

Modeling wheat and triticale winter hardiness under current and predicted winter scenarios for Central Europe: A focus on deacclimation

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ABSTRACT

Winter hardiness depends on the ability of plants to tolerate a wide spectrum of environmental stresses, which can be affected by climate change in complex ways. Here, empirical Partial Least Squares Regression (PLSS) models of winter survival (WS) of winter wheat (*Triticum aestivum* L.) and triticale (*Triticosecale* × Wittmack) were created using data from six years of field experiments at multiple locations throughout Poland. These included 553 winter wheat and 155 triticale accessions. Our aims were to: 1) predict WS on the basis of meteorological data; 2) identify the most critical weather events affecting WS of winter wheat and triticale under Polish conditions; and 3) predict WS for the simulated winters of 2040, 2060 and 2080 under climate change scenarios RCP2.6, RCP4.5, RCP6.0 and RCP8.5 for the experimental site with the lowest mean WS rate during the field experiments. The empirical models showed a high R^2 for winter wheat (0.751), and a low R^2 for winter triticale (0.160), because of the low winter damage to triticale observed during the experiments. The key climate factors affecting WS varied between species. Winter wheat was affected by winter severity, the number of freezing-thawing cycles, the thermal vegetation index and the freezing index in various winter months. Triticale was affected by late winter ice encasement and high numbers of freeze-thaw events. The predictions indicated that the WS of both winter wheat and triticale may decrease in the future, especially when more extreme climate change scenarios were considered. The main issue will be cold deacclimation connected with climate warming which will be more important for WS than the general increase in minimum winter temperatures. This finding indicates that deacclimation tolerance should be included in wheat and triticale breeding programs as a trait crucial for WS under future winters, at least in Central Europe.

1. Introduction

Winter hardiness is the ability of plants to survive the winter. It depends on the plant's potential to tolerate a wide spectrum of environmental stresses, such as freezing, rapidly changing temperatures, low light intensity, desiccation, wind, snow cover, ice-encasement, or various winter-related diseases (Rapacz et al., 2014). Climate change is a major challenge for the world economy, especially for the agricultural sector, where climate conditions strongly and directly influence crop yields. Thus, knowledge about the effects of climate change on crop yields and the plant biology mechanisms underlying crop yields are crucial for adapting crops to potentially greater climate variability.

An increase in the surface temperature of the Earth indicates a lower risk of crop exposure to extremely low temperatures. However, the risk

of winter damage to crops may not decrease proportionally because of the complex interactions among environmental factors (Rapacz et al., 2014). For example, the frequency, degree and length of extreme winter warming events leading to snowmelt may increase, especially in locations experiencing a transition from cold to warm winter climatic conditions (Johansson et al., 2011; Shabbar and Bonsal, 2003). This may increase the risk of freezing injury in crops that are not covered with snow. Future climate projections suggest that cold acclimation will occur later in the autumn, which may affect energy partitioning between elongation growth, the accumulation of organic reserves and cold acclimation (Dalmansdottir et al., 2017). Also, temporary warming during winter may cause decrease in snow cover and deacclimation, eventually reducing winter hardiness (Rapacz et al., 2014; Rapacz et al., 2017). All these factors, often with contradictory effects on winter

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survival (WS), make plant overwintering viability under future climates an open question (Rapacz et al., 2014).

Research on the impact of projected climate change on the overwintering of major agricultural crops is limited, especially in Central Europe, including Poland which lies on the border between temperate and continental climates. In Poland, the cold winter climate is currently a major limiting factor in crop production. In common wheat, the major agricultural crop in the country, yield reduction owing to unfavorable winter conditions may, in extreme cases, exceed 32% (representing a loss of approximately 6 billion Euros) (GUS, 2012). Basic research on winter hardiness has focused on freezing tolerance and the mechanisms of cold acclimation with decreasing temperature (Gusta and Wisniewski, 2013). The effects of different winter stress conditions on winter hardiness have not been fully identified.

Simulation models are essential tools for understanding climate change and its impact on vegetation, including agricultural crops. Each model provides a unique representation of plant processes in the form of mathematical functions. These models often simulate important features of the micro-climate around the plant. For example, a large number of process-based models are available that simulate the yield-building processes in winter common wheat e.g., the eight models that were compared for simulating wheat under contrasting conditions in Europe (Palosuo et al., 2011). Some of existing models as CropSyst (Stockle et al., 1994) and CERES-Wheat (Ritchie et al., 1988) consider WS but the models do not explicitly allow for predicting WS. This limits their usefulness for predicting the impact of climate change on crops in regions like Poland where WS is a key issue. Estimating the risk of winter injury in crops under climate change is limited to a fairly simple approach (Trnka et al., 2011, 2014), where the risk of frost injury in winter wheat is related to the number of days with a daily minimum temperature below a fixed freezing tolerance level (-20°C) on the days without a continuous snow cover. In those studies, weather data were processed through a snow cover model, thus accounting for the insulating effect of snow against frost exposure. However, this approach ignores the fact that in reality the freezing tolerance of plants varies greatly over the winter, being affected by a range of external and internal factors. Other, most comprehensive approaches to estimate the risk of winter injury in winter cereals were also developed but have not been used for the WS predictions under climate change (Bergjord et al., 2008; Bergjord Olsen et al. 2018; Fowler et al., 1999; Persson et al., 2017).

A number of researchers have modelled the freezing tolerance or WS of winter plants of agricultural importance. For example, a well-established model, FROSTOL, (Bergjord et al., 2008), calculates changes in the freezing tolerance of winter wheat (the temperature at which 50% of plants were killed — LT_{50}) as a function of temperatures from sowing onwards. The FROSTOL model was further validated for winter hardiness for two winter seasons in 20 field experiments with four cultivars of known LT_{50} (Bergjord Olsen et al., 2018). However, this model was not developed to predict the WS under climate change. In another model developed for wheat for the same climatic zone, factors such as the presence of snow cover and the occurrence of freezing-thawing cycles were also considered (Vico et al., 2014). Another approach in WS modeling was presented by Waalen et al. (2013). In this study PPLS regression using a set of agrometeorological indices from autumn and winter was successfully used in WS modeling of oilseed rape and turnip oilseed rape (Waalen et al., 2013). A very similar approach has been used in our work because this approach makes it possible both to show what the impact of particular factors in the course of autumn and winter weather is on WS and at the same time it is possible to calculate the values of the same agrometeorological indices for climate change scenarios and thus predict the future changes in WS.

Most projections of future climate conditions, for example, those provided by the IPCC, operate on a relatively coarse spatial and temporal resolution. Typically, they provide annual or seasonal values for temperature and rainfall for large regions (Bowyer et al., 2014). To

assess the consequences of climate change for the WS of crops, regional data needs to be spatially and temporally downscaled, as WS mechanisms operate at a field level and are largely influenced by the day-to-day variations in many weather variables (eg. extreme freezing, the presence of snow cover, temperature fluctuations causing de-acclimation). The studies predicting the future changes in WS are rare and have not been systematically carried out for agricultural crops in Poland. However, some work in this field has been done for grasslands in Northern Europe (Höglind et al., 2013; Thorsen and Höglind, 2010). In these studies, simulations of micro-climatic conditions were combined with simulations of frost and ice-encasement tolerance to assess the risk of frost- and ice-related damage under future climate conditions.

