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Modelling the course of frost tolerance in winter wheat
I. Model development

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Abstract

A Canadian model that simulates the course of frost tolerance in winter wheat under continental climatic conditions was adopted and further developed for use in an oceanic climate. Experiments with two cultivars were conducted during two winters in Central Norway. All plants were hardened at the same location. After hardening, in mid November, they were distributed to three locations with contrasting winter climates. Plants were sampled several times during autumn and winter and tested for frost tolerance, expressed as LT_{50} (the temperature at which 50% of the plants were killed). Results from the experiment were used in parameterization and cross validation of the new model, called FROSTOL, which simulates LT_{50} on a daily basis from sowing onwards. Frost tolerance increases by hardening and decreases by dehardening and stress, the latter caused by either low temperatures, or by conditions where the soil is largely unfrozen and simultaneously covered with snow. The functional relationships of the model are all driven by soil temperature at 2 cm depth. One of them is in addition affected by snow cover depth, and two of them are conditioned by stage of vernalization. Altogether five coefficients allotted to four of the functional relationships produced a good agreement ($R^2 = 0.84$) between measured and modelled values of LT_{50}. A cross validation of the model indicated that the parameters were satisfactorily insensitive to variation in winter weather.
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1. Introduction

A plant's tolerance to freezing temperatures changes during the course of the winter as a consequence of complex interactions between the plant and various environmental factors.

Anticipated future changes in temperature, precipitation and snow cover caused by global warming may affect winter wheat cropping in different ways. On one hand, a warmer climate may make it possible to expand winter wheat cropping into new locations where the growing season now is too short. On the other hand, if climatic changes imply more variable weather conditions, the conditions for overwintering may be worse for the plants since significant dehardening may be anticipated. Semenov and Porter (1995) found, when modelling winter wheat yield in response to future weather scenarios, that changes in the variability of either temperature or precipitation during summer had a larger effect on the yield than changes in average conditions.

Several models simulating crop performance of winter wheat in response to environmental factors have been developed and used in different studies during recent years (Ghaffari et al., 2002; Semenov and Porter, 1995; Jamieson et al., 1998; Rickman et al., 1996). However, only a few models account for genetic and environmental factors on overwintering performance. Such an approach will be needed more in areas where winter damage may affect crop performance heavily.

Overwintering models quantifying relationships between climatic factors and winter survival of plants will make it possible to perform risk calculations for winter wheat production. This kind of risk calculations will be useful not only in a changing climate and at new locations, but also for present winter wheat areas and climate (e.g. Tveito et al., 2005). The weather conditions during winter vary, and hence also the risk of winter damage. Thus, overwintering subroutines may be major contributions to

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crop growth models of perennial, biennial, and winter annual crops. Calculations of overwintering risks could be a necessary supplement to existing models of crop performance for use in various contexts (e.g. Vatn et al., 2006).

An early attempt upon modelling winter survival was the use of the CERES crop growth model to map the potential of winter wheat production and risk of winterkill in western Canada under the present climatic conditions (Savdie et al., 1991). Further steps towards a physiological basis were the model of Fowler et al. (1999), simulating daily development of frost tolerance in winter wheat based on temperature and a cultivar dependent coefficient of frost tolerance, and that of Lecomte et al. (2003) modelling daily changes in frost tolerance and estimates of the temperature below which the first leaf damage in winter wheat may occur.

The Canadian model developed by Fowler et al. (1999) was chosen as a base model in this work. However, it is well known that model concepts working well under one set of climatic conditions may fail under contrasting climates. Our objective has been to further develop the Canadian model such that it could simulate daily fluctuations in frost tolerance of winter wheat grown in oceanic climates. The new model, called FROSTOL, can use easily obtainable input data and be used to evaluate possibilities for winter wheat survival during various winter conditions.

2. Materials and methods

2.1. Plant material and experimental design

Two cultivars of winter wheat, Bjørke and Portal, were sown in perforated and well-drained polythene boxes filled with soil at the 4 September and 1 September in 2003 and 2004, respectively. All boxes were placed outdoors at the Norwegian Institute for Agricultural and Environmental Research in Stjørdal right after sowing. The soil was a sandy loam, and mineral fertilizer was initially added at rates of 3.7 g N, 1.0 g P, and 2.8 g K m^{-2}. Each box (37 × 27 × 15 (depth) cm) contained 20 plants of each cultivar, giving a plant population similar to 400 plants m^{-2}. To prevent fungal infections which could reduce cold hardiness, the plants were sprayed with 45 mg prochloraz m^{-2} in mid October.

The boxes were kept in Stjørdal until the 11 November so that all plants gained most of their frost tolerance under the same weather conditions. They were then distributed to three different trial sites located in Stjørdal, Selbu, and Oppdal. Stjørdal (63° 29′ N, 10° 52′ E, 26 m a.s.l.) has an oceanic climate, as situated near a fjord that is free of ice during winter. Selbu (63° 20′ N, 11° 01′ E, 165 m a.s.l.) and the more highland site Oppdal (62° 34′ N, 9° 40′ E, 590 m a.s.l.) are both located more inland with lower temperatures and a more stable snow cover during winter. At each trial site, the boxes were placed in pits in the soil so that the plants stayed at the same level as the grass sod (Stjørdal and Oppdal) or grain field stubble (Selbu) surrounding them. To prevent the boxes from being firmly frozen into the surrounding soil and being impossible to recover during winter, the pits were lined with a layer of straw.

