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The effect of various factors (light, temperature, salt, and drought) on germination of *Bromus sterilis* L.

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Abstract: *Bromus sterilis* L. (barren brome) is one of the most economically important noxious grass weeds in the winter cereal fields of Europe. Its ecological behaviour in this agro-climatic region should be assessed for effective weed control strategies. The present study was conducted to assess the dormancy and germination response of the *B. sterilis* population from the Czech Republic under thermal, light, and stress conditions. The dormancy loss experiment revealed that seeds exposed to the light regime showed a remarkably lower percentage of germination, and under alternating temperatures of 10/20 °C in dark conditions, rapid loss of primary dormancy was observed. This population was found to germinate across a wide temperature range of 5–35 °C, with the highest germination rate at 25 °C (T_{50} = 1.14 days in dark, 1.21 days in light) and the germination time increased with decreasing temperatures below 25 °C. Further, due to fitness advantage, herbicide-resistant (R) biotypes were found to be more stress-tolerant than susceptible (S) biotypes under salinity and drought conditions. In the highest stress conditions, the germination of S biotypes was negligible, while R biotypes can germinate under high stress, but germination decreased below 25 °C. The current findings may add value to effective weed control strategies using prediction models based on seed dormancy and germination values under different hydrothermal conditions.

Keywords: drought stress; herbicide resistance; salinity stress; competition

Barren brome (*Bromus sterilis* L., syn. *Anisantha sterilis* (L.) Nevski) is an emerging annual weed in Europe and some regions of South and North America (Andersson et al. 2002). Chytrý et al. (2008) found *B. sterilis* among the twenty most common archaeophytes occurring in most habitats in the Czech Republic (suboceanic climate) and Great Britain (oceanic climate). Its ecological behaviour in central European regions with semi-continental climates is not well understood, and there is a knowledge gap about its dormancy and germination patterns.

For effective weed control strategies on agricultural land, prediction models are being developed, which are usually based on seed dormancy and germination values from different hydrothermal conditions. For most of the weed species, freshly matured seeds do not germinate because of the primary dormancy. Sometimes, seed germination is limited due to conditional dormancy (Baskin and Baskin 1998). A proper study on the annual pattern of the dormancy cycle is required to understand soil seed bank dynamics in contexts with the emergence timing of weed species for modelling weed-crop competition dynamics and optimising weed control schedules (Forcella 1998, Batlla et al. 2004). Germination and dormancy patterns can vary due to a population's adaptation to the actual environmental conditions and agricultural practices.

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There are many key environmental factors influencing dormancy and germination, mainly temperature, water potential, and light. Many studies have highlighted that seeds in a seed bank can adjust the depth of dormancy through temporal and spatial sensing (Finch-Savage and Leubner-Metzger 2006). Footitt et al. (2011) found that the germination pattern can be significantly influenced by subtle differences in the expression of key genes linked to temporal and spatial sensing.

B. sterilis emerges in late summer and early autumn with winter cereals, overwintering in the crop. Its seeds germinate with sufficient soil moisture after losing dormancy. Long-term adaptation to local agro-climatic conditions can influence germination. While articles mention minimal innate dormancy, the dormancy duration is unspecified (Peters et al. 2000). It is crucial to assess germination ecology and dormancy cycles in different conditions for accurate prediction models. However, there is no research broadening concern on the germination ecology of *B. sterilis* in different environmental conditions. Hence, this study is the first detailed exploration focusing on the influence of thermal, light, and stress conditions on the dormancy and germination of *B. sterilis* in the Czech Republic. Following that, we determined the germination speed and optimal temperature under various temperature, light, and stress conditions, specifically tailored for crop and weed emergence in Central Europe. This information is intended for predictive use in decision support systems.

MATERIAL AND METHODS

Seed material. Seeds of *B. sterilis* were harvested at maturity from ten locations in the Czech Republic in winter wheat stands (Table 1). Collected seeds were air-dried, and the weight of 1 000 seeds (WTS) was determined for all populations before the experiment. Dry seeds were stored under dark conditions at 20 °C in the lab.

