

The Survival Strategy of *Crepis tectorum* L. under Conditions of Chronic Atmospheric Pollution

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Abstract—The results of demographic studies on *Crepis tectorum* L. populations from polluted and clean habitats are presented. They show that these populations significantly differ from each other in a number of parameters, including the seasonal dynamics of seed germination, the number of generations, the time of plant transition to reproduction, and the rate of generation succession in general. These data provide evidence that populations of annual or biennial plants can employ different survival strategies when growing under conditions of pollution or its absence.

Keywords: monocarpic plants, life cycle, seed germination, population, dynamics, fluorine, sulfur dioxide.

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Plants growing under unfavorable conditions employ different survival strategies, including a stress avoidance strategy. In plants reproducing by seeds, one of mechanisms to avoid stress involves a shift in the time of seed germination (Harper, 1977; Markov, 1990; Donohue, 2002). In temperate climates, for instance, seed germination delayed until spring excludes the possibility of seedling death during winter. On the other hand, seed germination in autumn can provide a selective advantage when the risk of high seedling mortality during winter is insignificant, since overwintered plants can enter the reproductive phase earlier, having grown to a greater size by that time.

Plants exposed to pollution can avoid stress due to mechanisms limiting the intake of toxic substances in excess concentrations or facilitating their effective removal (Il'kun, 1978; Taylor, 1978; *Zagryaznenie...*, 1988). The rate of toxicant intake depends on environmental conditions. In particular, temperature is regarded as a major factor determining the response of plants to pollution stress. At high temperature, plants take in greater amounts of toxic agents, and damage they cause becomes more severe as temperature increases (Nikolaevskii, 1979; Norby and Kozlowski, 1981; Taylor et al., 1985; Umbach and Davis, 1987). Taking into account the close dependence between temperature and the rates of gas exchange and plant growth, it may be assumed that, under conditions of pollution, the vulnerability and mortality of seedlings developing at higher temperatures (in spring and summer) will be higher than those of seedlings developing at relatively low temperatures (in autumn). The transition from the spring to the autumn germination strategy may be a mechanism providing for the survival of a

population. In temperate climates, however, autumn seedlings are at high risk of death during winter. Moreover, low temperatures enhance the impact of pollutants on plants (Caporn et al., 1991; Kleier et al., 1998; Yoshida et al., 2004), and, conversely, plants exposed to pollution are more vulnerable to frosts (Dueck et al., 1990/1991; Power et al., 1998; Caporn et al., 2000). Thus, the transition from the spring to the autumn strategy may take place only on condition that the winter mortality of seedlings in a polluted area is fairly low and that the spring strategy gives no apparent advantage to the population.

To verify the above assumptions, we performed demographic studies on a *Crepis tectorum* L. population growing under conditions of long-term atmospheric pollution with fluorine compounds and sulfur dioxide.

MATERIAL AND METHODS

Narrow-leaved hawk's beard, *Crepis tectorum* L. (Asteraceae), is a widespread monocarpic, semirosette plant (Andersson, 1989) growing mainly in arable fields, roadsides, and other areas with a disturbed soil and plant cover. Studies were performed in the vicinity of the cryolite plant located near the city of Polevskoy (the Middle Urals). The plant (founded in 1907) is the source of emissions amounting to 6000–7000 t per year, with sulfur dioxide and fluorine compounds being the main pollutants. Characteristics of the study region and specific features of plant community transformations in the vicinity of the plant were described in detail previously (Makhnev et al., 1990; Trubina and Makhnev, 1997).

