

CLIMATE CHANGE AND AGRICULTURE PAPER

Sensitivity of barley varieties to weather in Finland

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SUMMARY

Global climate change is predicted to shift seasonal temperature and precipitation patterns. An increasing frequency of extreme weather events such as heat waves and prolonged droughts is predicted, but there are high levels of uncertainty about the nature of local changes. Crop adaptation will be important in reducing potential damage to agriculture. Crop diversity may enhance resilience to climate variability and changes that are difficult to predict. Therefore, there has to be sufficient diversity within the set of available cultivars in response to weather parameters critical for yield formation. To determine the scale of such ‘weather response diversity’ within barley (*Hordeum vulgare* L.), an important crop in northern conditions, the yield responses of a wide range of modern and historical varieties were analysed according to a well-defined set of critical agro-meteorological variables. The Finnish long-term dataset of MTT Official Variety Trials was used together with historical weather records of the Finnish Meteorological Institute. The foci of the analysis were firstly to describe the general response of barley to different weather conditions and secondly to reveal the diversity among varieties in the sensitivity to each weather variable. It was established that barley yields were frequently reduced by drought or excessive rain early in the season, by high temperatures at around heading, and by accelerated temperature sum accumulation rates during periods 2 weeks before heading and between heading and yellow ripeness. Low temperatures early in the season increased yields, but frost during the first 4 weeks after sowing had no effect. After canopy establishment, higher precipitation on average resulted in higher yields. In a cultivar-specific analysis, it was found that there were differences in responses to all but three of the studied climatic variables: waterlogging and drought early in the season and temperature sum accumulation rate before heading. The results suggest that low temperatures early in the season, delayed sowing, rain 3–7 weeks after sowing, a temperature change 3–4 weeks after sowing, a high temperature sum accumulation rate from heading to yellow ripeness and high temperatures (≥ 25 °C) at around heading could mostly be addressed by exploiting the traits found in the range of varieties included in the present study. However, new technology and novel genetic material are needed to enable crops to withstand periods of excessive rain or drought early in the season and to enhance performance under increased temperature sum accumulation rates prior to heading.

INTRODUCTION

Reducing vulnerability to climate change is a key to sustaining future agriculture. Vulnerability is defined as a function of exposure, sensitivity and adaptive capacity of a system (IPCC 2007a). It has been suggested that increasing diversity of cropping systems and livelihoods may enhance resilience and provide adaptation options to climate change (Howden *et al.*

2007). Crop cultivar diversity could also reduce sensitivity to climate variability and thus be important for adaptation, supposing a wide diversity exists in response to critical agro-meteorological variables within the available cultivar set.

Temperature sum, length of growing season and critical temperatures during important phenological stages, as well as timing and amount of precipitation, are key variables that influence potential and attainable agricultural crop yields (Kontturi 1979; Wheeler *et al.* 1996a,b; Porter & Semenov

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2005; Peltonen-Sainio *et al.* 2009c; Rajala *et al.* 2009, 2011; Trnka *et al.* 2011). Short and intensive growing season, early and late season frosts and low accumulated temperature sum are the main reasons for low yield levels in Finland. Also, precipitation early in the season is generally too low to fully satisfy the water requirements of cereals to reach full yield potential (Peltonen-Sainio *et al.* 2009c; Trnka *et al.* 2011). If conditions become more favourable later in the growing season, increase in grain weight may compensate for some of the potential yield losses, such as reduction in grain number/m², but the yield level may still be lower than the higher initial yield potential (Mitchell *et al.* 1993; Wheeler *et al.* 1996a, b; Peltonen-Sainio *et al.* 2011; Rajala *et al.* 2011). In addition to responses to drought, cereals, especially spring barley (*Hordeum vulgare* L.), are sensitive to waterlogging early in the season (Zhou *et al.* 2007; Peltonen-Sainio *et al.* 2010). Despite the trend of generally dry early season conditions, Finland, like many other European countries, has periodically suffered from heavy rains and flooding early in the season, with consequent losses in yields (Olesen *et al.* 2011). Late in the season, if harvest is delayed because of excessive rain, sensitive cereals such as wheat (*Triticum aestivum* L.), barley and rye (*Secale cereale* L.) may suffer loss of quality through pre-harvest sprouting.

Climate change is generally predicted to improve growing conditions in the North (Carter *et al.* 1996; Rötter & van de Geijn 1999; IPCC 2007a; Peltonen-Sainio *et al.* 2009a; Olesen *et al.* 2011). For example, the growing season is expected to become longer and the accumulated temperature sum higher (IPCC 2007b; Kaukoranta & Hakala 2008; Peltonen-Sainio *et al.* 2009a). However, rainfall is expected to increase only little in the spring, offering no solution to early season drought problems, but may increase in the autumn and winter, rendering the harvesting conditions worse than today (IPCC 2007b; Peltonen-Sainio *et al.* 2009c). However, the uncertainty of climate projections is high, and changes in variability of weather, including more frequent extreme events, is not usually taken into account in impact studies (Harris *et al.* 2010; Soussana *et al.* 2010; Rötter *et al.*, *in press*). Increased temperatures during the growing season (Trnka *et al.* 2011) and increased occurrence of extreme weather events such as heat waves (IPCC 2007b) may lower the yields due to accelerated development and also due to flower abortion (Mitchell *et al.* 1993; Wheeler *et al.* 1996a, b; Porter & Semenov 2005). The warm and dry growing season of 2010 provides

an example of future extreme conditions that may become more frequent in Finland; it resulted in 18% lower yield/ha for spring wheat and 39% lower yield/ha for spring barley compared with the yield levels in 2009 (Matilda Agricultural Statistics 2011). In addition to the climate-induced physical stresses, new stresses may be caused by increased occurrence of pests and pathogens (Hakala *et al.* 2011; Olesen *et al.* 2011), emphasizing the need for stress tolerance more than high productivity.

For a farmer, selection of crop cultivar is often a gamble between yield stability and potentially high attainable yields. Risk-taking farmers tend to prefer cultivars that give them a bumper harvest in good years but may lead to considerable losses in poor years, while risk-averse farmers go for cultivars that show reduced yield variations (Olesen *et al.* 2011). What then would ensure farms were well-prepared for increasing weather uncertainty and climate change, e.g. extreme weather events, changed temperatures and precipitation patterns in the future? Crop and cultivar selection are obvious factors. Historically, crop varieties have been bred to be stable under certain 'average' conditions, with the variety tests lasting usually for 10–15 years before a variety can be considered stable enough for commercial release for a particular climatic zone (Kangas *et al.* 2009). While plant breeding has succeeded in continuously producing new, more adaptive and higher yielding crop cultivars (Peltonen-Sainio *et al.* 2009b), varieties producing extremely high yields in exceptionally good conditions may be lost in the process, as the variety tests aim to find varieties that perform well on average, not just in certain years favouring an individual variety (Öfversten *et al.* 2002). Expectations for climate change derived improvement of crop production potential in Finland (Carter *et al.* 1996; Peltonen-Sainio *et al.* 2009a) emphasize the need for higher-yielding varieties with a longer growing time, especially as the climatic conditions in the future may change in favour of them. In the crossfire of alternative, both positive and negative, factors that affect crop production, it would be very important to have a diverse set of crop varieties to select from. This would offer the farmer greater flexibility and enable selection of either a more or less risky adaptation strategy in terms of increasing weather instability.

Many previous studies have attempted to predict crop responses to weather based on temperature sum and seasonal precipitation (e.g. Carter *et al.* 1996; Peltonen-Sainio *et al.* 2009a). However, the timing

of the weather variables in relation to sensitive crop phenological stages might be much more meaningful in predicting actual yields (Peltonen-Sainio *et al.* 2010; Trnka *et al.* 2011). Detailed observations of phenological and weather variables are needed to explain yield levels and to identify the most vulnerable development stages for a specific crop species (Porter & Semenov 2005). Long-term field trials, including a large set of differentially responsive varieties, offer one approach to identifying the most meaningful weather events regarding yield level and the constraints of their timing with crop phenology.