Germination experiment. Seed germination tests were conducted in 12-cm-diameter Petri dishes, with 7-cm-diameter dishes inserted upside-down and enveloped in 50 × 200 mm cellulose filter paper strips. Each Petri dish received 20 mL of distilled water, with 25 seeds in four replicates per treatment. Two light regimes (12 h light/12 h darkness and constant darkness) were used. Germination tests were conducted in a growth chamber (Sanyo MLR-350H, Osaka, Japan) under light 160 µE/m/s, R/FR (red/far red) ratio of 15. Petri dishes were covered with a layer of aluminium foil for dark conditions. Daily germination records were maintained, considering a seed germinated when the radicle exceeded 1 mm. Dishes in the dark regime were inspected under light at 532 nm wavelength. Germination results are presented as a percentage of viable seeds from all tested seeds in all experiments.

Dormancy loss experiment. After-ripening was tested with seeds originating from the Opolany location only. The length of primary dormancy was tested under regimes typically common in autumn for this region (10 °C, 20 °C, and alternating 10/20 °C) and under two

Table 1. Characterisation of tested seed collections of *Bromus sterilis* used in experiments

Number	Locality	Altitude (m a.s.l.)	GPS coordinates		WTS (g)	Herbicide efficacy (Pyroxsulam) (%)
			N	E		
1	Vykáň	194	50°7'20"	14°48'59"	7.08	91.75
2	Lovčice	222	50°09'55"	15°23'05"	8.02	36.75
3	Líbeznice	219	50°19'19"	14°49'35"	8.78	92
4	Třebívlice	275	50°27'28"	13°53'56"	6	33.75
5	Hospozín	196	50°30'68"	14°17'17"	8	91.5
6	Žižice	234	50°24'62"	14°15'38"	6.36	48
7	Libčice n. Vltavou	207	50°11'45"	14°22'	6.3	92.75
8	Kostelec n. Labem	172	50°13'36"	14°35'11"	8.75	92.75
9	Dřemčice	281	50°28'27"	13°54'45"	6.33	17.5
10	Opolany	195	50°13'05"	15°22'07"	5.88	18.75

WTS – weight of thousand seeds

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light regimes (12 h light/12 h darkness and constant darkness). Six subsequent tests were conducted in one-week intervals during the first 6 weeks after seeds were harvested. Germinated seeds were counted and removed from Petri dishes every day. Non-germinating seeds were inspected for viability by tetrazolium chloride staining, as Patil and Dadlani (2009) described.

Speed of germination experiment. Germination dynamics of seeds were studied in two experiments: (*i*) recently ripened seeds (6 weeks) and (*ii*) fully matured non-dormant one-year-old seeds. Redundancy analysis (RDA) was employed to explore the impact of different seed collection locations. Seeds were incubated at 10, 15, 20, and 25 °C and 0/15, 5/15, 10/20, and 15/20 °C under two light regimes (see above). Analysis of variance with interactions (ANOVA) in Statistica software analysed the effects of location, incubating temperature, light regime, and their interactions on germination data. Tukey *HSD* (honestly significant difference) test ($P < 0.05$) identified significant differences among treatments. Seed germination (%) and T_{50} values were obtained. T_{50} is a measure of the time required to achieve 50% of maximum germination. T_{50} values were calculated using a log-logistic four-parameter Gompertz model in R-project software (version 2.12.2, R Core Team, 2014), and a lack-of-fit analysis (build-in-function in R-project software) was conducted.

Temperature optimum experiment. Optimum germination was only tested for one-year-old seeds collected at two locations (Opolany and Dřemčice). For the optimum germination calculation, the germination test was conducted under the following temperatures: 0, 3, 5, 10, 15, 20, 25, 30, 35, 40 and 45 °C. Obtained data were modelled according to the Eq. (1):

$$\Theta_T\,(g) = (T - T_b) \times t_g \quad (1)$$

where: Θ_T (g) – thermal time to germination of percentage g; g – germination of a specific fraction; T – germination temperature; T_b – base temperature; t_g – time to germination of seed population.

The germination rate was calculated according to the Eq. (2) (Bradford 2002):

$$GR = 1/t = (T - T_b)/\Theta_T\,(g) \quad (2)$$

where: GR – rate of germination. The germination rates have been calculated for different fractions (percentages) of the seed population (10, 50, and 90%, respectively).

