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Effect of Temperature and Fluorides on Growth and Development of *Crepis tectorum* L. Seedlings From Populations of Polluted and Nonpolluted Habitats

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Abstract—The effect of temperature and soil contamination by fluorides on the early stages of the growth and development of narrowleaf hawksbeard plants from polluted and nonpolluted habitats has been studied. The character and degree of manifestation of the combined effects of pollution and temperature, as well as the variations in the direction of response depending on temperature, a measured parameters, and the origin of population are shown. In the populations of polluted habitats, the alteration of phenotypic plasticity in relation to temperature is revealed.

Keywords: plants, stress, adaptation, low and high temperature, pollution, phenotypic plasticity

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INTRODUCTION

Fluorides are among the most phytotoxic air pollutants, and the concentrations of fluorides in the atmosphere continue to increase (Rozhkov and Mikhailova, 1989; Weinstein and Davison, 2003). Despite the possibility of some species adapting to pollution through the selection of tolerant ecotypes, vegetation in the zones of hard pollution remains essentially sparse. In the presence of viable seeds, the high toxicity of soils and the continuing input of toxicants prevent the colonization of free space (Komulainen et al., 1994). The increased susceptibility of plants of polluted habitats to the action of natural stressors, especially at early stages of growth, may be one more reason for the observed phenomenon.

Temperature is one of the most important factors that define the response of plants to stress caused by pollution. At high temperatures, plants take up a greater quantity of toxicants, and the damages caused by toxicants increase as the temperature rises (Nikolaev, 1979; Norby, Kozlowski, 1981; Taylor et al., 1985; Umbach and Davis, 1987). Under the influence of low temperatures, the negative effect of pollution also reinforces (Kleier et al., 1998; Yoshida et al., 2004); the addition of pollutants results in an increase in the susceptibility of plants to frosts (Caporn et al., 2000; Laine et al., 1993; Power et al., 1998; Taulavuori et al., 2005).

The early growth stages of living organisms are the most sensitive to the influence of unfavorable environment factors. Taking into account the close relationship between temperature, intensity of growth processes, and rate of the absorption of toxic substances, it is possible to propose that, in the conditions of pollution, the viability of seedlings which develop at high temperatures will be lower than the viability at low temperatures. Some plants that have a strongly pronounced positive reaction to an increase in temperature will be characterized by greater damaging. In the case of a prolonged input of pollutants, such plants can be eliminated from populations, and, as a whole, the phenotypic plasticity of populations in relation to temperature decreases.

To verify the stated assumptions, the influence of temperature and fluorine on the early stages of growth and development of the *Crepis tectorum* L. plants from populations of polluted and nonpolluted habitats was studied. The experiment was organized in this way to answer the following questions. How does the temperature modify the reaction of plants to pollution at early stages of growth? Does the reaction of seedlings to pollution depend on their susceptibility to temperature? Are there are any distinctions between populations of polluted and nonpolluted places in reaction to temperature and pollution at the early stages of growth?

MATERIALS AND METHODS

Narrowleaf hawksbeard (*Crepis tectorum* L., family Asteraceae) is the widespread monocarpic semirosette species of plants (Andersson, 1989). In nonpolluted habitats the species usually behaves like a summer or autumnal annual plant (Andersson, 1989, 1992; Trubina and Makhnev, 1999). These plants grow mainly in cultivated fields, waysides, and in other places with disrupted vegetative and soil cover. In this study the seeds of narrowleaf hawksbeard plants, which grow in the different toxic load zones in the vicinity of the Polevskii cryolite factory near the town of Polevskii (Central Ural) were used for the experiment. The factory was founded in 1907; the volume of emission is 6000–7000 tons a year, in which the dioxide of sulphur and fluorine compounds prevail. The characteristic of the studied area, as well as the effect of pollution on the particular features of the transformation of plant communities, as well as on the structures of narrowleaf hawksbeard plant populations, have been described earlier (Makhnev, et al, 1990; Trubina and Makhnev, 1997, 1999; Trubina, 2005, 2011).

The seeds for experiments were collected on a distance of 300 m, 4 km and 50 km from a source of emissions in the impact zone, buffer zone, and background zone of pollution, respectively. The concentrations of acid-soluble fluorine compounds in the humus soil horizon of the impact, the buffer, and the background zones were 420 μg/g, 93 μg/g, and 8 μg/g, respectively (Trubina, 1990). The seeds were collected in June–July from 20 maternal plants individually in each population. The average weight of 100 seeds in background (BGP), buffer (BP) and impact (IP) populations was 27.0 ± 1.0, 28.6 ± 1.2 and 32.5 ± 1.1 mg, respectively. The weight of seeds from different maternal plants within populations varied from 20.0 to 36.4 mg (IP), from 20.2 to 36.7 mg (BP), and from 21.4 to 40.3 (BGP).