The aim of the present study was to establish the degree of response diversity to Northern climatic variables that exists among the present selection of barley varieties cultivated in Finland. Barley was chosen as the example crop as it is the most widely grown cereal in Finland and has high variety diversity. Those weather variables most critical for yield performances were first selected according to published literature and knowledge of farmers and researchers. Preliminary tests of the sensitivity of barley in general to these variables were then conducted with a large collection of varieties extending back 40 years. The weather variables found to markedly affect yields were further tested with a selection of modern barley cultivars. Diversity in the responses of this set of cultivars to the selected weather parameters was then sought in order to assess the current capacity of barley to adapt to different present and future climatic conditions in the North. The aim was to contribute to assessments of resilience of Northern crop production towards climatic variability and change.

MATERIALS AND METHODS

Variety trials

Variety trial data from MTT research stations were used whenever weather records were available from a nearby weather observatory or station (Table 1). During the first phase, all varieties from the last 40 years were included in the tests to establish general responses of barley as a species to selected weather variables under Finnish climatic conditions. After a univariate analysis, combinations of weather variables were further tested in a multivariate analysis with variables selected on the basis of the results of the univariate analysis. This first phase test data included 13 242 yield records. In the second phase, a set of modern cultivars of both Finnish and foreign origin, from the late 1980s to the present, and older cultivars

Table 1. Selected experimental sites, their latitudes, longitudes, average sowing dates and number of trials

Location	Latitude		Longitude	Sowing date	Trials
	North	East			
Piikkiö	60°23'	22°33'		13 May	12
Pernaja	60°26'	26°02'		7 May	5
Mietoinen	60°38'	21°55'		15 May	67
Anjalankoski	60°41'	26°48'		18 May	37
Jokioinen	60°49'	23°30'		15 May	28
Kokemäki	61°17'	22°15'		16 May	20
Pälkäne	61°20'	24°13'		14 May	44
Mikkeli	61°40'	27°10'		15 May	30
Tohmajärvi	62°14'	30°21'		20 May	38
Laukaa	62°19'	26°19'		21 May	53
Ylistaro	62°57'	22°30'		13 May	118
Maaninka	63°09'	27°19'		21 May	35
Sotkamo	64°01'	28°22'		22 May	18
Ruukki	64°40'	25°06'		22 May	59

that are still cultivated during the 2000s were tested, amounting to 2384 records. These cultivars are listed in Table 2. The northernmost test site was Ruukki (64°40'N, 25°06'E).

Most of the variety trial experiments were part of the MTT Official Variety Trials and all followed procedures specified for that purpose (Kangas *et al.* 2009; Peltonen-Sainio *et al.* 2011). In addition to MTT Agrifood Research Finland, which has numerous regional research units in Finland, some of the experiments were organized by plant breeding companies and private agricultural research stations.

All experiments were arranged as randomized complete block designs or incomplete block designs. Numbers of replicates varied between 3 and 4. Each year the test set of varieties changed, but long-term control varieties were used. Plots were 7–10 × 1.25 m, depending on location and year. Fertilizer use depended on cropping history, soil type and fertility and was comparable with standard practices in Finland.

Yield was combine-harvested and weighed (t/ha) after removing straw, weed seeds and other particles. Grain moisture content was determined by weighing grain samples before and after oven drying or more recently by using a Dickey John apparatus. Yield was adjusted to 150 g moisture/kg.

Selection of climatic variables and their thresholds

Based on the literature (e.g. Trnka *et al.* 2011) and local observations regarding barley performance under

Table 2. *Modern barley cultivars tested and selected agronomic information*

Cultivar	Owner	Year of release	First test	Last test	<i>n</i>	Tests in 2000s	Heading (DAS)	Yellow maturation (DAS)	Average yield (kg/ha)	Diff. average heading	Diff. average maturity
Kustaa	SW	1979	1976	2001	417	25	52.7	94.3	4171	−1	1
Pohto	Bor	1987	1984	2001	345	28	51.1	89.9	4758	−2	−3
Arve	Gr	1989	1987	2003	301	56	48.7	85.8	4733	−5	−7
Artturi	Bor	1992	1989	2008	141	14	49.3	84.4	4641	−4	−9
Botnia	Bor	1996	1989	2003	132	1	51.0	90.7	4959	−2	−2
Saana	Bor	1996	1992	2008	141	75	54.3	92.7	4612	1	0
Rolfi	Bor	1997	1990	2009	189	86	48.7	85.1	4805	−5	−8
Erkki	Bor	1998	1992	2008	107	25	50.8	89.7	5027	−3	−3
Scarlett	SJB	1998	1995	2009	136	106	53.9	94.0	4851	1	1
Jyvä	Bor	2000	1997	2008	76	32	48.1	89.8	4871	−5	−3
Kunnari	Bor	2001	1997	2009	155	111	51.0	91.8	5240	−2	−1
Gaute	Gr	2003	2001	2005	42	42	51.8	88.6	5182	−2	−4
Annabell	NS	2003	2001	2009	80	80	55.6	97.2	5208	2	4
Maaren	SW	2004	2002	2008	40	40	55.1	96.2	5073	2	3
Edel	Gr	2004	2001	2009	43	43	52.8	93.0	5319	−1	0
Voitto	Bor	2005	2002	2009	48	48	49.1	86.3	5052	−4	−7
Vilde	Gr	2005	2003	2009	38	38	51.3	90.0	5539	−2	−3
Pilvi	SW	2005	2003	2009	40	40	49.1	86.1	5000	−4	−7
Braemar	SS	2005	2002	2007	37	37	53.9	95.8	4807	1	3
Tocada	KWS	2006	2004	2009	37	37	54.8	97.7	5479	1	5
Olavi	Bor	2006	2003	2009	45	45	51.2	90.3	5165	−2	−3
Tiril	Gr	2006	2004	2009	37	37	49.1	87.1	5340	−4	−6

SW, Svalöf Weibull AB, Sweden; Bor, Boreal Plant Breeding Ltd, Finland; Gr, Graminor AS, Norway; SJB, Saatzucht Josef Breun GdbR, Germany; NS, Nordsaat Saatzuchtgesellschaft GmbH, Germany; SS, Syngenta Seeds Ltd, England; KWS, KWS Lochow GmbH, Germany.

DAS, days after sowing. Diff. average heading and Diff. average maturity, difference of heading or yellow maturation (DAS) compared to average of all cultivars (negative number means earlier than average). Average yields for the cultivars are national averages up to 64°40'N.

Table 3. Pre-selection of agro-meteorological variables expected to have a marked influence on growth and yield formation, and the expected yield response in barley. In parentheses, the name of the tested variable in Tables 4 and 5 and in Figs 1 and 2

Variable	Expected yield response
1. Rain for 1 month before sowing.	May lead to delayed sowing if soil is too wet to carry tractors, and consequently to lower yields if conditions become too hot and dry for optimal yield formation (Peltonen-Sainio <i>et al.</i> 2009c).
2. Delayed sowing (sowing date).	See variable 1.
3. Early season drought and waterlogging (rain 0–3 weeks after sowing).	Early season drought may delay germination and early development, water logging may significantly reduce yields (Zhou <i>et al.</i> 2007; Peltonen-Sainio <i>et al.</i> 2010).
4. Drought at yield potential determination (rain 3–7 weeks after sowing).	Drought at yield potential formation may reduce grain number and yield (Rajala <i>et al.</i> 2009, 2011).
5. Frost damage during early growth (lowest temperature during 0–4 weeks after sowing).	Early season frost may cause significantly reduced yield of e.g. turnip rape, but has not been tested previously with barley, although general opinion is that Finnish cereals are not susceptible to mild early season frosts (Peltonen-Sainio <i>et al.</i> 2009a, c).
6. Temperatures at tillering phase (temperatures during 3rd and 4th weeks after sowing).	Traditionally it is held that a slow start to growth (low temperatures during vegetative phases of cereals) may increase yields, but this has not been tested previously.
7. High temperature stress (number of days with maximum temperature of 25 °C or higher 1 week before to 2 weeks after heading).	Very high temperatures during early generative phases have been shown to reduce grain number and yield (Wardlaw <i>et al.</i> 1989a; Mitchell <i>et al.</i> 1993; Wheeler <i>et al.</i> 1996a).
8. Very high temperature stress (number of days with maximum temperature of 28 °C or higher 1 week before to 2 weeks after heading).	See variable 7.
9. Rate of temperature sum (Tsum) accumulation before heading (Tsum accumulation rate from 14 days before heading to heading).	Increased rate of development at yield potential formation has been shown to reduce grain number and yield (Mitchell <i>et al.</i> 1993; Wheeler <i>et al.</i> 1996a; Hakala 1998).
10. Rate of Tsum accumulation at grain filling (Tsum accumulation rate from heading to yellow ripeness).	Increased temperature has been shown to shorten the duration of grain filling (Evans & Wardlaw 1976; Kontturi 1979; Wardlaw <i>et al.</i> 1989a; Wheeler <i>et al.</i> 1996b; Hakala 1998) and may thus reduce grain yield.
11. Mean daily temperature sum accumulation rate at grain filling (Tsum accumulation rate (per day) from heading to yellow ripeness).	See variable 10.

