in soil per m² x ± SD</th>
<th>Density of seedlings per m² x ± SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>I. Meadow</td>
<td>2012 ± 1734 *</td>
<td>107 ± 38</td>
</tr>
<tr>
<td>II. Macroforbs</td>
<td>1186 ± 668 N.S.</td>
<td>125 ± 45 **</td>
</tr>
<tr>
<td>III. Willows brushwood</td>
<td>912 ± 970</td>
<td>40 ± 24</td>
</tr>
</tbody>
</table>

* – P<0.05; ** – P<0.01; N.S. – not significant.

---

**Fig. 6.** Effect of the plant cover on seedling emergence of *C. palustre* in meadows followed 5 years (I), 10 years (II) and 15 years (III).  
C – plots with plant cover.  
E – plot without plant cover.
and shading (Holt 1972; Werner 1975; Harper 1977; Pons 1977; Silvertown 1987; Kelly 1985a, b). All these factors affect the survivorship and life history of *C. palustre*, but each of them plays a different role in the particular life cycle stages of the individuals, which agrees with Grime's (1979) concept of different life strategies of the juvenile and mature stages.

For many species evidence has been found to prove that a close vegetation cover limits the appearance and survivorship of seedlings (Platt 1975; Grubb 1977; Gross 1984; Peart 1989a, b, c). For instance, at all succession stages the removal of the vegetation cover was followed by a considerable increase of the number of *C. palustre* seedlings (Fig. 6). The above findings are similar to those described by Collins and Pinder (1990). The removal of macroforbs and sedges was followed by a twofold increase of the rosette size of *C. palustre*. A comparison of the rosette size of *C. palustre* growing among various neighbours indicates that the size is most limited by sedges and willows (Table 1). If the latter fill all the free spaces, most *C. palustre* rosettes fail to attain the size they need to be able to produce the flowering shoot in the second growing season. They flower only in the third or fourth growing season, and for this reason, more and more individuals extend their life span to several years (Fig. 9).

*Cirsium palustre*’s neighbours thus affect the individual longevity and age of attainment the generative phase, and thereby the demographic processes in its populations. Successional species turnover causes changes in the habitat conditions and affects the growth and size of the rosettes, thus determining the *C. palustre* population size.

Essential to the reproductive phase of biennials is a suitable rosette size (Gross and Werner 1982; Zedler et al. 1983; Bullock et al. 1994), e.g. in *Cirsium palustre* the rosette must be at least about 20 cm in diameter, and almost all individuals with rosette diameters 30-40 cm long produce flowers. Thus, every rosette-size limiting factor retards the reproductive phase, and individual longevity is extended to several years (Grubb 1977; Falińska and Pirożnikow 1983; Schenkeveld and Verkaar 1984; Lee and Hamrick 1983; Grubb 1976). For instance, the number of gaps in the plant cover of meadows affects the germination of *C. palustre* seeds, while neighbours affect survivorship of the seedlings and attainment by them
the flowering phase. The overgrowth of gaps with macroforbs and scrub limits the appearance of *C. palustre* new individuals, and reduces (due to shading) the chance of the vegetative-stage (rosette) individuals to flower.

In meadows that had been followed for 9 years the influence of willows on the survivorship and flowering of *C. palustre* individuals was stronger, and the numbers of *C. palustre* much lower (Fig. 10). However, the impact of willows varies. For example, individuals growing under the canopy of willows flower sporadically. Though the rosettes attain a size (17-20 cm) similar to that necessary to produce the flowering shoot, a close willow canopy and considerable shading reduce the number of individuals attaining the generative stage (Fig. 4). On the edges of willow aggregations 2 and 3 years old individuals were seen with flowering shoots about 2 m high, that is, of a size similar to that attained in the greenhouse, where optimum conditions had been provided. The behaviour of individuals growing on willow scrub edges is called the "edge effect" (Kershaw 1978), i.e. increased viability and size of individuals at the boundary of the niche occupied. A similar phenomenon was observed in forest-meadow ecotones where *C. palustre* individuals attained the size of about 2 m (Falińska 1991). Jakucs (1972) thinks that the edge effect on the boundary of a forest is the result of favourable microcli-
matic, especially thermic conditions for growth and flowering. Changes in environmental conditions in the course of succession caused the changes in *C. palustre* population abundance and age structure that occurred during the 15-year study-period. The presence of the species is maintained by such features of its life strategy as: numerous airborne seeds, seed bank, ability to germinate during the whole growing season, and the occurrence of 2-3 seasonal cohorts. Cessation of mowing is usually followed by an increase in *C. palustre* population size. Several years later, however, when plants with a clontype growth (which grow very quickly after the cessation of mowing) fill all empty spaces, a decrease in *C. palustre* population abundance begins, and the encroachment of willows is followed by its regression.