Soil temperature in 2 cm depth (plant crown temperature) was recorded hourly both by automatic weather stations (Campbell Scientific LTD) and by HOBO® H8 Pro Series temperature loggers placed in some of the boxes at each trial site. Snow cover at the trial sites and a representative snow depth were observed at least once a week and interpolated for days in between.

Samplings of plants were carried out according to specifications (Table 1). In 2003 one initial sampling was carried out in Stjørdal, just before distribution to the different trial sites in November. In 2004 three such presamplings were conducted from early October. Samplings from all trial sites were done five times, about once a month from December until late April/early May. Six randomly selected boxes containing both cultivars were taken from each trial site at every sampling. Sampled boxes with frozen soil were kept at 2–4 °C for 3 days for thawing before the plants were tested for cold hardiness.

2.2. Cold hardiness determination

The test of cold hardiness was performed according to the method described by Limin and Fowler (1988). Plants were washed free from soil, cut to 2 cm root and 3 cm top, and placed in moist sand in aluminium trays in a programmable freezer. The temperature was lowered from 2 to −3 °C by 1 °C h^{-1} and thereafter kept at this temperature for 12 h. Thereafter temperature was lowered by 1 °C h^{-1} until the set minimum temperature of each test was reached. During this period, two

Table 1
Sampling dates at trial sites in Stjørdal, Selbu, and Oppdal during the two winters 2003–2004 and 2004–2005

2003–2004			2004–2005		
Stjørdal	Selbu	Oppdal	Stjørdal	Selbu	Oppdal
			4 October		
			18 October		
3 November			12 November		
8 December	12 December	12 December	3 December	10 December	10 December
12 January	16 January	16 January	14 January	21 January	21 January
16 February	20 February	20 February	11 February	18 February	18 February
22 March	26 March	26 March	4 March	11 March	11 March
			1 April		
26 April	3 May	3 May	22 April	29 April	29 April

samples of 10 plants per cultivar were removed at intervals of 2–3 °C for each of five test temperatures. The sampled plants were placed at 2 °C over night for thawing and then transplanted into pots with fertilized peat. Survival of individual plants rated dead or alive, and LT_{50} (the temperature at which 50% of the plants were killed) were determined after 3 weeks of regrowth in a growth chamber at 18 °C and long day (18 h) conditions. Light was supplied by a combination of high-pressure sodium lamps and high-pressure mercury halogen lamps, yielding light at a fluence rate of approximately 120 μmol m^{-2} s^{-1}.

2.3. Parameter estimation, optimization and cross validation

Calibration of the model was based on LT_{50} values from the tests of cold hardiness. Results from both cultivars, the three locations and both winters were used. PowerOpt, a simplex optimizer of Nelder and Mead type (Nelder and Mead, 1965) for optimization of Powersim models was used to estimate a set of five parameters that minimized the root mean square error (RMSE) of the simulation (Table 2). A cross validation was also performed. One of the six different combinations of year and location was in turn left out during optimization of parameter values on the remaining five, to be used as a validation sample afterwards.

2.4. Model description

Frost tolerance is expressed as LT_{50}, and calculated on a daily (t) time step from sowing onwards as:

$$LT_{50t} = LT_{50t-1} - RATEH + RATED + RATES + RATER \tag{1}$$

Frost tolerance increases by hardening (RATEH) and decreases by dehardening (RATED) and stress. Two stress terms are included in the model. One of them is caused by exposure to low temperatures (RATES), and the other one is caused by conditions where the soil temperature is about 0 °C and the ground simultaneously covered with snow (RATER).

Necessary input data are maximum frost tolerance for the cultivar used, and daily measurements of soil temperature in 2 cm depth (plant crown temperature) and snow cover.

2.5. Hardening

The daily change in LT_{50} caused by hardening was in accordance with Fowler et al. (1999) calculated as:

$$\begin{aligned} &RATEH = H_{\text{param}}(10 - TC)(LT_{50t-1} - LT_{50c}) \\ &\text{when } TC < 10 \end{aligned} \tag{2}$$

where TC is diurnal mean crown temperature, LT_{50c} is the maximum frost tolerance of the cultivar, and H_{param} is a constant assumed to be independent of cultivar, set to 0.0093 after optimization.

Low-temperature acclimation is a cumulative process (Roberts, 1979). It can be stopped and reversed if the plants are exposed to high temperatures, and restarted if the temperature is lowered to levels within the acclimation range again (Mahfoozi et al., 2001a; Pomeroy et al., 1975). Limin and Fowler (1985) found that temperatures above approximately 10 °C had a limited effect to increase cold hardiness. Once the temperature fell below 10 °C, the frost tolerance started to increase rapidly. Rate of hardening increased as the temperature declined towards 0 °C (Limin and Fowler, 1985; Gay and Eagles, 1991). Below 0 °C the rate of hardening in Eq. (2) is assumed to be equal to that at 0 °C.

Several experiments have shown a curvilinear relationship between number of acclimation days and the level of frost tolerance achieved. The plants gain frost tolerance rapidly in the beginning of an acclimation period, before the rate of change gradually slows down and eventually starts to decline (Fowler et al., 1996b; Gay and Eagles, 1991; Limin et al., 1995; Brule-Babel and Fowler, 1989). This is accounted for by the term ($LT_{50t\text{-}1}$–LT_{50c}).