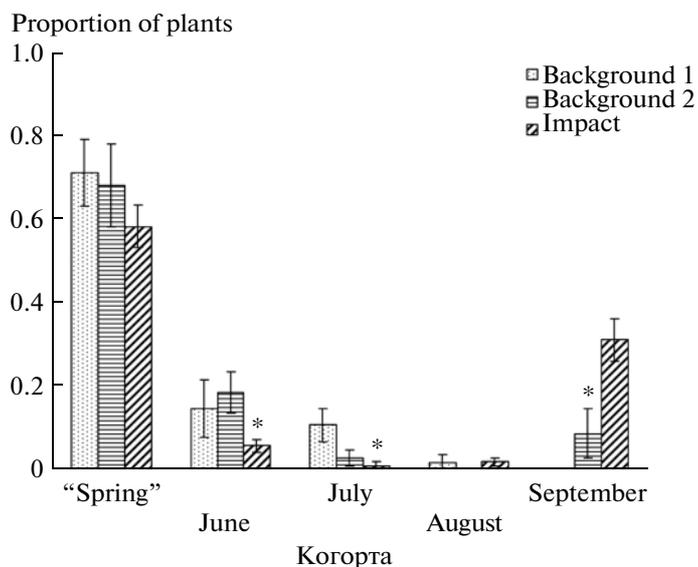


Fig. 1. Proportions of plants from different cohorts (means \pm standard errors) in *Crepis tectorum* L. populations in the background and impact zones. Asterisks indicate significant differences by the Mann–Whitney test ($P < 0.05$).

Two populations were included in analysis: one in the impact pollution zone (300 m from the plant) and the other in the background zone (50 km north of the pollution source). Plants of the impact population (IP) are characterized by the increased contents of acid-soluble fluorine compounds in their aboveground parts, which reach, on average, 4159 $\mu\text{g/g}$ (Trubina, 1990). They grow in disturbed areas with a sparse ground vegetation layer (total coverage about 30%) consisting mainly of *Cirsium arvense*, *Artemisia absinthium*, *Festuca pratensis*, *Sonchus arvensis*, *Tussilago farfara*, *Leucanthemum vulgare*, *Elytrigia repens*, *Potentilla anserina*, *Pimpinella saxifraga*, *Lathyrus pratensis*, and *Tanacetum vulgare*. Plants of the background (control) population (BP) grow in a field sown with oats (*Avena sativa*) and vetch (*Vicia sativa*) and at its edges. The most abundant weed species in the field are *Thlaspi arvense*, *Sonchus arvensis*, *Cirsium arvense*, *Galium aparine*, *Tripleurospermum inodorum*, *Capsella bursa-pastoris*, *Elytrigia repens*, and *Chenopodium album*. The total coverage (including cultivated plants) at the peak of plant development (July) averages 60% in the field and 90% at its edges, where the herbaceous layer consists of the above weeds (*Elytrigia repens*, *Sonchus arvensis*, *Cirsium arvense*, and *Tanacetum vulgare* are dominant).

In late May 2005, ten 25 \times 25-cm test plots located no less than 1 m from each other were established and mapped in areas occupied by *C. tectorum* in the impact zone. In the background zone, ten 50 \times 50-cm plots were established in the field, and ten more squares, at its edges. The distance between these transects was 300 m. Below, the respective parts of the background population are referred to as BP₁ and BP₂. The size of test

plots in the background population was increased because of a low plant density. All *C. tectorum* plants found in the plots in late May were marked with colored sticks and conditionally designated as the "spring cohort," since the exact time of their emergence was unknown. At the end of each subsequent month, all newly emerging plants were marked with sticks of a different color and designated as a cohort of the corresponding month (the June cohort, July cohort, etc.). The numbers of living and generative plants in each cohort were recorded every month. After plowing (in early September), the plots in the field were restored to continue monitoring. Observations in 2005 were stopped in October, after the establishment of snow cover. In mid-July 2006, the assessment of plant survival and enumeration of generative plants were performed for cohorts of the last year. On the whole, 688 *C. tectorum* plants were marked.

RESULTS AND DISCUSSION

The impact population was characterized by a higher plant density, compared to the background population (table), with plants of the spring cohort prevailing in both of them. New seedlings in BP₁ emerged mainly in June and July; in BP₂, in June and September. Summer cohorts in IP were extremely sparse, especially the July cohort, and the bulk of new seedlings emerged in September. The relative abundance of June and July cohorts in IP was markedly lower than in BP₁ and BP₂, while that of the September cohort was higher (Fig. 1).