Seeds were stored dry at room temperature for 3 months and then at 0°C until the beginning of the experiment. Ten seeds in rolls from a filter paper from each family were placed in plastic vessels containing soil suspension (5 g of soil per 50 mL of distilled water). The plants were cultivated in climatic rooms at a 12-h-long photoperiod and at a constant humidity of 60% supported by means of a steam generator. Throughout the experiment, the initial volume of suspension was supported to be constant by the addition of water. The vessels were moved daily to minimize the effect of the position. Patterns of temperature conditions such as 12, 22, and 32°C and two samples of soil suspension such as noncontaminated (NS) and contaminated by fluorides (CS) were used in the experiments. The soils for the experiments were collected in the background and in the impact zones of pollution. In these soils the concentrations of $F_{(HClO_4)}$ were 6.3 and 358.2 μg/g; the values of pH were 4.96 and 5.39; the contents of C_{org} were 3.93 and 4.21%; the concentrations of K were 11.38 and 15.73 mg/100 g and those of P were 3.53 and 7.57 mg/100 g; Ca contents were 12.0 and 16.0 mg-eq./100 g; the contents of Mg were 8.0 and 10.0 mg-eq./100 g; and N_{hyd} concentrations were 157.2 and 262.0 mg/kg, respectively. The full design of the experiment was presented by three patterns of temperature condition in two soil samples for three populations. Each population was presented by 20 families. The total quantity of sowed seeds was 3600.

The intensity of germination was evaluated from the 3rd to the 12th days of experiment. The portion of germinated seeds (germination) and the survival of seedlings (the portion of the surviving seedlings in relation to number of germinating seeds) were evaluated on the 21st day after the experiment began. For each seedling, the length of the greatest leaf, the number of true leaves, the length of the main root, and the portion of damaged seedlings with disorders such as a chlorosis, necrosis, either deformation or an absence of organs, and the heliotropism disorder were determined. For each temperature condition, the tolerance index (TI) of the family was calculated according to the following formula: TI is the ratio between the average values of the parameter of seedlings of the family in the contaminated suspension and the average value of the parameter in noncontaminated suspension. The negative effect of CS was shown only in aboveground parts of plants; therefore, TI for families and TI averages for populations were calculated according to the length of the leaf (TI_{leaf}). For an evaluation of the degree of manifestation of the response of the family to the temperature change (phenotypic plasticity in relation to temperature), we used the variance of values of leaf length in the NS at different temperatures standardized by means of an average (Taylor and Aarssen, 1988).

To evaluate the influence of treatments on the intensity of seed germination, a two-way and three-way mixed effects repeated-measurements ANCOVA was used. The influence of treatment on other measured parameters was evaluated using a two-way and three-way mixed effects ANCOVA. In all cases temperature and soil were the fixed effects; population was a random factor. The weight of seeds was used as a covariant. The average values of seedling parameters in the family were used as replications. The nonparametric Mann–Whitney test and the Kolmogorov–Smirnov criterion were used for a pair comparison of average values of parameters and distributions. The dependence between parameters was evaluated using the Spirmen's rank factor of correlation.

RESULTS AND DISCUSSION

The Combined Effect of Temperature and Fluorine on the Germination of Seeds and the Viability of Seedlings

The temperature and contamination significantly influenced the germination of seeds and the viability of seedlings, and populations differed in reaction to the influence of these factors (Table 1).

Table 1. Results of the evaluation of the effects of temperature, contamination, the origin of population, and the interaction of these factors by means of variance analysis

The source of variation (df)	Parameter						
	IG[a]	*G*	*LL*	*NL*	*RL*	*DIS*	*S*
Population (2, 323)	5.53**	2.82†	14.17***	2.82†	4.82**	13.99***	7.30***
Contamination (1, 2)	2.24	4.41	50.71*	28.52*	29.92*	20.01*	12.10†
Temperature (2, 4)	39.51**	15.25*	32.08**	57.91**	12.85*	3.00	1.44
Interaction of population and contamination (2, 323)	3.02†	2.03	3.49*	2.63†	7.26***	3.41*	4.44*
Interaction of population and temperature (4, 323)	5.09***	4.49**	9.86***	6.69***	6.56***	6.43***	9.51***
Interaction of contamination and temperature (2, 4)	1.68	51.03**	21.17**	3.53	1.69	1.81	0.55
Interaction of population, contamination, and temperature (4, 323)	3.30*	0.41	2.73*	4.33**	3.24*	3.51**	10.07***

The F-ratio values at $P < 0.1$ (†), $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$ (***) are presented.
[a] *IG* is the intensity of germination, *G* is germination, *LL* is the length of leaf, *NL* is the leaf number, *RL* is the length of root, *DIS* is the portion of seedlings with disorders, and *S* is the survival.