2.6. Dehardening

Loss of frost tolerance by dehardening is calculated according to the equation of Fowler et al. (1999) as:

$$\begin{aligned} &RATED = D_{\text{param}}(LT_{50i} - LT_{50t-1})(TC + 4)^3 \\ &\text{alternatively } TC \geq 10 \text{ or } TC \geq -4 \end{aligned} \tag{3}$$

where D_{param} is a constant assumed to be independent of cultivar, set to 2.7×10^{-5} after optimization. LT_{50i} is the LT_{50} of an unacclimated plant. The value of LT_{50i} depends on LT_{50c}, the maximum frost tolerance of the cultivar, and it is calculated as $LT_{50i} = -0.6 + 0.142\ LT_{50c}$.

Table 2
Symbols and estimated values of parameters of the FROSTOL model based on the full data set of three locations, two winters, and two cultivars

Description	Symbol	Eq.	Estimate	S.D.	Std.%
Hardening coefficient (°C^{-1} d^{-1})	H_{param}	2	0.0093	2.3×10^{-4}	2.4
Dehardening coefficient (°C^{-3} d^{-1})	D_{param}	3	2.7×10^{-5}	1.9×10^{-6}	7.0
Low temperature stress coefficient (°C^{-1} d^{-1})	S_{param}	5	1.90	0	0.0
Respiration stress coefficient (d^{-1})	R_{param}	4	0.54	0.015	2.8
Minimum snow depth to allow for full respiration stress (cm)	T_S_max	4	12.5	0	0.0

Standard deviations (S.D.) of six estimates of the same parameter values when in turn optimized on five subsets of locations and winters collectively for two cultivars (cross validation). Std.% = 100 × S.D./estimate.

The term (LT_{50i}–LT_{50t-1}) accounts for the findings of Gusta and Fowler (1976a, 1976b), who showed a rapid decrease in frost tolerance during the first 3 days of exposure to 15 °C both in autumn- and spring-collected plants of winter wheat. After these 3 initial days, loss of frost tolerance levelled off in autumn-collected plants. For the plants collected in spring, the same reduction in rate of dehardening was, however, not found. This more rapid loss of frost tolerance in spring-collected plants than in plants sampled in the autumn is accounted for in the model by: (1) lowering the temperature threshold for dehardening, and (2) not allowing the plants to reharden after the vernalization requirement is fulfilled. Before the plants are fully vernalized, dehardening in the FROSTOL model only occurs at temperatures above 10 °C. After saturation of the vernalization requirement, dehardening starts when the temperature rises above −4 °C.

2.7. Stress

Plants in unfrozen soil may have a higher respiration rate than those in frozen soil. Further, a snow cover may, as ice encasement, create more or less anaerobic conditions for respiration and capture metabolites like CO_2, ethanol and lactate (Andrews and Pomeroy, 1979; Gudleifsson, 1997), thereby increasing the stress level and reducing the frost tolerance of the plants. Frost tolerance of hardened winter wheat seedlings was found to decrease rapidly after only a short time exposure to ice encasement in an experiment performed by Andrews and Pomeroy (1977). Loss of frost tolerance assumed to be caused by respiration under snow is calculated in the model as:

$$\mathrm{RATER} = R_{\mathrm{param}} \times \mathrm{RE} \times f(\text{snow depth}) \tag{4}$$

where R_{param} is a constant independent of cultivar, set to 0.54. RE is a respiration factor, fitted by Sunde (1996) from respiration measurements presented by Sjøseth (1971), which is calculated as [exp(0.84 + 0.051 TC) − 2]/1.85. The *f*(snow depth) is a function of snow depth that takes a value between 0 and 1. It increases linearly with snow depth up to 12.5 cm (T_S_max) and thereafter levels off.

Prolonged exposure to near lethal temperatures has in experiments resulted in decreased survival of winter wheat plants (Pomeroy et al., 1975; Gusta and Fowler, 1977). According to the winter survival model developed by Fowler et al. (1999), loss of frost tolerance caused by low temperatures may be calculated as:

$$\mathrm{RATES} = (\mathrm{LT}_{50t-1} - \mathrm{TC})/ \times \exp[-S_{\mathrm{param}}(\mathrm{LT}_{50t-1} - \mathrm{TC}) - 3.74] \tag{5}$$

where S_{param} is a constant independent of cultivar, set to 1.90 after optimization of the model.

2.8. Phenological development

Calculation of both RATEH and RATED requires state of vernalization to be estimated. Temperatures in the vernalization range shorten the duration of the vegetative phase of winter wheat (Wang et al., 1995), and expression of frost tolerance genes is found to be connected with stage of phenological development (Fowler et al., 1996b). In experiments performed by Fowler et al. (1996b) and Mahfoozi et al. (2001b), a close association was observed between time to vernalization fulfilment and start of decline in frost tolerance.

