Ecogenetic plasticity and genetic variation in *Populus* hybrids under the impact of simulated climate change related stressors

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Abstract

To meet the needs of carbon sequestration and production of raw materials from renewable natural resources for the timber market of the European Union, it is necessary to expand forest plantation areas. The efficiency of short-rotation forestry depends primarily on the selection of hybrids and clones, suitable for the local environmental conditions. We postulate that ecogenetic response, ecogenetic plasticity and genotypic variation of different hybrids of poplars (*Populus* L.) depend both on the type of stressors (spring frosts, summer drought, increased UV-B radiation, warm winters) and peculiarities of the cross-bred species as well as on their genetic preadaptations to native environmental conditions of their origin. The aim of the study was to estimate the ecogenetic plasticity, genotypic variation of adaptive traits and adaptability of *Populus* hybrids under simulated conditions of the expected climate change.

The research was performed with the cultivars and experimental clones of three different intraspecific crosses of poplars (*P. nigra* L., *P. deltoides* Bartr. ex Marsh, and *P. trichocarpa* Torr. & Gray.) and four interspecific hybrids of poplars (*P. deltoides* L. × *P. nigra*, *P. deltoides* × *P. trichocarpa*, *P. maximowiczii* A. Henry × *P. trichocarpa*, and *P. balsamifera* L. × *P. trichocarpa*).

Simulated spring frosts and summer drought treatments had a substantial impact on growth of trees, but the hybrid and clone effects were also significant and showed that many hybrids and clones in general retain their features/differences under stressful environmental conditions. A strongly expressed hybrid and clone interactions with simulated frost and drought effects (genotype-environment interaction, G × E) showed different ecogenetic response, plasticity and specific ecological preferences of the clones and hybrids. The sensitivity of hybrids to UV-B radiation varied and depended on the origin of their parental trees and this sensitivity partially reflected their susceptibility also to other stressors. Warm winters adversely effected the growth of some hybrids while others, *P. nigra* × *P. nigra* and *P. trichocarpa* × *P. trichocarpa*, which parents originated from the southern part of their natural distribution range have increased their growth. This treatment also resulted in reduction of the heritability and genotypic variation of growth traits.

Keywords: poplars, clones, genotype-environment interaction, genetic variation, heritability

Introduction

Biomass-production-oriented short-rotation forestry is based on the most advanced and intense forestry technologies: hybridization, introduction, extremely intensive breeding and biotechnology. To meet the needs in raw materials from renewable natural resources on the timber market of the European Union, it is necessary to expand forest plantation areas (Coaloa, Nervo 2011, FAO 2016). Barua et al. (2014), cited in McEvan et al. (2019), predicts demand for roundwood will reach 6 billion m³ by 2050, and will be the main driver for the expansion of industrial plantations. This is also important in order to increase carbon sequestration to mitigate greenhouse effect and global climate change. In 2011, hybrid poplar plantations in Europe covered a total area of 9,402 km² (Coaloa

and Nervo 2011, Nervo et al. 2011). The forest products proportions of end use reported for native poplars were: sawnwood (67%), wood pulp (14%), logs/pulplogs (8%), woodchips (7%), particle/fibre boards (2%) and fuelwood, veneer and plywood (2%) (FAO 2016). The proportions of forest products end use of planted poplars were the following: particle/fibre board (51%), plywood (17%), veneer (16%), wood pulp (6%), sawnwood (5%), woodchips (4%) and logs/pulplogs and fuelwood (1%) (FAO 2016). High productivity of *Populus* hybrids is related to the prolonged vegetation period, in comparison to the parental species (Yu et al. 2001). Many of these hybrids can be grown beyond the natural range of their parents (Sykes et al. 1996).

The efficiency of short-rotation plantation forestry depends primarily on the selection of appropriate clones for the relevant regional environmental conditions. With climate change, the rising temperature, CO_2 concentration and an increase of precipitation, growth conditions for many species of deciduous trees in Baltic countries should improve. However, climate change also causes a number of adverse events – extremes of weather conditions such as strong spring frosts, droughts, heat waves, etc., which distorts a tree growth rhythm, has a negative impact on growth and vitality of trees. This also results in change of genetic variation of various traits.

In many countries, cultivation of hybrid poplar is based on a small number of clones, e.g. clone I-214, which was bred in 1929 and is grown on about 80% of poplar plantations in Europe. These monoclonal or oligoclonal plantations have low genetic diversity and therefore are vulnerable to disease or insect outbreaks and to changing or extreme climatic conditions. Multiclonal plantations, although they require the breeding and selection of multiple hybrids and clones, provide an alternative solution that limits these risks (Beuker 2000). Lithuania is situated at the northern limit of *P. nigra* natural dis-

tribution range (Vanden Broeck 2003). Thus, this tree species can be considered as native and its hybrids as well as hybrids of other poplar species have good potential for wide use in short-rotation forestry.

The aim of this study was to evaluate genetic variation of growth and other adaptive traits and ecogenetic plasticity and adaptability of different poplar hybrids under simulated conditions of the expected climate change, such as frost, drought, warm winter and increased UV-B radiation.

Materials and methods

Materials

For the study under controlled environmental conditions, 44 clones and cultivars of 3 different intraspecific crosses of poplar (*P. nigra* L., *P. deltoides* Bartr. ex Marsh, *P. trichocarpa* Torr. et Gray.) and 4 interspecific hybrids (*P. deltoides* L. × *P. nigra*, *P. deltoides* × *P. trichocarpa*, *P. maksimovicii* A. Henry × *P. trichocarpa*, *P. balsamifera* L. × *P. trichocarpa*) were used. The clones were vegetatively propagated by shoot cuttings and for two years were grown in 3.5-liter pots filled with peat substrate in the greenhouse of the Dubrava SFE nursery. For the substrate, bog peat with the fragmentation of 5–10% was used. The peat substrate was weakly acidic, i.g. $p_{HKCl} = 5$. Chalk (4–5 kg per 1 m³ of peat) was added to reduce acidity. Vegetatively propagated poplars were grown in the substrate with the introduction of 0.17 kg of N, 0.50 kg of P and 0.50 kg of K fertilizers per 1 m³. The substrate was enriched with micro fertilizers, viz. 15 g of copper, 15 g of manganese, 15 g of magnesium sulfate and 10 g of boric acid per 1 m³ of peat were introduced.

Treatments and measurements

Portion of the saplings (7–10 saplings of each clone) early in the growing season (mid-May, spreading of leaves) in climatic chamber were affected (for 20 min.)