different temperature and precipitation patterns, agro-meteorological variables that were expected to have a marked influence on growth and yield formation of barley were pre-selected (see Table 3). The Zadoks scale (Zadoks *et al.* 1974) was applied for characterizing crop phenology.

Imputation of missing values

The set of varieties varied from trial to trial. Sowing day was the same for all varieties in a trial, but the dates of heading (growth stage (GS) 55) and yellow ripeness (GS92) depended on variety. To calculate mutually comparable heading and yellow ripeness days for all

trials, the following analysis of variance model was fitted:

$$\text{date}_{kl} = \mu + \text{trial}_k + \text{variety}_l + \varepsilon_{kl} \quad (1)$$

where date_{kl} is observed heading or yellow ripeness date, μ is intercept, variety_l is the effect of l^{th} variety, trial_k is the effect of k^{th} trial and ε_{kl} is the residual.

Dates of sowing, heading and yellow ripeness were not available for all trials. The number of missing dates was 8 for sowing, 267 for heading and 29 for yellow ripeness for the 514 trials. Latitude plays a key role in timing in Finland. Missing dates were estimated using known days and latitudes. In addition, trials for oats (*Avena sativa* L.) and spring wheat were used to make

Table 4. Correlation among the tested climatic variables*. The upper value is the Pearson correlation coefficient, the lower value is significance for the coefficient

	var1	var2	var3	var4	var5	var6	var7	var8	var9	var10	var11
var1		0.33	0.01	-0.10	0.23	0.25	0.09	0.09	0.15	0.02	0.04
		<0.001	0.832	0.022	<0.001	<0.001	0.040	0.037	<0.001	0.673	0.356
var2			0.19	0.06	0.36	0.32	-0.08	-0.08	-0.04	-0.02	-0.38
			<0.001	0.144	<0.001	<0.001	0.067	0.048	0.353	0.589	<0.001
var3				-0.05	0.09	-0.13	0.21	0.15	0.19	-0.02	0.02
				0.287	0.043	<0.01	<0.001	<0.001	<0.001	0.623	0.684
var4					-0.02	-0.05	-0.14	-0.19	-0.24	-0.02	-0.05
					0.662	0.213	<0.001	<0.001	<0.001	0.704	0.218
var5						0.23	-0.08	-0.03	-0.05	0.16	-0.02
						<0.001	0.065	0.490	0.275	<0.001	0.672
var6							-0.11	-0.05	-0.03	0.17	0.04
							0.010	0.200	0.478	<0.001	0.331
var7								0.83	0.58	-0.07	0.59
								<0.001	<0.001	0.120	<0.001
var8									0.54	-0.06	0.57
									<0.001	0.184	<0.001
var9										-0.10	0.44
										0.017	<0.001
var10											0.15
											<0.001
var11											

* var1, rain for 1 month before sowing; var2, sowing date; var3, rain 0–3 weeks after sowing; var4, rain 3–7 weeks after sowing; var5, lowest temperature during 0–4 weeks after sowing (whole period); var6, temperatures during 3rd and 4th weeks after sowing; var7, number of days with maximum temperature of 25 °C or higher 1 week before to 2 weeks after heading; var8, number of days with maximum temperature of 28 °C or higher 1 week before to 2 weeks after heading; var9, Tsum accumulation rate from 14 days before heading to heading; var10, Tsum accumulation rate from heading to yellow ripeness; var11, Tsum accumulation rate (per day) from heading to yellow ripeness.

latitude-based estimates more accurate. The following model was used to estimate missing dates:

$$\text{date}_{ijk} = \mu + \text{species}_i + \text{year}_j + \beta_1 \text{ latitude} + \text{year}_j \times \beta_1 \text{ latitude} + \varepsilon_{ijk} \quad (2)$$

where date_{ijk} is the known date for k th trials (in analysis of heading and yellow ripeness date is estimates of trial_k from the Eqn 1), μ is the intercept, species_i is the effect of i th species ($i = \text{barley, oats, spring wheat}$), year_j is the effect of j th year ($j = 1976, \dots, 2009$), β_1 is the regression slope from latitudes presented in Table 1. $\text{Year}_j \times \beta_1 \text{ latitude}$ allows for regression slope to vary from year to year (i.e. in some years sowing occurs simultaneously in the whole study area, in some years differences can be more than 3 weeks). Finally, ε_{ijk} is the residual. Residuals showed that the difference between true and estimated date was typically less than 3 days.

General responses of barley to weather conditions

A univariate approach was used to find general responses to weather conditions, i.e. regression analysis was used to model response for each weather parameter separately. If the response was not linear (e.g. early season drought and waterlogging), the weather parameter was classified into 2–3 groups.

A multivariate approach was taken after univariate analyses using a multiple regression model. The initial model included all the climatic variables from the univariate analysis. However, moderately and highly correlated variables ($r > 0.50$) were not accepted because of the potential multi-collinearity problem. A correlation matrix of climatic variables is presented in Table 4. After this, backward selection was used to reduce the model, i.e. the least significant variable was dropped, one at a time, until only statistically significant or almost significant effects ($P < 0.10$) were left.

Responses of selected modern barley varieties to weather conditions

Modern and also older, but currently cultivated, varieties were selected when interactions between varieties and weather parameters were tested (Table 2). Weather parameters were classified into three categories of equal numbers of trials, e.g. rain during 1 month before sowing was classified according to monthly rainfall at: up to 23, 23–41 and 41–113 mm of rain/month. Interaction was analysed using the following mixed model:

$$y_{ijk} = \mu + \text{variety}_i + \text{category}_j + \text{variety} \times \text{category}_{ij} + \text{trial}(\text{category})_{kj} + \varepsilon_{ijk}$$

where y_{ijk} is the observed yield, μ is the intercept, variety_i is the average yield level of i th variety, category_j is the average yield level at j th level of categorized environment ($j=1, 2, 3$) and $\text{variety} \times \text{category}_{ij}$ is the variety-by-environment interaction. All the above effects are fixed in the model. $\text{trial}(\text{category})_{kj}$ is the random effect of k th trial within j th category and ε_{ijk} is normally distributed residual error.

When comparing modern cultivars, the effects of various weather variables on crop yields are presented as percentage of the average national yield calculated for the variety. This approach was taken as the differences in the average yields of the studied cultivars were large, ranging from 4000 to 5500 kg/ha (Table 2), and thus losses or gains in kilograms would not be a meaningful measure of cultivar sensitivity. As the statistical testing was performed only for variety trials where there was also a weather observatory close by, and the results were compared with the total cultivar average, the columns in the figures do not always reach 100%, even when all possible conditions are included in the results.

All statistical analyses were performed using the MIXED and REG procedures in SAS software (version 9.1).

RESULTS

General yield responses of barley to rainfall and temperature

In general, yield levels of barley varieties differed significantly ($P < 0.001$) from each other in all tested weather conditions. High rainfall before sowing and delayed sowing reduced barley yields (Table 5). During the first 3 weeks after sowing, the general

effect of rainfall was negative. However, when the rainfall was divided into three classes: low (0–18.2 mm), moderate (18.3–33.6 mm) and high (33.7–122.4 mm), moderate rainfall resulted in high yields, while both high rainfall and low rainfall reduced yields considerably. At later stages, when the crop had already established (3–7 weeks after sowing), increase in rainfall increased yield (Table 5).