Daily rate of vernalization (VR) is in the model calculated according to Wang and Engel (1998):

$$\mathrm{VR} = [2(T - T_{\min})^{\alpha}(T_{\mathrm{opt}} - T_{\min})^{\alpha} - (T - T_{\min})^{2\alpha}]/ \times (T_{\mathrm{opt}} - T_{\min})^{2\alpha} \tag{6}$$

where $\alpha = \ln 2/\ln[(T_{\max} - T_{\min})/(T_{\mathrm{opt}} - T_{\min})]$. Porter and Gawith (1999) have reviewed literature on temperature effects in wheat and summarized minimum ($T_{\min}$), optimum (T_{opt}), and maximum ($T_{\max}$) temperatures for vernalization to −1.3, 4.9, and 15.7 °C, respectively. No vernalization is assumed to occur if $T < T_{\min}$ or $T > T_{\max}$.

The accumulated VR gives number of vernalization days (VD). One VD is attained when the plants are exposed to optimum temperature for vernalization during 1 day. For temperatures departing from optimum, but within the temperature range for vernalization, only a fraction of a vernalization day is added. The plants' state of primary induction as related to number of accumulated VD is described by a function given by Streck et al. (2003):

$$f(V) = \frac{(\mathrm{VD})^5}{[(22.5)^5 + (\mathrm{VD})^5]} \tag{7}$$

$f(V)$ varies from 0, when the plants are unvernalized, to 1, for fully vernalized plants. A number of 50 VD is assumed to be sufficient to saturate the vernalization requirement in winter wheat (Ritchie, 1991). In experiments performed by Mahfoozi et al. (2001b) and Fowler et al. (1996a,b), all the winter cultivars included, both of wheat and rye, were fully vernalized after 49 vernalization days. Eq. (7) attains values of $f(V) > 0.98$ when $\mathrm{VD} > 50$. When $f(V) \geq 0.99$ in the model, the plants lose their ability to reharden, and the temperature threshold for dehardening is lowered from 10 to −4 °C as described above. There is no further response to continuing accumulation of VD when $f(V) \geq 0.99$.

3. Results and discussion

As expected, there were significant differences in LT_{50} among years, locations and sampling times ($p < 0.0001$) in the experiment, and also significant interactions among these factors. The only significant effect of cultivar was an interaction between cultivar and sampling time ($p = 0.02$), caused by the fact that Portal had acquired less frost tolerance than Bjørke in November and December. This cultivar difference was taken care of in the model by giving Bjørke and Portal different values for LT_{50c} (maximum frost tolerance of the cultivar). Based on the tests of cold hardiness, LT_{50c} for Bjørke and Portal was set to −24 °C and −22 °C, respectively. Since only minor differences were found between the cultivars at other sampling times, results just for one of them (Bjørke) are presented in Figs. 3 and 4.

Both measured and modelled LT_{50} reached lower values in 2003 than in 2004 (Figs. 3 and 4). The autumn of 2004 was milder than that of 2003 (Figs. 1 and 2), thus estimated hardening started about 10 days later in 2004. The modelled hardening period did also end somewhat earlier that year, caused by a higher rate of vernalization and hence an earlier saturation of the vernalization requirement of the plants.

In the FROSTOL model, the hardening ability of the plants is switched off after vernalization saturation. Vernalization requirement was, in the model, reached about 11 November in