In BP₁ and BP₂, more than half of plants in the spring cohort were in the generative state in late May (Fig. 2), and all plants completed the developmental cycle by late June. Plants of the June cohort in BP₁ entered the reproductive phase in August, but only 39% of them completed the developmental cycle during the season. All other plants perished in the vegetative phase because of plowing. In BP₂, almost 60% of plants in this cohort began reproducing in July, and all plants completed the developmental cycle by the end of September. The July cohort in BP₁ was third in numbers; 60% of its plants completed the developmental cycle in August, while the rest perished in the vegetative phase because of plowing. In BP₂, plants of this cohort failed to enter the generative phase and died during winter. The August cohort was absent in BP₂ and extremely sparse in BP₁. Plants of this and September cohorts in BP₂ did not reproduce and died during winter.

In IP, plants of the spring and, partly, June cohorts began reproducing during the first season, but the proportion of generative plants was very low (no more than 40%). Not only plants that completed their developmental cycle but also some plants at the vegetative phase died during the season. Their number depended on the initial plant density. Pearson's coefficients of correlation between the initial number of

Dynamics of the abundance of cohorts and total plant density (D , ind./m²) in *Crepis tectorum* L. populations (mean values with standard errors)

Cohort	Year and month of census					
	2005					2006
	May	June	July	August	September	July
Background 1						
“Spring”	20.8 ± 6.9	0	0	0	0	0
June	—	7.2 ± 3.4	7.2 ± 3.4	4.4 ± 2.5	0	0
July	—	—	4.4 ± 2.1	0.8 ± 0.5	0	0
August	—	—	—	0.4 ± 0.4	0	0
September	—	—	—	—	0	0
D , ind./m ²	20.8	7.2	11.6	6.6	0	0
Background 2						
“Spring”	8.4 ± 1.2	0	0	0	0	0
June	—	3.6 ± 1.1	1.2 ± 0.6	0.8 ± 0.5	0	0
July	—	—	0.8 ± 0.5	0.8 ± 0.5	0.8 ± 0.5	0
August	—	—	—	0	0	0
September	—	—	—	—	2.4 ± 1.7	0
D , ind./m ²	8.4	3.6	2.0	1.6	3.2	0
Impact						
“Spring”	537.6 ± 147	385.6 ± 72	310.4 ± 67	212.8 ± 41	174.4 ± 37	73.6 ± 25
June	—	68.8 ± 31	59.2 ± 26	33.6 ± 16	32.0 ± 14	19.2 ± 13
July	—	—	8.0 ± 8.0	3.2 ± 3.2	3.2 ± 3.2	0
August	—	—	—	19.2 ± 9.5	19.2 ± 9.5	11.2 ± 7.9
September	—	—	—	—	275.2 ± 86	166.4 ± 50
D , ind./m ²	537.6	454.4	370.4	268.8	504.0	270.4

plants and the number of plants that died per month were 0.92 ($P < 0.05$) in June, 0.54 ($P < 0.11$) in July, 0.88 ($P < 0.05$) in August, and 0.25 in September. During summer and autumn, a peak of plant mortality was observed in August. The highest mortality was characteristic of the July cohort.

In winter, plant mortality within the cohorts was significantly higher than in the summer–autumn season ($P < 0.05–0.001$). The highest and lowest values of mortality were recorded in the July and September cohorts, respectively. The numbers of plants that died during winter also depended on the initial plant density in the plot (Pearson’s correlation coefficient 0.82 at $P < 0.05$). The proportions of plants of the spring, June, July, August, and September cohorts that entered the reproductive phase in the next season were 19, 25, 33 and 5%, respectively.

Thus, *C. tectorum* populations in polluted and clean habitats proved to differ significantly in the dynamics of seed germination and, therefore, in the relative abundance of plants in different cohorts. Both parts of the background population were characterized by a

very low abundance of the autumn cohort, with plants of this cohort being found only at the edge of the field. In the impact population, conversely, the abundance of summer cohorts (especially of the July cohort) was markedly lower than that of the autumn cohort.

