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Published in:
Agriculture, Ecosystems and Environment

Link to article, DOI:
10.1016/j.agee.2018.01.025

Publication date:
2018

Document Version
Peer reviewed version

Highlight

- A 10-day heatwave was superimposed to elevated temperature and CO_2 around flowering
- The applied heatwave decreased barley yield by 52%
- Aboveground vegetative biomass increased from heatwave exposure
- 22 barley accessions showed variation in decreased yield and stability of yield

How a 10-day heatwave impacts barley grain yield when superimposed onto future levels of temperature and CO_2 as single and combined factors

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Abstract

Heatwaves pose a threat to crop production and are predicted to increase in frequency, length and intensity as a consequence of global warming. Future heatwaves will occur in addition to the ongoing increase of mean temperature and CO_2. To test effects of heatwaves superimposed to future climate scenarios, 22 barley accessions were cultivated with elevated temperature (+5°C) and CO_2 (700ppm) as single factors and in combination. The control treatment mimicked ambient Scandinavian early summer conditions (19/12°C, day/night; 400ppm CO_2). Around flowering a 10-day heatwave of 33/28°C (day/night) was superimposed to all treatments. The lowest average grain yield was observed when the heatwave was superimposed onto the combined elevated temperature and CO_2 treatment. Here the yield decreased by 42% compared to no heatwave and 52% compared to ambient conditions. When the heatwave was superimposed onto ambient conditions the average grain yield decreased by 37% compared to no heatwave. There was no significant difference between the relative grain yield decrease caused by the heatwave in the ambient and future climate scenarios. In contrast, the vegetative aboveground biomass increased upon heatwave exposure, leading to a strong decline in the harvest index. Our results strongly emphasize the need to produce heatwave resilient cultivars.

Keywords: Biomass, extreme events, genotype differences, heat exposure, *Hordeum vulgare* L., multifactor treatment, stability

1. Introduction

Extreme weather events like heatwaves, floods, droughts and storms cause acute changes in growth conditions determining primary production (Fischer and Schär, 2009; Hajat *et al*., 2010; Collins *et al*., 2013). Collected data from recent decades together with results from simulation studies suggest that the variability within seasons can be more unfavorable for crop production than the general changes from season to season (Reyer *et al*., 2013; Gourdji *et al*., 2013, Tack *et al*., 2015). In a statistical study, inter-annual climate variability was shown to account for >60% of maize, rice, wheat and soybean yield variability (Ray *et al*., 2015). Hence, large variations in the climate within the crop seasons, such as a heatwave, are detrimental for the end result.

In the 2012-2013 growth season Australia experienced what became known as the 'angry summer', where over 100 temperature records were broken (BoM, 2014). An extreme heatwave caused large scale yield failures in Russia in 2010 (Trenberth and Fasullo, 2012), and Europe experienced extreme heatwaves in 2003 and 2006. In 2003, the European heatwave caused a 21% decrease in the French wheat production as temperatures were up to 6°C above long-term means and precipitation being less than 50% of the average (Ciais *et al*., 2005). Losses in cereal crop production from heat and drought in the period from 1964 to 2007 were showed to reach 9-10% globally with the highest losses in recent years (Lesk *et al*., 2016). Unfortunately, predictions are that global warming will make summer heatwaves more frequent and severe together with decrease in precipitation during the summer period (Meehl and Tebaldi, 2004; Fischer and Schär, 2010; Collins *et al*., 2013).

In the north of Europe, barley (*Hordeum vulgare* L.) - especially spring barley - is the cereal species occupying most of the cultivated area (19%), and the grains are predominantly used for feed and malt (FAOSTAT 2017). The annual average increase in grain yield of barley and wheat (*Triticum aestivum* L.) observed up to 1995 has ceased in Scandinavia (FAOSTAT, 2017). Stagnation of grain yield might, at least partly, is alleviated by the development of climate resilient cultivars. However, to develop climate resilient cultivars, assessing the effects of the most likely and relevant climate changes to a range of genotypes is essential. Studying the effects of future extreme events are challenging due to the high complexity of their timing, frequency and intensity, and the fact that they will be superimposed on the seasonal changes.