An analysis of variance in the Statistica program (version 12, Prague, Czech Republic) was conducted for data evaluation. The non-linear regression (log-logistic model) was calculated in R-Project (version 2.12.2, Vienna, Austria). Statistical differences were tested on the probability level 0.05 in all experiments presented in this study.

Stress response experiment. Susceptible (S) and herbicide-resistant (R) biotypes of *B. sterilis* have been identified through primary herbicide efficacy screening (Table 1) as described by Sen et al. (2021), and these identified seeds were used for stress response experiments. Seed germination was carried out according to the above-described method with 4 replications. For drought stress, 20 mL of different concentrations (0, −0.001, −0.005, −0.1, −0.5 and −1 MPa) of polyethylene glycol (PEG) 6000 solution was used in each Petri dish, along with 10 seeds in each. The following temperatures of 5, 15, 20, and 25 °C with a light regime of 16 h have been used for the stress experiment. NaCl concentrations of 0, 25, 50, 100, 200, and 250 mmol for the salinity stress experiment were used according to the USDA 2020 table (https://www.usda.gov, accessed April 2022). Regression equations (MS Excel, Redmond, USA) with different models (exponential, logarithmic) which best fit the data were used.

RESULTS AND DISCUSSION

Dormancy loss. Dormancy loss in *B. sterilis* was significantly influenced by temperature, light regime,

Table 2. Analysis of variance for germination as affected by the interaction of temperature and light regime ($F = 5.1$, $P = 0.008$) of after-ripening *Bromus sterilis* seeds

Effect: regime	Effect: temperature	Percentage of germination (mean value)	Homogeneous groups (Tukey *HSD*, α = 0.05)
Light	10/20°C	56.0	a
	20°C	59.2	a
	10°C	62.5	a
Darkness	20°C	82.1	c
	10°C	91.9	b
	10/20°C	92.7	b

HSD – honestly significant difference

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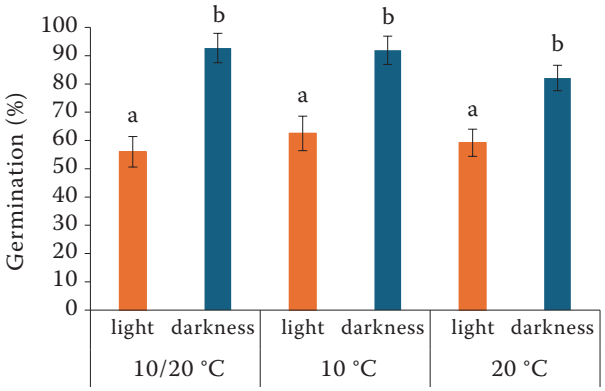

Figure 1. *Bromus sterilis* germination is affected by the interaction of temperature and light regime. Different letters indicate statistically significant differences according to the Tukey *HSD* (honestly significant difference) test ($P < 0.05$)

and the week of testing, indicating a complex germination response to varied environmental conditions. Seeds exposed to the light regime exhibited notably lower germination percentages consistently across all tested conditions (Table 2); seeds were found to have lower germination percentages under conditions of constant light compared to seeds germinated under constant and alternating light/dark regimes (Figure 1). Rapid dormancy loss occurred under alternating temperatures of 10/20 °C and dark conditions, with 99% germination in the first week (Figure 2A). Subsequent germination showed no significant differences over the next 5 weeks ($F = 0.386$, $P = 0.85$), but under light conditions, only 49% germinated in the first two weeks, increasing to 78% in the following four weeks (Figure 2B). At a constant 20 °C, germination progressed gradually over 6 weeks in both light regimes. In dark conditions, 90% of seeds germinated in the first week, increasing to 99% and 96% in the fifth and sixth weeks (Figure 2C). Under light, germination was 48% in the first weeks, gradually increasing to 89% and 84% in the fifth and sixth weeks (Figure 2D). Significant differences in germination were noted between the first and sixth weeks in the dark ($F = 3.51$, $P = 0.022$) and between the first four weeks and the last two weeks in light

