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Published in:
Genetic Resources and Crop Evolution

Link to article, DOI:
[10.1007/s10722-013-0021-1](https://doi.org/10.1007/s10722-013-0021-1)

Publication date:
2013

[Link back to DTU Orbit](#)

Citation (APA):
Alemayehu, F. R., Frenck, G., van der Linden, L., Mikkelsen, T. N., & Bagger Jørgensen, R. (2013). Can barley (*Hordeum vulgare* L. s.l.) adapt to fast climate changes? A controlled selection experiment. *Genetic Resources and Crop Evolution*, 61, 151–161. DOI: 10.1007/s10722-013-0021-1

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Can barley (*Hordeum vulgare* L. s.l.) adapt to fast climate changes? A controlled selection experiment

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Received: 22 February 2013 / Accepted: 1 July 2013 / Published online: 7 August 2013
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Abstract The projected future climate will affect the global agricultural production negatively, however, to keep abreast of the expected increase in global population, the agricultural production must increase. Therefore, to safeguard the future crop yield and quality, the adaptive potential of crops to environmental change needs to be explored in order to select the most productive genotypes. Presently, it is unknown whether cereal crops like spring barley can adapt to climate stressors over relatively few generations. To evaluate if strong selection pressures could change the performance of barley to environmental stress, we conducted a selection experiment over five plant generations (G0–G4) in three scenarios, where atmospheric [CO₂] and temperature were increased as single factors and in combination. The treatments represented the expected environmental characteristics in Northern Europe around year 2075 [700 ppm

CO₂, 22/17 °C (day/night)] as well as a control mimicking present day conditions (390 ppm CO₂, 19/12 °C). Two different barley accessions, a modern cultivar and an old landrace, were evaluated in terms of yield and biomass production. In all treatments representing future environmental scenarios, the G4-generation of selected plants did not improve its reproductive output compared to the G0-generation, as G4 produced less seeds and had a lower yield than unselected plants. These results indicate that barley might not respond positively to rapid and strong selection by elevated [CO₂] and temperature, contrary to previous results from oilseed rape. The two barley accessions analyzed presented almost the same response pattern in a given treatment, though the modern cultivar had the highest yield in the climate scenarios, while the landrace was superior in yield under present day climate conditions.

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Keywords Barley genotypes · Breeding ·
Generational selection · Genetic adaptation ·
Hordeum vulgare L. s.l.

Introduction

Crop yields are predicted to decrease under increased climatic stress (Taub et al. 2000), why the adaptive capacity of crop genotypes needs to be explored to select suitable lines for breeding towards stress tolerance. The use of environmentally tailored genotypes is

one of the measures that can be applied to secure a primary production providing for a growing world population with minimum costs to the environment (Araus et al. 2008). The globe is facing an increase in temperature, elevated atmospheric carbon dioxide and other greenhouse gases (Taub et al. 2000; Prasad et al. 2002; IPCC 2007). If radical decreases in greenhouse gasses are not achieved, the global mean temperature may incase about 4.0 °C [degrees Celsius; likely range: 2.4–6.4 °C (IPCC 2007)] within this century. More recent projections assume an even larger increase in average global temperature of up to 5 °C (<http://climateprediction.net/>). Increased temperatures and heat stress are primarily linked with high evapotranspiration, acceleration of plant development and consequently shortening of developmental phases, leading to an early maturation and decreased yields (Altenbach et al. 2003; Barnabas et al. 2008; Elke et al. 2011). The negative effects of higher temperatures might partially be compensated by elevated carbon dioxide concentrations. Elevated [CO₂] (square brackets are used to designate concentrations of chemical substances) has often been reported to promote crop yields and overall performance through increased photosynthesis (Long et al. 2006a, b; Makino 2011) and improved plant-water relations (Warren et al. 2011). At the end of this century the atmospheric [CO₂] is expected to increase to nearly 700 ppm (IPCC 2007) from its current level of about 394 ppm. Although elevated [CO₂] may affect crop production positively, its combination with other environmental factors may well result in lower plant productivity. The evidence is limited, but Tubiello et al. (2000), Prasad et al. (2002) and Frenck et al. (2011) documented that the increase in yield as a result of elevated [CO₂] may be counteracted and even more so, when combined with higher temperature.