The aim of our study was to build empirical models linking different agrometeorological indices characterizing winter microclimate in the experimental fields in Poland with WS of two cereal species – winter common wheat (*Triticum aestivum* L.) and triticale (*Triticosecale* x Wittmack.). These models suggest various winter microclimate characteristics most important for WS during the years of the study and were used to project the future WS at the selected experimental point by including simulated microclimate data in the empirical models to assess the future risks for WS, with the hypothesis that deacclimation during winter will seriously affect the risk of WS under predicted climate change.

2. Material and methods

2.1. The development of winter hardiness models

To fill the existing gaps in knowledge concerning the present and future risks for the winter hardiness of cereals in Central Europe, we built empirical models of winter hardiness based on six years of multiple field studies in more than ten environmental conditions in Poland. We looked at the winter hardiness of winter common wheat (*Triticum aestivum* L.) as well as triticale (*Triticosecale* x Wittmack.). Wheat was selected because of its economic importance and triticale, because it is winter hardy to a level where winter damage is economically unimportant. The models were built on the basis of previous studies (Waalen et al., 2013) with some important modifications.

2.1.1. Field studies of winter hardiness

The empirical models were based on a 6-year experiment (2013–2019) performed in 11 (seven for wheat and seven for triticale) locations in Poland (Fig. 1): Borowo (52.115°N , 16.777°E , elevation (elev.) 77 m), Dębina (54.130°N , 19.032°E , elev. -1 m), Kobierzyce (50.973°N , 16.948°E , elev. 133 m), Krzemlin (53.072°N , 14.872°E , elev. 80 m), Matyszyn (52.744°N , 15.174°E , elev. 77 m), Nagradowice (52.318°N , 17.145°E , elev. 85 m), Laski (51.810°N , 21.141°E , elev. 125 m), Polanowice (50.203°N , 20.085°E , elev. 259 m), Smolice (51.699°N , 17.184°E , elev. 107 m), Strzelce (52.317°N , 19.405°E , elev. 123 m), and Szelejewo (51.859°N , 17.159°E , elev. 125 m).

In the assessment of winter hardiness, hundreds of accessions (533 and 155 for wheat and triticale, respectively) were studied. The set of accessions was different between the years with common standard varieties (wheat: Ozon, KWS Lochow; Patras, Saaten Union; triticale: Fredro, Danko Plant Breeding; Meloman, Strzelce Plant Breeding). The remainder of the accessions originated from Polish breeding companies (Danko Plant Breeding, Choryń, Poland; Małopolska Plant Breeding, Kraków, Poland; Smolice Plant Breeding, Smolice, Poland; Strzelce Plant Breeding, Strzelce, Poland; Poznań Plant Breeders, Tulce, Poland) and were advanced breeding materials (F₈–F₁₀). The complete list of accession used is available on request from the corresponding author.

Plants of both species were sown in 10 m^2 experimental plots at a density of 400 seeds per m^2 with three replicates using a fully randomized block design. Winter survival was estimated on the basis of visual observations of plant condition after winter using a score ranging from 1 to 9 (Rapacz et al., 2015), where 9 mean that 0%–5% of plants were winter-killed; 8: 5–15%; 7: 15–25%; 6: 25–40%; 5: 40–60%; 4:

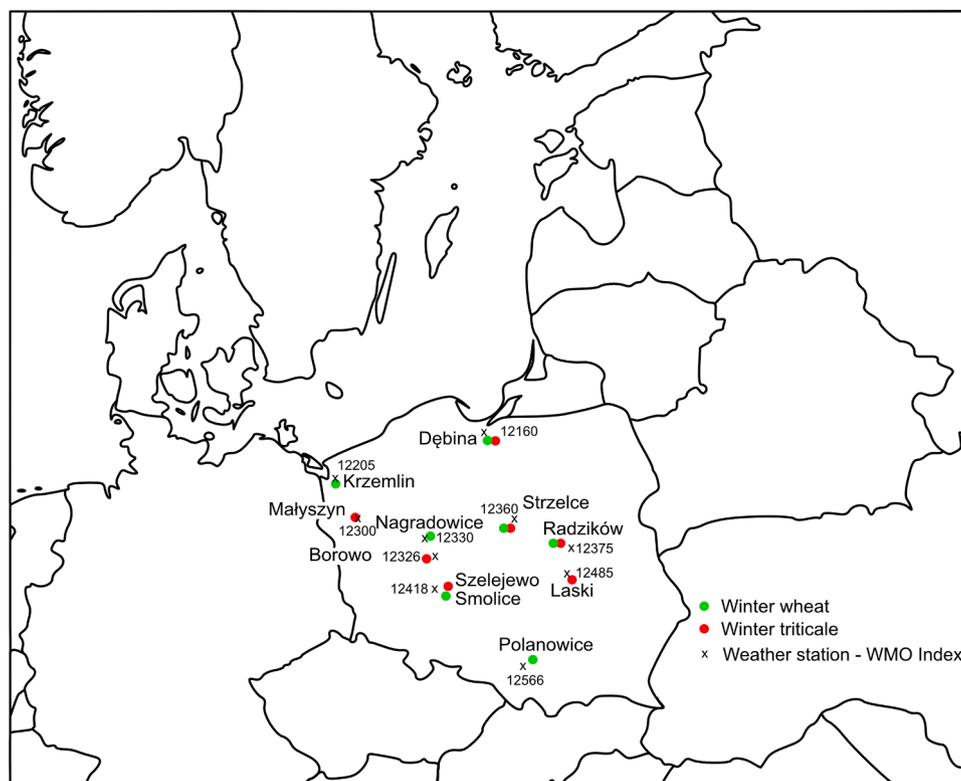


Fig. 1. Location of field trials and weather stations used for the development of the empirical models of winter survival (WS) of wheat and triticale in Poland.

60–75%; 3: 75–85%; 2: 85–95%; and 1: 95–100%. Observations were carried out between 10 and 14 days after the start of cereals vegetation defined as the beginning of regrowth, when old, undamaged leaves straighten up and become firm, and new leaves appear on damaged plants (Najewski et al., 2013). This is usually observed at times when the maximum daily air temperature remains above 5 °C for several days.

The weather data used for the model development were taken from SYNOP available at: <http://www.ogimet.com> (Valor and López, 2016). SYNOP data were used because of missing data and a lack of standardization in direct field observations as explained in Rapacz et al. (2017). The World Meteorological Organization indices of the weather stations are shown in Fig. 1. The data from SYNOP were adjusted for local microclimate conditions when necessary to accurately document critical minimum temperatures and snow cover depth at this time were measured directly in the experimental fields.

2.1.2. Weather data processing

Table 1 presents the list of weather variables calculated on the basis of meteorological data from 11 locations (taken from SYNOP). Agroclimatic indices were calculated on a monthly bases except for heat units (twice during the winter) and DIs (before the maximum day temperature drops below 0 °C). All agroclimatic indices were normalized by dividing by their own standard deviation.