Early season frost had no effect on yield. However, cool start of season increased yields: the yield was significantly reduced by increases in temperatures during the 3rd and 4th weeks after sowing (Table 5a). Very high temperatures (≥ 25 °C) during a period of 1 week before and 2 weeks after heading reduced yields significantly. The effect was increased with increasing temperature. High temperature sum accumulation rate during a period of 2 weeks before heading decreased the yield slightly, while at a later phase, during the period from heading to yellow ripeness, increase in temperatures (higher temperature sum for the period) increased the yields, especially when calculated as a rate of temperature sum accumulation (°C d/day) (Table 5a).

A multivariate analysis was performed to establish how the different weather variables tested individually would affect yields when they coincide during a growing season. The results are shown in Table 5b. Of the variables affecting the yields significantly when tested alone, sowing date, rain during the first 3 weeks after sowing (when grouped into three categories), rain 3–7 weeks after sowing, temperatures during 3rd and 4th weeks after sowing, number of days with maximum temperature of 25 °C or higher and temperature accumulation rate from heading to yellow ripeness (°C d/day) affected the yields statistically significantly (Table 5b). It was found that when tested together, drought during the early phases of development caused a bigger effect than when tested alone, while heavy rain during the early phases of development caused a lower effect than when tested alone. High (≥ 25 °C) and very high (≥ 28 °C) temperatures around heading caused more yield reduction and with higher statistical significance when tested together with other variables than when tested alone. Increased temperature sum accumulation rate, again, had a bigger effect on yield when tested together with other weather variables. Effects of delayed sowing, as well as rain and temperatures at early tillering, affected the yields only slightly differently when tested together with other variables than when tested alone. When experimental site was included in the multivariate model (Table 5c),

Table 5. Effects of the tested climatic variables on yield of all barley varieties tested during the last 40 years, at sites where weather information was also available (total of 13 242 yield records). (a) Univariate analysis, (b) multivariate analysis and (c) multivariate analysis where experimental site is included in the model. *beta_hat*=estimated yield effect (kg/ha) per parameter unit; *s.e.*, standard error; *P*, statistical significance of the response of barley to the climatic variable

<i>beta_hat</i>	<i>s.e.</i>	<i>P</i>	Climatic variable
(a) Univariate analysis			
– 6.29	3.04	0.039	Rain for 1 month before sowing
– 35.12	7.66	<0.001	Sowing date
– 8.38	2.60	<0.01	Rain 0–3 weeks after sowing
– 257/– 551*		<0.001	Rain 0–3 weeks after sowing: 3 groups
5.19	1.99	<0.01	Rain 3–7 weeks after sowing
– 7.22	23.91	0.763	Lowest temperature during 0–4 weeks after sowing (whole period)
– 53.74	21.16	0.011	Temperatures during 3rd and 4th weeks after sowing
– 41.20	13.80	<0.01	Number of days with maximum temperature of 25 °C or higher 1 week before to 2 weeks after heading
– 76.85	32.20	0.017	Number of days with maximum temperature of 28 °C or higher 1 week before to 2 weeks after heading
– 4.51	2.10	0.033	Tsum accumulation rate from 14 days before heading to heading
2.50	0.96	<0.01	Tsum accumulation rate from heading to yellow ripeness
59.63	29.92	0.047	Tsum accumulation rate (per day) from heading to yellow ripeness
(b) Multivariate analysis			
– 20.84	9.51	0.029	Sowing date
– 357/– 492*		<0.001	Rain 0–3 weeks after sowing: 3 groups
3.93	1.94	0.043	Rain 3–7 weeks after sowing
– 48.52	23.74	0.041	Temperatures during 3rd and 4th weeks after sowing
– 82.27	17.78	<0.001	Number of days with maximum temperature of 25 °C or higher 1 week before to 2 weeks after heading
138.97	41.60	<0.001	Tsum accumulation rate (per day) from heading to yellow ripeness
(c) Multivariate analysis with experimental site included			
– 24.48	10.17	0.022	Sowing date
– 263/– 403*		<0.01	Rain 0–3 weeks after sowing: 3 groups
3.45	1.94	0.077	Rain 3–7 weeks after sowing
– 53.84	23.51	0.022	Temperatures during 3rd and 4th weeks after sowing
– 79.28	17.89	<0.001	Number of days with maximum temperature of 25 °C or higher 1 week before to 2 weeks after heading
114.52	44.15	<0.01	Tsum accumulation rate (per day) from heading to yellow ripeness

* The weather parameter was classified into three classes: low (0–18.2 mm), moderate (18.3–33.6 mm) and high (33.7–122.4 mm), as with the selected modern cultivars. The figures denote difference of low/high compared to moderate.

most of the tested variables remained significant and the effects on yield were only slightly altered.

Diversity of modern barley varieties in response to rainfall at different growth stages

In accordance with the general variety trial results described above, high rainfall before sowing resulted

in yield reduction also when tested separately with the selected modern cultivars (Table 2, Fig. 1a). The lowest rainfall category resulted in consistently higher yields than the highest category. In general, the cultivars tended to react differently to rain before sowing ($P=0.103$). For example, cultivars Saana, Kustaa and Maaren had equal yields with low or moderate rain before sowing, and yield decreased only when

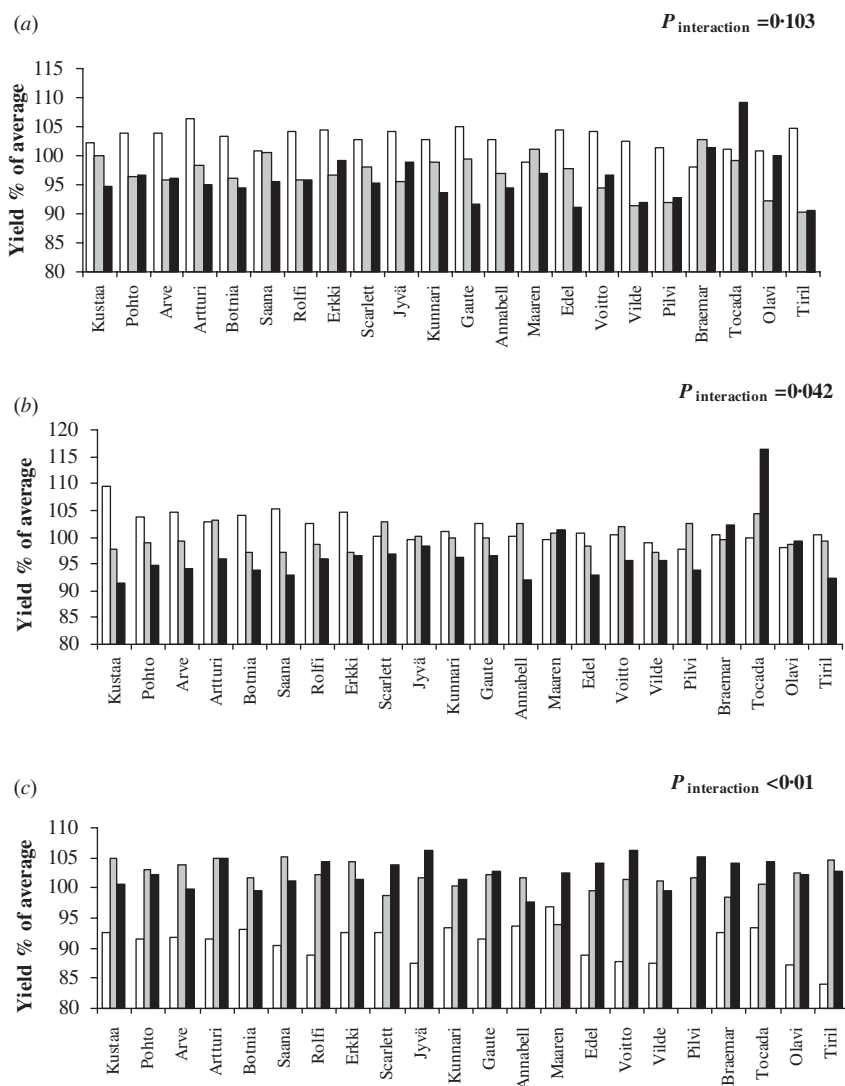


Fig. 1. Responses of the chosen modern barley cultivars to (a) rain for 1 month before sowing (mm/month), (b) delay of sowing (sowing date) and (c) rain during 3–7 weeks after sowing (rain sum mm/period). P , statistical significance for the interaction between the cultivar and the climatic parameter. White, grey and black columns denote, respectively, categories low, moderate and high (extreme), or in: (a) rain sum: 1.1–23.1, 23.2–40.7 and 40.8–112.9 mm; (b) dates: 25 April–12 May; 13–19 May and 20 May–6 June; (c) rain sum: 2.3–39.4, 39.5–63.3 and 63.4–176.7 mm. P values for the interaction between the cultivar and the categories and the average standard error of difference (S.E.D.) of the categories within cultivars are 0.103 and 4.8%, 0.042 and 4.5% and <0.01 and 4.6% in (a), (b) and (c), respectively.