In the NS, the highest intensity of the germination of seeds from the BGP was observed at 32°C; that of seeds from the IP and BP was observed at 22°C (Fig. 1). At 12°C, the intensity of germination of seeds from the IP and BP was higher than that of seeds from the BGP; at 32°C, on the contrary, this value was essentially lower than that at 12°C ($F_{4.170} = 9.22$; $P < 0.001$). At 12°C the contamination did not influence the intensity of germination, but at 22 and 32°C the intensity of germination in CS was higher, than that in NS. At 22°C an increase in germination intensity was observed in all populations; at 32°C the increased intensity of germination was observed only in seeds from the BP and IP. In the case of the cultivation of seeds in CS, the differences between populations in the germination intensity were observed at 12°C only. The germination intensity of seeds from the BP and IP was higher than that from the BGP throughout the experiment.

In the case of cultivation in NS, by 21st day after the experiment began, the germination of seeds from the BGP was lowest at 12°C, and that from both the IP and BP was the least at 12 and 32°C (Table 2). At 32°C the values of this parameter for the IP and BP were significantly lower than those of the BGP. At 12°C the contamination slightly inhibited the germination of seeds from all populations, but an almost statistically significant ($P < 0.055$) influence was noted for seeds from only the BGP. At 22°C and especially at 32°C, the contamination stimulated the germination. Somewhat higher values of the parameter were observed with seeds from the IP in comparison with the BGP at 12°C, whereas at 32°C these values were lower.

The most pronounced positive response to temperature was noted in plants of the BGP. At 12 and 22°C, the sizes and number of leaves on the plants of the BGP, as a rule, were essentially less than those of the BP and IP, but at 32°C, on the contrary, the values of these parameters were higher in plants of the BGP. At all temperature modes, the root length of plants of the BGP, as a rule, was less, than that of the BP and IP. The contamination negatively influenced the sizes and number of leaves in the plants of the BGP at 32°C only. In the plants of the BP, the negative effect of pollution on size and leaf number was observed at all temperature modes. The contamination resulted in a decrease in the sizes and quantity of leaves of the plants of IP at 12 and 22°C. In plants of all populations, the length of root in PS increased at all temperature modes used. At all temperature modes, in CS the sizes of seedlings differed slightly between the populations with a few exceptions as follows: at 32°C the root length of the seedlings from the IP was less than that from the BGP; at 22 and 32°C the sizes of leaves and the root length of sprouts from the BP were less than those from the BGP and IP.

At all treatments, chlorosis and necrosis were the most often observed disorders in the development of seedlings. In NS the significant influence of temperature on the portion of seedlings with disorders was revealed in the BGP only; the smallest portion of such seedlings was noted at 32°C. At 12 and 22°C in the BGP, the portion of seedlings with disturbances was more than that in the IP and BP, and at 32°C, on the contrary, this value was less in the BGP. In all populations, the contamination reduced the quantity of development disorders of seedlings, especially at 12 and 22°C, and statistically significant differences between populations in this parameter, as a rule, were absent.

The temperature considerably ($F_{2.103} = 18.78$; $P < 0.001$) influenced the survival of the seedlings from the