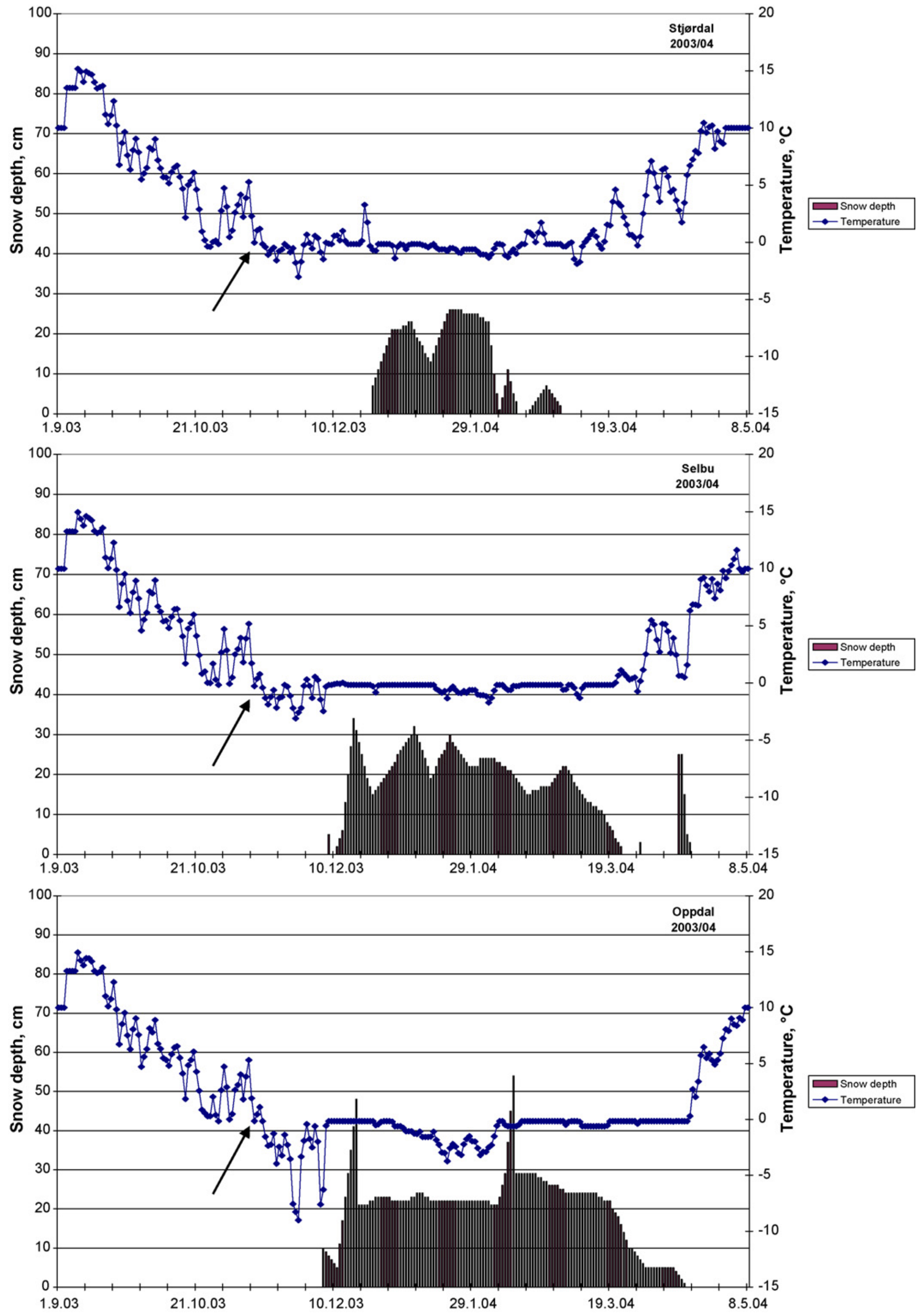

Fig. 1. Soil temperature (2 cm) and snow depths at the trial sites in Stjørdal, Selbu, and Oppdal in 2003/04. All plants were kept in Stjørdal until 11 November (arrow), before they were distributed to the three different trial sites.

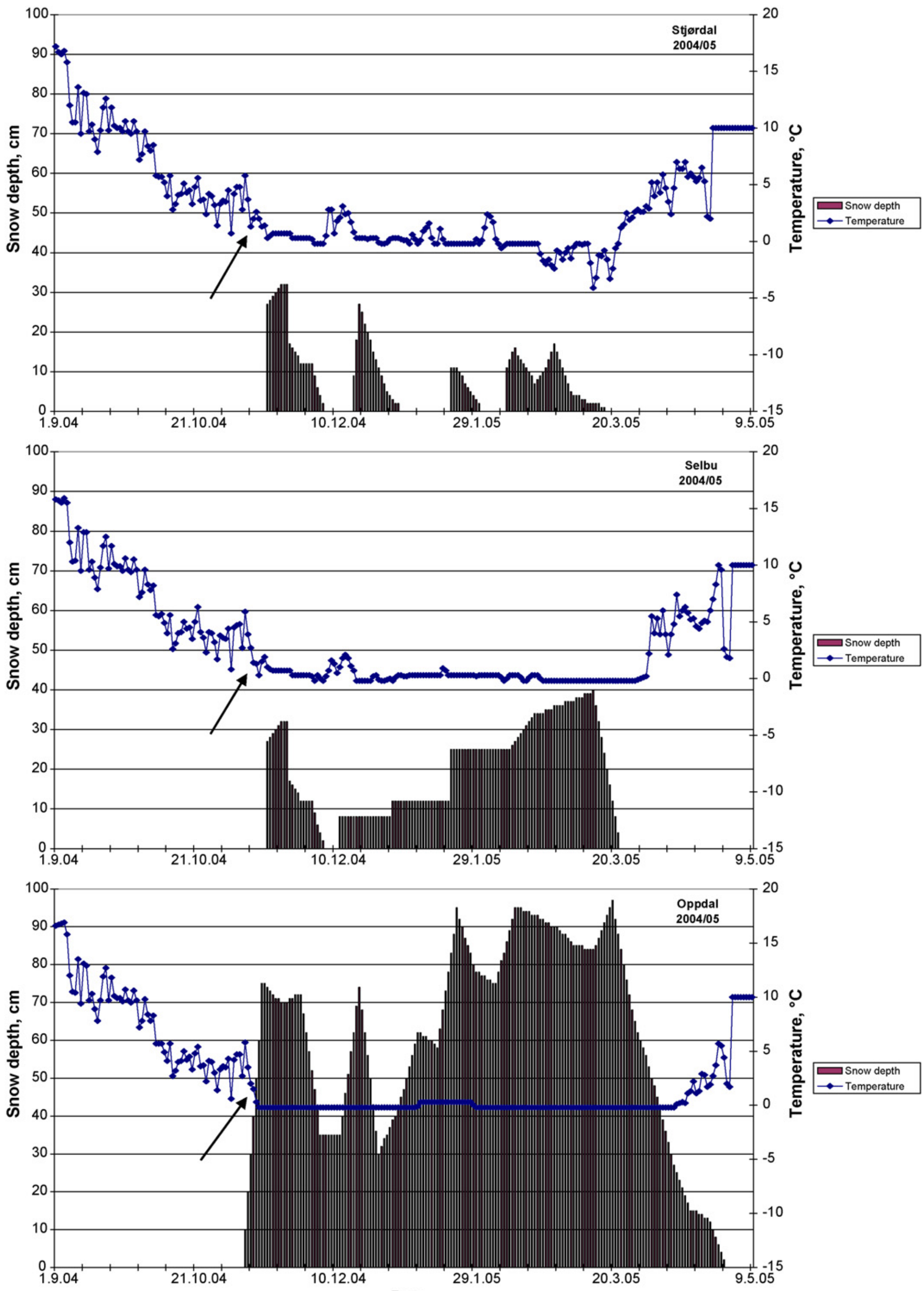

Fig. 2. Soil temperature (2 cm) and snow depths at the trial sites in Stjørdal, Selbu, and Oppdal in 2004/05. All plants were kept in Stjørdal until 11 November (arrow), before they were distributed to the three different trial sites.