Variation in environmental stress tolerance between and within landraces and cultivars is little explored (Luo et al. 2009; Ceccarelli et al. 2010; Anderson et al. 2011), and therefore, targeted breeding efforts should involve screening of existing accessions. High genetic diversity may enhance the environmental adaptation potential of a cultivar (Hakala et al. 2012), however, it is often anticipated that the recurrent breeding leading to modern crops have reduced their genetic variation and thus their adaptability. In barley—the crop under study here—the genetic variation has been analyzed e.g. by Kraakman et al. (2004) and Brantestam et al. (2007) using AFLP and SSR markers, respectively. They found

marker variation that could easily differentiate between spring cultivars. In the SSR analysis of 22 loci, Brantestam et al. (2007) did not detect a decrease in genetic variation between old accessions (e.g. landraces) and modern cultivars. To what extent the apparent genetic variation in barley will translate into tolerance to the prevailing abiotic stress under climate change is yet unexplored. If not present in the present crop cultivars, this highly requested environmental tolerance might be found in the landraces or cross compatible wild relatives (Ellis et al. 2000; Newton et al. 2010). In a long term monitoring program Nevo et al. (2012) for example found that natural climate stress created profound adaptive changes in wild barley (*Hordeum spontaneum* K. Koch).

Barley (*Hordeum vulgare* L. s.l.) is one of the most widely cultivated cereals worldwide ranking fourth after wheat, maize and rice (USDA 2011). Barley plays a huge role in the economy as it is essential for global production of animal fodder, beer and whisky. The present study represents one of few studies in plants, where the adaptive potential to the future climate stressors is analyzed in a manipulative experiment; such studies have not previously been reported for barley. In this experiment we exposed two different barley accessions, a landrace and a modern cultivar, to a selection pressure over several generations in climate scenarios representing the climate in Northern Europe around 2075 (IPCC 2007, scenario A1FI).

Materials and methods

Experimental conditions

In future climate scenarios mimicked (Table 1 for details) within the climate phytotron Risø Environmental Risk Assessment Facility (RERAF), two spring barley accessions, a modern cultivar ‘Anakin’, and an old landrace “Gammel Dansk” were analyzed. Each of the two barley accessions was represented by the first (G0-generation) and the fourth (G4-generation), from a preceding selection performed under the same climate scenarios as the present comparison (for details see Frenck et al. 2011): Each of four identical chambers in the phytotron accounted for a specific climate scenario. A chamber had the dimension in meters 4.0 m × 6.0 m × 3.1 m (w × l × h) and was

equipped with an individual control of light level, temperature, humidity, CO₂ and ozone concentration. The gas concentrations were verified by sequential gas sampling from all chambers connected to one set of analyzers. Twenty eight high pressure mercury and 14 halogen lamps (1,000 and 400 W, respectively) per chamber generated a 16/8 h day/night light regime. Daily simulation of sunrise and sunset was performed within the first and last hour of the day period by gradually changing light intensity. During day time, photosynthetic photon flux density (PPFD) averaged 520 μmol photons m⁻² s⁻¹ at the height of mature crop canopy. All climate scenarios were provided with the same amount of water: At the beginning of the day, plants were watered by an automatic irrigation system providing 4.4 L m⁻² day⁻¹ to the plants. This is more than average for Danish summer precipitation, but extra water was given to compensate for higher losses from the pot soil relative to natural conditions, e.g. due to the pot-constrain of the root distribution and the loss of excess water due to pot drainage. The amount of water delivered was decreased at the beginning of leaf senescence (approximately within the third month after sowing) in a stepwise fashion to promote maturation and seed ripening. A relative humidity of 55/70 % (day/night) was established for all treatments. To ensure complete air mixing, two tube enclosed fans (Ø 0.45 m, outlet wind speed average was 5 m s⁻¹) in every chamber circulated air day and night.

The conditions in control and manipulated treatments are summarized in Table 1. The control treatment was designed to simulate present Nordic/Danish early summer climate. In all treatments a low background ozone concentration of approximately 30 ppb was added continuously to mimic the natural tropospheric ozone outside the phytotron. Plants were cultivated in 11 L polypropylene pots each filled with 4 kg of a standard soil (Pindstrup substrate No. 6, Pindstrup Mosebrug A/S, Denmark), and each pot was supplemented with 10 g of NPK fertilizer 21-3-1 (Kemira, Denmark A/S). As 8 barley plants were evenly distributed per pot, a competition regime for below ground resources including water was created. In every climate treatment, 48 plants per genotype (6 pots with 8 plants each) and generation founded experimental core population. The different plant populations ('Anakin' and "Gammel Dansk", with generations G0 and G4) were spatially separated on individual moveable tables. Plant density was 130 individuals/m². Plants of each population were restricted from growing over the table margins by lightweight fencing. To avoid chamber specific biases and minimize confounding effects of micro-environmental variations, the tables with the plants and their corresponding treatment were relocated among the chambers of the phytotron every week, at which time the relative position of a given population within a chamber was also changed. This weekly rotation was accomplished within 1 h, the time period necessary for