The spring cohort was the most abundant in all populations. Data on the survival of plants during winter indicated that this cohort in both parts of the background population consists mainly of plants emerged in spring. In the impact population, the spring cohort is largely represented by plants that emerged during the previous season. It is noteworthy that the differences in the time of seed germination observed in natural populations are in good agreement with the results of experiments on the effect of temperature on the early growth and development of seed progeny from the same populations in the absence of toxic impact (Trubina, 2006). In particular, the intensity of seed germination and the viability of seedlings at elevated temperatures were higher in the progeny from the background than from the impact population, whereas the situation observed at decreased temperatures was

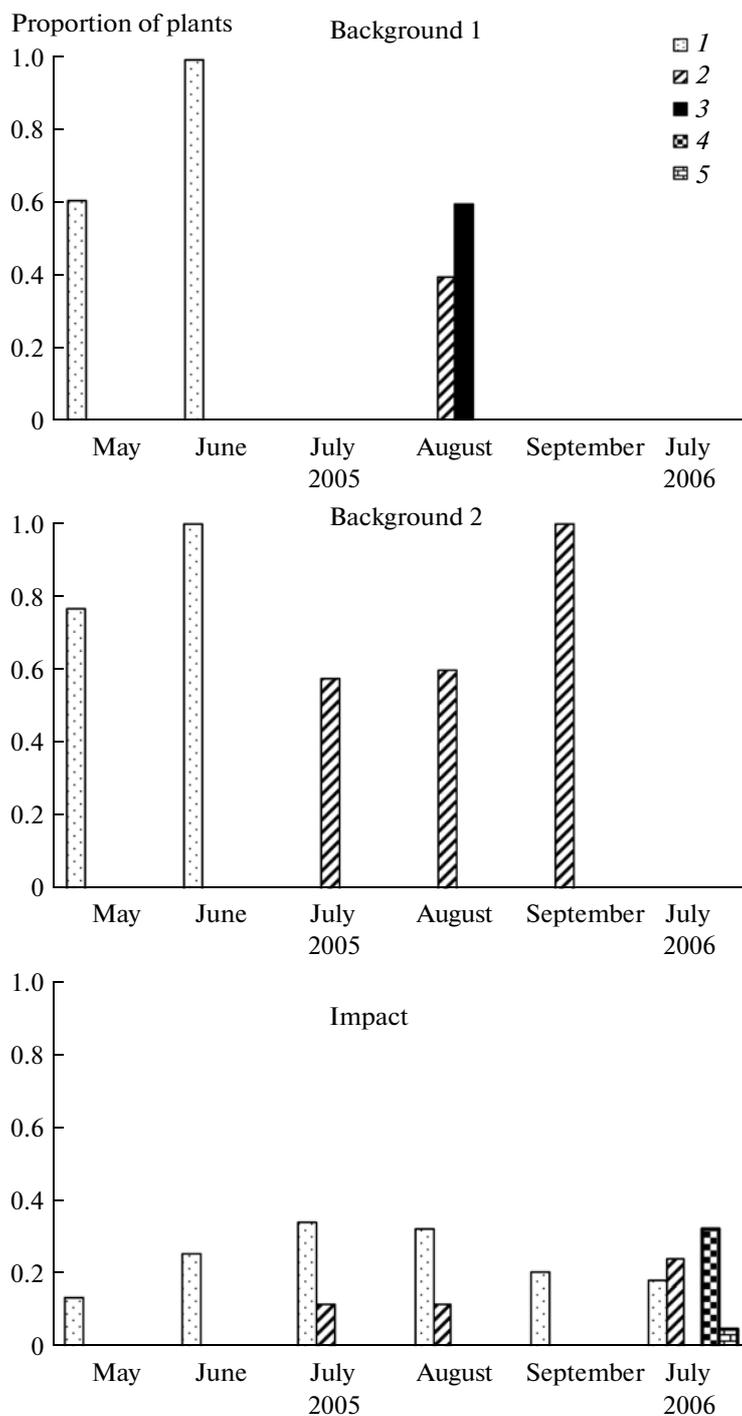


Fig. 2. Time-related changes in the proportions of generative plants in different cohorts of *Crepis tectorum* L. populations from the background and impact zones. Cohorts: (1) “spring,” (2) June, (3) July, (4) August, and (5) September.

opposite. In general, these data indicate that the background and impact population employ mainly the spring–summer and autumn germination strategies, respectively.