The factor ensuring the presence of *C. palustre* until the formation of forest communities is undoubtedly the ever-increasing patchiness of the vegetation in abandoned meadows. The dynamics of patches dominated by various species provides diverse habitat conditions, some of which enable *C. pa-

lustre to succeed. For example, necromass patches and gaps in the vegetation that arise during the species turnover are as a rule colonized only by *C. palustre*. In such situations individuals develop from seeds that have been present in the soil even if the species had been absent from a particular site for several years. A permanent seed bank, even though it decreases during succession, persists there until the initial forest phase. *C. palustre* rosettes grow in size within 2-3 months and fill the site they occupy, where they can stay several years by prolonging their life history to 4 or 5 years. Several of them attain the flowering phase in each season. Only the growth of willows leads to a decrease in the size or complete elimination of their population (Fig. 12).

Population density is an important number-regulating factor, particularly in short living species. No such a direct relationship has been found in *C. palustre* populations. Although in experimental studies the presence of 4 individuals in a 0.25m² plot had a negative effect on the growth of the rosettes, and thereby on the flowering time, it has also been found that under natural conditions such situations are rare and comprise only 25% of the individuals in a population. Interactions between individuals depend on the size of the space they occupy, called the "individual area", phytogenetic field (Uranov 1967), or polygon (Mithen et al. 1984). It has been stressed recently that it is not enough to know the population density to understand the mutual relations between plants (Mithen et al. 1984), it is rather necessary to evaluate their individual areas and the distances between them. Even if their number is the same, individuals in an area of the same size may be dispersed or form aggregations. For example, at early successional stages there grew 53 *C. palustre* individuals in a 25 m² plot, and 56 at a later stage (Fig. 3).

In the former case most of the individuals grew singly or in twos in 0.25 m² plots, and in the latter as many as 30% of the individuals occurred in common areas, where their density was 4 per 0.25 m². In this case density was found to have a negative effect on the growth and size of *C. palustre* rosettes (Table 3).

So, what traits of *C. palustre*, a biennial species are, responsible for its presence in the long-lasting succession process in abandoned meadows?

One of the mechanisms responsible for the presence of mature (fruiting) individuals, and recruitment of young ones under deteriorating habitat conditions (shade, close vegetation cover) is the rosette growth pattern. *C. palustre* rosettes begin
to grow fast in the early spring when other species have not yet started their growth. They are therefore the first to start growing and filling the area. In summer, the rosettes attain large sizes, and their numerous leaves (12-20) form disks which eliminate other species by pressure, shading, and by the necromass into which they turn. *Cirsium palustre* seedlings emerge under the canopies formed by the mature individuals of the species, or on their edges. After fruiting, the mature individuals die and are replaced by juvenile ones that have developed in the areas of the large rosettes. Large rosettes thus provide "safe havens" for the offspring, and since rosettes in an aggregation are uneven-aged, in each season at least one individual attains the reproductive phase, ensuring a supply of several thousand seeds to the population. Uneven rosette size and age within the aggregations are the mechanisms regulating the demographic processes of *C. palustre*, called the "rosette mechanism" (Falińska 1991).

The above suggest the question: Why do seedlings of other species seldom occur in the areas of mature *Cirsium palustre*? There seem to be two causes of this: with a progressing succession the dominance of clonal plants and vegetative reproduction increase. The number of seedlings of all the species taking part in a succession usually decreases (Symonides 1979, 1985; Peart 1989a, b, c; Falińska 1991). As confirmed also by experiments (Fig. 6), seedlings as a rule appear in gaps or in uncovered spaces. Gaps are more numerous at early- than at late-succession stages. Another possible cause could be biochemical changes in the environment, caused by the decomposition of *C. palustre* leaves. Such changes have been discovered experimentally, and it has been demonstrated that in *C. palustre* some allopstasy limits the development of seedlings in close vicinity to mature individuals (Ballegard and Warncke 1985a). This thesis has not been proved by the studies here presented, as indicated by the maps showing the distribution of seedlings, juvenile and mature individuals which form common aggregations. However, the lack of seedlings of other species among *C. palustre* rosettes permits the assumption that under natural conditions this species brings about some biochemical changes in the habitat which eliminate the seedlings of other species, but not those of *C. palustre*. Further precise experimental studies under natural conditions are needed to clarify this process.