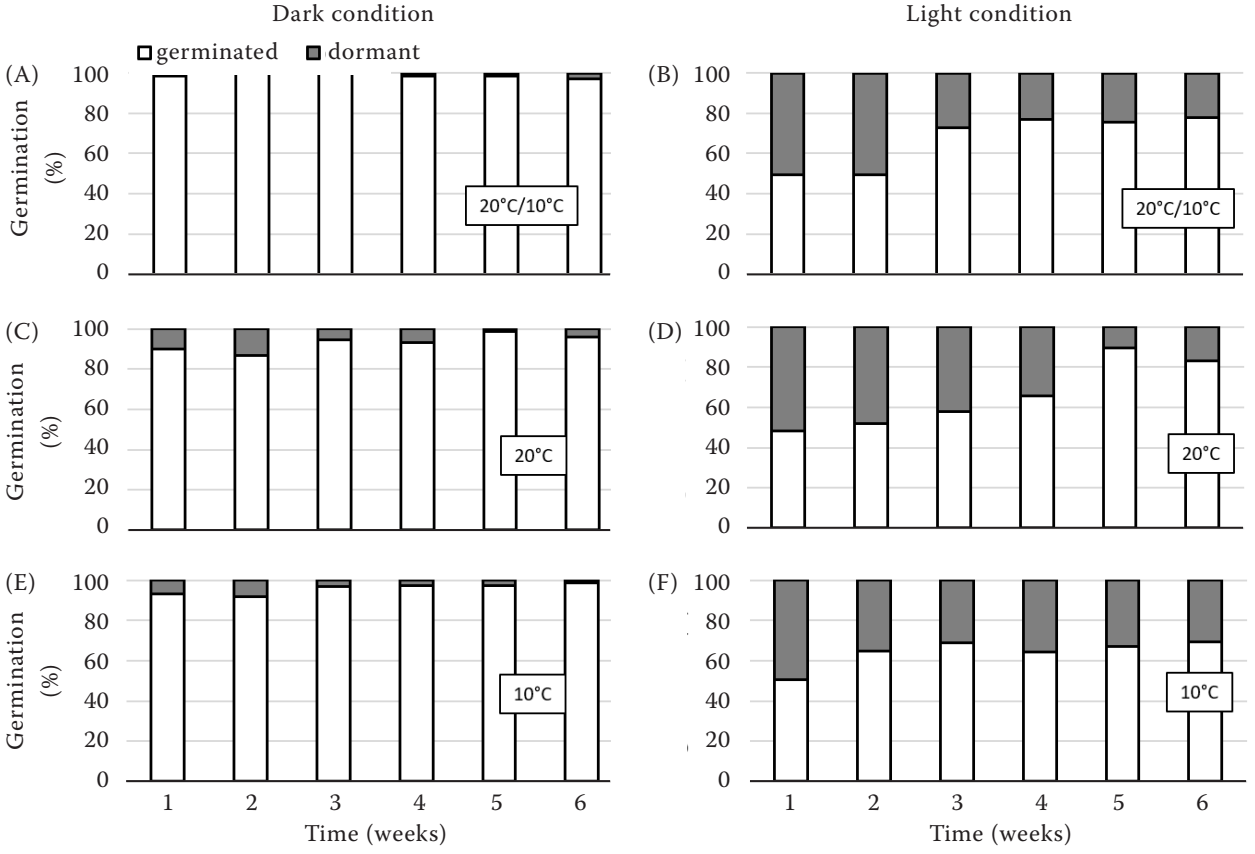

Figure 2. Percentage of germinated and dormant seeds of *Bromus sterilis* during after-ripening: (A) in darkness and alternating temperature of 20/10 °C; (B) in light and alternating temperature of 20/10 °C; (C) in darkness and 20 °C; (D) in light and 20 °C; (E) in darkness and 10 °C, and (F) in light and 10 °C