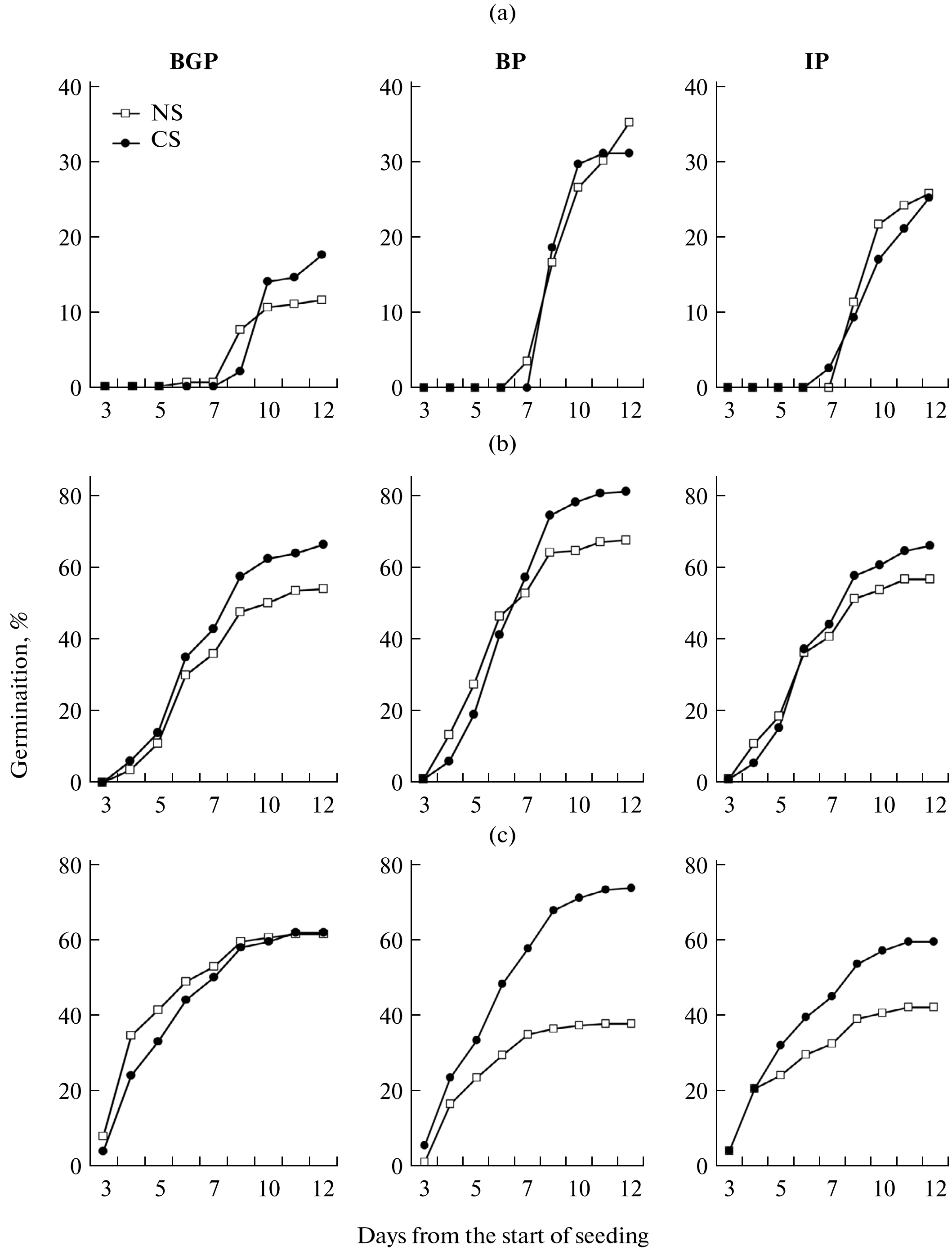

Fig. 1. Intensity of seed germination in the background (BGP), the buffer (BP), and the impact (IP) populations at 12°C (a), 22°C (b), and 32°C (c) in noncontaminated suspension (NS) and in suspension contaminated by fluorides (CS).

BGP, which were grown in NS. An increase in temperature resulted in a value increase (Fig. 2). The survival of seedlings from the BP considerably decreased at 32°C ($F_{2.103} = 6.96$; $P < 0.002$). In comparison with the IP and BP, the survival of seedlings from the BGP was lower at 12 and 22°C, but at 32°C the survival of these seedlings was, on the contrary, higher than that of the IP and BP. In all populations the survival of seedlings in CS was considerably higher than that in NS, with a few exceptions. At 32°C the values of this parameter for seedlings from the BGP decreased under the influence of contamination ($P < 0.05$). A statistically significant increase in the survival of seedlings from the IP grown in CS was noted at 12°C only ($P < 0.01$). The results of a two-factor analysis of covariance confirm the interaction between such factors as "temperature"

Table 2. Characteristics of the *Crepis tectorum* L. seed progeny from the populations of polluted and nonpolluted habitats at different temperatures and soils. The mean values with standard errors are presented