2004, and about 15 (Oppdal) and 19 (Stjørdal and Selbu) November in 2003. Both Bjørke and Portal did, however, continue the hardening process for some time after estimated vernalization saturation, and maximum frost tolerance was, according to the tests of cold hardiness, not observed until December for most of the trial sites. These observations could indicate that a gradual decline in the hardening ability after vernalization saturation would be more in accordance with the reality than a simple switch off.

If all the frost tolerance genes were to be switched off after vernalization saturation, the plants would not be able to reharden after passing this point of development. Andrews et al. (1974) found, however, that plants collected from field in March had increased their frost tolerance after snow thaw and exposure to lower temperatures. The frost tolerance thereafter decreased again in April when spring growth started. The same observation was done in Stjørdal 2004/05. Other experiments have also shown that cereal plants still seem to have the ability to reharden to a certain degree after their vernalization requirement has been completed (Fowler et al., 1996b; Prasil et al., 2004). The hardening rate does, however, seem to be lower after vernalization saturation, which could mean that the hardening ability of the plants after transition to a generative stage of development depends on another mechanism, and other genes, than their hardening ability in a vegetative stage. Results from Mahfoozi et al. (2001a) show that plants advanced to the generative stage only reached the level of frost tolerance that can be expected for spring-wheat when rehardened. Further knowledge about a possible rehardening mechanism of plants in a generative stage of development is necessary to be able to implement this in the model. Our field experiments did not contain enough variation in dehardening and rehardening of plants after vernalization saturation to outline any functional relationship for such a mechanism.