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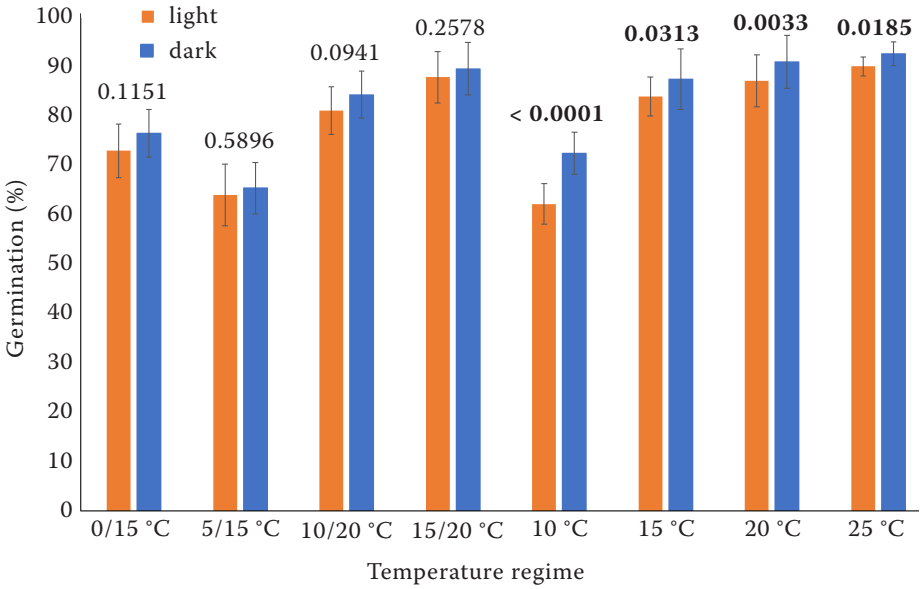

Figure 3. Germination as affected by temperature and light regime of fully matured non-dormant one-year-old *Bromus sterilis* seeds. Numbers calculation based on analysis of variance indicate *P*-value, bold values denote statistical significance at the 0.05 level

conditions (F = 8.68, P = 0.000). Under the lowest constant temperature (10 °C) and dark conditions, rapid dormancy loss occurred, with 93% germination in the first week, reaching 99% in the sixth week (Figure 2E). No significant difference was observed between the first two and the next four weeks. In light conditions, germination was 51% in the first week, gradually increasing to over 70% in the last two weeks (Figure 2F). Significant differences in germination were found between the first and sixth weeks under light conditions (F = 3.493, P = 0.022). The dormancy length for *B. sterilis* is often described as very short without specific duration (Peters et al. 2000). Andersson et al. (2002) showed a gradual increase in germination within 2–6 weeks after harvest, primarily influenced by light conditions. Alternating light temperature conditions resulted in a rapid dormancy loss, with over 90% of seeds germinating in the first week, consistent with findings by Peters et al. (2000). In a comparable experiment using an alternating temperature of 10/20 °C Froud-Williams et al. (1984) found 90% germination under dark conditions. Shallow incorporation of seeds in soil or coverage by plant residues, providing darkness and availability of soil moisture, may promote dormancy loss and seed germination. This strategy allows subsequent control measures, such as herbicide application/s or soil tillage operations, before sowing new winter crops.

Speed of germination. The populations of *B. sterilis* seeds tested in the study originated from similar environmental and farm conditions. The redundancy analysis showed the statistically insignificant effect of different locations characterised by ecological parameters (altitude, annual sum of precipitation, annual mean air temperature, latitude, longitude, WTS) on the occurrence of *B. sterilis* and/or dormancy and germination characteristics (Table 3). Therefore, all 10 populations were statistically evaluated together. After-ripening of freshly harvested *B. sterilis* seeds reduced germination time by over 50% within one week, particularly at 20 °C. One-year-old non-dormant seeds exhibited faster germination, especially in the dark. Temperature significantly influenced germination, favouring higher and faster rates in the dark compared to light, especially at constant temperatures. Germination of one-year-old seeds

Table 3. Analysis of variance for germination as affected by location (where *Bromus sterilis* was sampled), temperature and light regime of fully matured non-dormant one year old *B. sterilis* seeds and time required for germination of 50% (T_{50}) of all seeds

Effect (all data)	*df*	*F*	*P*
Regime	1	31.60	< **0.0001**
Temperature	7	117.81	< **0.0001**
Location	9	1.32	0.2745
Regime × temperature	7	2.13	**0.0376**
Regime × location	9	1.15	0.3227
Temperature × location	63	1.4	0.3863
Regime × temperature × location	63	0.54	0.9988

Bold number indicates significance at the 0.05 level; *df* – degree of freedom; *F*-value and probability at statistical significance level 0.05