precipitation before sowing was very high. In contrast, the cultivar Braemar had the highest yield at moderate and high rainfall levels before sowing and cultivar Tocada had the highest yield at the highest rainfall before sowing.

The effect of high pre-sowing rainfall on yield might be explained by the weather-forced delay of sowing in the spring due to soil water saturation (Trnka *et al.* 2011). Therefore, delayed sowing should also decrease yields. This seemed to hold true in most cases (Fig. 1b). However, the cultivars significantly differed

in their responses ($P=0.042$). Cultivars Jyvä, Olavi, Maaren and Braemar showed little response to sowing date at the tested sowing windows (end of April–12 May; 13–19 May and end of May–beginning of June). Cultivar Tocada, again, produced its highest yield at the latest sowing.

All the tested modern barley cultivars responded similarly ($P=0.539$) to rainfall during the first 3 weeks after sowing (results not shown). When rain increased from the lowest class 0–18 mm to 18–34 mm, the yield increased. The only exception here was cultivar

Maaren, the yield of which seemed to decrease consistently with increasing precipitation. When rainfall increased from 34 up to 122 mm during the 3 weeks from sowing, the yield decreased for all cultivars tested. At a later phase, during 3–7 weeks after sowing, yield increased when precipitation increased from low (2.3–39.4 mm) to moderate (39.5–63.3 mm) in all but one (Maaren) cultivar tested (Fig. 1c). When rainfall increased further, to a rain sum of 63.4–176.7 mm, the yield response was rather small, but more variability within the tested cultivars appeared. The yields either increased further, decreased or there was no change. Even though cultivars differed in their responses to rainfall at this stage ($P < 0.01$), all produced the lowest yield at the lowest rainfall level.

Diversity of modern barley cultivars in response to temperatures at different growth stages

All tested modern barley cultivars yielded best when the average temperatures during early growth (3–4 weeks after sowing) were low (Fig. 2a). Even though the lowest temperature category resulted in higher yields in all cultivars, the cultivars differed in their reactions to early season temperatures ($P < 0.001$). Cultivars Tocada, Braemar, Scarlett and Maaren were characterized by a pattern of reduced yield at moderately increased early season temperatures, but yield increased when the temperatures rose to an even higher level (Fig. 2a). Yields of other cultivars were either stable or decreased under higher temperatures compared with moderate temperatures. During the period of 2 weeks before heading, increased average temperatures decreased yield (Fig. 2b). However, the decrease was significant only between the first two threshold temperature sums, 63–135 °C d and 139–159 °C d. When the temperatures increased further during this phase, the yields seemed to increase consistently, but the increase was not statistically significant. All barley cultivars tested behaved similarly ($P = 0.725$).

When maximum day temperatures increased to very high (≥ 25 °C or even ≥ 28 °C) levels during the period of 1 week before and 2 weeks after heading (the period in which anthesis takes place), the effect depended on the duration of exposure to the high temperatures (Fig. 2c). No change in yield was detected when the exposure to temperatures reaching or exceeding 25 °C was short, but when the exposure lasted for more than 6 days, there were yield penalties

in most of the barley cultivars studied. The cultivars differed statistically significantly from each other in their responses to high temperatures ($P = 0.052$ for ≥ 25 °C and $P = 0.023$ for ≥ 28 °C) and in the extent of the yield penalty. Under conditions with maximum daily temperatures of 25 °C for more than 6 days, there was no yield penalty for two cultivars: the old cultivar Kustaa and the Finnish cultivar Botnia (results not shown). Under even higher temperatures (daily maximum temperatures of 28 °C or higher for more than 6 days), the yield penalties were in some cases very serious, with yields decreasing to only 70–80% of the average yield level (Fig. 2c). The German bred cultivars Annabell and Scarlett and the Scandinavian Maaren and Vilde suffered the biggest losses, while there were small yield losses in cultivar Kustaa.

Temperature sum accumulation rate from heading to yellow ripeness affected the yields of the tested barley cultivars significantly. The lowest accumulation rates resulted in most cases in lower yields than the highest accumulation rates, but the highest yield levels were reached at moderate temperature sum accumulation rates (Fig. 2d). Although the general responses were relatively consistent, the cultivars differed in their responses ($P < 0.001$). In cultivars Jyvä, Annabell and Braemar, the yields were the same at both moderate and high accumulation rates. The highest yield penalties following low accumulation rates were in cultivars Olavi and Annabell (Fig. 2d). The cultivar Jyvä seemed to yield equally well at all temperature conditions compared in the present work.

DISCUSSION

The spectrum of response among diverse barley varieties to northern weather conditions was established. The main findings are that under Finnish conditions there is a relatively high diversity of response among varieties that should be fully exploited for developing local adaptation strategies. There was, however, no response diversity to drought and excess rain early in the season or to high temperature sum accumulation rate before heading which severely reduced yields of all cultivars.

Yield responses to rainfall

The effect of delayed sowing seemed to be more significant than the effect of high rainfall *per se*, yet with high response diversity among cultivars. Some of the cultivars, irrespective of their origin, responded