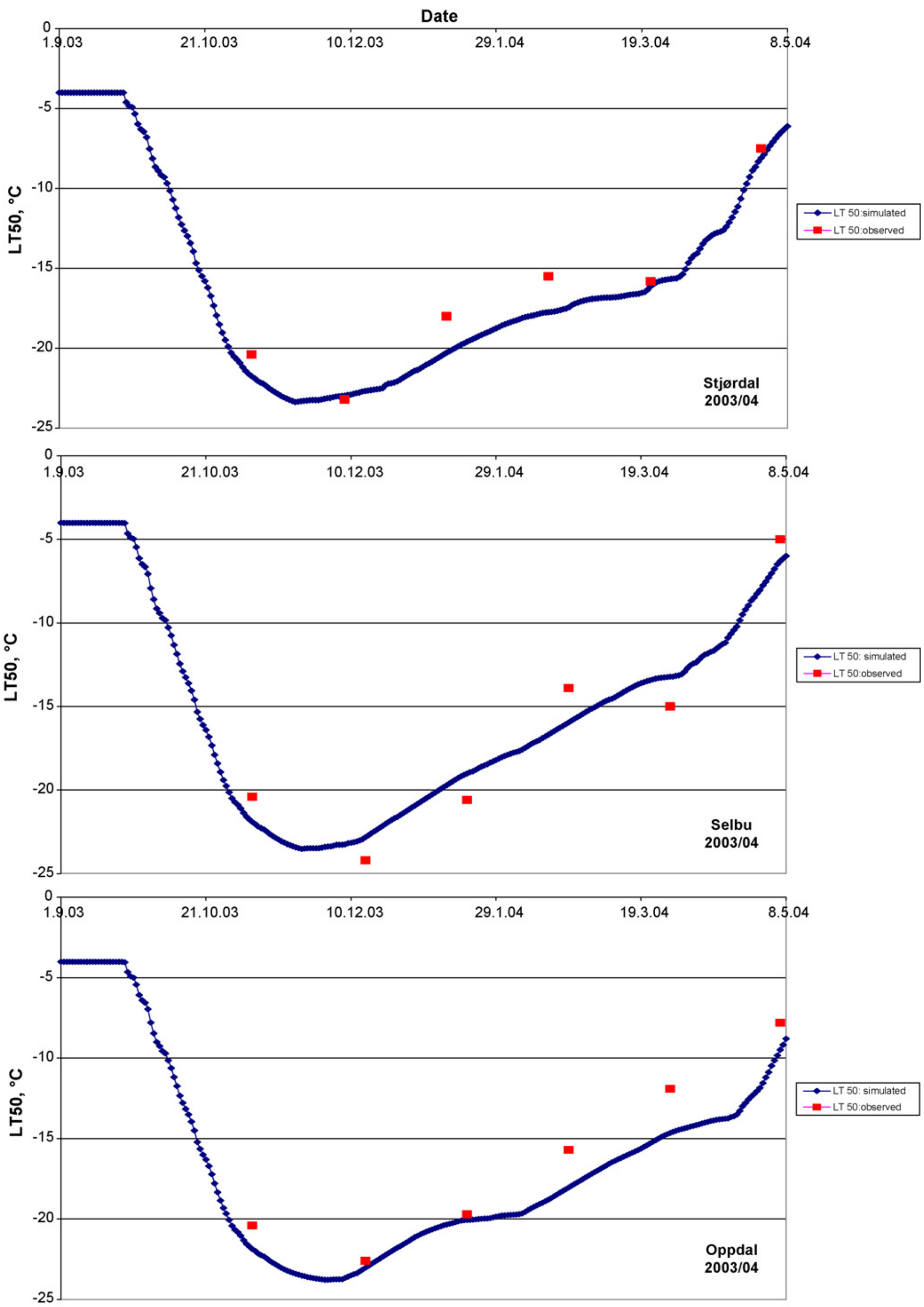

Fig. 3. Simulated and observed frost tolerance (LT_{50}) in Bjørke winter wheat from Stjørdal, Selbu, and Oppdal in 2003/04.

Modelled frost tolerance started to decrease by dehardening when the vernalization requirement was fulfilled (Figs. 3 and 4). Tests of cold hardiness showed that, during the winter 2004/05, plants from Selbu and Oppdal lost their frost tolerance faster than they did in 2003/04. A more durable snow cover, combined with a somewhat higher plant crown temperature, more often above 0 °C during the winter that year, was thought to be the reason for this rapid loss of frost tolerance. Olien (1967) and Roberts (1979) found that plants exposed to low, above freezing temperatures for longer periods of time gradually lost their frost tolerance. A long lasting snow cover may also have caused accumulation of anaerobic metabolites to toxic levels, thereby reducing the vigour and frost tolerance of the plants, as estimated in the model by the term RATER [Eq. (4)]. Frost tolerance was lost more slowly at Stjørdal, where the snow cover was not that stable and long lasting. The rapid loss of frost tolerance associated with rising temperatures in spring did, however, both years start first in Stjørdal, then in Selbu, and last in Oppdal, as expected due to the climatic differences between these locations. Only at two occasions during the experiment, in Oppdal 2003/04 (Fig. 1), did the temperature get low enough to cause loss of frost tolerance due to low temperature stress, RATES [Eq. (5)].