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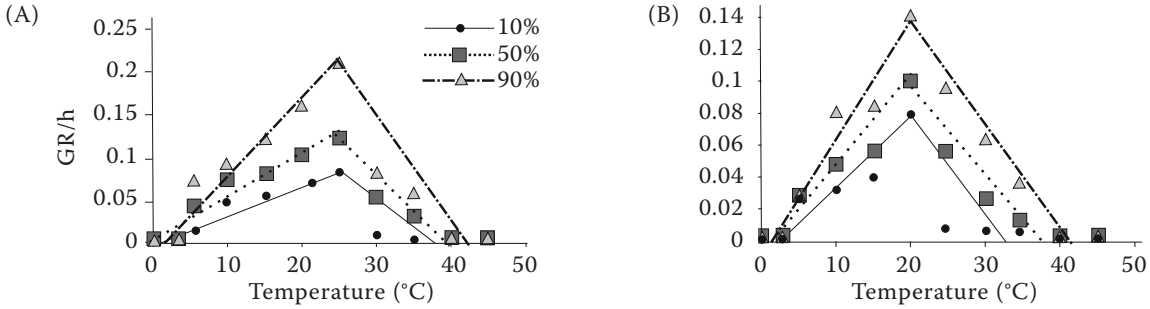

Figure 4. The germination rate of fully ripened *Bromus sterilis* seeds under different temperature treatments (A) with light and (B) under dark conditions based on germination rate (GR) for 10, 50 and 90%

was significantly affected by temperature, light, and their interaction. The fastest germination occurred at 25 °C (T_{50} = 1.14 days in the dark, 1.21 days in the light). At 20 °C and 15 °C, T_{50} values were 1.50 and 2.22 days in the light and 1.48 and 1.94 days in the dark. Under alternating temperatures, the quickest germination was observed at 15/20 °C under both light regimes (T_{50} = 1.64–1.74 days), while slower germination occurred at 10/20 °C (T_{50} > 2 days) under both light conditions (Table 4). Lower temperatures led to longer germination times, with 4–5 days needed for 50% germination. Under a constant temperature of 10 °C, a T_{50} = 4.41 days was found with light and 4.28 days under dark conditions. Faster germination was observed at 0/15 °C compared to 5/15 °C. For most tested lower temperatures under both light regimes, full germination was achieved within 4–8 days. This study marks the first comprehensive examination of *B. sterilis* germination dynamics during the after-ripening period. Freshly harvested seeds experienced brief germination inhibition, with a subsequent decrease in germination time after 6 weeks, akin to after-ripened seeds. After-ripened seeds exhibited exceptionally rapid germination, slightly slower under light, likely due to the inhibitory effect of phytochrome red/far-red photoreceptor (Bewley et al. 2013). The shortest time for 50% germination of *B. sterilis* seeds was at 25 °C and 15/20 °C (~1 day), while lower temperatures (10 °C, 0/15 °C, 5/15 °C) increased T_{50} to 3–5 days. Chilling temperatures (< 5 °C) in alternating conditions suggested a stimulation effect on the germination rate at higher temperatures. A significant finding is that low night temperatures only marginally increased germination time for a few days. Comparing our data with Hulbert's (1955) testing of one-year-old seeds of *Bromus commutatus*, our study reveals that *B. sterilis* seeds from Central Europe can germinate much more rapidly. On the other hand, it is documented that at the optimum temperature of 20/30 °C, fully after-ripened seeds of *B. tectorum* germinated with a mean T_{50} of 1.6 days for 21 populations from a wide array of habitats (Meyer et al. 1997). *B. sterilis's* fast germination suggests early crop competition, potentially exploited

Table 4. The percentage of germinated *Bromus sterilis* seeds assessed under various temperature and regime conditions through analysis of variance

Effect: temperature and regime	*F*	*P*	% of germinated seeds		T_{50}	
			under light[aa]	under dark[aa]	under light[ab]	under dark[ab]
0/15 °C	2.48	0.1155	72.4[c]	75.9[c]	4.2 (0.602)	3.57 (0.175)
5/15 °C	0.29	0.5896	63.5[a]	64.9[a]	5.33 (0.787)	5.16 (0.129)
10/20 °C	2.81	0.0941	80.5[d]	83.7[d]	2.74 (0.179)	2.51 (0.748)
15/20 °C	1.28	0.2578	87.2[f]	88.9[f]	1.74 (0.259)	1.64 (0.421)
10 °C	20.8	< **0.0001**	61.7[a]	71.9[b]	4.41 (0.138)	4.28 (0.234)
15 °C	4.65	**0.0313**	83.3[d]	86.8[e]	2.22 (0.099)	1.94 (0.611)
20 °C	8.65	**0.0033**	86.5[e]	90.3[g]	1.5 (0.124)	1.48 (0.147)
25 °C	5.57	**0.0185**	89.4[f]	91.9[g]	1.21 (0.347)	1.14 (0.452)