Temperatures	Suspension	Population		
		background	buffer	impact
The portion of germinated seeds				
12°	Noncontaminated	0.56 ± 0.05	0.62 ± 0.04	0.56 ± 0.04
	Contaminated	0.40 ± 0.05	0.51 ± 0.06	0.54 ± 0.06†
22°	Noncontaminated	0.76 ± 0.04	0.80 ± 0.03	0.71 ± 0.03
	Contaminated	0.82 ± 0.03	0.88 ± 0.03†	0.78 ± 0.04
32°	Noncontaminated	0.71 ± 0.03	0.61 ± 0.04†	0.51 ± 0.05***
	Contaminated	0.85 ± 0.03	0.81 ± 0.03	0.76 ± 0.03†
The length of leaf, cm				
12°	Noncontaminated	0.45 ± 0.05	0.61 ± 0.02*	0.63 ± 0.02**
	Contaminated	0.43 ± 0.02	0.41 ± 0.02	0.44 ± 0.02
22°	Noncontaminated	0.71 ± 0.03	0.81 ± 0.02*	0.79 ± 0.04*
	Contaminated	0.74 ± 0.03	0.68 ± 0.02†	0.74 ± 0.02
32°	Noncontaminated	1.32 ± 0.06	1.05 ± 0.09*	1.28 ± 0.08
	Contaminated	0.84 ± 0.03	0.68 ± 0.02***	0.78 ± 0.03
The number of leaves				
12°	Noncontaminated	0.70 ± 0.21	1.49 ± 0.12**	1.33 ± 0.13*
	Contaminated	0.71 ± 0.08	0.58 ± 0.09	0.76 ± 0.05
22°	Noncontaminated	2.13 ± 0.12	2.38 ± 0.07†	2.21 ± 0.10
	Contaminated	2.21 ± 0.09	2.05 ± 0.07	2.16 ± 0.09
32°	Noncontaminated	3.58 ± 0.16	2.91 ± 0.27*	3.09 ± 0.20†
	Contaminated	2.51 ± 0.09	2.28 ± 0.10	2.30 ± 0.11
The length of root, cm				
12°	Noncontaminated	2.99 ± 0.76	4.47 ± 0.31	4.12 ± 0.30
	Contaminated	5.38 ± 0.54	6.65 ± 0.64	6.07 ± 0.55
22°	Noncontaminated	4.78 ± 0.30	6.13 ± 0.15***	5.41 ± 0.39†
	Contaminated	9.79 ± 0.47	7.95 ± 0.32**	9.45 ± 0.46
32°	Noncontaminated	6.56 ± 0.22	5.69 ± 0.39†	7.20 ± 0.26*
	Contaminated	10.48 ± 0.52	8.16 ± 0.26***	8.53 ± 0.41**
The portion of seedlings with disorders				
12°	Noncontaminated	0.81 ± 0.08	0.29 ± 0.06***	0.46 ± 0.08*
	Contaminated	0.32 ± 0.06	0.15 ± 0.05*	0.23 ± 0.06
22°	Noncontaminated	0.81 ± 0.04	0.42 ± 0.07***	0.54 ± 0.06**
	Contaminated	0.33 ± 0.03	0.28 ± 0.06	0.26 ± 0.04
32°	Noncontaminated	0.18 ± 0.03	0.28 ± 0.10	0.38 ± 0.08†
	Contaminated	0.21 ± 0.03	0.14 ± 0.03	0.23 ± 0.05

The significance levels of differences between the BGP and other populations (Mann–Whitney test) were as follows: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; † $P < 0.1$.

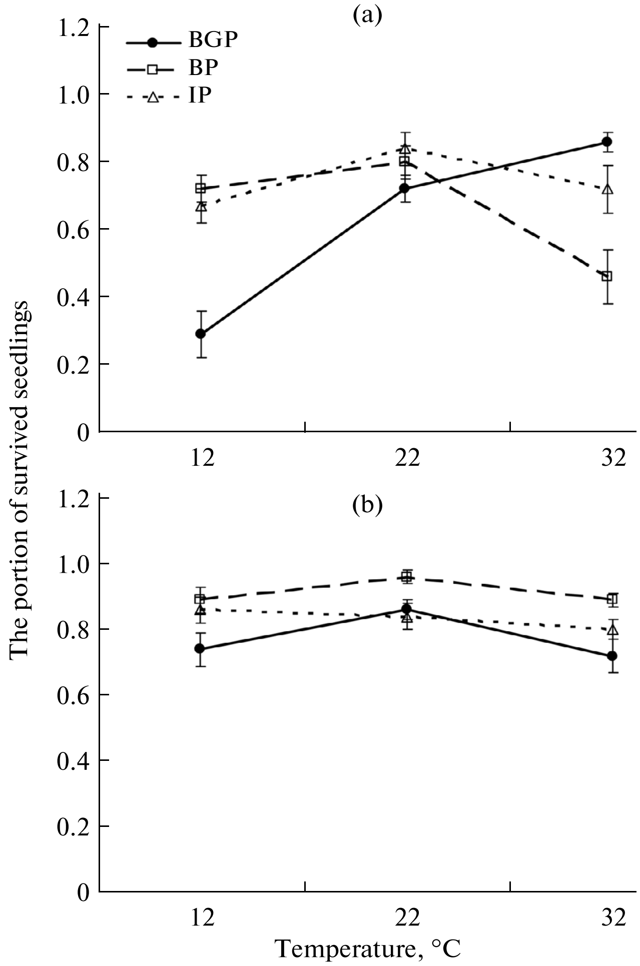

Fig. 2. Portion of survived seedlings in the background (BGP), buffer (BP), and impact (IP) populations at different temperatures in a noncontaminated suspension (a) and in a suspension contaminated by fluorides (b). The mean values with standard errors are presented.