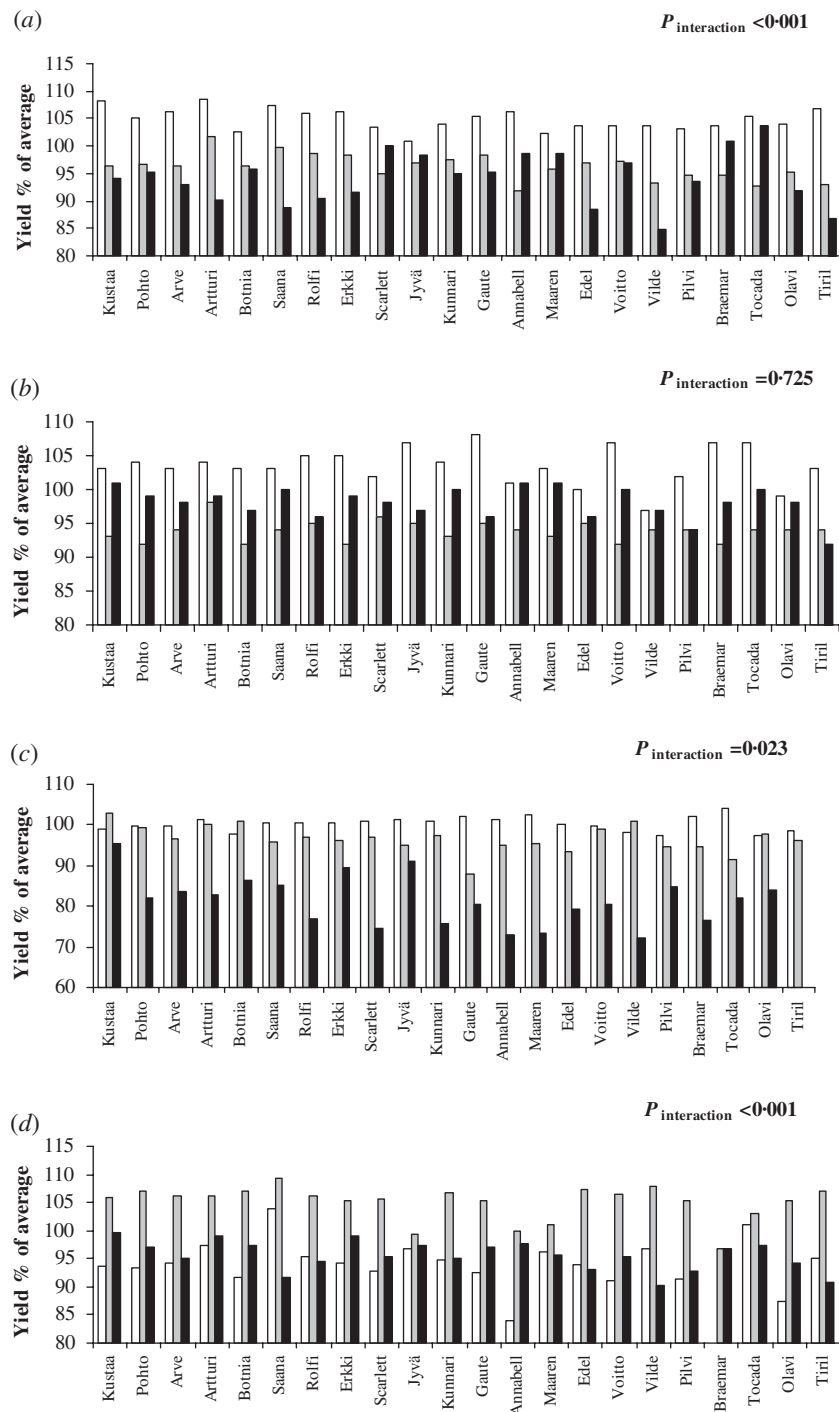


Fig. 2. Responses of the chosen modern barley cultivars to (a) temperatures during 3rd and 4th weeks after sowing (average temperature, °C for the period), (b) temperature sum accumulation rates during the period of 2 weeks before heading (Tsum, °C d for the period), (c) very high temperatures (maximum day temperatures 28 °C or higher) during the period of 7 days before and 14 days after heading and (d) temperature sum accumulation rate during the period of grain filling (heading to yellow ripeness) (°C d/day during the period). *P*, statistical significance for the interaction between the cultivar and the climatic parameter. White, grey and black columns denote, respectively, categories low, moderate and high (extreme), or in: (a) average temperatures: 6.3–11.6, 11.6–13.7 and 13.8–19.1 °C; (b) temperature sum: 63–135, 136–159 and 160–237 °C d; (c) duration: 0–2, 3–5 and more than 6 days; (d) temperature sum accumulation rate: 5.2–10.2, 10.3–11.5 and 11.6–16.6 °C d/day. *P* values for the interaction between the cultivar and the categories and the average S.E.D. of the categories within cultivars are <0.001 and 4.5%, 0.725 and 4.8%, 0.023 and 3.8% and <0.001 and 4.7% in (a), (b), (c) and (d), respectively.

little if at all to a delay in sowing. Tocada differed clearly from the other cultivars, giving the highest yield at the highest rainfall before sowing and also at the latest sowing. Tocada was the latest maturing and the longest-growing cultivar in the present study. It is possible that it can benefit not only from a long growing season but also from a warm early season, requiring a high temperature sum for optimal yield, as would be expected for a cultivar originating from Germany. In the expected warmer future conditions, with an earlier start to the growing season, the problems that occur today with soil moisture and delayed sowings in the spring may still prevail (Kaukoranta & Hakala 2008). Cultivars such as Tocada might be the best types to cultivate under such conditions, at least in southern Finland.

The effect of rainfall on barley yield during the 3-week period after sowing was negative (Table 5). This contradicts the hypothesis that drought, rather than heavy rain, early in the season leads to decreased yield potential and lower yield. When the total rain sum for this period was divided into three categories, it was found that both low and high rain sum during the first 3 weeks after sowing resulted in lowered yield compared with moderate rain, with no difference in response between the cultivars. Heavy rains after sowing can have at least two kinds of effect: mechanical disturbance and water logging. If heavy rain occurs just after sowing and is followed by a dry and warm period, the soil surface can be sealed and crusted, hampering seedling emergence and resulting in sub-optimal stand density and lower yields. Heavy and long lasting rains after emergence, again, can result in water logging and anoxia. Mechanical damage such as crust formation on the soil surface is difficult to combat. Breeding new barley varieties with water logging resistance, however, is in progress (Zhou *et al.* 2007), but until substantial breakthroughs in performance of commercial cultivars have taken place, more conventional drainage measures have to be used to remove the excess water from the fields. An expected increase in heavy rains as climate changes calls for new methods and innovations to control water in the fields, especially as extensive periods of drought may occur between the heavy rains.

The present results showed a general and significant increase in yield with increased rain during 3–7 weeks after sowing (Table 5). It seems that no barley cultivar currently grown can produce maximum yields if drought limits formation of yield potential (number of tillers, ears and grains/m²). Drought is a very common

problem in Finland during early growth stages of spring cereals (Peltonen-Sainio *et al.* 2009c), and it has been previously reported that every 10 mm increase in precipitation during this phase increases yields by 45–75 kg/ha (Peltonen-Sainio *et al.* 2011). Later in the season, even if precipitation increases, the reduced sink size cannot recover, although the grains may grow bigger to compensate (Rajala *et al.* 2009, 2011). In barley, an increase in grain size has not been found to compensate for the yield losses caused by reduced grain number (Peltonen-Sainio *et al.* 2011; Rajala *et al.* 2011), whereas in spring wheat, even full compensation has been reported, caused partly by more grains developing from the smaller number of florets (Rajala *et al.* 2009). The current results show, however, that the yield increase from higher precipitation has a limit, at least in some barley cultivars: after a certain precipitation level, more rain fails to increase yields further (Fig. 1c). A comparable result was found with winter wheat, where rain first increased yields but, after an optimum, started to decrease yields (Kristensen *et al.* 2011). It would be tempting to suggest that the varieties with the highest yield potential would benefit from higher precipitation levels, but among the tested cultivars this seems not to hold true; the differences in yield responses to the highest precipitation levels do not coincide with the yield levels (Table 2, Fig. 1c).

Unless breeding succeeds in enhancing drought resistance of barley, future conditions may cause even worse cultivation problems than is currently the case (Rötter *et al.*, *in press*). According to the most recent scenarios (Harris *et al.* 2010; Trnka *et al.* 2011) for future climatic conditions in high latitudes, precipitation in the spring and summer will increase slightly. However, major uncertainties exist in climate projections, especially regarding precipitation (Harris *et al.* 2010). Even though areas in the North are likely to become wetter in the future, the increases in precipitation are predicted to take place mainly in the autumn and winter. This offers no solution for the early season drought problems, especially as the temperatures, and thus evaporation rates, will increase simultaneously (Harris *et al.* 2010; Trnka *et al.* 2011). The situation may be even more difficult in the future if the already insufficient precipitation falls increasingly as heavy rains, as suggested by the IPCC (2007b). Heavy rains may result in both waterlogging and run-off water escaping from the field; neither phenomena benefiting the plants as would moderate rain falling over a longer time period.

Yield responses to temperature

The last frosts in Finland may occur as late as June even in the southernmost parts of the country. This means that crops such as spring barley, which are currently sown around mid-May (13–22 May, Table 1), may have emerged and already be growing when freezing occurs. However, barley seems to be rather resistant to frosts during its early growth phases (Table 5a). The result was the same whether the lowest temperatures during early growth were -7 to -2 , -2 to -0 or -0 to 9 °C (results not shown), and there were no differences in the responses among varieties. The frosts occurring during the early season are mostly night frosts and typically last only for a few hours. In addition, during the initial stages of barley development the canopy is low enough to be partly protected by the relatively warm soil, even when frost is measured at 2 m above the soil surface. Also, during early stages of growth grass meristems remain buried in the ground, and even if the leaves were to suffer frost damage, the meristems usually remain undamaged. If leaves are destroyed by frost, there is a delay in growth, but typically other conditions later on affect the growth of the plant more than this early delay.