Table 1. Code list of hybrid poplar clones by crossing types and combination of crossed poplar species

Crossing type	Hybrid abbreviation	Crossing combination	Clone number or cultivar name abbreviation
Inter-specific	D × N	*P. deltoides* × *P. nigra*	Gr-Comp, Gr-F-488, Gr-F7258, Gr-I-214, Gr-I4551, Gr-It-1, Gr-It-2, Gr-It-3, Gr-It-5, Gr-It-6, Gr-It-7, Gr-It-8, Gr-It-9, Gr-It-10, Gr-Xe-3, Nyd-Albe, Nyd-Degr, Nyd-Elle, Nyd-Hess, Nyd-Kost, Nyd-Pola, Nyd-Sano, UK-AgatF, UK-Arges, UK-Banic, UK-Casal, UK-DeltA, UK-FrPEF, UK-Gaver, UK-Gelri, UK-I-214, UK-Primo, UK-RobuH, UK-Robus, UK-Spitk
	D × T	*P. deltoides* × *P. trichocarpa*	Isl-15, Isl-70, Isl-90, Isl-171, Isl-192, Isl-215, Isl-247, UK-Boela, UK-Donk, UK-Rap
	M × T	*P. maximowiczii* × *P. trichocarpa*	SvSFPo2, SvSFPo6, SvSFPo7, UK-Andro
	B × T	*P. balsamifera* × *P. trichocarpa*	SvSFPo1, SvSFPo3, SvSFPo4, SvSFPo5, SvSFPo13
Intra-specific	N	*P. nigra* × *P. nigra*	Gr-I-64, Gr-I-64B, Gr-K-7
	T	*P. trichocarpa* × *P. trichocarpa*	SvSFPo10, SvSFPo11, SvSFPo12, SvSFPo14, SvSFPo15, SvSFPo9, UK-FrPau
	D	*P. deltoides* × *P. deltoides*	Ser-B-81, Ser-B229, Ser-P-19, Ser18281

by simulated –4ºC frost. Frost treatment were done at the same date for each clone. Another portion of the test material (7–10 saplings of each clone) in the middle of the growing season (second half of July) was exposed to simulated drought without watering for two weeks (up to leaf withering stage). *P. nigra* × *P. nigra* intraspecific hybrid and clones (crosses) were not included in a drought treatment. Pots with 3–5 ramets of each clone were placed in two rows randomly distributing them across two beds (= blocks).

Warm winter was simulated by keeping saplings in an unheated greenhouse from late autumn to early spring. The temperature in the greenhouse was by 5–10ºC degrees higher than outside and the saplings were protected from the wind and sudden changes in temperature while humidity was kept at 40–60%. For the study 7–10 saplings of each clone were used.

Ambient UV-B radiation was enhanced by 10–15% (in sunny days) 8 hours per day for three weeks in July using the UV-B lamps, which were hung 1.0 m above the hybrid poplar trees. For the UV-B radiation measurement the Delta OHM HD 2302.0 light meter was used with LP 471 UVB Probe sensor. Damaged tree leaves were evaluated using a 5-point scale, where 5 denotes healthy leaf, 1 denotes the whole leaf is heavily damaged. For the study 7–10 saplings of each clone were used.

Neither treatment overlapped with another one. The effect of one stress factor on the plant was studied.

The height of saplings was measured three times: at the beginning (April), in the middle (July) and at the end (September) of the growing season. Stem diameter at the root collar was measured twice: at the beginning and at the end of the growing season. The survival was evaluated in September by counting dead and alive trees.

Statistical analysis

To estimate significance of the effects of various factors, such as treatments (frost, drought, warm winter or UV-B radiation), blocks, clones and hybrids and their interaction with treatments, the multifactor variance analysis was performed on single-tree data using the MIXED procedure (procedure option is "Covparms") of SAS software (SAS® Analytics Pro 12.1, 2015) which is based on mixed model equations (MME) and the restricted maximum likelihood (REML) method. The following linear models were used for joint analyses (1) of treatment, hybrids and clones, (2) a treatment and hybrids, (3) treatment and clones and for separate analyses (4) of clones in individual treatment and control:

$$y_{ijklm} = \mu + t_j + h_k + c_{i(k)} + c_{i(k)tj} + h_k\,t_j + b_m + e_{ijklm}, \quad (1)$$
$$y_{jklm} = \mu + t_j + h_k + h_k\,t_j + b_m + e_{jklm}, \quad (2)$$
$$y_{ijlm} = \mu + t_j + c_i + c_i\,t_j + b_m + e_{ijlm}, \quad (3)$$
$$y_{iklm} = \mu + h_k + c_{i(k)} + b_m + e_{iklm}, \quad (4)$$

where

y_{ijklm} is an observation on the lth ramet from the ith clone in the kth hybrid in the mth block in the jth treatment,

y_{iklm} is an observation on the lth ramet from the ith clone in the kth hybrid in the mth block,

μ is the overall mean,

t_j is the fixed effect due to the jth treatment,

b_m is the fixed effect due to the mth block,

h_k is the fixed effect due to the kth hybrid,

$c_{i(k)}$ is the random effect due to the ith clone,

$c_{i(k)}\,t_j$ is the random effect of interaction between the ith clone and jth treatment,

$h_k\,t_j$ is the fixed effect of interaction between the kth hybrid and jth treatment,

e_{ijklm}, e_{jklm}, e_{ijlm} and e_{iklm} are the random residuals.

The model assumes that the random effects are normally distributed with the expectation of zero and corresponding variances: σ_c^2, σ_{ct}^2 and σ_e^2. Assumptions of normal distribution of residuals and variance homogeneity in all experiments were tested using the GLM and UNIVARIATE procedures of the SAS software (SAS® Analytics Pro 12.1, 2015).

Statistical significance of the effects of fixed factors – treatments, blocks and interactions between treatments and blocks – was estimated by P-test (Tests3 option) using the MIXED procedure of the SAS software (SAS® Analytics Pro 12.1, 2015). Z tests were carried out to determine where random effects were significantly different from zero.

Least-squares means estimates were obtained for treatments, as well as for hybrids and clones in each treatment. Statistical significance (at $P < 0.05$) of differences between least-squares means was tested using t-test (the PDIFF option under the LSMEAN statement of the MIXED procedure of the SAS software (SAS® Analytics Pro 12.1, 2015).

Estimates of genetic parameters

Using statistical model 2, clonal variance components were estimated:

$$VC_c^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_{c\cdot b}^2 + \sigma_e^2}, \quad (5)$$

where

VC_c^2 is the clonal variance component,

σ_c^2 is the clonal variance,

$\sigma_{c\cdot b}^2$ is the variance of interaction between clones and blocks,

σ_e^2 is the random residual.

The variance component of each effect was expressed as a percentage of dispersion of all analyzed (included in the model) random effects.

The means of trial conditions, blocks, hybrids and clones by blocks and test conditions as well as their standard errors were determined using the MEANS procedure of the SAS software (SAS® Analytics Pro 12.1, 2015). Genetic parameters were estimated using variance analysis results separately for each treatment.

Clonal heritability coefficient on the level of individuals for each trait was calculated by the following formula:

$$H_i^2 = \frac{\sigma_c^2}{\sigma_{phen}^2} \,, \qquad (6)$$

where:

H_i^2 is the coefficient of clonal individual heritability,

σ_c^2 is the clonal variance,

σ_{phen}^2 is the phenotypic variance.

The standard errors of heritability coefficient under unequal number of trees per family were calculated according to Becker (1984).

Clonal heritability coefficient (repeatability) on the level of means was estimated using the following formula:

$$H_m^2 = \frac{\sigma_c^2}{\sigma_c^2 + \frac{\sigma_e^2}{k}} \,, \qquad (7)$$

where

H_m^2 is the clonal heritability coefficient on the level of means,

σ_c^2 is the clonal variance,

σ_e^2 is the random variance,

k is the coefficient showing mean number of trees per clone.

The errors of heritability coefficients were estimated according to Swiger et al. (1964) by the corresponding method modified by Becker (1984) for an uneven number of observations.