The agroclimatic indices were selected on the basis of similar model developed before for oilseed (Waaen et al., 2013). Additionally, due to increasing problem of the role of deacclimation tolerance in the WS of wheat and triticale observed in Poland de-acclimation indices (DIs) which showed the link between the temperature proceeding freezing events in winter and the cold acclimation/deacclimation status of the plants (Rapacz et al., 2017) were included in our empirical models.

2.1.3. PLSR regression models

PLSR (named also PPLS; Partial Least Squares Regression) is a multivariate regression method especially suitable for modeling if there are many, possibly correlated, predictor variables (colinearity between

variables), and relatively few samples. The PLSR models were developed using the R package ‘pls’ v.2.7–3 (Mevik et al., 2020). In brief, observed WS, measured for 2214 and 559 individual cases (accession × location) of wheat and triticale, respectively, and weather variables (73 and 68 for wheat and triticale) were used as possibly correlated predictor variables. Both data sets were randomly sampled into training (1500 and 400 cases) and testing (714 and 199 cases) data sets. The PLS models were based on training datasets. The optimum number of components to be incorporated in the model was selected using leave-one-out cross-validation so that the cross-validation RMSEP was minimized. For consistency, the selection of the optimal number of components was done on the basis of both a one-sigma heuristic (Hastie et al., 2009) and a permutation approach (van der Voet, 1994). The final models were fitted using an optimal number of components. Models were verified by predicting WS for the testing dataset and comparing the predicted and measured values. Pearson correlations and linear regressions were calculated using the R package ‘stat’ v.3.6.2. The importance of variables was evaluated using the VIP and the vector of RC (β), calculated with the R package ‘plsVarSel’ v.0.9.6 (Mehmood et al., 2012). The RMSEP (root mean squared error of prediction) values plotted against the component numbers showed a gradual decline, indicating a good model performance, without the risk of bias due to high variance (Faber and Rajkó, 2007). The optimal number of components, based on low RMSEP values without the loss of predictive power, was set to 10 for wheat and two for triticale. The predictive ability of the PLS regression models was evaluated using testing data sets that were not used for model development. The optimal number of components, based on low RMSEP values without the loss of predictive power, was set to 10 for wheat and two for triticale. The predictive ability of the PLS regression models was evaluated using testing data sets that were not used for model development.

2.2. Modeling wheat and triticale winter hardiness under climate change

To simulate the changes in winter hardiness under climate change

Table 1
Weather variables included in the PPLS analysis.

Weather variable	Calculation method	Reference
Deacclimation index based on maximum daytime temperature (DI_{Tmax})	$DI_{Tmax} = (\sum_{n=-14}^{-1} (T_{max} - 5) \geq 0) - (\sum_{n=-14}^{-1} (5 - T_{max}) > 0)$ 5 °C threshold was assumed between acclimation/deacclimation (calculated during the 2-week period before the maximum day temperature dropped below 0 °C)	Rapacz et al., 2017
Deacclimation index based on minimum daytime temperature (DI_{Tmin})	$DI_{Tmin} = (\sum_{n=-14}^{-1} (T_{min} - 5) \geq 0) - (\sum_{n=-14}^{-1} (5 - T_{min}) > 0)$ 5 °C threshold was assumed between acclimation/deacclimation (calculated during the 2-week period before the maximum day temperature dropped below 0 °C)	Rapacz et al., 2017
Heat units	Heat units = $\sum [(T_{max} + \frac{T_{min}}{2}) - T_{base}]$, $T_{base} = 3$ °C, days with a $T_{min} < 3$ °C are not included (calculated twice: October–November, December–March)	Waaen et al., 2013
Mean air temperature	Arithmetic mean of the mean daily air temperature (calculated monthly October–March)	Waaen et al., 2013
Maximum air temperature	The highest air temperature (calculated monthly October–March)	Waaen et al., 2013
Minimum air temperature	The lowest air temperature (calculated monthly October–March)	Waaen et al., 2013
Number of freeze-thaw events	Freeze thaw events were counted when the mean daily temperature dropped below 0 °C (calculated monthly November–March)	Waaen et al., 2013
Monthly sum of the mean daily air temperature	(calculated monthly October–March)	Waaen et al., 2013
Number of days with minimum air temperature < -5 °C	(calculated monthly October–March)	Waaen et al., 2013
Freezing index	Freezing index = $\sum T_{mean}$, days with a $T_{mean} > 0$ °C are not included, T_{mean} mean daily air temperature (calculated monthly November–March)	Waaen et al., 2013
Freezing period	Number of days with $T_{mean} < 0$ °C (calculated monthly November–March)	Waaen et al., 2013
Intensity of winter	Intensity of winter = freezing index / freezing period (calculated monthly November–March)	Waaen et al., 2013
Mean snow depth	(calculated monthly November–March)	Waaen et al., 2013
Number of days with snow cover	(calculated monthly November–March)	Waaen et al., 2013
Number of days with ice enhancement	(calculated monthly November–March)	Waaen et al., 2013

the experimental site in Dębina was chosen because it had the lowest mean WS of winter wheat during the experiment and because at this site both species were assessed for winter hardiness (in the case of triticale, the mean survival rate was lower in Laski, but wheat was not tested at that site).

2.2.1. Weather data generation

To model wheat and triticale winter hardiness under climate change, generated meteorological data were used according to climate change scenarios based on RCPs. The choice of RCP scenarios in relation to the SRES, including the A1B scenario most frequently used in Poland. RCP scenarios were better at describing climate changes in the earlier period (using data from the 20th century and the beginning of the 21st century) than SRES scenarios, which allows us to assume that projections to 2080

will also be better (van Vuuren et al., 2011). This fact follows from the IPCC report (2013), which changed the philosophy of model construction by adopting RCP scenarios.

The climatic data that formed the baseline for the study were a series of observations in the months October–February for the years 1999–2020 from the weather station at Dębina (54.130° N, 19.032° E, 1 m above sea level). These data were used to generate a 500-year series of minimum and maximum temperatures for each of the RCP2.6, RCP4.5, RCP6.0 and RCP8.5 scenarios and for the forecast horizon for 2040, 2060 and 2080 and for 2010, the reference year of the study (mid-year of the period 1999–2020). The RCP2.6, RCP4.5, RCP6.0 and RCP8.5 scenarios, according to new models of the Earth system including CH₄ and N₂O gasses, correspond to predicted CO₂ concentrations for 2100 of 475 ppm, 630 ppm, 800 ppm and 1313 ppm respectively (IPCC, 2013).

The WGENK model (Kuchar, 2004) was used to generate the weather data, which is a modification of the commonly used WGEN model (Richardson and Wright, 1984).