Interpopulation differences in the timing of seed germination apparently reflect opposite directions of selection in the habitats studied. Selection for germi-

nation in spring or autumn depends on the risk of seedling death during winter and the relative advantage of spring germination and development (Masuda and Washitani, 1992; Donohue, 2002), with the timing of germination being regulated via the interactions of maternal plants with the environment (Byers et al., 1997; Galloway, 2002). In the background population,

no natural mortality of plants in the vegetative phase has been observed during the season, and the prevalence of the spring–early summer germination strategy is explained by a high risk of death for plants emerging in late summer or autumn. Arable fields in the study region are usually plowed in late August to September or in early May. In either case, the probability of survival and transition to reproduction for plants from the late-summer and autumn cohorts is significantly lower than for plants emerging in late spring or summer. The results of demographic analysis confirm this conclusion.

Available data show that the prevalence of the autumn germination strategy under conditions of long-term pollution (chronic stress exposure) is explained by a high mortality of seedlings emerging and developing at relatively high temperatures as well as by a high winter survival rate of autumn seedlings. A low viability of spring seedlings may be due to the combined impact of high temperatures and pollution, since the rate of toxicant intake and vulnerability of plants increase at higher temperatures (Nikolaevskii, 1979; Norby and Kozłowski, 1981; Taylor et al., 1985; Umbach and Davis, 1987). The results of experiments on the combined effect of temperature and fluorine pollution on early stages of *C. tectorum* growth and development (Trubina, 2007) also show that the adverse effect of pollution on the size and viability of seedlings manifests itself stronger at higher temperatures. Moreover, the viability of summer seedlings may decrease under the combined effect of drought and pollution, which may be additionally enhanced due to the sparseness of ground vegetation in polluted habitats. The fact that these stress factors have an additive effect has been confirmed in a number of experiments (Gordon et al., 1999; Takács et al., 2001). It is noteworthy that in populations of *Crepis tectorum* ssp. *pumila* growing in dry habitats, where the risk of plant death from drought in summer is especially high, the seeds germinate mainly in autumn (Andersson, 1992). The low viability of summer generations in the impact population may also result from enhanced competition for resources in the period of the most active plant growth under conditions of high plant density.

One more difference between the impact and background populations concerns the time of transition to the reproductive phase and the duration of the life cycle. The majority of plants from the background population entered the reproductive phase and completed the developmental cycle during the same growing season. Moreover, a considerable proportion of these plants began reproducing within one month. The spring cohort completed the developmental cycle after 2 months; the June cohort, after 3 months. The main contribution to the total seed pool in the field came from the spring, June, and July cohorts; at the field edge, from the spring and June cohorts. The delay in the development of plants from the June cohort at the field edge could be accounted for by higher density

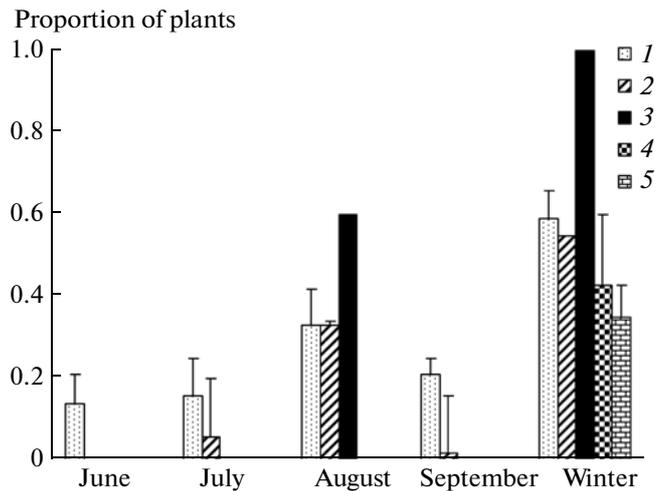


Fig. 3. Time-related changes in the proportions of dead generative plants (means \pm standard errors) in different cohorts of *Crepis tectorum* L. populations from the impact zone. Cohorts: (1) “spring,” (2) June, (3) July, (4) August, and (5) September.

of the herbaceous layer, compared to that in the field (see above). In the impact population, none of the cohorts succeeded in completing the developmental cycle during one season. Plants that began reproducing during the first season were mainly from the spring cohort, with the proportion of generative plants in the population remaining small throughout the season. A major part of overwintered plants from this cohort still remained in the vegetative phase in the middle of the next growing season. Plants from other cohorts usually began reproducing only in the next year, with the proportion of generative plants in each cohort (the September cohort in particular) remaining very small even in the middle of the growing season.