Table 1 Summary of manipulated environmental conditions for the four treatments in the present study

	CO ₂ (ppm)	CO ₂ std (±ppm)	Temperature (°C)	Temperature std (±°C)	RH (%)	RH % std (± %)
Day treatment						
Ambient	405.5	37.2	17.8	1.8	57.9	4.1
CO ₂	655.9	30.6	18.3	2.1	57.9	4.1
CO ₂ T	684.2	31.7	22.3	1.9	58.0	4.2
Temp	398.9	21.1	22.4	2.2	58.0	4.2
Night treatment						
Ambient	430.2	20.6	15.3	1.7	64.8	4.4
CO ₂	622.5	20.7	15.0	1.6	64.8	4.4
CO ₂ T	677.9	19	18.2	1.9	64.9	4.5
Temp	410.9	15	17.8	1.4	64.9	4.4

The CO₂ concentration intended was 390 ppm (ambient) or 700 ppm (elevated), and the temperature was set to 12/17 °C night/day (ambient) and 17/22 °C (elevated). All treatments had a background ozone concentration of 30 ppb (intended; realized 23–34 ± 3.8–7.1 ppb)

the new environmental conditions of experimental treatment to equilibrate within a chamber.

Plant material

The Danish spring barley ‘Anakin’, is a modern cultivar released in 2006 by Nordic Seed A/S (<http://www.nordicseed.dk/>; Denmark) and “Gammel Dansk” is a landrace cultivated around 1850; “Gammel Dansk” is stored and propagated by NordGen (The Nordic gene bank; <http://www.nordgen.org/>; Sweden). Both accessions are two-rowed (i.e. only the central spikelet is fertile). ‘Anakin’ has a medium height and some tendency to lodging, while “Gammel Dansk” has long straws and therefore also lodges very easily. To confirm the inherent levels of genetic variation present in the accessions investigated, they were screened by AFLP according to Johannessen et al. (2002) using one primer combination for the specific amplification (EcoRI + AGC/MseI + CGA) before the start of the selection experiment. Both accessions presented polymorphic markers; 12 of 62, and 30 of 64 markers, were polymorphic in ‘Anakin’ and “Gammel Dansk”, respectively. The production of the material for the present experiment was generated in a pre-study: The first experimental generation of plants, G1, was cultivated to maturity under selective conditions from seeds of G0 [G0 = ‘Anakin’ (certified seed from the breeder) and “Gammel Dansk” (gene bank accession)]. Generation G2 was based on seeds chosen randomly from the pooled seed stock of G1—and so on for the subsequent generations. Generations G1–G4 were all cultivated in the same selective scenario as the G0-generation, viz. one of the 4 treatments in Table 1. All seeds were stored at 4 °C for the short periods before the next generation was sown.

During the final cycle of cultivation, the populations that were exposed to selection pressure under the future climate scenarios for five generations, G4-plants, were cultivated simultaneously with unselected G0 plants from the original seed stock. For ‘Anakin’ and “Gammel Dansk” each of the two generations, G0 and G4, were divided into two batches, which were temporally delayed by 28 days in their cultivation (hereafter called groups).

Harvests

At maturity, the plants were harvested as pooled samples. The 8 plants per pot were harvested 4 by 4, providing a

total of 12 pooled samples per accession, generation and treatment (2 pools per pot × 6 pots per treatment and accession). After drying, the seeds were separated from the vegetative biomass. Seed and shoot dry weight, seed number and thousand grain weight (TGW) were determined. Harvest index (HI) was calculated as the ratio of seed dry weight over shoot dry weight.