2.2.2. Simulation of field survival data

The appropriate selection of the variables used in model development reduces the analysis time and facilitates the interpretation of the results. The suggested cut-off for the importance of variables, expressed as a VIP value, is $VIP > 1$; however, a threshold between 0.83 and 1.21 is acceptable (Chong and Jun, 2005). Generally, the VIP values for most variables were above 0.83. However, the weather variables related to the rainfall or snowfall in each month showed low RC values. Additionally, these data were not used to calculate other weather variables with relatively high VIP and RC values, e.g., DI_{Tmax} and DI_{Tmean} . Therefore, we repeated the PLSR modeling, described in Section 2.1.3, using data sets without weather variables related to rainfall/snowfall. The comparison of measured and predicted WS obtained from the testing data sets for both species were satisfactory, thus only temperature data were simulated. The final set of 54 weather variables was calculated as described in Section 2.1.2, using a personal Python script (Supplementary File 1). The fitted models for wheat and triticale were used to predict future WS based on simulated variables. Before predicting the future WS under different climate scenarios, additional validation of models was done using a simulated data set, containing current temperatures. To keep the predicted WS consistent with the scale used for measured data, all predicted values were normalized by multiplying the value by the calculated factor $meanWS_{measured}/meanWS_{predicted}$ (Supplementary Fig. 2). The maximum value of measured WS was nine, reflecting 0–5% of winter-killed plants. However, the simulated weather data included combinations that were not observed in the experimental data, that were used for model development. Therefore, a combination of variables that favorably affects WS may result in values greater than 9, although any value above 9 does not reflect better performance of plants. Those, predicted WS values for each species and scenario were transformed so that values higher than nine were replaced by the maximum.

3. Results

3.1. The development of empirical models of winter survival for wheat and triticale

In the case of winter wheat, the predictive power of the model was high ($R^2 = 0.75$; Fig. 2). The correlation between measured and predicted WS values of triticale suggested a lower predictive power of the model ($R^2 = 0.16$, Fig. 3). This approach of model validation required a large number of samples for both training and evaluation. The low R^2 for triticale was likely because of the use of a low number of different cases (accession \times location) and also a high rate of survival, which meant that in case of triticale 14% of plants had $WS < 6$, while in case of triticale number of plants with low rate of survival was higher (21%). However, the predicted values were within the range observed for the measured

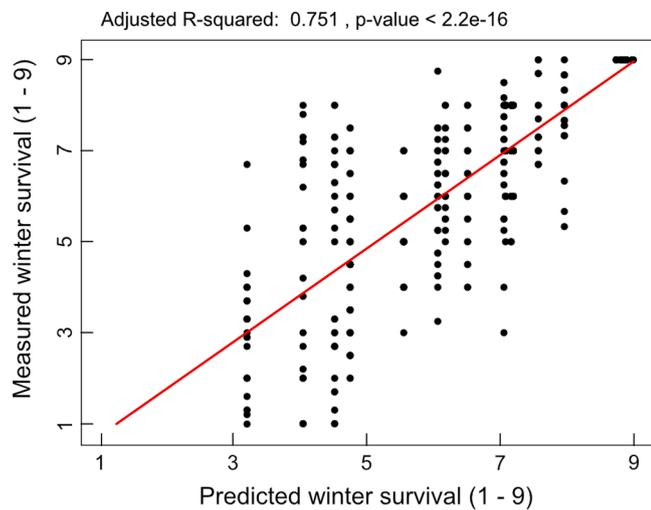


Fig. 2. Predicted vs. measured winter survival (WS) of winter wheat using linear regression. The model was developed using 73 variables and 10 components. In WS score, 9 means that 0%–5% of plants were winter-killed and 1: 95–100%.

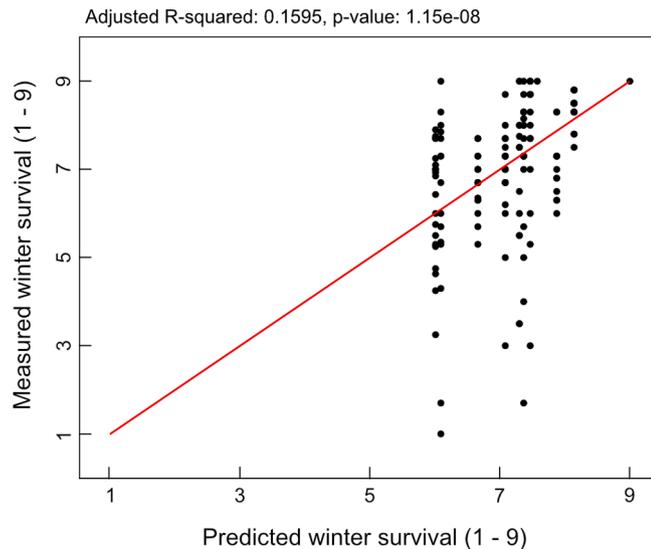


Fig. 3. Predicted vs. measured winter survival (WS) of winter triticale using linear regression. The model was developed using 68 variables and two components. In WS score, 9 means that 0%–5% of plants were winter-killed and 1: 95–100%.

values and the Welch two-sample *t*-test (*p*-value = 0.5384) supported the hypothesis that there was no difference between the means of measured and predicted values. Therefore, both models were used to predict WS on the basis of the simulated data.

The initial PLS investigation was focused on evaluating which weather variables had the strongest impact on WS. The variable importance was reflected by two commonly accepted measures, VIP that shows the contribution of each variable according to the variance explained by each PLS component, and the vector of regression coefficients (RCβ) which is a measure of the association between each variable and the response. The calculated values shown in Table 2 were also used for variable selection to develop the final models to predict the future impact of temperatures on WS, described below.

Table 2

Importance of each meteorological factor used in the PLS model, reflected by VIP and the regression coefficient (RCβ) of winter wheat and triticale. VIP values above 1 are in bold.