Genotypic variation coefficient in every clonal trial was estimated based on Falconer (1989), Falconer and Mackay (1996). The genotypic gain (genetic improvement effect) was estimated according to Nanson (1989):

$$\Delta G_x = i_x \sqrt{R_x} \sigma_p \,, \qquad (8)$$

where

i_x is the intensity of selection based on selection of n clones from N clones tested (in this study the selection intensity is assumed to be equal to 1.271 which corresponds to selection of 20 clones out of 100),

R_x is repeatability (heritability) coefficient,

σ_p is the phenotypic standard deviation of clonal means.

Expected gain was expressed in percents of the trait mean in each treatment and control.

Phenogenetic plasticity of different hybrids by individual growth traits was estimated as the difference between means in treatments and the control. To determine the contribution of each hybrid to the overall $G \times E$ interaction, an A-type Wricke ecovalences were calculated according to the modified Wricke (1962) method using ls-means estimates ('lsmeans' option) and variances obtained by the SAS MIXED procedure (SAS® Analytics Pro 12.1, 2015). Shukla stability variance and the statistical significance of ecovalences were estimated by the F-test based on Shukla (1972) method using variances obtained by the SAS MIXED procedure.

Results

Performance of different poplar hybrids under the stressors – simulated frost and drought

The ANOVA showed that the effect of simulated spring frost on the growth in height was highly significant ($P < 0.001$), while hybrid effect was of low significance ($P = 0.039$) (Table 2). Hybrid × frost treatment interaction ($G_H \times E$) was also significant ($P < 0.032$) indicating that hybrids differ in their response to the stressor. The effect of drought treatment and hybrid, and their interaction on tree growth was highly significant ($P < 0.001$).
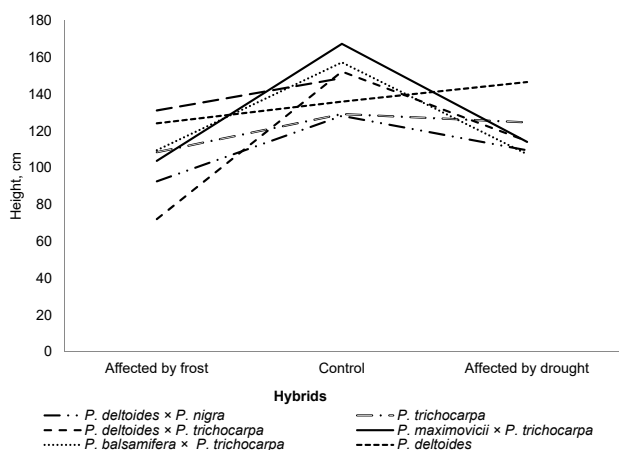
Simulated spring frost and summer drought affected different hybrids in different ways. Both simulated spring frost and summer drought led not only to growth decrease but also to the withering of a portion of tree stem or even entire tree which reduced mean height. Mean height of trees affected by simulated spring frost was lower than that affected by simulated summer drought (Figure 1). An exception was the *P. deltoides* × *P. deltoides* hybrids which were not affected by drought to a larger extent. After summer drought mean height of *P. deltoides* × *P. deltoides* was higher than that of the control trees. The height of this hybrid affected by drought was significantly higher than that of the others.

The lowest growth losses were experienced by the *P. trichocarpa* × *P. trichocarpa* and *P. deltoides* × *P. deltoides* infraspecific hybrids. However, under ambient (the control) conditions their growth was one of the poorest. After simulated summer drought the height of the *P. deltoides* × *P. deltoides* intraspecific cross was even higher than in the control.

Table 2. Results of multivariate ANOVA: *F*-criteria and significance (*P*) of effects of hybrids, simulated spring frost and summer drought treatments on tree height, stem diameter and tree survival of *Populus* hybrids

Treatments and factors		Tree height			Stem diameter			Survival		
	DF	MS	F	P	MS	F	P	MS	F	P
Spring frost										
Hybrid	6	3936.1	2.21	0.039	2114.8	2.21	0.039	0.2	1.96	0.067
Frost	1	20999.7	11.80	<0.001	23262.1	24.30	<0.001	2.0	13.80	<0.001
Hybrid × frost interaction	5	4352.1	2.44	0.032	2314.8	2.42	0.034	0.5	3.63	0.001
Summer drought										
Hybrid	6	8833.4	4.99	<0.001	4493.4	3.62	0.001	0.3	4.31	<0.001
Drought	1	107816.1	61.01	<0.001	11962.6	9.64	0.001	2.6	28.50	<0.001
Hybrid × drought interaction	6	6874.4	3.89	0.001	4888.3	3.94	<0.001	0.3	3.64	0.002

Figure 1. Tree height of different *Populus* hybrids after simulated spring frost and summer drought treatments and under control (ambient) environment at the end of growing season

The greatest differences of mean height between trees in the control and stress-damaged trees were recorded for the *P. deltoides* × *P. trichocarpa* hybrids (Figure 1). The effect of simulated spring frost for all hybrids was stronger than effect of summer drought. The mean height of hybrids due to frost-caused growth losses, or death, decreased by 26.4%, while due to drought by 18.4%.

In our studies the hybrid progenies of *P. balsamifera* or *P. trichocarpa* (*P. maximowiczii* × *P. trichocarpa*, *P. balsamifera* × *P. trichocarpa* and *P. deltoides* × *P. trichocarpa*) were among the tallest ones. Although they suffered significant growth losses due to simulated spring frost, all of them, except for *P. deltoides* × *P. trichocarpa*, remained among the tallest.

The ANOVA showed a highly significant (*P* < 0.001) effect of simulated frost on tree diameter as well, while hybrid effect (*P* = 0.039) and hybrid × frost treatment interaction effect were of low significance (*P* = 0.034) (Table 2). In the trial of simulated summer drought, highly significant effects of drought treatment, hybrid, and hybrid × drought treatment interaction (*P* < 0.001) were also found.

The greatest losses in diameter increment due to simulated frost were experienced by the *P. balsamifera* × *P. trichocarpa* and *P. deltoides* × *P. trichocarpa* hybrids. The greatest losses due to simulated drought were experienced by the *P. deltoides* × *P. trichocarpa* and *P. balsamifera* × *P. trichocarpa* hybrids. However, drought positively influenced the growth in diameter of the *P. deltoides* × *P. deltoides* hybrid.

The ANOVA of tree survival after the impact of different stressors showed a significant frost and frost interaction with hybrid (G_H × E) effect rather than hybrid effect (Table 2). Drought treatment and hybrid effects were highly significant when considered separately, however the effect of their interaction was of moderate significance (0.001 < *P* < 0.01).

Mostly *P. balsamifera* × *P. trichocarpa* hybrid trees were killed – mortality was 35%, the least affected were
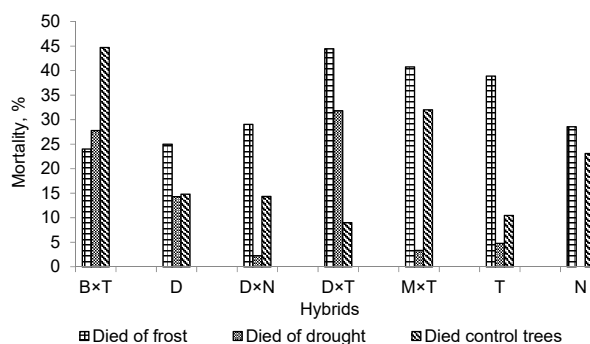
Figure 2. Tree mortality of different Populus hybrids after simulated spring frost and summer drought treatments and under control (ambient) environment at the end of growing season.