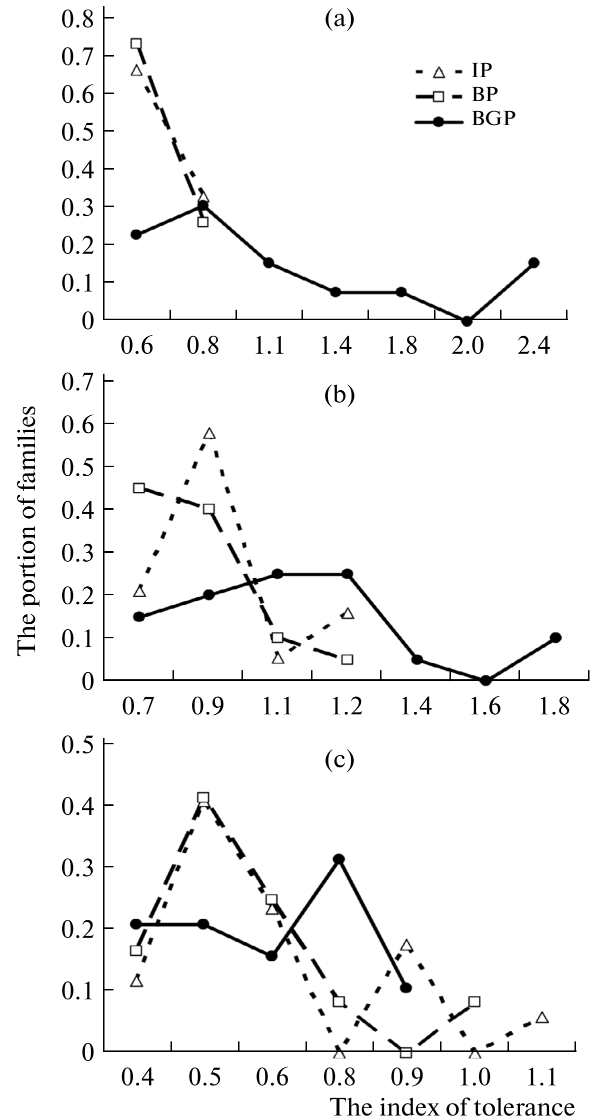

Fig. 3. Distribution of families from the background (BGP), buffer (BP), and impact (IP) populations according to the index of tolerance (IT_{leaf}) at 12 (a), 22 (b), and 32°C (c).

and "soil" both for seedlings from BGP ($F_{2.103}$ = 15.28; $P < 0.001$) and BP ($F_{2.103} = 3.59$; $P < 0.05$). At 12 and 32°C in CS, the survival of seedlings from BGP was considerably lower than that obtained from IP and BP.

Phenotypic Plasticity and Index of Tolerance

The average values of the standardized variance of the sizes of seedlings were the greatest in the BGP, and these values were the least in the BP. For the length of leaf, these values were 0.26 ± 0.04, 0.07 ± 0.01, and 0.13 ± 0.03 in the BGP, BP, and IP, respectively. The differences of variances between the BGP and two other populations were statistically significant ($P <$ 0.023–0.001); the differences between the IP and BP were near-significant ($P < 0.087$). The values of the standardized variances of the parameter among families within a population varied from 0.02 to 0.71 (BGP), from 0.0001 to 0.23 (BP), and from 0.01 to 0.46 (IP).

At 12°C a decrease in the leaf sizes of plants grown in CS was noted in all families of IP and BP, and families with a strongly pronounced negative reaction to contamination prevailed in these populations (Fig. 3). One-half of the BGP families only at 12°C reacted negatively; other families were characterized either by a neutral or positive reaction. The average values of TI_{leaf} were 1.17 ± 0.19, 0.68 ± 0.03, and 0.68 ± 0.02 for BGP, BP, and IP, respectively. At 22°C, in the BGP the families with neutral and positive reactions to pollution prevailed, in the BP families with negative and neutral reactions to pollution prevailed, and most families of the IP possess a feebly marked negative

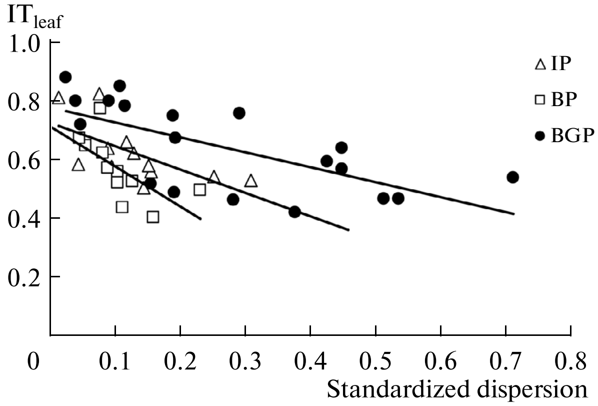

Fig. 4. Dependence of tolerance index (IT_{leaf}) at 32°C on the phenotypic plasticity of families in relation to temperature in the background (BGP), buffer (BP), and impact (IP) populations.

response. The average values of TI_{leaf} were 1.10 ± 0.07, 0.85 ± 0.04, and 0.92 ± 0.04 for BGP, BP, and IP, respectively. At 32°C all families of BGP negatively reacted to pollution. In IP and BP, families with negative reactions also prevailed, but families with neutral reactions also occurred. The average values of TI_{leaf} were 0.64 ± 0.03, 0.60 ± 0.04, and 0.64 ± 0.04 for BGP, BP, and IP, respectively. The distributions according to TI_{leaf} essentially ($R < 0.05$) differed in populations at 12 and 22°C only.