Data treatment and statistical analysis

In the analysis of experimental responses, shoot and aboveground dry weight and TGW data was log transformed, while values for seed dry weight, total seed number and HI were square-root transformed, to improve normality and homoscedasticity of the data sets. All statistical procedures were performed in R (version 2.11.1; R Development Core Team, 2010). Linear-mixed-effects models were fitted to each response parameter in two ways: (a) Modelling the effects of CO₂, temperature, generation and their interactions, as represented in the experiment, as fixed effects and modelling the effects of genotypic origin as a random factor. (b) Integrating all individual and interactive effects of CO₂, temperature, generation and genotype as fixed effects. For both procedures, all effects were nested within group and treatment, since the two temporal groups were assumed to be true replicates of the experiment. This procedure allowed the elucidation of directional responses common to the genotypes from the first statistical model structure, and the evaluation of the differences in the responses among the investigated genotypes, by the second. Subsequently, analysis of variance (ANOVA) was performed on the linear-mixed-effects models to reveal the effects of carbon dioxide, temperature, generation and their corresponding interactions on biomass responses to the applied treatments for the two genotypes. All effects resulting in a *p* value <0.05 in the ANOVA were considered and reported as significant.

Results

Comparing yield and biomass of plants exposed to selection pressures and unselected

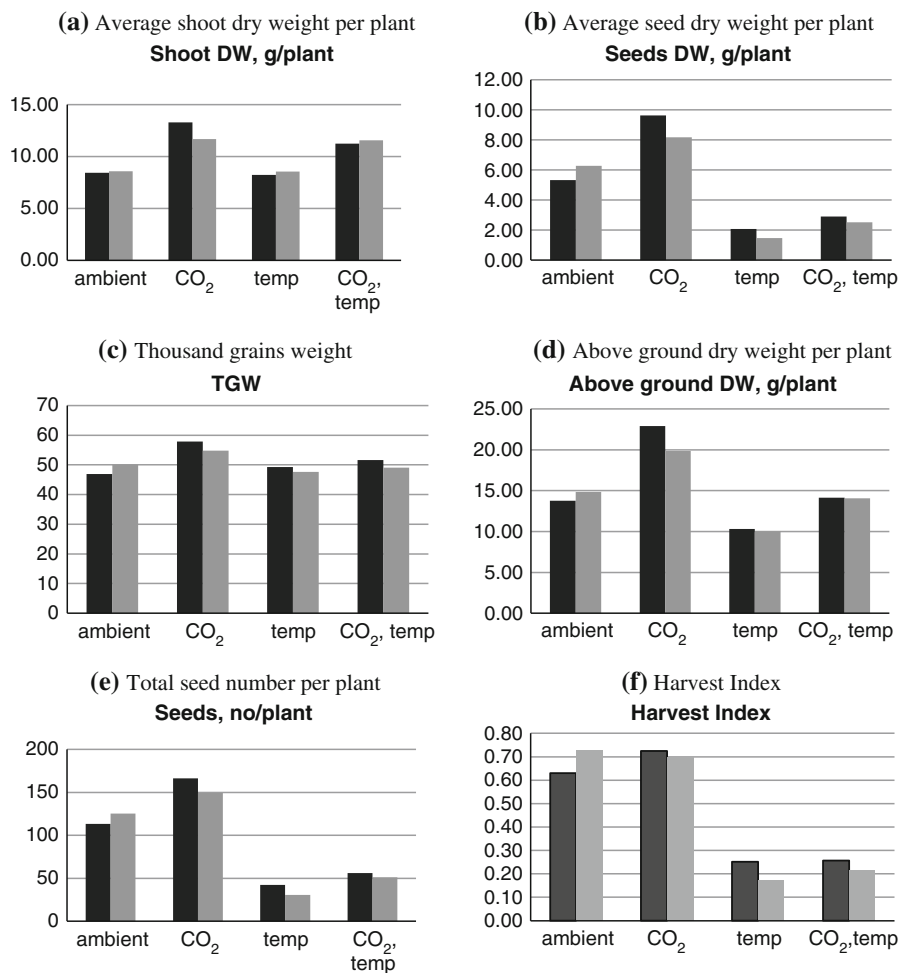
The production parameters for the G0- and G4-generations are given in Figs. 1a–f and 2. There was no statistical support for generational differences

between G0 and G4, even though the trend was that for reproductive parameters, generation G4 on the whole performed worse than G0 except in the ambient treatment. Highest yield and biomass were observed under the conditions with elevated CO₂, while the temperature treatment had the lowest yield and seed number. Vegetative biomass seemed to be less affected by the elevated temperature than the reproductive traits. In the combined treatment with both elevated [CO₂] and temperature, the negative effect from the +5 °C to seed number and yield per plant was not compensated for by the positive effects of elevated [CO₂].