* Hybrid abbreviations are explained in Table 1.

P. deltoides × *P. nigra*, 16% (Figure 2). The largest portions of trees killed by drought, 31.8% and 27.8%, were in the hybrids of *P. deltoides* × *P. trichocarpa* and *P. balsamifera* × *P. trichocarpa*, respectively. The least affected by drought were the *P. deltoides* × *P. nigra* hybrids, of which only 2.2% of all trees died. Due to spring frosts mostly *P. deltoides* × *P. trichocarpa* and *P. maximowiczii* × *P. trichocarpa* hybrid trees were killed, 45% and 41%, respectively (Figure 2). The smallest portion of trees killed by frost was recorded for the *P. balsamifera* × *P. trichocarpa* hybrids, 24%. In general, simulated spring frost caused higher losses than summer drought.

As indicated by Wricke's ecovalence, the strongest response to different environmental conditions by tree height was shown by the *P. balsamifera* × *P. trichocarpa* hybrids, and the weakest by the *P. deltoides* × *P. nigra* hybrids (Table 3). The lowest ecovalence values of the *P. deltoides* × *P. nigra* hybrid were also in terms of tree diameter and survival. The highest ecovalence by tree diameter was estimated for the *P. balsamifera* × *P. trichocarpa* hybrids, while by the survival of trees for *P. deltoides* × *P. trichocarpa*. The highest value of Shukla's parameter in tree height was obtained for the *P. balsamifera* × *P. trichocarpa* hybrids (estimates for *P. nigra* are biased because of its absence in the draught treatment), and the lowest for *P. trichocarpa*. The highest value of Shukla's parameter in diameter of trees was estimated for the *P. deltoides*, and the lowest for *P. trichocarpa*.

Genotypic variation and plasticity of clones under the stressors – simulated frost and drought

Analyzing at the clonal level, the ANOVA revealed that tree height was significantly (*P* < 0.001) affected by drought treatment effects, and clone and genotype by drought treatment interaction (*G* × *E*) indicating that clones respond differently (Table 4). In the trial with simulated spring frosts a highly significant effect of frost was also found, clone and clone by frost treatment interaction (*P* < 0.001) (Table 4).

Table 3. Stability characteristics of different poplar hybrids for tree height, diameter and survival under frost and drought treatments and control

Hybrid	Estimate in frost treatment	Estimate in control treatment	Estimate in drought treatment	Mean estimate	Phenotypic plasticity under effect of frost	Phenotypic plasticity under effect of drought	Wricke ecovalence (stand.)	Wricke ecovalence, %	Shukla stability variance	F	P
					Tree height						
B × T	1.551	−0.189	−1.408	−0.015	1.739	2.958	55.423	25.19	28.022	36.00	<0.001
D	−0.050	2.122	2.489	1.520	−2.172	−2.539	48.888	21.47	23.449	14.43	<0.001
D × N	−0.549	−0.762	−0.641	−0.651	0.212	0.091	11.439	0.13	0.2765	.	.
D × T	0.548	0.050	0.587	0.395	0.498	−0.039	13.008	1.02	0.1667	.	.
M × T	1.096	1.333	−0.413	0.672	−0.237	1.508	29.153	10.22	0.9633	7.91	<0.001
N	−0.387	2.648	.	1.130	−3.035	.	.	26.26	58.650	23.43	<0.001
T	−0.609	1.274	1.547	0.737	−1.882	−2.155	38.764	15.70	16.362	24.56	<0.001
					Tree diameter						
B × T	16.90	11.41	−9.41	6.29	54.87	263.17	4.5	13.25	2.2	14.80	<0.001
D	−2.90	24.60	40.54	20.74	−275.08	−434.45	1.0	33.19	6.2	11.20	<0.001
D × N	−9.99	−3.84	−6.78	−6.87	−61.56	−32.13	8.7	0.65	.	.	.
D × T	12.25	−22.35	−0.40	−3.50	346.14	126.62	6.8	21.08	3.8	27.18	<0.001
M × T	26.28	6.26	−0.94	10.53	200.21	272.30	4.6	13.68	2.3	9.83	<0.001
N	8.99	30.91	.	19.95	−219.23	.	.	8.26	2.3	4.98	<0.001
T	−9.19	10.48	12.54	4.61	−196.77	−217.45	3.5	9.90	1.5	11.96	<0.001
					Tree survival						
B × T	0.162	−0.070	0.195	0.096	0.231	−0.033	0.0410	28.06	0.0260	30.78	<0.001
D	−0.074	−0.024	0.060	−0.012	−0.049	−0.134	0.0091	6.20	0.0039	1.71	0.181
D × N	−0.035	−0.073	−0.060	−0.056	0.038	0.025	0.0007	0.51	.	.	.
D × T	−0.108	0.135	0.203	0.077	−0.243	−0.311	0.0536	36.21	0.0350	35.73	<0.001
M × T	0.151	0.098	−0.048	0.067	0.052	0.198	0.0212	14.33	0.0123	8.58	0.162
N	0.100	−0.024	.	0.038	0.123	.	0.0076	5.16	0.0057	1.95	.
T	−0.804	0.079	−0.035	−0.013	−0.163	−0.049	0.0141	9.53	0.7400	7.94	<0.001

Hybrid abbreviations are explained in Table 1.

Table 4. Results of multivariate ANOVA: *F*-criteria and significance (*P*) of effects of clones, simulated spring frost and summer drought on tree height, stem diameter and tree survival of *Populus* hybrids' clones

Treatments and factors		Tree height			Stem diameter			Survival		
	DF	MS	F	P	MS	F	P	MS	F	P
				Spring frost treatment						
Clone	44	8449.6	6.02	<0.001	5077.3	6.87	<0.001	0.8	7.29	<0.001
Frost	1	32021.7	22.8	<0.001	49777.6	67.40	<0.001	0.3	3.33	0.068
Clone × Frost interaction	28	4470.8	3.19	<0.001	2876.0	3.89	<0.001	0.6	5.95	<0.001
				Summer drought treatment						
Clone	44	7995.1	5.98	<0.001	32.2	3.64	<0.001	0.7	7.40	<0.001
Drought	1	145548.0	108.0	<0.001	56.7	6.21	0.013	2.2.	23.1	<0.001
Clone × Drought interaction	22	7973.5	5.96	<0.001	26.2	2.88	<0.001	0.5	5.94	<0.001

The highest mean height among the clones and cultivars of the *P. deltoides* × *P. nigra* hybrid was characteristic of *Degroso*, Delta × Nigra (UK–I), *Banica*, *Albelo*, *Compedor* cultivars and Svel1 test clone, but all of them responded to stressors very differently. The best growing in the control conditions *Degroso* variety was characterized by high ecogenotypic plasticity, i.e. high sensitivity to stressful growing conditions: spring frost and summer drought not only decreased their increment in height but also caused dieback of some portions of tree stems or even entire trees.