At 12°C the families of the BGP, which possessed high values of variance, were characterized by high TI_{leaf} ($r = 0.62$, $P < 0.023$). At 22°C the relationship between the parameters was also positive, but weaker ($r = 0.41$, $P < 0.076$). At 12 and 22°C there was no dependence between variance and TI_{leaf} in BP and IP. At 32°C the character of dependences between variance and TI_{leaf} was the same in all populations: families with high variance were characterized by the lowest values of TI_{leaf} (Fig. 4). The correlation factors between parameters were as follows: –0.70 ($P < 0.001$), –0.89 ($P < 0.001$), and –0.77 ($P < 0.002$) for BGP, BP, and IP.

The Modifying Influence of Temperature

At low temperatures the pollution did not influence the intensity of germination of seeds and slightly inhibited the germination. When temperature increased, a stimulating effect was observed. The stimulation may be induced by an increase in permeability of seedcoat under the influence of fluorine at high temperatures, as well as by the intensification of metabolic processes, which is noted at the initial stages of the influence of fluorides or at small concentrations of these compounds (Il'kun, 1978).

In the BGP, the strongest negative influence of pollution was shown at high temperatures, which appeared as a strong inhibition of growth of assimilating organs, as well as a decrease in the survival of seedlings. At lower temperatures a considerable part of families in the BGP was characterized by a neutral or even positive reaction to pollution. Moreover, in all populations, the families, the sizes of which increased the most strongly with an increase in temperature, were characterized by a more pronounced negative reaction to pollution at high temperatures.

Most likely, the different degree of negative effects display at low and high temperatures is connected with different intensities of growth processes and with the rate of fluorine absorption. The absence of visible symptoms of damage and the stimulation of plant growth at small concentrations of toxicants, including fluorine, is a known fact. In a number of experiments it was also shown that, with an increase in temperature, the rate of toxicant absorptions and plant damage increase (Nikolaev, 1979; Norby and Kozlowski, 1981; Taylor et al., 1985; Umbach and Davis, 1987), and the results of our experiment confirm this conclusion. Moreover, a study on the dynamics of the mortality of *Crepis tectorum* sprouts in natural habitats shows that the highest mortality among seedlings in the polluted environment occurs in August, i.e., after the hottest month (July) (Trubina, 2011). At the same time, in the control population the death of seedlings was not observed during summer.

The pollution of the BGP at low and optimum temperatures promoted both a decrease in the part of seedlings with disorders and an increase in the survival of seedlings. At high temperatures the survival of seedlings under the influence of pollution in this population decreased. Most likely, a positive effect at low temperatures was induced by an intensification of protective processes under the influence of small concentrations of toxicants and, on the contrary, a negative effect at high temperatures occurred due to the suppression of most processes, including protective, because of the high concentration of the toxicants. In particular, it was shown in a number of experiments that either at the initial stages of action or at a low concentration of stressors the activity of enzymes, which perform protective functions, essentially increases from the beginning. On the contrary, an increase in the concentration of the stress factor or in the duration of the action of this factor leads to the inhibition of these enzyme activities (Il'kun, 1978; Nikolaev, 1979; Rozhkov and Mihailova, 1989; Demirevska-Kepova et al., 2004; Sharma and Dubey, 2005; Liu et al., 2004).

It is interesting that at all temperature modes the pollution caused an increase in the length of seedlings roots and the progeny of hawksbeard plants grown in the polluted places was characterized by elongated roots. The intensification of the root growth under the action of fluorine may be caused by the stimulation of the synthesis of cytokinins under conditions of stress. The cytokinins participate in the regulation of a great number of processes in plants, including the stimulation of prochlorophyllide synthesis, the division of chloroplasts, and the inhibition of chlorophyll degradation (Zubo et al., 2005; Yaronskaya et al., 2006; Srivastava et al., 2007). The positive role of cytokinins or cytokinin-like substances in an increase in tolerance of plants to the action of various stressful factors was shown in a great number of experimental investigations (Gadallah, 1999; Gadallah and El-Enany, 1999; Musatenko et al., 2003; Lukatkin et al., 2007). A study of other plant species revealed that fluorine inhibits the growth of both aboveground and underground organs, and in some species the growth of underground organs was only inhibited by fluorine (Stevens et al., 1998; Stevens et al. 2000). The inconsistence with our data may be a result of the species specificity of the reaction to pollution.