Elevated [CO₂] had highly significant positive effects ($p < 0.001$) on all measures of plant production except for HI (Table 2). In contrast to the increase in production noted for elevated [CO₂], higher temperatures had significant negative impact

($p < 0.001$) on seed dry weight, seed number, aboveground dry weight and HI. The interactive effect of increased temperature and elevated [CO₂] was negative for all parameters, but was only significant for seed dry weight and aboveground dry weight ($p < 0.01$). There was no significant effect of generation (as a single factor) across all production parameters measured. An interactive effect of elevated CO₂ and generation was detected for seed dry weight and aboveground dry weight ($p < 0.05$), in which the G4-generation was inferior to G0. The interactive effect of high temperature and generation was significant for seed dry weight, seed number and HI; here again the G4-generation was less productive than G0. Significant positive interactions were found between CO₂, temperature and generation for all production parameters except shoot dry weight and TGW (Table 2).

Fig. 1 a–f Production parameters for the two barley generations G0 (black columns) and G4 (gray columns) in the four different treatments. **a** Average shoot dry weight per plant. **b** Average seed dry weight per plant. **c** Thousand grains weight. **d** Above ground dry weight per plant. **e** Total seed number per plant. **f** Harvest index



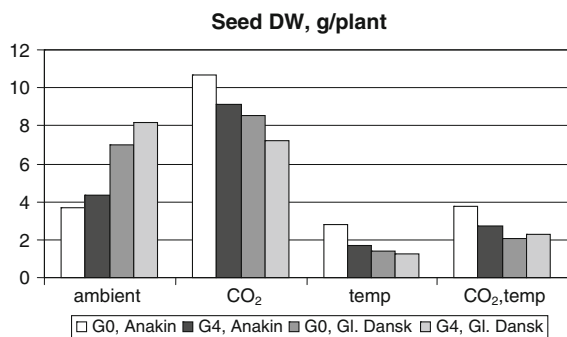


Fig. 2 Seeds dry weight (DW) for two barley cultivars, ‘Anakin’ and “Gammel Dansk”, and two plant generations (G0 and G4) cultivated in different environments

Discussion

As a consequence of the projected increase in global population (UN 2010) and current trends in global average diet, total global food production will have to increase by 50–70 % within the next 40 years to satisfy demand (Smil 2005; FAO 2009; Jaggard et al. 2010). To aggravate this pressure on primary production, the energy crisis raises the demand for crops to be used for bioenergy, e.g. it is expected that 14 % of all cereals will be used for bioenergy by 2021 (OECD-FAO 2012). There is severe concern that primary production may not meet the food and energy demands of the future due to the increasing global temperature, increase in concentration of ozone in the troposphere and uncertainty about the amount and seasonality of precipitation (Jaggard et al. 2010; OECD-FAO 2012). OECD-FAO in their agricultural outlook 2012–2021 projects that for the next decade the growth in the global food production will decrease from presently 2.0–1.7 % per year, and they emphasize the demand for increasing agricultural productivity. Among a number of measures for optimizing the future crop production is the development of cultivars adapted to the future climate stress. Such cultivars can best be bred if more knowledge is available on the effects from multi-factorial climate changes and generational stress selection to different genotypes. The present experiment attempted to analyze the impacts of environmental stressors on the natural selection trajectory in barley.

Effects of elevated [CO₂] on the primary production

Our findings from the treatment applying elevated [CO₂] as a single factor seem to correspond well with other published data. For example, in a meta-analysis comprising 79 crop and wild species, Jablonski et al. (2002) documented an average increase in yield of 28 % due to CO₂ enrichment. The effects of elevated [CO₂] on wheat were reviewed by Long et al. (2006a), and they found that the average yield increase at 700 ppm [CO₂] could be predicted to be about 1.4 times that of ambient [CO₂], a result that is well in accordance with the present result from barley. In our treatment with 700 ppm [CO₂] the yield in barley increased by 54 %. There are only few other studies in barley on this topic; in one cultivar of winter barley, Manderscheid and Weigel (2006) evaluated effects of elevated [CO₂] using free air carbon dioxide enrichment (FACE) at 550 ppm, and they obtained yield increases of 7–15 %. For spring barley cultivated just one generation at 700 ppm [CO₂], Clausen et al. (2011) observed, on average, a 57 % increase in yield in four cultivars and three F₁ hybrids using the same climate phytotron (RERAF) as the present experiment. These authors allowed the plants unlimited access to water, while water availability under our experimental conditions was limited, as all future climate scenarios obtained the same amount as the ambient treatment. The yield increase at elevated [CO₂] was almost identical in these two phytotron experiments, possibly indicating that due to reduced stomatal conductance under elevated [CO₂], water was not the limiting factor. Both experiments sought to reproduce the nutrient availability found in a normal fertilized barley field, but the future cultivation of barley may not only be affected by the changed atmospheric composition and temperature, but low input conditions would also be a challenge to plant production. With a shortage of plant nutrients (e.g. phosphorus via rock phosphate supply limitation or nitrogenous fertilizer limitation via energy-economic pressures) and more stringent regulations on fertilizer applications, it is possible that the biomass gain under elevated [CO₂] will be limited by nutrient availability and allocation of extra biomass will primarily increase root biomass (Martín-Olmedo et al. 2002).