The tallest clone of the *P. trichocarpa* × *P. trichocarpa* intraspecific cross under control conditions was Svel2. Interestingly, mean height of the clone Svel4 in drought conditions was slightly higher than that of Svel2 in the control conditions and much higher than that of the same Svel4 in the control conditions. Mean height of the Svel4 clone under normal growing conditions was the lowest of all. However, after its exposure to both drought and frost conditions, it was higher. The lowest ecogenetic plasticity was characteristic of Svel2: its growth was relatively stable in all conditions. Mean height of the clone affected by

the stressors decreased insignificantly. In the control conditions, among the clones and cultivars of the *P. trichocarpa × P. maximowiczii* hybrid the tallest was *Androscogin* with not too far behind Sve2 and Sve6 clones. The Sve2 was more affected by drought: its mean height decreased almost twice. The Sve6 and Sve7 clones were characterized by greater sensitivity to spring frosts.

Analysis of variance of the data revealed that the effect of simulated spring frosts or summer drought and effect of clone, taken both separately or in combination, were highly significant ($P < 0.001$) for tree growth in height (Table 4). The interaction of clone with the drought treatment ($G_C \times E$) was also very significant in terms of tree growth in diameter after the effect of drought stressor. The general effect of summer drought was significant on diameter ($P = 0.013$) (Table 4).

The best survival under different environmental conditions was characteristic of the Gra-Xe-3 and *Degroso* poplars. Not a single clone of the *P. deltoides × P. nigra* hybrid was killed. It is surprising that all the control trees of *Hess* (Nyd) cultivar died. The drought killed all the Isl 90 trees. The frost heavily damaged the trees of the Isl-70 clone and *Donk* (UK) cultivar and 77% and 55% of the trees respectively, were killed. All 192 control trees of the Isl clone died. The obtained results are confirmed by the ANOVA: the general effect of frosts on survival was not significant but the effect of clone and the interaction between clone and frost were highly significant. A significant effect of clone and drought as well as clone × drought interaction ($G_C \times E$) shows that clones have different plasticity in response to drought.

In the control conditions the highest heritability coefficient was obtained for tree survival ($H_i^2 = 0.32$) and the lowest for autumn diameter ($H_i^2 = 0.17$). The values of heritability coefficient were altering along with stressful environmental conditions. In drought conditions heritability was moderate ($H_i^2 = 0.41$), while in the case of spring frosts it was low ($H_i^2 = 0.11$).

The lowest genotypic variation was found for tree height in autumn (in all conditions) – CV_g ranged from 0.60% to 0.90% – while the highest one was that of survival, CV_g ranged from 49.90% to 220.98% (Table 5). The indicators of clonal variation in drought conditions were not significant for any trait except for a higher significance of tree mortality ($P < 0.01$). But this happened due to the decline of the number of trees per clone which consequently decreased the accuracy of analysis of variance.

Table 5. Genetic parameters of different traits of *Populus* hybrids in simulated spring frost and summer drought treatments and in the control environment

Treatment	Tree trait	Trait mean ±se	Clonal variance component, % ±se	P	CV_G, %	H_i^2 ±se	H_m^2 ±se	CV_{ph}, %	dG, %	dGm, %
Control	Stem diameter in spring, cm	3.44 ±0.16	22.58 ±6.72	***	24.27	0.23 ±0.01	1.00 ±0.01	49.79	24.11	49.58
	Stem diameter in autumn, cm	10.66 ±0.14	16.66 ±5.91	**	13.03	0.17 ±0.04	0.74 ±0.04	32.95	5.49	24.53
	Tree height in spring, cm	43.01 ±0.70	17.40 ±5.30	***	19.21	0.17 ±0.04	0.79 ±0.04	46.42	8.08	36.72
	Tree height in autumn, cm	140.05 ±1.84	22.58 ±6.72	***	0.60	0.23 ±0.05	0.81 ±0.03	34.00	7.68	27.53
	Survival	0.19 ±0.01	32.46 ±9.63	***	126.01	0.32 ±0.05	0.90 ±0.02	209.23	67.91	187.52
Spring frost	Stem diameter in spring, cm	3.85 ±0.10	26.75 ±10.77	**	22.61	0.27 ±0.02	0.99 ±0.01	42.81	11.45	42.35
	Stem diameter in autumn, cm	7.99 ±0.23	7.71 ±7.35	.	10.66	0.08 ±0.06	0.34 ±0.09	38.59	2.98	13.06
	Tree height in spring, cm	48.65 ±1.23	26.11 ±10.46	**	19.44	0.26 ±0.07	0.75 ±0.05	40.16	10.49	30.29
	Tree height in autumn, cm	96.93 ±3.09	26.75 ±10.77	**	0.90	0.27 ±0.08	0.69 ±0.07	42.60	11.40	29.43
	Survival	0.31 ±0.03	10.99 ±6.38	*	49.90	0.11 ±0.05	0.52 ±0.08	149.65	16.45	77.45
Summer drought	Stem diameter in spring, cm	4.45 ±0.12	28.68 ±12.35	*	21.98	0.29 ±0.02	0.99 ±0.01	7.40	11.49	39.59
	Stem diameter in autumn, cm	10.43 ±0.19	7.64 ±7.14	.	6.39	0.08 ±0.06	0.39 ±0.09	24.54	1.88	9.65
	Tree height in spring, cm	41.12 ±1.32	19.76 ±10.32	*	19.1	0.20 ±0.07	0.68 ±0.07	46.16	12.09	31.31
	Tree height in autumn, cm	114.85 ±26.20	28.68 ±12.35	*	0.85	0.29 ±0.08	0.76 ±0.06	27.02	7.75	20.51
	Survival	0.08 ±0.02	41.45 ±16.81	**	220.98	0.41 ±0.09	0.86 ±0.04	334.24	138.55	286.90

Parameters: trait means, clonal variance component, coefficient of genotypic variation (CV_G), coefficient of individual heritability (H_i^2), clonal mean heritability (H_m^2), coefficient of phenotypic variation (CV_{ph}) and expected genetic gain (dG); 'se' is the standard error Level of significance of effects is denoted by: * – $0.01 < P < 0.05$, ** – $0.001 < P < 0.01$, *** – $P < 0.001$.

The greatest changes in genotypic variation were found for the survival of trees: *CV* decreased in the case of frost but significantly increased due to drought effect.

The highest phenotypic plasticity of tree height under the effect of frost was observed in the *P. deltoides × P. trichocarpa* hybrid, the lowest – in *P. deltoides*, however the results were somewhat different under the impact of drought. The plasticity of *P. deltoides* remained the lowest while that of *P. maximowiczii × P. trichocarpa* the highest. Estimating the plasticity of trees by their survival, the lowest plasticity both under the effect of drought and frost was characteristic of the *P. deltoides × P. trichocarpa* hybrid. The highest plasticity in drought had the *P. maximowiczii × P. trichocarpa* hybrid, while under the effect of frost had *P. balsamifera × P. trichocarpa*.

Sensitivity of poplar hybrids to warm winters and UV-B radiation

Analysis of variance showed that the effect of warm winter as a stress factor on the growth in height and diameter was not significant (Table 6), however hybrid effect was highly significant ($P < 0.001$) on the diameter of trees but not on the height.