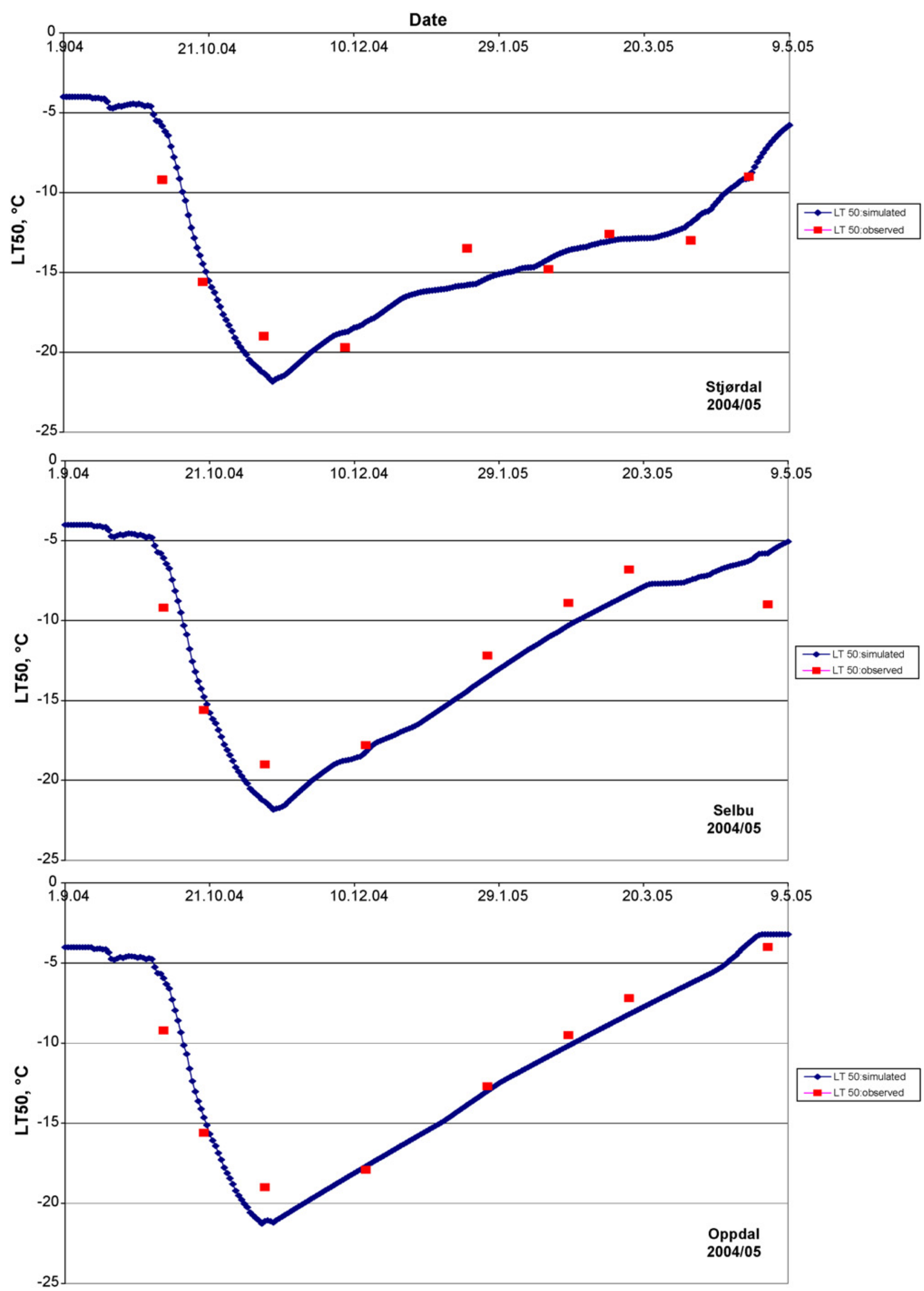

Fig. 4. Simulated and observed frost tolerance (LT_{50}) in Bjørke winter wheat from Stjørdal, Selbu, and Oppdal in 2004/05.

Table 3
Root mean square error (RMSE) in LT_{50} from cross validation of the FROSTOL model

Subset left out	2003/04			2004/05		
	Stjørdal	Selbu	Oppdal	Stjørdal	Selbu	Oppdal
RMSE	1.99	2.29	2.01	2.90	2.52	2.78

The six different combinations of year and location were left out, one at a time, during optimizing of the model parameter values on the remaining five subsets, and the subset left out was used for RMSE calculation, all collectively for two cultivars.

The only cultivar dependent character in the FROSTOL model is maximum attainable level of LT_{50} (LT_{50c}). Studies of cultivar differences in rate of hardening and dehardening have shown diverging results (Brule-Babel and Fowler, 1989; Fowler and Limin, 2004; Gusta and Fowler, 1976a, 1976b). Possible genotypic differences in rate of hardening and dehardening have been taken care of in the model by including LT_{50c} in both these functions. Hence, according to Eqs. (2) and (3), a cultivar with high maximum attainable frost tolerance would harden faster and deharden somewhat slower than a cultivar with lower maximum frost tolerance. The observed difference in LT_{50} between Bjørke and Portal in November and December is in accordance with this. The impact of LT_{50c} on rate of dehardening is smaller than the effect on rate of hardening. The difference in LT_{50c} between Bjørke and Portal was too small to give any significant difference in estimated rate of dehardening in the experiment, and no significant difference in observed LT_{50} was established.

Generally, there was a good agreement between measured and modelled values of LT_{50}. A simple correlation between observed and modelled LT_{50} values gave a coefficient of determination R^2 of 0.84 for the whole data set. Thus, the two climatic input variables, soil temperature (2 cm depth) and snow cover depth, were by the dynamics of the functional relationships able to explain most of the different courses in frost tolerance during winter.

The six different optimizing runs performed during cross validation of the model resulted in only minimal variation in the parameter values of H_{param}, D_{param} and R_{param}, and no variation in S_{param} and T_S_max (Table 2). The relatively largest variation was in D_{param} with a standard deviation amounting to 7% of the estimate from the entire data set. Hence, the parameters seem to be satisfactorily insensitive to variation in winter weather.

The parameter values of H_{param} and D_{param} are at the same order of magnitude as in the corresponding functional relationships of Fowler et al. (1999), even though two different parameterization procedures have been used. The S_{param} is about three times higher in FROSTOL than in the Canadian model. This may be quite fortuitous as only one incident with low temperature stress occurred at Oppdal in December 2003.

Mean difference between modelled and observed LT_{50} was larger for every location in 2004/05 than in 2003/04 (Table 3). Two additional tests of LT_{50} during the hardening period were included in the material from 2004/05, as compared with 2003/04. Frost tolerance increased rapidly during this period, and the model was not able to keep entirely track of the fast development. Testing the model against observations from Stjørdal 2004/05 gave the largest value of RMSE. This could largely be explained by a cold spell without any snow cover during mid March in Stjørdal that winter. In this period the plants seem to have attained some rehardening that the model has no functional relationship to account for.

Results from the simulation of frost tolerance can be translated into predictions of winter damage in the field by comparing modelled frost tolerance with the actual crown temperature. Further, a reduction in crop growth potential may be estimated based on the reduction in plant density caused by freezing injury (Kanneganti et al., 1998), thereby providing needed supplemental information to existing crop growth models of winter wheat.

Winter survival of winter wheat depends on many different biotic and abiotic factors. Snow mould, desiccation and ice encasement are all major causes of winter damage. Further, growing conditions, soil moisture, sowing time and nutritional status may also affect to what extent the plants survive winter (Andrews et al., 1997; Szucs et al., 2003; Fowler and Gusta, 1977; Tyler et al., 1981). Weather conditions during winter may vary from 1 year to another, especially in coastal areas, causing different stress factors to predominate in winter wheat fields over years. There are, however, several examples of positive correlation between frost tolerance and tolerances to other stresses (e.g. Gudleifsson and Larsen, 1993; Ergon et al., 1998). Thus, quantifying and modelling relationships between temperature, snow cover and fluctuations in frost tolerance may be considered a suitable first step towards understanding and prediction of winter damage.

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