[aa]numbers are means of germination over locations; different letters have statistically significant differences according to Tukey *HSD* (honestly significant difference) test (P < 0.05); [ab]lack-of-fit test value is presented in parentheses

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through post-harvest herbicide treatments for better weed control between crop rotations.

Temperature optimum. Germination rates (GR = 1/tg) showed a linear increase with temperatures above the calculated common base temperature (T_b; 3 °C), reaching up to 25 °C in light and 20 °C in dark conditions (Figure 4). No germination occurred at very low (0 °C) or very high temperatures (40 °C and 45 °C). *B. sterilis* seeds exhibited germination across a wide temperature range of 5–35 °C, with the highest rate at 25 °C. In contrast to Guillemin et al. (2012), who reported no germination at 35 °C, our study recorded a 65–68% germination rate. Hilton (1984) observed optimal germination between 11 °C and 23 °C, with Pfr phytochrome inhibition causing delayed germination outside this range. Our results, showing a broad germination temperature range, underscore *B. sterilis*' adaptability and its ability to germinate across various temperatures common in the region, from summer to late autumn. This wide germination range indicates the potential for *B. sterilis* to pose significant competition to winter crops, unlike many winter cereals in Europe that exhibit a narrow germination range (Olesen et al. 2012).

Stress response. The findings from a germination test of pyroxsulam (an ALS-inhibiting herbicide) resistant and susceptible biotypes of *B. sterilis*, conducted under salt and drought stress conditions, are illustrated as the percentage of germination loss (refer to Figure 5). This study marks the initial report documenting the germination ecology of herbicide-resistant *B. sterilis* under stress conditions. Significant temperature-dependent differences in germination were observed between resistant (R) and susceptible (S) biotypes for both stress conditions. The R biotype demonstrated germination resilience under high salinity and drought compared to S biotypes, albeit with decreased percentages below 25 °C. A sigmoid