In the control, the largest stem diameter was in *P. deltoides × P. trichocarpa*, *P. maximowiczii × P. trichocarpa* hybrids, and the smallest in *P. deltoides × P. nigra* (Figure 3). After a warm winter the *P. deltoides × P. trichocarpa*, *P. maximowiczii × P. trichocarpa* hybrids suffered from losses in diameter growth. Mean diameter of the remaining hybrids at the end of the growing season followed by a warm winter stress was higher than that of trees growing in the control conditions; meanwhile differences for *P. deltoides* and *P. balsamifera × P. trichocarpa* were not significant.

Under the control (ambient) conditions the tallest at the end of the growing season were the *P. deltoides × P. trichocarpa* and *P. maximowiczii × P. trichocarpa* hybrids, while the lowest were the intraspecific *P. deltoides × P. deltoides* and *P. nigra × P. nigra* crosses (Figure 4). After a warm winter, losses of growth in height were recorded for the *P. deltoides × P. trichocarpa*, *P. maximowiczii × P. trichocarpa* and *P. deltoides × P. deltoides* hybrids. Meanwhile effect on growth was minimal in the *P. deltoides × P. deltoides*, *P. deltoides × P. nigra* and *P. balsamifera × P. trichocarpa* hybrids.
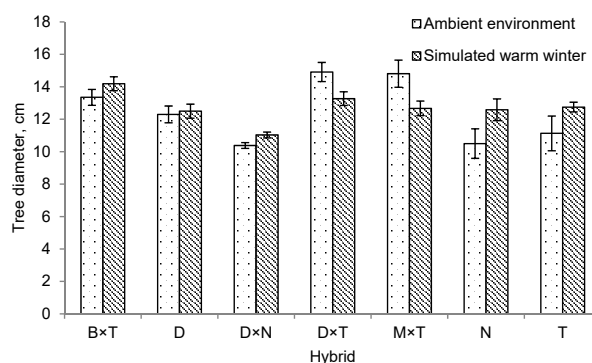
Figure 3. Mean tree stem diameter of hybrids affected by simulated warm winter and tested in control (ambient) environment at the end of growing season

Hybrid abbreviations are explained in Table 1.
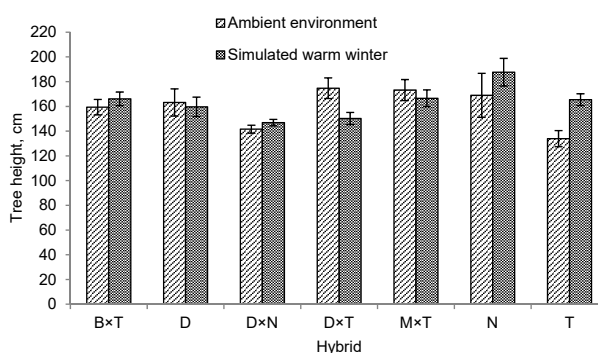
Figure 4. Mean height of hybrids affected by simulated warm winter and tested in the control (ambient) environment at the end of growing season

Hybrid abbreviations are explained in Table 1.

All the other hybrids after a warm winter demonstrated a better growth. The biggest increase was observed in the *P. nigra × P. nigra* and *P. trichocarpa × P. trichocarpa* hybrids since their mean height increased the most.

The condition of trees both in the control and those overwintering in warm conditions was quite good and the differences were insignificant. The condition of the *P. deltoides × P. deltoides* and *P. trichocarpa × P. trichocarpa* hybrids after warm winter was better than that of the control. The condition of the *P. maximowiczii × P. trichocarpa* hybrids was stable regardless of the environmental conditions.

The most damaged by UV-B radiation were the leaves of the *P. balsamifera × P. trichocarpa* and *P. max-*

Table 6. Results from joint mixed linear models analysis of variance of growth traits of hybrid *Populus* clones affected by simulated warm winter

Trait*	Random effects				Fixed effects					
	Clones, %		Clones × Warm winter treatment, %		Hybrids		Hybrids × Warm winter treatment		Warm winter treatment	
					F	*P*	*F*	*P*	*F*	*P*
Stem diameter in autumn	3.69 ±3.81	*	11.2 ±4.44	**	5.84	<0.001 ***	1.24	0.311 .	0.00	0.953 .
Tree height in autumn	10.73 ±5.35	.	11.0 ±4.31	**	1.00	0.441 .	0.85	0.538 .	0.04	0.849 .

F-criteria and probability (*P*) of fixed effects and variance components and their standard errors for random effects as percent of the total random variation. Level of significance of effects is denoted by: * – 0.01 < *P* < 0.05; ** – 0.001 < *P* < 0.01; *** – *P* < 0.001.
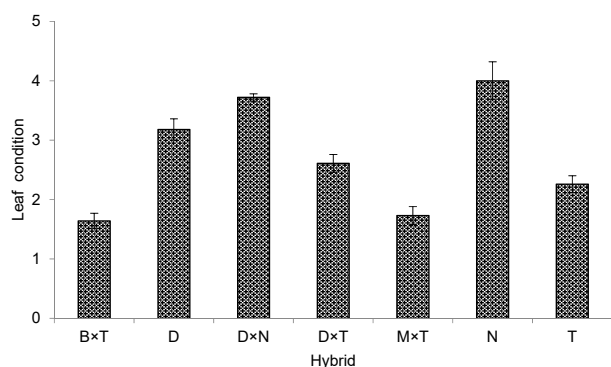
Figure 5. Leaf condition (5 – healthy leaf, 1 – the whole leaf is heavily damaged) of *Populus* hybrids after UV-B treatment

Hybrid abbreviations are explained in Table 1.

imowiczii × *P. trichocarpa* hybrids (Figure 5). Both hybrids are characterized by a rapid growth in the field trials. In the test under controlled conditions the hybrids experienced significant growth losses due to spring frosts and summer drought. The *P. maximowiczii* × *P. trichocarpa* hybrid also suffered from warm winter. After UV-B radiation treatment the healthiest leaves were observed on the *P. nigra* × *P. nigra* and *P. deltoides* × *P. nigra* hybrids.

Sensitivity of clones to warm winters and UV-B radiation

The ANOVA showed a significant clone and warm winter interaction effect ($G_C \times E$) on tree height ($P < 0.01$) (Table 6). The tallest in the control were the Sve-11, Gr-K-7, Serb-182 clones (Figure 6). They all responded differently to the warm winter stress. Mean height of the Sve-11 and Serb-182 clones at the end of the growing season followed by overwintering in warmer conditions decreased. The clone Gr-K-7 after a warm winter was growing faster than in the control conditions. Warm winter intensified the growth of one half of the clones. The greatest height increment as compared to the control was received for the Sve-14, *Degroso*, and Uk-I-214 clones. Mean height of the Sve-14 clone in the control conditions was 100.89 ±5.51 cm while after a warm winter – even 183.19 ±10.4 cm. The greatest growth loss due to the stress was experienced by the Isl-70 clone. The mean height of the *Hess* (Nyd) clone was the same regardless of the environmental conditions and differed only the magnitude of error.
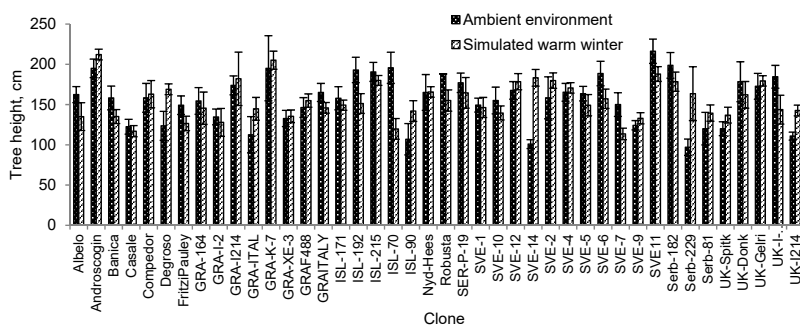
The ANOVA showed that the effect of warm winter and clone interaction ($G_C \times E$) on the growth in diameter was significant ($P < 0.01$), while clone effect was weakly significant ($P < 0.05$) (Table 6). Thus, no significant differences between mean diameters of the majority of clones in different environments were found. The greatest losses of growth in diameter were suffered by the Sve-11 and Sve-6 clones. The maximum value of diameter (20.29 ± 8.33 cm) was obtained by measuring trees growing in the control conditions. The Sve14, Serb-229 clones were characterized by the most vigorous growth in diameter during the summer drought.