Weather variables	Wheat		Triticale	
	VIP	RC(β)	VIP	RC(β)
DI T _{max}	1.03	-0.28	0.66	-0.02
DI T _{mean}	1.21	-0.37	0.86	-0.03
Heat units Oct.–Nov.	1.01	0.06	0.78	0.00
Heat units Dec.–Mar.	1.38	-0.33	0.29	0.00
Mean air temperature [°C] (Oct.)	1.07	0.00	1.08	0.01
Mean air temperature [°C] (Nov.)	0.73	-0.06	0.13	0.00
Mean air temperature [°C] (Dec.)	0.92	-0.10	0.48	-0.01
Mean air temperature [°C] (Jan.)	1.10	0.16	0.86	-0.01
Mean air temperature [°C] (Feb.)	0.80	0.08	-	-
Mean air temperature [°C] (Mar.)	0.06	-0.01	1.45	0.03
Maximum air temperature [°C] (Oct.)	0.90	-0.14	0.48	0.00
Maximum air temperature [°C] (Nov.)	0.83	-0.03	0.44	-0.01
Maximum air temperature [°C] (Dec.)	0.99	0.22	0.23	0.00
Maximum air temperature [°C] (Jan.)	0.88	0.05	0.70	0.01
Maximum air temperature [°C] (Feb.)	0.82	0.08	1.79	0.05
Maximum air temperature [°C] (Mar.)	0.52	-0.02	1.45	0.02
Minimum air temperature [°C] (Oct.)	1.16	-0.12	0.59	0.02
Minimum air temperature [°C] (Nov.)	1.15	0.11	0.27	0.01
Minimum air temperature [°C] (Dec.)	1.12	0.14	1.03	0.03
Minimum air temperature [°C] (Jan.)	0.95	0.02	1.20	-0.04
Minimum air temperature [°C] (Feb.)	1.20	0.21	1.75	-0.05
Minimum air temperature [°C] (Mar.)	0.73	0.07	0.68	0.00
Number of freeze thaw events (Nov.)	0.89	0.07	0.93	-0.02
Number of freeze thaw events (Dec.)	1.06	0.31	1.14	0.03
Number of freeze thaw events (Jan.)	0.68	0.06	1.67	0.04
Number of freeze thaw events (Feb.)	1.04	-0.07	0.77	-0.02
Number of freeze thaw events (Mar.)	0.78	-0.06	1.88	-0.06
Sum of the mean daily air temp [°C] (Oct.)	1.07	0.02	1.05	0.01
Sum of the mean daily air temp [°C] (Nov.)	0.73	-0.02	1.21	-0.04
Sum of the mean daily air temp [°C] (Dec.)	0.90	-0.09	0.45	0.00
Sum of the mean daily air temp [°C] (Jan.)	1.11	0.17	0.85	-0.01
Sum of the mean daily air temp [°C] (Feb.)	0.80	0.06	0.43	0.01
Sum of the mean daily air temp [°C] (Mar.)	0.05	0.00	1.42	0.03
Days with min. air temp < -5 °C (Oct.)	1.36	0.05	-	-
Days with min. air temp < -5 °C (Nov.)	1.05	0.05	1.27	0.04
Days with min. air temp < -5 °C (Dec.)	1.03	0.09	1.78	-0.05
Days with min. air temp < -5 °C (Jan.)	1.04	-0.07	0.66	0.00
Days with min. air temp < -5 °C (Feb.)	0.91	0.17	1.35	0.04
Days with min. air temp < -5 °C (Mar.)	0.71	-0.11	0.56	0.01
Freezing index (Nov.)	1.14	0.27	0.48	-0.01
Freezing index (Dec.)	1.03	-0.11	1.26	0.04
Freezing index (Jan.)	1.15	0.22	0.78	-0.01
Freezing index (Feb.)	0.66	0.08	0.82	-0.02
Freezing index (Mar.)	0.65	0.11	0.62	-0.02
Freezing period [days] (Nov.)	0.97	-0.05	0.58	0.00
Freezing period [days] (Dec.)	0.93	0.09	0.54	-0.02
Freezing period [days] (Jan.)	1.12	-0.11	0.84	0.01
Freezing period [days] (Feb.)	0.88	0.00	0.08	0.00
Freezing period [days] (Mar.)	0.59	-0.11	0.53	-0.01
Intensity of winter (Nov.)	1.32	-0.42	0.40	-0.01
Intensity of winter (Dec.)	1.09	-0.21	0.97	-0.02
Intensity of winter (Jan.)	0.96	-0.03	0.91	0.03
Intensity of winter (Feb.)	1.22	-0.44	1.23	0.03
Intensity of winter (Mar.)	0.69	-0.07	0.74	-0.02
Mean snow depth (Oct.)	1.17	0.04	-	-
Mean snow depth (Nov.)	0.78	-0.15	1.45	-0.03
Mean snow depth (Dec.)	1.01	0.16	0.99	0.03
Mean snow depth (Jan.)	0.89	-0.10	1.20	-0.01
Mean snow depth (Feb.)	0.65	0.09	1.48	0.05
Mean snow depth (Mar.)	0.52	-0.07	0.87	0.03
Number of days with snow cover (Oct.)	1.36	0.05	-	-
Number of days with snow cover (Nov.)	0.72	-0.03	1.00	-0.01
Number of days with snow cover (Dec.)	1.11	0.18	1.15	0.04
Number of days with snow cover (Jan.)	1.23	0.12	0.69	0.01
Number of days with snow cover (Feb.)	1.03	-0.13	0.24	0.01
Number of days with snow cover (Mar.)	0.59	0.07	0.32	0.01
Days with ice enhancement (Oct.)	1.09	-0.04	0.30	0.01
Days with ice enhancement (Nov.)	0.64	-0.07	0.32	0.01
Days with ice enhancement (Dec.)	0.73	0.04	0.16	0.00
Days with ice enhancement (Jan.)	1.00	0.28	0.79	-0.01
Days with ice enhancement (Feb.)	0.82	0.17	1.83	-0.05
Days with ice enhancement (Mar.)	1.07	-0.06	1.83	-0.04

3.2. The weather variables affecting the winter survival of winter wheat and triticale

The effects of different weather indicators on WS were complex and differed for winter wheat and triticale (Table 2). In the case of winter wheat, the factors that were highly correlated with WS were: winter severity in November and February, DIs and the number of freezing-thawing cycles in December, the thermal vegetation index during the winter and the freezing index in November as well as the number of days with ice enhancement in January (although the VIP value was low in this case). Thus, it seems that the main impacts on winter wheat survival were connected with an insufficient level of cold acclimation caused by warm temperatures both at the beginning of the winter (November), after deacclimation during the winter, and at the end of the winter (February).

In the case of triticale, all the RC values were low, thus, no weather variables were found that clearly affected WS. However, looking at the highest VIP values, ice encasement (February and March) and a higher

number of freeze-thaw events in March decreased the survival rate of triticale. This suggested that triticale was more susceptible to extreme winter conditions at the end of the winter. The maximum air temperature in February together with a higher number of freezing–thawing cycles in January increased WS suggesting that this species may not be susceptible to deacclimation during winter under present conditions. WS also decreased by days with air temperature <5 °C in December.

3.3. Predictions of future winter damage risks in wheat and triticale under different climate change scenarios

The reduction of variables required re-fitting of the models. The optimum number of components for the reduced data sets was nine for the wheat model and three for the triticale model. The other data for model development and validation of predictive power were unchanged.

In the case of wheat, the predictive power of the model, evaluated on the basis of the correlation between the measured and predicted values,