According to an old Finnish saying ‘shivering sets the seed’, which means that cold weather at the beginning of the season promises good yield. This old wisdom seems to hold true, as in the present test all barley varieties yielded best when the average temperatures during early growth (3–4 weeks after sowing) were low (Table 5, Fig. 2a). One of the reasons for the beneficial effects of low temperatures early in the season may be slower development. When the shift from the vegetative to the generative growth phase is delayed, roots may penetrate deeper into the soil and grow larger, which helps the plant to acquire nutrients and water later on in the season from the larger soil mass. In addition, tillering may be enhanced, leading to a denser canopy with more reproductive organs, higher grain number per unit area and ultimately increased yield (Evans & Wardlaw 1976). Also in a recent study with winter wheat, high winter temperatures resulted in lowered yields, possibly due to hastened development leading to sub-optimal canopy density and reduced tiller and ear number (Kristensen *et al.* 2011). A cool start to a season also usually means higher moisture levels in the soil and lower evapotranspiration, thus less limiting moisture conditions early in the season. Although a cool early season increased yield in general, the cultivars differed in their reactions to

early season temperatures. Cultivars originating from lower latitudes than Finland, such as Tocada, Braemar, Scarlett and Maaren, showed a pattern of lowered yield at moderately increased early season temperatures, but regained some of the yield when the temperatures rose (Fig. 2a). Yields of other cultivars, either of Finnish or foreign origin, were either stable or decreased at higher temperatures, compared with at moderate temperatures. The differing reactions of the cultivars tested to high early season temperatures emphasize the importance of looking at the timing of climatic events when assessing effects on yield: the effect seems to depend particularly on the development stage of a variety. The fact that the responses of the cultivars in the present work differed gives hope for finding suitable varieties adapted to future warmer conditions, with markedly earlier sowing dates (Peltonen-Sainio *et al.* 2009a) and somewhat lowered frost risk (Trnka *et al.* 2011).

High temperature sum accumulation rates during a period 2 weeks before heading decreased yield levels, with all barley varieties behaving similarly (Table 5, Fig. 2b). In earlier investigations, yield responses of barley to increases in temperatures were found to be most marked exactly during the developmental phase just prior to heading (Peltonen-Sainio *et al.* 2011). The cause for this may be accelerated development that may result in smaller numbers of grains/m² and thus reduced yield, especially if the grain-filling period is also shortened (Evans & Wardlaw 1976; Kontturi 1979; Wheeler 1996a,b; Hakala 1998; Kristensen *et al.* 2011; Peltonen-Sainio *et al.* 2011). Higher temperatures also lead to a higher evapotranspiration and resulting drought problems, which can lower yield potential and lead to a lower yield (Peltonen-Sainio *et al.* 2009c, 2011; Rajala *et al.* 2011).

In general, barley suffered significantly from periods with very high temperatures (≥ 25 °C) that occurred just before and after anthesis, when the exposure lasted longer than 6 days (Fig. 2c). Very high temperatures during early phases of heading and anthesis may damage the florets of the developing ears in addition to accelerating development, leading to reduced grain number (Wardlaw *et al.* 1989a; Mitchell *et al.* 1993; Wheeler *et al.* 1996a). During grain filling, high temperatures may still cause damage to grains and yield, but this results not so much from reductions in grain number as from a decrease in grain weight (Wardlaw *et al.* 1989a). In an Australian experiment with wheat, the varieties under study differed in their sensitivity to high temperatures so that those sensitive at booting were less sensitive at later phases of grain

development (Wardlaw *et al.* 1989a). As the number of florets was not counted in the variety trials reported here, it is not clear whether the high temperatures simply accelerated growth rate and shortened the period during which florets were turning into grains or physically damaged the florets.

In a study of wheat, Wardlaw *et al.* (1989b) found that the varieties originating from warmer conditions were not necessarily the least sensitive to hot weather. In the present study, the biggest losses attributable to very high temperatures were associated with a number of cultivars originating from lower latitudes than those typical for Finland. While some Finnish cultivars also suffered in hot weather, the old cultivar Kustaa, which has been cultivated widely in Finland for many years, coped better with hot conditions than any other cultivar tested. This surprising result may at least partly be explained by the low average yield of Kustaa (Table 2): it seems to be one of those varieties that have been selected due to yield stability rather than high yielding performance. Despite the fact that the last 10 years have been among the warmest ever (IPCC 2007b), some of the newest cultivars tested here were among the most sensitive. The same phenomenon has been recorded for turnip rape (*Brassica rapa* L.) in Finland: surprisingly, the newest cultivars have been found to be quite sensitive to high temperatures at late seed set and seed filling stages (Peltonen-Sainio *et al.* 2007). In the future, when heat waves and extreme temperatures become more common (IPCC 2007b), it will be increasingly important to find varieties that suffer minimal yield penalties under increasing temperatures. Luckily, based on the present results, there seem to be suitable genetic resources present among current varieties to breed such varieties that can better tolerate high temperature stress.

When the grain filling period is shortened at elevated temperatures, the yield tends to be lower, despite the acceleration of grain growth at higher temperatures (Evans & Wardlaw 1976; Kontturi 1979; Wardlaw *et al.* 1989a; Wheeler *et al.* 1996b; Peltonen-Sainio *et al.* 2011). The present results showed a clear effect of increased temperature sum accumulation rate from heading to yellow maturation on yields of the tested barley cultivars. The lowest accumulation rates resulted in most cases in lower yields than the highest accumulation rates, but the best yield levels were attained at moderate temperature sum accumulation rates (Fig. 2d).

Cultivars bred and selected in Finland are mostly adapted to perform best at current Finnish conditions

with short and intensive growing seasons and low temperature sums (Peltonen-Sainio *et al.* 2009c). Thus, they most often thrive best under the historically typical climatic conditions and suffer if conditions deviate. The same acclimation phenomenon was found also in a European study, where any deviation of weather conditions from 'seasonal normal' after the vegetative phase of a crop led to decreases in yield (Peltonen-Sainio *et al.* 2010). The present study suggests, however, that considerable diversity exists in responsiveness of the modern barley cultivars to early season temperatures, delay of sowing, rain 3–7 weeks after sowing, very high maximum day temperatures and temperature sum accumulation rate from heading to yellow ripeness.

CONCLUSIONS

Selection of suitable crop genotypes for future climatic conditions could be more easily done where diversity in the important responses already exists than for where all the varieties respond negatively to various extents. The present results suggest that diversity exists in responsiveness of barley cultivars to all temperature-related variables studied, except for temperature sum accumulation immediately prior to heading. However, regarding precipitation-related variables, there appeared to be significant response diversity only to the rain sum during the phase of linear growth (3–7 weeks after sowing). Thus, temperatures 2 weeks prior to heading and precipitation after sowing seemed to be the weather factors where there was least diversity in response to exploit. To combat drought and excess rain early in the season, and to deliver a high yield despite high temperature sum accumulation before heading, either new technologies or new genetic material has to be introduced to enhance adaptive capacity of barley to climate change and variability in the North.