These data are in good agreement with the results of previous studies, which show that *C. tectorum* populations from polluted habitats are characterized by the prevalence of plants in the pregenerative state, with the generative component consisting mainly of biennial plants (Trubina and Makhnev, 1999). Moreover, this retardation of growth and development also manifests itself in the *C. tectorum* seed progeny grown in the absence of pollution impact (Trubina, 2005).

The retardation of growth and development and decrease in reproductive activity are a widespread response of plants to adverse environmental conditions. In ruderal species, however, the response to stress factors often manifests itself in the reduction of the period of vegetative growth and redistribution of resources in favor of seed production (Grime, 1977; Harper, 1977; Markov, 1990), which eventually leads to a reduced duration of the life cycle.

The fact that the life cycle of *C. tectorum*, a typical ruderal species, becomes longer under pollution impact can be accounted for by several factors. In the

majority of annual and biennial rosette and semi-rosette plants, rosette growth is a distinct phase of individual development during which practically all assimilatory plant organs are formed (Markov, 1990). The size and leaf area of the rosette largely determine the probability of plant survival, transition to flowering, and contribution to reproduction (Harper, 1977; Gross, 1981; Maddox and Antonovics, 1983; Farris and Lechowicz, 1990; Markov, 1990; Holderegger, 2000). Thus, the delayed transition to reproduction in the impact population may be due to insufficient development of the rosette and its assimilatory surface. Suppression of rosette growth may be a result of direct exposure to toxic agents, additive action of pollutants and natural stress factors, or high plant density and, consequently, deficiency in resources for normal growth and development. The delay in transition to reproduction can also be explained by an increase in the proportion of plants with a low rate of growth and development in populations from polluted habitats (Cox and Hutchinson, 1981; Wilson, 1988; Trubina, 2005).

Reduction of metabolic rate is a widespread mechanism to improve resistance to stress factors, and a low rate of growth and development is a common feature of stress-tolerant plant species (Grime, 1977). Selection in favor of individuals with a low rate of growth and development under conditions of pollution may be due to deficient nutrient supply in such habitats (Jowett, 1964). Another relevant factor is that slow-growing plants are more resistant to pollution because of a low intake rate of toxic substances and the possibility of their metabolic redistribution and release (Nikolaevskii, 1979; Rozhkov and Mikhailova, 1989). A low rate of growth and development may also be determined by the necessity of increased resource expenditure for the formation of protective mechanisms allowing plant survival under chronic stress (i.e., by an increased adaptation cost), but this aspect needs special evaluation.

On the whole, the relevant data indicate that populations of annual and biennial plants can employ different survival strategies when growing under conditions of pollution or its absence. Population success in species reproducing by seeds depends on the size of total seed pool (Harper, 1977; Markov, 1990). Seed production and individual size depend on specific features of the life cycle (an annual or biennial strategy, or a spring or winter annual strategy), which, in turn, are closely connected with the timing of seed germination (Harper, 1977; Farris and Lechowicz, 1990; Markov, 1990; Donohue, 2002).

Ruderal plant species typically grow in potentially productive environments periodically subject to severe disturbances. Under such conditions, population reproductive success is achieved via rapid succession of several generations during the growing season, which, in turn, is accounted for by the prevalence of plants with a high rate of growth and development and

the spring–summer germination strategy. A high rate of growth and development is regarded as a basic feature of ruderal plants adapted to environments with periodically deteriorating conditions (Grime, 1977), since rapid seed production ensures restoration of populations after disturbances. Adherence to the spring–summer germination strategy is a way to cope with the adverse consequences of high seedling mortality during winter and as a result of regular plowing.

Thus, factors accounting for success in reproduction of plant populations under conditions of chronic pollution include delayed transition to reproduction, longer individual life span (slow succession of generations), and prevalence of the autumn germination strategy. Prolongation of the pregenerative period of development allows plants exposed to chronic stress to form the assimilatory surface sufficient for transition to the reproductive phase, and the autumn germination strategy allows the population to avoid the adverse consequences of combined impact of toxic pollutants and natural summer stress factors.

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