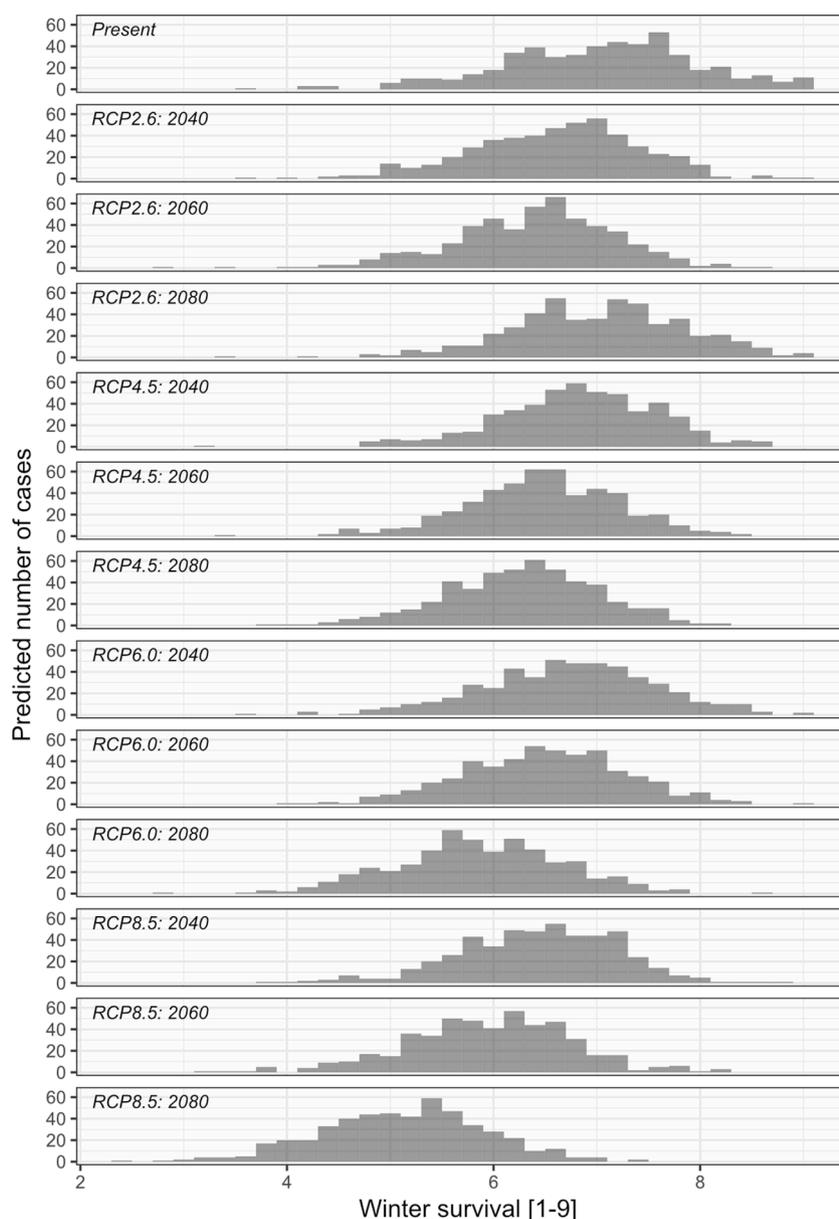


Fig. 4. Distribution of predicted winter wheat winter survival (WS), based on simulated weather conditions in Dębina, Poland, calculated for the reference year of the field experiments (2010), and in 2040, 2060, and 2080 for four climate change scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5). In WS score, 9 means that 0%–5% of plants were winter-killed and 1: 95–100%.

was slightly weaker when nine components were used ($R^2 = 0.73$, Supplementary Fig. 3a) as compared to the initial model. There was no difference in the means of measured vs. predicted values (Welch two-sample t -test, p -value = 0.3515). The variable selection improved the triticale model, as reflected by the slightly higher R^2 (0.18, Supplementary Fig. 3b).

3.3.1. Winter wheat

The predicted WS rates of winter wheat at Dębina were clearly lower than calculated for the current conditions with the exception of RCP2.6 (especially in 2080) (Fig. 4, Supplementary Fig. 4). Winter hardiness got worse with an increasing time horizon and level of assumed temperature increase. The greatest decrease in the winter hardiness of winter wheat was predicted for 2080 and 2060 in the RCP8.5 scenario and for 2080 in RCP6.0. In these cases, the probability of WS below the critical value of 5, which can cause considerable economic loss (see Discussion), was also

clearly higher. In the case of RCP2.6 (all the years of prediction) and RCP4.5 (2040, 2060) the probability decreased.

3.3.2. Winter triticale

In the case of the hardier triticale WS decreased for the more extreme climate change scenarios (Fig. 5, Supplementary Figure 5). This was especially visible in the case of RCP8.5 for 2080 and 2060. Under RCP2.6 winter hardiness stayed at the same level or even increased. It must be also emphasized that neither the calculations for 2020 nor the future predictions pointed to the possibility of economic losses owing to lower winter hardiness of triticale because no WS values <5 were reported (see Discussion).

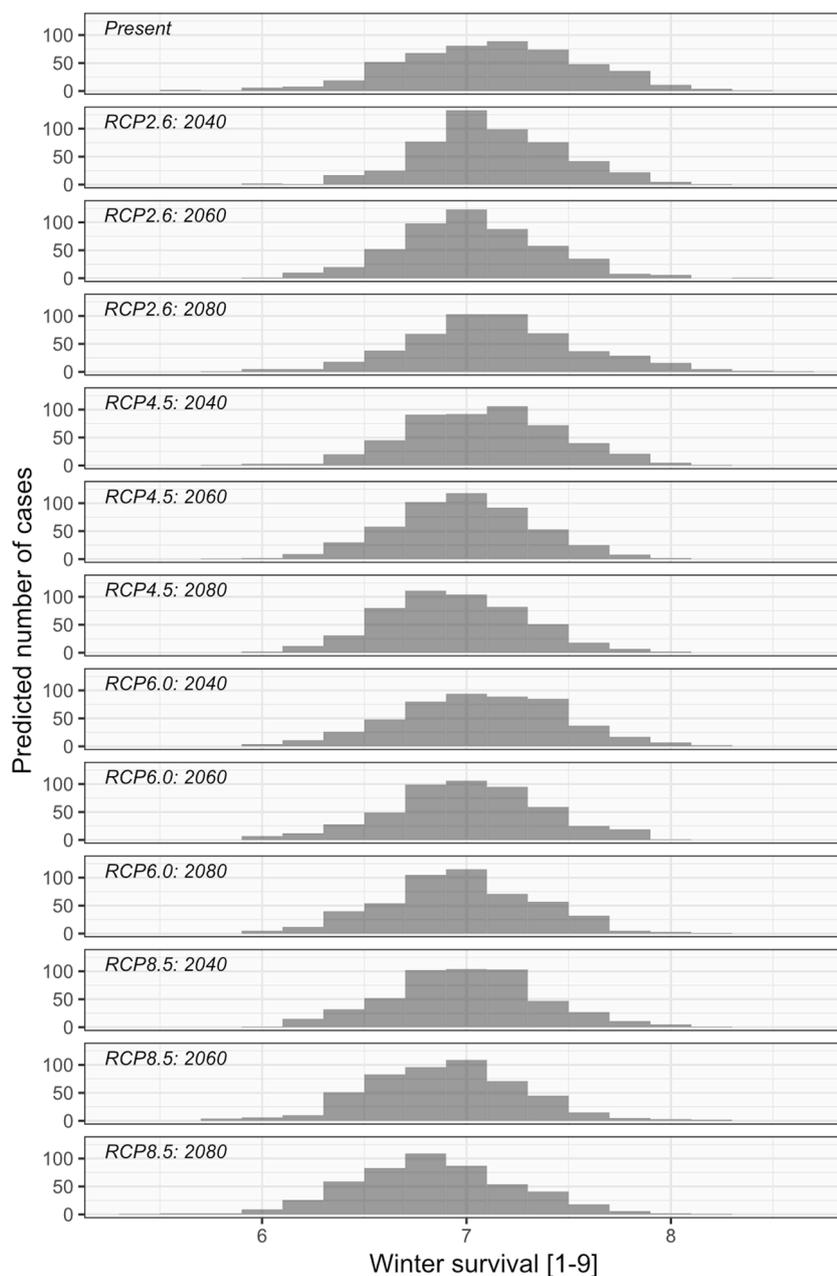


Fig. 5. Distribution of predicted triticale winter survival (WS) in Dębina (Poland), based on simulated weather conditions, calculated for the reference year of the field experiments (2010), and in 2040, 2060, and 2080 for four climate change scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5). In WS score, 9 means that 0%–5% of plants were winter-killed and 1: 95–100%.