The traits of trees growing in the control were characterized by a higher clonal variance component than those growing in warm winter conditions. Clonal variance component of tree height decreased the most: from 23.58% down to 18.29% ($P < 0.005$).

Stressful environmental conditions reduced also genotypic variation and trait heritability. The greatest genotypic variation both in the control and in warm winter conditions was obtained for tree height. Genotypic variation of tree diameter in warm winter conditions decreased the most: from 15.1 to 8.72% (Table 7). Genotypic variation of hybrid performance depending on environmental conditions (control vs. warm winter) varied insignificantly.

Discussion

Performance of different poplar hybrids under the stressors – simulated spring frost and summer drought

Simulated spring frost and summer drought affected different hybrids in different ways. Both simulated spring frost and summer drought led not only to growth decrease but also to the withering of a portion of tree stem or even entire tree which reduced mean height. An exception was the *P. deltoides* × *P. deltoides* hybrids which were not affected by drought to a larger extent.

After summer drought mean height of *P. deltoides* × *P. deltoides* was higher than that in the control. The height of this hybrid affected by drought was significantly higher than that of the others. This phenomenon could be attributed to the eustress, a positive form of stress having a beneficial effect on performance of organisms. Although *P. deltoides* naturally grows in moist habitats but it also

Figure 6. Mean height of clones affected by simulated warm winter and tested in the control (ambient) environment at the end of growing season

For clone descriptions see Table 1.

Table 7. Genetic parameters of different traits of *Populus* hybrids in simulated warm winter and in the control environment

Treat-ment	Tree trait*	Clonal variance component ±se, %	P	CV_G, %	H_m^2 ±se	H_i^2 ±se	CV_F, %	dG, %	dGm, %
Control	Stem diameter	16.53 ±6.33	**	15.1	0.68 ±0.05	0.17 ±0.05	39.18	6.48	26.64
	Tree height	23.58 ±7.66	**	16.96	0.77 ±0.04	0.24 ±0.05	35.05	8.38	27.03
	Tree condition	5.84 ±5.21	.	1.54	.	.	6.34	0.37	2.53
Warm winter	Stem diameter	11.15 ±4.52	**	8.72	0.64 ±0.06	0.11 ±0.04	27.30	3.04	17.37
	Tree height	18.29 ±6.05	**	12.47	0.76 ±0.04	0.18 ±0.05	29.15	5.33	22.08
	Tree condition	3.13 ±2.62	.	1.14	.	.	6.48	0.20	2.01

Parameters: trait means, clonal variance component, coefficient of genotypic variation (CV_G), coefficient of individual heritability (H_i^2), clonal mean heritability (H_m^2), coefficient of phenotypic variation (CV_F) and expected genetic gain (dG). Level of significance of effects is denoted by: * – $0.01 < P < 0.05$; ** – $0.001 < P < 0.01$; *** – $P < 0.001$.

needs higher air temperature (Burns et al. 1990) which in a greenhouse was higher than under natural weather conditions in the field trials.

In our studies the hybrid progenies of *P. balsamifera* or *P. trichocarpa* (*P. maximowiczii* × *P. trichocarpa*, *P. balsamifera* × *P. trichocarpa* and *P. deltoides* × *P. trichocarpa*) were among the tallest ones. Although they suffered significant growth losses due to simulated spring frost, all of them, except for *P. deltoides* × *P. trichocarpa*, remained among the tallest. Similarly, McKown et al. (2014), in Canada, found a significant dependence of phenological and biomass parameters on climatic and geographical conditions of the environment. In our study all hybrids, which parents originated from the northern regions, experienced more intensive leaf damages due to spring frosts or summer drought than hybrids, whose parents originated from the southern regions. This can be due to mismatching phenology with environment changes.

The greatest losses in diameter increment due to simulated spring frost were experienced by the *P. balsamifera* × *P. trichocarpa* and *P. deltoides* × *P. trichocarpa* hybrids. The simulated spring frost disrupted the vegetation period, which resulted in small diameter increments (Elferjani et al. 2016). It is known that cold hardiness is tend to increase with age, and show significant differences between the adult individuals and trees in the juvenile stage for a number of deciduous species (Lim et al. 2014, Hofmann et al. 2014), therefore at field trials *P. balsamifera* × *P. trichocarpa* has one of the greatest diameter among all hybrids despite climatic factors (Pliūra et al. 2014). Moreover, tree ring width of hybrid poplar correlated with climatic factors not only in the current year but also previous ones (Šēnhofa et al. 2016).

In our studies as indicated by high ecovalences the strongest response to different environmental conditions by tree height showed *P. balsamifera* × *P. trichocarpa* hybrid, the weakest showed *P. deltoides* × *P. nigra*. Ecovalence shows how strongly varies genotype response to different environmental conditions of treatments or, in other words, the ecovalence of the genotype is its interaction with the environments (Fasahat et al. 2015). Ecovalence characterizes the relative lability of a population in relation to other populations and describes what part

of the $G × E$ interaction is determined by ecogenetic variability of a hybrid. High Wricke's ecovalence shows that the *P. balsamifera* × *P. trichocarpa* hybrid is sensitive to ecological environmental conditions. In Sweden clone *Boleare* showed poor survival and high sensitivity to frost (Karacic et al., 2003), but at our studies none of *Boleare* tree died.

Plasticity and genotypic variation of clones under the stressors: simulated spring frost and drought

We found that clone genotype by environment interaction ($G_C × E$) significantly affected tree height under simulated spring frost and summer drought conditions. Lazdina et al. (2016) found significant ($P < 0.01$) clone effect on the phenological stage, leaf and stem frost damage, height and biomass at field trial in Latvia as well. Nielsen et al. (2014) also found a significant effect of environment × clone interaction on tree height but not on the volume. Similar results were obtained studying hybrid aspen (Yu et al. 2003, Ma et al. 2015). Meanwhile, Wu and Stettler (1996) pointed out that clones and silvicultural measures (e.g. plant spacing and others) interaction strongly influence adaptation possibilities of clones and their performance.