Table 2 Analysis of variance (ANOVA, response coefficients) result for a linear-mixed effects model integrating the independent and interactive effects of carbon dioxide (CO₂), temperature (temp) and generation (gen) on achieved shoot dry

weight (Shoot DW), seeds dry weight (Seed DW), seed number (Seed No), above ground dry weight (Above DW), thousand grains weight (TGW) and harvest index (HI) for two spring barley cultivars each with two generations (G0 and G4)

Sources of variation	Response					
	Shoot DW	Seed DW	Seed No.	Above DW	TGW	HI
CO ₂	4.8418***	0.6997***	0.0721***	8.2152***	6.2331***	0.0519
Temp	-0.1976	-0.9776***	-0.1356***	-4.3803***	-2.4347	-0.3041***
Gen	0.1507	0.1267	0.0154	0.6057	0.8325	0.0442
CO ₂ :temp	-1.8436	-0.4568**	-0.0434	-4.4013**	-3.8776	-0.0459
CO ₂ :gen	-1.7517	-0.3878*	-0.0395	-3.6589*	-3.8828	-0.0655
Temp:gen	0.1671	-0.4303*	-0.0551*	-1.0216	-2.4051	-0.1619**
CO ₂ :temp:gen	1.7577	0.5796*	0.0699*	4.0186*	2.8949	0.1507*

The presented coefficients were determined from the mixed effects model including cultivar as a random factor

Significant effects indicated by bold and significant indices: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Effects of elevated temperature on the primary production

In the treatment with elevated temperature as a single factor, a reduction in average yield of 69 % was observed. Clausen et al. (2011) recorded a reduction in yield of 27 % from a similar temperature treatment with barley, but as mentioned above plants in their experiment experienced little or no water limitation. In line with that, negative effects of high temperature will get stronger under conditions of low rainfall or drought (IPCC 2007). While the effects from elevated [CO₂] seemed to affect generative and vegetative biomass almost equally, the effect of high temperature was more pronounced on generative traits like seed dry weight and seed number than on vegetative biomass. It seems likely that higher temperatures will lead to diminished efficiency in seed filling as increased temperatures and heat stress accelerate plant development and shorten developmental phases, resulting in early maturation and decrease in yield (Barnabas et al. 2008; Hatfield et al. 2011). Especially the plant's reproductive stage is sensitive to high temperature, and optimum temperature for yield is generally lower than optimum for vegetative growth (Hatfield et al. 2011). Hakala et al. (2012) in a study of Finnish barley cultivar trials from year 1976 to 2004 documented that when temperatures were high—more than 28 °C—over several days just before and after heading in barley, yield was substantially depressed. In our study we also observed substantial depression in yield under increased temperatures of 22/17 °C

(day/night). Also a modeling study of wheat by Semenov and Shewry (2011) demonstrated that heat stress around flowering will be more detrimental to yield than drought later in the season, because cultivars will mature earlier.

Effects of the multifactor treatment with elevated [CO₂] and temperature on the primary production