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REFERENCES

- CARTER, T. R., SAARIKKO, R. A. & NIEMI, K. J. (1996). Assessing the risks and uncertainties of regional crop potential under

- a changing climate in Finland. *Agricultural and Food Science in Finland* **5**, 329–350.
- EVANS, L.T. & WARDLAW, I.F. (1976). Aspects of the comparative physiology of grain yield in cereals. *Advances in Agronomy* **28**, 301–359.
- HAKALA, K. (1998). Growth and yield potential of spring wheat in a simulated changed climate with increased CO₂ and higher temperature. *European Journal of Agronomy* **9**, 41–52.
- HAKALA, K., HANNUKALA, A. O., HUUSELA-VEISTOLA, E., JALLI, M. & PELTONEN-SAINIO, P. (2011). Pests and diseases in a changing climate: a major challenge for Finnish crop production. *Agricultural and Food Science* **20**, 3–14.
- HARRIS, G. R., COLLINS, M., SEXTON, D. M. H., MURPHY, J. M. & BOOTH, B. B. B. (2010). Probabilistic projections for 21st century European climate. *Natural Hazards and Earth System Science* **10**, 2009–2020.
- HOWDEN, S. M., SOUSSANA, J.-F., TUBIELLO, F. N., CHIHETRL, N., DUNLOP, M. & MEINKE, H. (2007). Adapting agriculture to climate change. *Proceedings of the National Academy of Sciences, USA* **104**, 19691–19696.
- IPCC (2007a). *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Eds M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden & C. E. Hanson). Cambridge, UK: Cambridge University Press.
- IPCC (2007b). *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Eds S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor & H. L. Miller). Cambridge, UK: Cambridge University Press.
- KANGAS, A., LAINE, A., NISKANEN, M., SALO, Y., VUORINEN, M., JAUHAINEN, L. & NIKANDER, H. (2009). *Virallisten Lajikekokeiden Tulokset (Results of Official Variety Trials) 2002–2009*. MTT Kasvu 6 (Partly in English). Jokioinen, Finland: MTT.
- KALKORANTA, T. & HAKALA, K. (2008). Impact of spring warming on sowing times of cereal, potato and sugar beet in Finland. *Agricultural and Food Science* **17**, 165–176.
- KONTTURI, M. (1979). The effect of weather on yield and development of spring wheat in Finland. *Annales Agriculturae Fenniae* **18**, 263–274.
- KRISTENSEN, K., SCHELDE, K. & OLESEN, J. E. (2011). Winter wheat yield response to climate variability in Denmark. *Journal of Agricultural Science, Cambridge* **149**, 33–47.
- Matilda Agricultural Statistics (2011). *Yield of the Main Crops 2010*. Helsinki, Finland: Information Centre of the Ministry of Agriculture and Forestry. Available online at http://www.maataloustilastot.fi/sites/default/files/viljelykasvien_sato_2010_0.xls (verified 13 July 2011).
- MITCHELL, R. A. C., MITCHELL, V. J., DRISCOLL, S. P., FRANKLIN, J. & LAWLOR, D. W. (1993). Effects of increased CO₂ concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant, Cell and Environment* **16**, 521–529.
- ÖFVERSTEN, J., JAUHAINEN, L., NIKANDER, H. & SALO, Y. (2002). Assessing and predicting the local performance of spring wheat varieties. *Journal of Agricultural Science, Cambridge* **139**, 397–404.
- OLESEN, J. E., TRNKA, M., KERSEBAUM, K. C., SKJELVÅG, A. O., SEGUIM, B., PELTONEN-SAINIO, P., ROSSI, F., KOZYRA, J. & MICALE, F. (2011). Impacts and adaptation of European crop production systems to climate change. *European Journal of Agronomy* **34**, 96–112.
- PELTONEN-SAINIO, P., JAUHAINEN, L. & HANNUKALA, A. (2007). Declining rapeseed yields in Finland: how, why and what next? *Journal of Agricultural Science, Cambridge* **145**, 587–598.
- PELTONEN-SAINIO, P., JAUHAINEN, L., HAKALA, K. & OJANEN, H. (2009a). Climate change and prolongation of growing season: changes in regional potential for field crop production in Finland. *Agricultural and Food Science* **18**, 171–190.
- PELTONEN-SAINIO, P., JAUHAINEN, L. & LAURILA, I. P. (2009b). Cereal yield trends in northern European conditions: Changes in yield potential and its realisation. *Field Crops Research* **110**, 85–90.
- PELTONEN-SAINIO, P., RAJALA, A., KÄNKÄNEN, H. & HAKALA, K. (2009c). Improving farming systems in northern European conditions. In *Crop Physiology. Applications for Genetic Improvement and Agronomy* (Eds V. O. Sadras & D. F. Calderini), pp. 71–97. Amsterdam: Elsevier.
- PELTONEN-SAINIO, P., JAUHAINEN, L., TRNKA, M., OLESEN, J. E., CALANCA, P. L., ECKERSTEN, H., EITZINGER, J., GOBIN, A., KERSEBAUM, K. C., KOZYRA, J., KUMAR, S., MARTA, A. D., MICALE, F., SCHAAP, B., SEGUIN, B., SKJELVÅG, A. O. & ORLANDINI, S. (2010). Coincidence of variation in yield and climate in Europe. *Agriculture, Ecosystems and Environment* **139**, 483–489.
- PELTONEN-SAINIO, P., JAUHAINEN, L. & HAKALA, K. (2011). Crop responses to temperature and precipitation according to long-term multi-location trials at high-latitude conditions. *Journal of Agricultural Science, Cambridge* **149**, 49–62.
- PORTER, J. R. & SEMENOV, M. A. (2005). Crop responses to climatic variation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **360**, 2021–2035.
- RAJALA, A., HAKALA, K., MÄKELÄ, P., MUURINEN, S. & PELTONEN-SAINIO, P. (2009). Spring wheat response to timing of water deficit through sink and grain filling capacity. *Field Crops Research* **114**, 263–271.
- RAJALA, A., HAKALA, K., MÄKELÄ, P. & PELTONEN-SAINIO, P. (2011). Drought effect on grain number and grain weight at spike and spikelet level in six-row spring barley. *Journal of Agronomy and Crop Science* **197**, 103–112.
- RÖTTER, R. & VAN DE GEIJN, S. C. (1999). Climate change effects on plant growth, crop yield and livestock. *Climatic Change* **43**, 651–681.
- RÖTTER, R., PALOSUO, T., PIRTIOJA, N. K., DUBROVSKY, M., SALO, T., FRONZEK, S., AIKASALO, R., TRNKA, M., RISTOLAINEN, A. & CARTER, T. R. (in press). What would happen to barley production in Finland if global warming exceeded 4°C? A model-based assessment. *European Journal of Agronomy*, doi: 10.1016/j.eja.2011.06.003.
- SOUSSANA, J.-F., GRAUX, A.-I. & TUBIELLO, F. N. (2010). Improving the use of modelling for projections of climate change impacts on crops and pastures. *Journal of Experimental Botany* **61**, 2217–2228.

- TRNKA, M., OLESEN, J. E., KERSEBAUM, K. C., SKJELVÅG, A. O., EITZINGER, J., SEGUIN, B., PELTONEN-SAINIO, P., RÖTTER, R., IGLESIAS, A., ORLANDINI, S., DUBROVSKÝ, M., HLAVINKA, P., BALEK, J., ECKERSTEN, H., CLOPPET, E., CALANCA, P., GOBIN, A., VUCETIC, V., NEJEDLIK, P., KUMAR, S., LALIC, B., MESTRE, A., ROSSI, F., KOZYRA, J., ALEXANDROV, V., SEMERÁDOVÁ, D. & ZALUD, Z. (2011). Agroclimatic conditions in Europe under climate change. *Global Change Biology* **17**, 2298–2318.
- WARDLAW, I. F., DAWSON, I. A., MUNIBI, P. & FEWSTER, R. (1989a). The tolerance of wheat to high temperatures during reproductive growth. I. Survey procedures and general response patterns. *Australian Journal of Agricultural Research* **40**, 1–13.
- WARDLAW, I. F., DAWSON, I. A. & MUNIBI, P. (1989b). The tolerance of wheat to high temperatures during reproductive growth. II. Grain development. *Australian Journal of Agricultural Research* **40**, 15–24.
- WHEELER, T. R., BATTS, G. R., ELLIS, R. H., HADLEY, P. & MORISON, J. I. L. (1996a). Growth and yield of winter wheat (*Triticum aestivum*) crops in response to CO₂ and temperature. *Journal of Agricultural Science, Cambridge* **127**, 37–48.
- WHEELER, T. R., HONG, T. D., ELLIS, R. H., BATTS, G. R., MORISON, J. I. L. & HADLEY, P. (1996b). The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO₂. *Journal of Experimental Botany* **47**, 623–630.
- ZADOKS, J. C., CHANG, T. T. & KONZAK, C. F. (1974). A decimal code for the growth stages of cereals. *Weed Research* **14**, 415–421.
- ZHOU, M. X., LI, H. B. & MENDHAM, N. J. (2007). Combining ability of waterlogging tolerance in barley. *Crop Science* **47**, 278–284.