Our results suggest that inter- and intraspecific crosses and clones of *P. nigra* are characterized by the lowest phenotypic plasticity, i.e. low response rates to stressful environmental conditions such as frost impact. However, *P. nigra* clones were characterized by difficulties in adaptation to low temperatures in the Czech Republic, where *P. nigra* is considered a native pioneer species (Benetka et al. 2014). The studies of Stecki (1980) also showed poor results for *P. nigra* in Poland. Benetka et al. (2014) concluded that fertile soils increase adaptation possibilities of *P. nigra* to low temperatures. The natural range of *P. nigra* in Europe is not extending far north indicating that cold is the limiting factor. Response to stressful environmental conditions depends on hybrid origin as well. Viger et al. (2016) revealed significant natural variation among populations of *P. nigra* originating from contrasting climatic conditions within Europe.

In our studies the values of heritability coefficient were altered along with environmental conditions. For

example, in drought conditions about 40% of survival variability was due to genotype ($H_i^2 = 0.41$) while in the case of spring frosts only 10% ($H_i^2 = 0.11$). Heritability of one of the most important traits – height in autumn – under stressful growth conditions was also higher than in the control. The high mean values of heritability coefficient indicate strong genotypic control of the trait. The decrease of values of heritability coefficients shows that in stressful environmental conditions ecological variation of these traits is greater in relation to genotypic variation. Slightly increased values of height heritability coefficients at individual level under the effect of stressors show that stressful environmental conditions augmented genotypic differences of clonal growth.

Our finding that the greatest variation of coefficients of genotypic variation of survival of trees with decreased *CV* in the case of frost but significantly increased due to drought effect corresponds to findings by other researchers. Monclus et al. (2009) found that biomass trait, leaf area and other characteristics of the *P. deltoides* × *P. trichocarpa* hybrids are marked by a high genotypic variation which increased under water deficit. The difference in genotypic variation in different environments is preconditioned by an uneven growth disruption scale of different clones and their different phenotypic plasticity. High genotypic variation of adaptive traits is favourable for genetic adaptation as well as for tree breeding as allows obtaining high genetic gain.

High phenotypic plasticity suggests that in a relatively short period of time trees can respond to climatic and environmental changes even in the absence of their selection. However, in our study simulated frost and drought have reduced the growth of many hybrids, thus high phenotypic plasticity apparently shows not a high adaptation but the deterioration of vitality and performance due to frost and drought damages. This plasticity aspect is emphasized in the work presented by Schlichting (1986). Under environmental changes high phenotypic plasticity in the short term may be useful but can be harmful in the long run as natural selection will not be able to operate in full force (Eriksson 1996).

Sensitivity of poplar hybrids to warm winters and UV-B radiation

Crossbreeding of different hybrids from different adaptive environments disbalances genotypically controlled adaptive preferences and makes it difficult to predict ecological behaviour of the offspring according to the ecological adaptation preferences of their parent trees. Studies of pioneer species show that populations growing in optimal for the species conditions have a higher adaptability (Hill et al. 1998). Results of our study show that *P. nigra* growing at the northern margins of its natural range can be easily adapted to warm winter conditions and its mean height was higher than that in the control conditions.

Interestingly, there are no clear differences between response of poplars of the southern and northern origin: response to warm winter was in general poorly dependent on the latitude of species origin. Warm winters adversely effected the growth of some hybrids while others – *P. nigra* × *P. nigra* and *P. trichocarpa* × *P. trichocarpa*, which parents originated from the southern part of their natural distribution range – have increased their growth. The observed height growth increase following warm winter treatment can be attributed to the eustress.

Characterized by a slightly better growth in warm winter conditions than in control *P. balsamifera* × *P. trichocarpa* and *P. deltoides* × *P. nigra* had a pronounced sensitivity to spring frosts which increases the possibility of frost damages. It was shown that temporary peaks of temperature (lasting for a few days to weeks) increase the sensitivity of trees to frost and cold (Pagter et al. 2013). Early leaf expansion and following frosts particularly increase the risk of damages and defoliation (Fairweather et al. 2008). Warm conditions in autumn significantly increases growth, in combination with short photoperiod it leads to a reduced capacity to establish dormancy (Soolanayakanahally et al. 2013). Due to climate warming, trees will initiate terminal buds at increasingly higher temperatures at their current locations, potentially compromising dormancy (Soolanayakanahally et al. 2013). Photoperiodic induction of dormancy is effective only in a restricted temperature range on *Populus* species (Rinne et al. 2018). Natural *Populus* ecotypes have evolved to avoid the adverse effects of high and low temperatures by initiating and completing dormant buds within an approximate temperature-window of 24–12°C. Global warming and erratic temperature patterns outside this range can therefore endanger the successful propagation of deciduous perennials (Rinne et al. 2018). In the study on *Populus* Howe et al. (1999) revealed that dormancy establishment at 25°C was strongly delayed.

Poplar hybrids from the northern latitudes suffered more from the increased UV-B radiation than those of southern origin which are better adapted to high UV-B radiation occurring during clear summer days in the southern latitudes. Sensitivity to UV-B is preconditioned not only by the origin of the tree but also by interaction with other stressors (temperature, irrigation regime) (Drilias et al. 1997, Zhao et al. 2012, Strømme et al. 2015) and by gender (Melnikova et al. 2017). The study by Duan et al. (2008) confirms that in drought conditions the negative effect of UV-B radiation on poplar growth is minimal or non-existent. It is known that there is a significant effect of UV-B radiation and temperature interaction on poplar bud set (Strømme et al. 2015). More intensive UV-B radiation determines an earlier growth cessation and bud set, but for bud break, there are no significant effects of UV-B radiation enhancement (Strømme et al. 2019).

Conclusions

The ecogenetic response of different poplar hybrids, ecogenetic plasticity and genotypic variation is changing and depending on the nature of stressors. The highest phenotypic plasticity of trees was found under simulated warm winter conditions, the lowest one under simulated spring frost condition. Simulated warm winter and summer drought reduced the genetic variation of growth traits.

Simulated spring frosts and summer drought had a substantial influence on the growth of trees, but the hybrid and clone effect was also significant and showed that many hybrids and clones in principle retain their features/differences under stressful environmental conditions.

Hybrid and clone interaction with simulated frost and drought effects ($G \times E$) found in present study indicates that some of the hybrids and clones respond differently to the stressors. Hybrids, which parents originated from the northern regions, experienced more intensive leaf damages due to spring frosts or summer drought than hybrids which parents originated from the southern regions which are due to mismatching phenology with changed environment. The clones of *P. maximowiczii × P. trichocarpa*, *P. balsamifera × P. trichocarpa*, and *P. deltoides × P. trichocarpa* hybrids performed the best under ambient conditions, but they experienced high growth losses due to frost and drought, therefore they are recommended to be grown only on sites with not much risk of these stressors.

Our study shows that the warm winters can alter the growth of hybrids and adversely affect the condition of trees. Warm winters had negative effect on growth of some hybrids while positively affected others, such as *P. nigra × P. nigra* and *P. nigra × P. trichocarpa* hybrids which parents originated from the southern part of their natural distribution range. Warm winter treatment also affected genetic parameters: reduced the heritability of growth traits and genotypic variation.

The sensitivity of hybrids to UV-B radiation varies and depends on the origin of their parental trees: poplar hybrids from the northern latitudes suffered more from the increased UV-B radiation than those of the southern origin, and this sensitivity partially reflects their susceptibility to other stressors too.

Acknowledgements

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