As stated above, for elevated [CO₂] and temperature as single factors, our study showed effects to barley, which correspond with findings from other crop studies (e.g. Amthor 2001; Lobell and Field 2007; Barnabas et al. 2008). However, climatic factors will affect plants simultaneously making the outcome for production less predictable. Therefore, the multifactor combination of elevated [CO₂] and higher temperature was studied. The positive effect of elevated [CO₂] is clearly reduced, when combined with a temperature elevation of 5 °C. Clausen et al. (2011) found a yield reduction in well watered barley of 14 % from a multifactor treatment with the same levels of elevated [CO₂] and temperature, while we observed a 53 % reduction in yield in the presumably water-limited multifactor treatment. In their review of potential future changes to arable crops, Jaggard et al. (2010) stated that elevated [CO₂] increases water use efficiency, and thereby the negative impacts of higher temperatures on crops would be approximately cancelled out. In agreement with this assumption our study documented that there was an improvement in yield compared to the treatment with only high

temperature. Nevertheless, on average the magnitude of improvement was not able to compensate yield losses to the degree of ambient conditions productivity, indicating that the yield promoting effect of high [CO₂] is minor, when linked to temperature increases in this range. Consequently, the future elevated [CO₂] may not guarantee a sufficiently strong “fertilizing” effects on crop yield (Tubiello et al. 2000; Prasad et al. 2002; Frenck et al. 2011), depending of course on the crop, and the attained levels of [CO₂] and temperature increase. Tubiello et al. (2000) in a modeling study of Italian cropping systems under climate change, predicted that a mean annual temperature increase of 4 °C and 10 % more annual precipitation combined with elevated [CO₂] at 700 ppm will lead to reductions in barley yield by more than 20 %. These authors suggested that early sowing of spring crops is an option to minimize the impacts of high temperature; that however, demands selection of early types that can cope with low spring temperatures. For final shoot biomass and TGW we did not observe major effects from the different climate treatments, indicating that these production factors were less responsive to the environmental selection procedure applied here.

Accession specific responses to the future climate scenarios

The cultivar ‘Anakin’ produced 55 hkg/ha (hectokilograms per hectare) in the ambient treatment, and “Gammel Dansk” produced 97 hkg/ha. The average yield of ‘Anakin’ in the field is about 65 hkg/ha (range 57.7–73.9 hkg/ha, the Nordic field trial system, data from 5 years; www.sortinfo.dk). As it is a landrace, “Gammel Dansk” has not been cultivated for many years; therefore yield data are not available. Based on the yield data for ‘Anakin’, the ambient conditions in the climate phytotron were almost as productive as field conditions. The plant density in this phytotron experiment and in the field—130 contra 300 plants per m² respectively—can likely explain the small divergence in yield (Scursoni and Satorre 2005). Despite the fact that “Gammel Dansk” performed significantly better than ‘Anakin’ under ambient condition, ‘Anakin’ showed its superiority under the future climate conditions. Differences in yield between old and new cultivars are the consequence of breeding; for example the modern cultivars have been selected by breeders for high input of nutrients, whereas landraces were

grown in environments of low input (Pswarayi et al. 2008). Also, the genotype’s response to high [CO₂] is likely related to age of the cultivar/landrace. One hypothesis is that as landraces were grown at times when the concentration of CO₂ was lower than today and therefore, in high [CO₂] environments, they are unable to exploit the extra CO₂. Contesting the validity of this hypothesis is the comparison of a total of 10 modern and previous wheat cultivars (Manderscheid and Weigel 1997; Ziska et al. 2004). These studies suggested that yield was more stimulated by high atmospheric [CO₂] in the old genotypes bred under pre-industrial levels of [CO₂], as the older cultivars responded to the higher [CO₂] by producing more tillers and ears. This is contrary to the yield pattern found in the new and old genotype analyzed in the present study. The observation that crop cultivars respond differently to climate change scenarios has been documented by others from studies with barley, oat and oilseed rape (Fangmeier et al. 2000; Chauhan et al. 2005; Johannessen et al. 2002, 2005; Clausen et al. 2011), and gives hope to that selection of specific cultivars with tolerance to abiotic stressors may help safeguarding the future primary production.

The potential for fast adaptation to abiotic stress in barley

In the future climate treatments, the G4-generation of both barley genotypes did not improve its production compared to the G0-generation; rather, G4 tended to have a lower reproductive output than G0. Especially at elevated [CO₂] the G4-generation responded worse than G0, and at elevated [CO₂] also the vegetative biomass was decreased. On the indicators of yield—seed dry weight, seed number and HI—significant effects were found by the ANOVA (Table 2), when generation was combined with higher temperature and elevated CO₂. In a review of the evolutionary aspects of past, present and future atmospheric [CO₂] Leakey and Lau (2012) concluded that on a geological timescale, adaptations to low [CO₂] could be verified, but periods of high [CO₂] apparently did not drive major events in plant evolution. Also for the increases in [CO₂] in recent times (last 60 years) there is no clear evidence of plant evolution (Leakey and Lau 2012). This is in accordance with our results, and we hypothesize that the negative response to future climate changes found in the two barley genotypes analyzed, indicate that they neither possessed

sufficient phenotypic plasticity nor the ability for fast genetic change necessary to counteract stress from elevated $[\text{CO}_2]$ and temperature. On the other hand, as suggested from the ambient treatment, adaptation might take place under conditions mimicking today's environment. In their review Leakey and Lau (2012) suggested targeted breeding towards high yield under the elevated $[\text{CO}_2]$ that we will experience in the future.