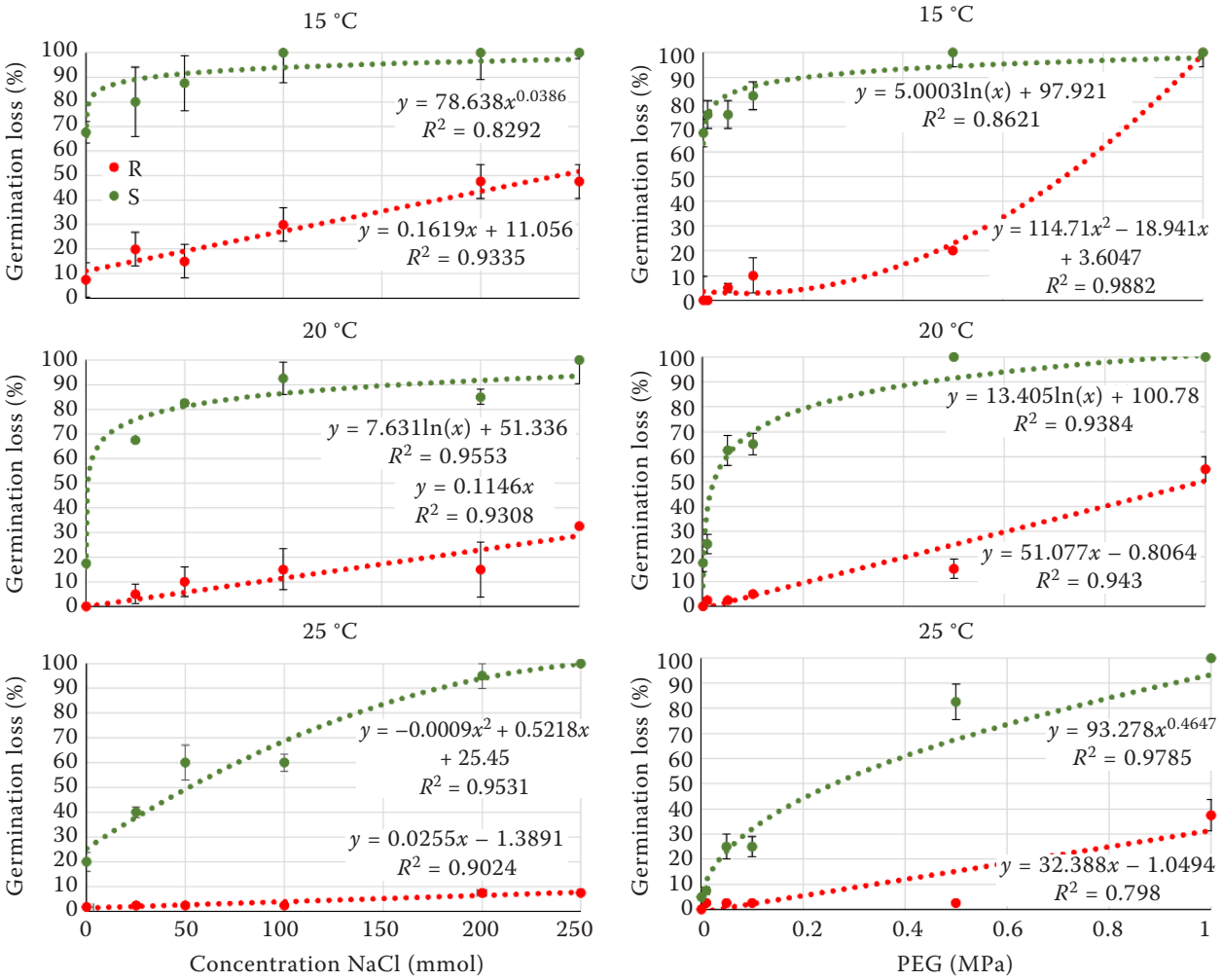

Figure 5. Germination loss percentage of *Bromus sterilis* resistant (R) and susceptible (S) biotypes under salt and drought stress. PEG - polyethylene glycol

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response was noted with increasing NaCl and PEG concentrations, with the highest stress conditions rendering negligible germination in S biotypes. In contrast, R biotypes exhibited over 50% germination in the maximum NaCl concentration and optimal germination at 25 °C in the maximum PEG concentration. Our findings align with previous reports that *Bromus* populations can germinate under low water potential but with decreased percentages below 25 °C (Valičková et al. 2017). Our observations suggest systemic acquired herbicide resistance with pleiotropic effects, indicating fitness benefits related to stress adaptation (Dyer 2018). Contrary to the often-hypothesised fitness cost of herbicide resistance, this study did not observe such costs in the R biotype. Previous studies reported key mechanisms, such as ALS gene overexpression and cytochrome P450-mediated enhanced metabolism, contributing to pyroxsulam resistance in this R biotype (Sen et al. 2021). Similar findings in glyphosate-resistant *Eleusine indica* and weedy rice highlighted overexpression of target genes as contributors to fitness benefits (Nam et al. 2020, Li et al. 2021). Additionally, non-target-site resistance in *Apera spica-venti* resulted in early germination and flowering, demonstrating fitness benefits (Babineau et al. 2017). These results confirm that overexpression of target genes and cytochrome P450 contributes to fitness benefits in the R *B. sterilis* under stress conditions, potentially aiding quicker germination in adverse soil conditions. The absence of fitness costs (such as reduced competitive ability, seed production, etc.) may contribute to the widespread resistance observed.

In conclusion, Czech *B. sterilis* seeds have a short and innate primary dormancy that can disappear within a few weeks in favourable conditions (darkness and 10/20 °C). Darkness is the key factor for dormancy loss, while light inhibits germination, with only 65% germinating across all temperature regimes. Non-dormant *B. sterilis* seeds can quickly germinate at a wide range of temperatures, taking 6–8 days for full germination. Under stress conditions, germination was affected by the temperature, and germination loss percentages were significant between the R and S biotypes as a fitness benefit. The dormancy and germination behaviour of *B. sterilis* resembled the results published earlier for maritime European populations but had a higher optimal germination temperature than in all studies published before. This suggests that it can be an indicator of species adaptation to continental summers and climate warming.

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