3.4. The possible role of deacclimation in winter survival under a changing climate

In the climate change scenarios that assumed the highest increase in CO₂ concentrations in the atmosphere, a clear decrease in predicted WS was shown for both cereal species (Figs. 4, 5; Supplementary Figures 4, 5). However, the increase in the minimum winter temperatures in our test site was within predicted changes under climate warming (Supplementary Fig. 6). Thus, the causes for the potential decrease in WS were connected with other weather variables.

The negative impact on WS observed in the RCP8.5 scenario, especially in 2060 and 2080, seemed to be related to changes in DIs ($DI_{T_{max}}$ and $DI_{T_{mean}}$). These indices indicate the effectiveness of deacclimation (when positive) or acclimation (negative) before the absolute minimum winter temperature (Rapacz et al., 2017). It was shown that, depending on the weather conditions during winter, both $DI_{T_{mean}}$ or $DI_{T_{max}}$ were able to characterize deacclimation and, thus, both were included in our models. The correlation calculated between WS and the two indices indicated that their increasing values, which reflected the higher temperatures before the period of frost, were negatively correlated with the WS predicted for wheat ($DI_{T_{max}}$ vs. WS $r = -0.32$, $r = -0.34$, $r = -0.37$ in RCP8.5_2040, RCP8.5_2060 and RCP8.5_2080, respectively) (Supplementary Table 7).

Other weather variables that negatively affected WS in RCP8.5_2080 were heat units Dec.–Mar. ($r = -0.32$), increase of T_{min} , monthly sum of the mean daily air temperature, and intensity of winter in February ($r = -0.34$, $r = -0.37$, and $r = -0.34$, respectively). All these factors, with the exception of the last relate to deacclimation and winter intensity in February, when deacclimation is most likely to occur before freezing, and may reveal the effect of prior deacclimation. RCP 6.0 and RCP 8.5). In WS score, 9 means that 0–5% of plants were winter-killed and 1: 95–100%.

A similar relationship was seen for triticale, although, as also observed for the present, the effects of the weather variables, especially $DI_{T_{mean}}$, seemed to be weaker than for wheat (Table 2): $DI_{T_{max}}$ vs. WS $r = -0.32$, $r = -0.33$, $r = -0.36$ in RCP8.5_2040, RCP8.5_2060, and RCP8.5_2080, respectively; $DI_{T_{mean}}$ vs. WS $r = -0.31$ and $r = -0.34$ in RCP8.5_2060, and RCP8.5_2080.

Moreover, for both species the deterioration of WS in RCP8.5_2080 was related to a decrease in the average number of days with T_{min} below -5 °C in February (wheat $r = 0.39$, triticale $r = 0.41$). If compared to the other scenarios, for which the average number of days with T_{min} below -5 °C varied between 7 and 8 days, in the RCP8.5_2080 scenario it was 6 days on average (Supplementary Table 7).

As suggested above, a major factor affecting the predicted future decrease in WS rate of both species seemed to be deacclimation. The values of the DIs increased considerably (which means that deacclimation will be more effective), the highest values being predicted for RCP8.5 and RCP6.0 scenarios for 2080 (Fig. 6, Supplementary Figures 8, 9). In the case of RCP2.6, an increase of DI values was predicted for 2040 only, while in 2060 and 2080 a considerable decrease was predicted. These data were comparable with the predictions of winter hardiness in both species, where an increase in WS was predicted under the RCP2.6 scenario with a final excess over the values estimated for 2020 in 2080 (Figs. 4, 5; Supplementary Figs. 4, 5).

4. Discussion

Empirical models linking local microclimate data and plant winter survival were developed for two cereal species. Similar efforts were performed also before. In Waalen et al. (2013) paper, PPLS regression models were created for oilseed rape and turnip oilseed rape on the basis of a 3-year study in two locations in Norway. Owing to the high variability in WS observed between studied accessions, these models were characterized by high determination coefficients (R^2 were 0.81 and 0.87, depending on species). In the case of the FROSTOL model the mean

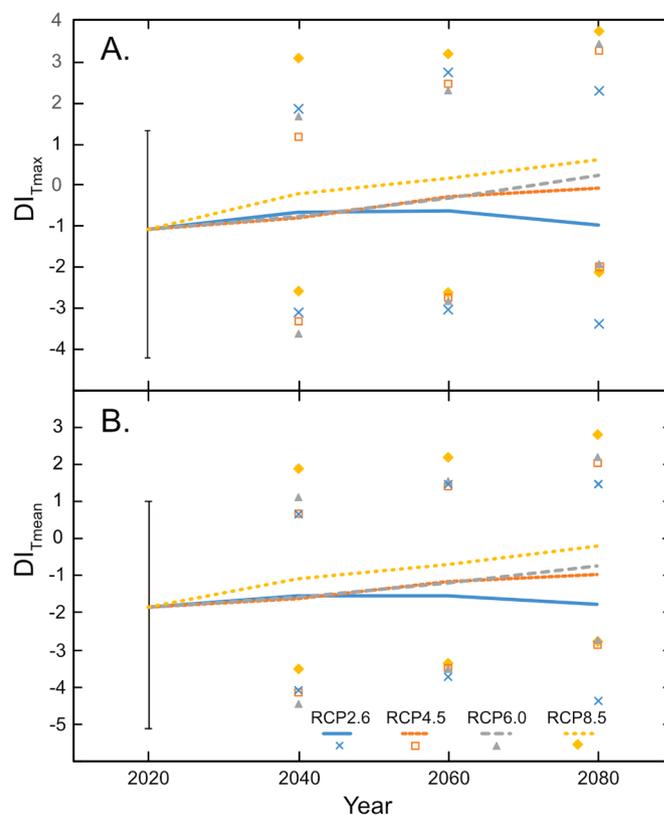


Fig. 6. Predicted changes in deacclimation indices calculated on the basis of (A) maximum day temperature ($DI_{T_{max}}$) and (B) mean day temperature ($DI_{T_{mean}}$) in Dębina (Poland) under different climate change scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5): mean, maximum and minimum values.

R^2 between the simulated and observed WS class model was between 37% and 75%, depending on the country (Sweden, Norway, respectively), which was explained as the occurrence of stress factors not included in the model at the Norwegian locations (Bergjord Olsen et al., 2018). In our model, based on a 6-year experiment performed in seven experimental sites for each species, the R^2 for wheat was similar (0.75) to the previous study but it was very low in the case of winter triticale (0.16). This was connected with very low variability of WS between the study years/accessions/sites. The mean winter hardiness of triticale was lower than 9 only in 3 years and only in a few experimental sites (two, one or six, depending on the year). We decided eventually to include all of these data in the model development to fit it with examples of 'winter comfort conditions' for triticale survival.