Features of the Reaction of Populations

At high temperatures and in the absence of pollution, the intensity of germination, the germination of seeds, and the viability of seedlings in populations from polluted places were lower than those in the BGP. At the same time, at lower temperatures, all the parameters in these populations were, on the contrary, higher than the parameters of the BGP. Moreover, in the populations from polluted places, there were no families with a strongly pronounced positive reaction to a rise in temperature and the phenotypic plasticity in relation to the temperature was considerably lower than in the BGP.

Most likely, the features of the populations from polluted places are related to the change in the survival strategy under conditions of long-term pollution. We have shown earlier (Trubina, 2005, 2011) that in nonpolluted places the existence of *Crepis tectorum* populations is supported, mainly, due to the use of the spring-and-summer strategy of seed germination and the fast replacement of generations because of the prevalence of plants with a high rate of growth and development in the population. In polluted places the existence is supported due to the primary use of the autumnal strategy of the germination of seeds, a considerable delay of reproduction, and an increase in the life longevity of individual plants (slow replacement of generation) because of the prevalence of plants with a low rate of growth and development in the populations. The results of this study, along with demographic research, indicate that under conditions of chronic pollution selection is directed against individuals that need raised temperatures for development and individuals that possess a strongly pronounced positive reaction to increase in temperature; i.e., the selection is directed against fast-growing individuals. As the results of the experiment show, the transition of populations from the polluted places to the autumnal strategy of seed germination, as well as the removal of individuals with high plasticity in relation to temperature from these populations, may be connected with differences between low and high temperatures in the character and intensity of the influence of toxicants on plants.

One more feature of populations from polluted places is a more pronounced inhibition of the growth of assimilating organs by fluorine when compared to the BGP. It is an unexpected result of the experiment. Populations of hawksbeard have existed under conditions of pollution for long enough time as it is (more than 20 years). Examples of the fast adaptation of some plant species to the excess of heavy metals or sulphur dioxide through the selection of tolerant ecotypes are well-known, and the high tolerance of plants from the polluted places to toxicants was shown in a number of investigations (Taylor and Bell, 1988; Wilson, 1988; Lehman and Rebele, 2004; Liu et al., 2004). In our experiment, a raised tolerance to fluorine in populations from the polluted habitats, in comparison with the BGP, appeared only in a higher survival rate of seedlings in the contaminated suspension at low and high temperatures.

A strong growth inhibition along with a simultaneous increase in survival in populations from the polluted habitats may be connected with the considerable redistribution of the energetic resources of a plant to protective processes. It was shown in a number of investigations that the plants growing in places polluted by heavy metals possess a higher activity of superoxide dismutase and peroxidase under the provocative influence of toxicants (Sharoiko et al., 2002; Liu et al., 2004). We have received similar results in an experiment with the seed progeny of hawksbeard from populations of places polluted and not polluted by fluorine under the provocative influence of NaF (Kiselleva and Trubina, 2008). The strongly marked decrease in the growth of seedlings under fluorine influence in populations from polluted habitats may be considered as a "price" for adaptation to chronic pollution, and also as a way to avoid stress at the early stages of growth, promoting an increase in seedling survival.

CONCLUSIONS

The results of our experiment testify that the character and the degree of manifestation of a response to temperature and pollution depend on a measured parameter and are different in populations from polluted and nonpolluted habitats. In the population from a nonpolluted habitat, at lowered temperatures, fluorine does not suppress the growth processes at the initial stages of influence and even promotes an increase in the survival of seedlings. At the same time, at high temperatures, fluorine considerably inhibits the processes of growth and development of assimilating organs of seedlings and causes a decrease in the survival of seedlings. In all populations, the negative effect of pollution is most strongly shown in plants with strongly a pronounced positive reaction to a temperature increase, i.e., in fast-growing plants. In the case of the prolonged input of pollutants, the difference between low and high temperatures in the magnitude of the negative effect of pollution and the selective mortality in early stages of growth and development may lead to a change in the susceptibility of populations to temperature and to a change of survival strategy as a whole. The transition of populations of the polluted habitats to the autumnal strategy of the germination of seeds, the elimination of plants with a strongly pronounced reaction to a rise in temperature from the populations, and a decrease in the level of phenotypic plasticity in relation to temperature as a whole may be considered one of the ways *Crepis tectorum* populations adapt to the chronic environmental pollution by acid gases, which makes it possible to avoid the negative consequences of the joint influence of toxicants and high temperature. Additionally, our data testify that an increase in the susceptibility of seedlings to the action of natural stressors such as low and, especially, high temperatures under conditions of pollution can not only accelerate the degradation of vegetation under the effect of pollutants, but also suppress the expansion of plant species that are tolerant to toxic substances on hard polluted territories.

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