The rarity of biennials is often considered in an evolutionary aspect (Schaffner and Gadgil 1975; Grime 1977; Hart 1977; Silvertown 1983; Thompson 1984; Jong et al. 1987; Stearns 1992). It is often stressed that they do not represent a life form equivalent to annual or perennial species (Harper 1977). Its transitional nature has many times been indicated, and trials have been made for distinguishing "strict biennials" and facultative biennials (Schenkeveld and Verkaar 1984; Kelly 1985a). The latter group of species (facultative) is most frequent among biennials, as indicated by many studies (e.g. Grubb 1976; Jong and Klinghamer 1988; Kelly 1985a, b; Klemov and Raynal 1985).

Factors limiting the growth and rosette formation have been reported to be the main causes of a prolonged individual longevity. The flowering phase is significantly correlated with the rosette size (Werner 1975; Gross and Werner 1982; Kelly 1982; Zedler et al. 1983; Fone 1989; Lotz 1990; Falińska 1991). Among these factors are the plant cover closure (Peart 1989a, b, c; Collins and Pinder 1990), competition and density (Platt 1975; Grime 1979; Symonides 1979; Silvertown...
1987), which has also been confirmed by the present researches on the life history of C. palustre.

Consequently, if any of these factors occurs in a habitat, individuals of biennial species prolong their life span. A high plasticity of the life-history pattern of biennials has been emphasized by many investigators (e.g. Van Groenendael 1983, 1986; Steel and Koella 1986; Pons and During 1987; Kelly 1989a, b, c). In case of deteriorating habitat conditions, some of these species may become monocarpic perennials. Studies indicate, however, that if the limiting factors are removed, individuals complete their life cycle within 2, or even 1.5 years.

The observable life history variability of C. palustre during succession probably reflects the life history variation of this species during its evolution. Experiments have demonstrated that individuals of this species can pass through the whole life cycle also in 1 or in 1.5 years. Variation in time is both variation within the life cycle and between successive generations, so life history plasticity is of adaptive nature.

LITERATURE CITED


ZMIENNOŚĆ HISTORII ŻYCIA CIRSIMUM PALUSTRE
I JEJ KONSEKWENCJE W DEMOGRAFIi POPULACJI PODCZAS SUKCESJI

STRESZCZENIE

Celem badań było opisanie historii życia dwuletniego gatunku Cirsium palustre. Wykazano, że w warunkach optymalnych, zapewnionych w szklarni, osobniki żyją od 1,5 roku do 2 lat, na łące koszonej od 2 do 3 lat, a podczas sukcesji na porzuconych łąках wydłużają czas życia do kilku lat. Towarzyszy temu sukcesywny spadek liczebności populacji C. palustre. Stwierdzono zależność między zmiennością wzorca historii życia podczas sukcesji a dynamicznością populacji. Wiek osiągana fazy reprodukcji jest skorelowany z wielkością rozet. Mimo pojawiania się podczas sukcesji wielu czynników ograniczających (zwarta pokrywa roślinna, zacienienie przez wysokie zioła, wierzbę) C. palustre utrzymuje się aż do uformowania się zbiorowisk leśnych. Sprzyja temu: wydłużanie cyklu życiowego, możliwość osiągania fazy generatywnej w różnym wieku (nie tylko w drugim roku), tworzenie trwałego banku nasion, mobilność nasion, a przede wszystkim pojawiające się sygnały przyciągające siewek, które w konsekwencji prowadzą do powstania nowych roztoczy. Cirsium palustre można zaliczyć do gatunków fakultatywnie dwuletnich. W każdym roku mogą fragmenty populacji osiągać fazę kwitnienia w drugim roku życia. W procesie sukcesji wzrasta udział form "trennial" i "quadriennial", a w terminalnym stadium – form wieloletnich monokarpicznych.

SŁOWA KLUCZOWE: Cirsium palustre, gatunki dwuletnie, wzorce historii życia, demografia, sukcesja.