As has been shown, multivariate regression analysis, using PPLS, also is useful for identifying the variables that affect WS (Waalen et al., 2013). Both in their study and in our study, the risks and favorable factors for overwintering were different between the species and this was more obvious with different climate zones. This observation has important consequences for building more reliable yield and productivity models that include WS, because the latter's dependence on changing climate factors should be treated differently for different species. For oilseed and turnip rapes, the most important factor affecting WS was the number of days without snow in December and, for turnip rape in January, as well as mean soil temperature in April (Waalen et al., 2013). The most important risk factor common to both species was ice encasement, which in our model, was only important for triticale.

In our model for winter wheat, the most important risk factors were DIs, thermal vegetation index (also connected with deacclimation) and the severity of winter in November (plant were not sufficiently cold-acclimated) and in February, when the plants started to de-acclimate passively (Rapacz et al., 2014). The key favorable factor for increased

WS was the number of freezing/thawing cycle in December. While such conditions increase freezing tolerance, the mechanisms of this effect are poorly recognized (Kacperska, 2000). Thus, we can summarize that winter hardiness of wheat under Polish climate depends on cold-acclimation.

In the case of triticale, when looking at VIP values (because the regression coefficients were very low) a similar positive dependence on freezing/thawing cycles at the beginning of winter was observed; however, the dependence on DIs was not sufficiently clear. Our studies indicate that at present triticale faces no problem with WS in Poland. However, the use of the model for winter hardiness prediction under climate change showed the same trend as in winter wheat, a decrease in WS with increased winter temperature, which again suggests a role for deacclimation.

Snow cover may be considered both as a risk for WS and a factor that decreases the risk of winter damage. Snow cover provides insulation against extreme freezing, where a 10–20 cm layer is often enough to smooth the fluctuations in air temperature and maintain the temperature near the plant close to freezing (Thorsen and Höglind, 2010). Many models have been proposed to describe the thermal effects of snow cover on the soil temperatures (e.g., Trnka et al., 2010). However, prolonged snow cover duration may increase the risk of ice encasement, anoxia, snow-mold infection and, because of the very low level of light, contribute to the depletion of assimilates or/and slowing down of the cold acclimation process, which is considered also as a factor that decreases survival rate (Vico et al., 2014; Waalen et al., 2013). Because of this complex relationship, the use of snow cover parameters in WS models may be subject to major errors. In our empirical models, the importance of snow cover for wheat and triticale overwintering in Poland was low. The main reason was that during the 6 years of our study the snow cover was absent or very thin and short-lasting in the majority of the experimental sites. Global warming is expected to decrease the duration of snow cover and snow depth, both globally IPCC (2013) and specifically in Poland (Szwed et al., 2019). Thus, we excluded factors connected to snow cover (snow cover depth, duration and ice-encasement) from our predictive models.

The most remarkable result of our study was that an increase in T_{mean} from climate warming during the winter may reduce WS in Poland's humid continental climate (Dfb in the Köppen-Geiger classification, Kottek et al., 2006). This is the first report suggesting this possibility in the case of winter annual plants, although similar suggestions have been implied for temperate and boreal-zone perennial grasses (Höglind et al., 2013) and woody plants (Arora and Taulavuori, 2016). The main proposed reason for this is an increased risk of plant deacclimation during warm breaks. The mechanisms of this phenomena, together with the deacclimation in the spring which is connected with dormancy break and/or depletion of assimilate reserves, are poorly understood (Kalberer et al., 2006; Pagter and Arora, 2013; Rapacz et al., 2014). Two recent reports examine the mechanisms and genetic backgrounds of cold deacclimation in annual plants (Horvath et al., 2020; Wójcik-Jagła et al., 2021). They conclude that deacclimation tolerance is genetically different from cold-acclimation capacity, which suggests there are different mechanisms for cold acclimation and deacclimation (Rapacz et al., 2017). Our study demonstrates the need to use existing and emerging knowledge on the mechanisms and genetic control of de-acclimation tolerance for breeding plants that are better adapted to the changing climate. This appears achievable because large variation in deacclimation tolerance has been shown for winter wheat, triticale and barley (Rapacz et al., 2017; Wójcik-Jagła et al., 2021).

Among potential applications of knowing the future risk for WS is the possibility of incorporating our models into crop production models. These models currently account for winter damage to varying degrees using a range of variables such as crop death, reducing seedling density, crop biomass or leaf area (Barlow et al., 2015; Zheng et al., 2018). It can be assumed that the main negative effect of winter on yield is connected with the death of seedlings (Barlow et al., 2015). Currently, the

economic damage threshold for winter cereal crops accepted by Polish insurance companies as so-called total damage is about 60% of winter-killed plants, which corresponds to a value of 4/5 on the WS scale we use (Gawrońska, 2014). In our models the frequency of wheat WS <5 will change from 2.4% in 2020 to 1%, 4.8%, 15.4% and 43.8% in 2080 (RCP2.6, RCP4.5, RCP6.0 and RCP8.5, respectively; Supplemental Table 10), while for triticale the lowest WS (lower than today) was 5.496, predicted for RCP8.5 in 2080. Thus the predicted increase of the risk of low WS may have a potential impact on the profitability of winter wheat in Poland.

Another risk from freezing damage in winter cereals, which is not considered in our model, is that plants will grow and develop faster because of increased temperatures, which increases their vulnerability to spring freezing events, which will potentially be of great economic importance owing to high sensitivity to sub-zero temperatures during anthesis (Alt et al., 2020; Barlow et al., 2015; Xiao et al., 2018). This means that the future effects of low winter/spring temperatures on cereal yields in Central Europe may be even worse than predicted in our models. Regardless of the climate projections and the changes expected with them, attention should also be drawn to the ongoing discussion around Arctic oscillation and the influence of the polar vortex on thermal fluctuations in winter (Kim and Choi, 2021), as the associated increasing variance in temperatures brings with it the threat of spring frosts and extreme winter freezing events.

5. Conclusion

The empirical models of winter survival showed that cold deacclimation during winter are one of the most important risk factors for overwintering of winter wheat and triticale in Poland. At our chosen representative experimental site global warming did not reduce of the risk of poor wintering of winter wheat and even more winter hardy triticale. The models used in our study indicate that the degree of damage to the crop may increase as a result of the increasing occurrence of warm breaks and subsequent frosts in winter. This suggests that tolerance to deacclimation should be the target of plant breeders in coming decades.

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Authors contribution

MR: project leader, conceptualization, methodology, data acquisition and visualization, writing the manuscript draft, manuscript editing; AMP: methodology, data calculations, models development, data acquisition and visualization, writing the manuscript draft, manuscript editing; BJ: weather variables calculation, manuscript editing; LK: conceptualization, generation of weather data, manuscript editing .

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2021.108739](https://doi.org/10.1016/j.agrformet.2021.108739).

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