This inability of barley to respond positively to fast selection under elevated $[\text{CO}_2]$ is contrary to the response pattern found in oilseed rape. In the only other study specifically addressing differences between crop generations in response to elevated $[\text{CO}_2]$, Frenck et al. (2013) documented that selection had the potential to improve plant fitness including yield in oilseed rape. This diverging response in oilseed rape and barley to selection can possibly be ascribed to their different life history and different levels of genetic diversity: In contrast to the diploid inbreeding barley, oilseed rape is a partly outbreeding tetraploid; the allopolyploidy provides the species with an extra set of genes, and possibly also with higher general genetic diversity, which may lead to more phenotypic plasticity—19 and 47 % polymorphic AFLP markers found in 'Anakin' and "Gammel Dansk", respectively is less than 60–68 % polymorphic markers found in the oilseed rape cultivars analyzed by Frenck et al. (2013). The higher phenotypic plasticity of oilseed rape is likely reflected in its "weedyness". Oilseed rape has several weedy characteristics that are not found in barley, e.g. abundant seed production, ability to cross- as well as self-pollinate, persistent seeds, seed production and seed germination in a wide variety of environments, etc. These are all characteristics that broaden the environmental range of oilseed rape, so that it can be found as a weed or ruderal plant in many places—simply providing oilseed rape with better adaptive capacity towards environmental change.

Barley is a crop adapted to the cooler climates, why negative effects from elevated temperature may be predicted, and as reported here adaptation to $+5\text{ }^\circ\text{C}$ is apparently not possible over five generations in the two study-genotypes. Like barley, oilseed rape did not show adaptation to elevated temperature during the generational selection experiment (Frenck et al. 2013). The results from the present study indicate that selection pressures over five generations did not improve the production of barley, neither under

elevated CO_2 , elevated temperature or their combination. In the ambient treatment, however, positive natural selection was apparently observed. As the response to the selection pressure had different directions in the different treatments, we may assume that the reaction-patterns recorded in the "elevated scenarios", were not just effects of small experimental population size, selfpollination and thus inbreeding over generations. Endogenous heterogeneity was present in the genomes of the two accessions at the start of the experiment, but the rate of gene flow between individuals within the population could have been a critical factor limiting rate of adaptation to climate change (Savolainen et al. 2004; Jump and Peñuelas 2005). Genetic drift is another factor that cannot totally be ruled out and may have affected the genetics of the experimental populations and caused the different directional responses to natural selection in the treatments.

Jump and Peñuelas (2005) stated that keeping all other factors constant, annual plants will adapt faster to a changing environment because of their short generation time. Based on a selection experiment using three generations of wild mustard under five stress regimes (high boron, high salt, low light, low nutrient or optimal conditions), Stanton et al. (2004) documented that selection in annual plants resulted in an evolutionary shift towards early flowering, a mechanism that could be described as stress avoidance. They also discussed that opportunity of selection varied based on origin of the crop cultivars, suggesting that artificial selection, inbreeding (most likely not the case in the present experiment—see above) and drift might influence adaptive responses to environmental stresses. Even though we used two accessions of barley of widely different age, breeding history and genetic diversity, we acknowledge that the plant material was limited. It cannot be ruled out that other barley cultivars can adapt quickly to climate stressors; therefore a larger array of genotypes should be screened. The experiment, however, may have its methodological merits showing, how a generational selection experiment can be conducted over at relatively short time frame. To follow the adaptation over many plant generations at lower selection pressures would possibly give a better reflection of the natural microevolution in barley, but such long time experiments are hardly feasible, and information is needed now to prepare for tomorrow.

Acknowledgments This study was funded by Risø DTU, Aarhus University and NordForsk (the Nordic Council of Ministers). Thanks to colleagues in the NordForsk network for “Sustainable primary production in a changing climate” for valuable discussions. The staff at Risø DTU is also thanked for their assistance.

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