The effect of elevated temperature (eTmp) and elevated atmospheric carbon dioxide concentration (eCO_2) on grain yield have been evaluated as single-factors and combined-factors under experimental conditions in FACE (free air carbon dioxide enrichment) and in enclosure studies as well as in simulation studies (Lawlor and Mitchell, 1991; Conroy *et al*., 1994; Jablonski *et al*., 2002; Ainsworth and Long, 2005; Lobell *et al*., 2011; Challinor *et al*., 2014; Ingvordsen *et al*., 2015a; Cai *et al*., 2016). The numerous studies generally report decreasing grain yield by eTmp and increasing grain yield from eCO_2. In combinations, the harmful effect of eTmp is not fully complemented by eCO_2, and therefore, grain yield generally decreased (Conroy *et al*., 1994; Long *et al*., 2006; Ingvordsen *et al*., 2015a). The above mentioned studies all reported results from a maximum of four accessions, and crop responses to climate change are almost exclusively reported from studies including a very limited number of genotypes. In contrast the present study includes 22 accessions representing a diverse genetic origin and thereby widening our knowledge on genotypic effects in response to eTemp and eCO_2.

Temperature stress caused by exposure to constantly increased eTmp affects cereal yield differently than exposure to an extreme temperature event like a heatwave. The negative effect of a heatwave on grain yield is mainly determined by the timing in relation to the cereal development stage, with the most susceptible stage being around flowering (Barnabas *et al*., 2008, Barber *et al*., 2017). In turn, the physiological response mechanisms of individual cultivars vary and are associated with their final yield (Stone and Nicolas 1994; Hakala *et al*., 2012). Under field conditions, the differences observed in development between the accessions together with time of sowing for each accession would have influenced at which development stage the heatwave would have had its effect. Sufficient variability in cultivar earliness/lateness, cultivation of mixed cultivars and agricultural management can enable partial escape from the deleterious effects of heatwaves (Tewolde *et al*., 2006).

Few studies have so far investigated the effect on crop production caused by heatwaves superimposed to projected future levels of temperature and/or CO_2. One study applied a 15-day heatwave of maximum 35°C, 8 hours a day during grain filling on three wheat cultivars under simultaneous exposure to eCO_2 (750ppm; Bencze *et al*., 2004). However, none have, to our knowledge, applied a heatwave under the realistic future climate scenario of eTmp and eCO_2 in combination and assessed a large number of genotypes.

In the present study a 10-day heatwave of 33/28°C (day/night) was induced around the time of flowering to 22 spring barley accessions. The heatwave was timed around flowering, which is known to be the most critical developmental phase of barley yield determination at high latitudes (Peltonen-Sainio *et al*., 2011). The heatwave was superimposed to projected future levels of temperature and CO_2 as single factors and combined, conditions close to IPCC's worst case scenario for the end of this century (~RCP8.5; Collins *et al*., 2013). We ask if heat waves will be more or less devastating when superimposed on future growth conditions with eTmp and eCO_2 considering grain yield, biomass, calculated harvest index (HI) and stability of grain yield.

2. Material and Methods

2.1 Plant material

Based on their performance, 22 barley (*Hordeum vulgare* L.) accessions were selected from a previous study on production under eTmp, eCO_2, and eCO_2 combined with eTmp (Ingvordsen *et al*., 2015a). The accessions represent both high and low yielding lines and include landraces, old (1924-1962) and new (1978-2010) cultivars. Details on the 22 accessions can be found in Table 1. The accessions were supplied by NordGen (the Nordic Genetic Resource Center; http://www.nordgen.org/) and Nordic breeding companies.

2.2 Growing conditions

The accessions were cultivated in the RERAF (Risø Experimental Risk Assessment Facility) phytotron at the Technical University of Denmark, Campus Risø, Roskilde. RERAF has the advantage of six identical 24 m^2 (6 m × 4 m × 3 m) gastight chambers individually programmed and with continuous measurements of the experimental conditions. The light regime mimicked the long days of southern Scandinavia (May-July) with 16 hours of light and 8 hours of dark. Lamps were controlled to imitate sunrise and sunset (one hour each) in the beginning and end of the light regime. Light intensity was in PAR (photosynthetically active radiation) averaged at approximately 400 mol photons m^{-2} s^{-1} at canopy height. Each accession was grown in 11 L pots filled with 4 kg of sphagnum substrate (Pindstrup Substrate No. 6, Pindstrup Mosebrug A/S, Denmark) supplemented with 10 g NPK fertilizer (21-3-10, Yara) at sowing. Per accessions twelve seeds were sown in each of two pots, and at the seedling stage thinned to eight experimental plants per pot. The pots were placed on wheeled growing tables; one pot remained in the basic treatment the other was moved to the heatwave treatment at Zadoks growth stage 49 (first awns visible; ZS, Zadoks *et al*., 1974; Fig. 1). Throughout the experiment 4.4 L m^{-2} day^{-1} of water was applied in all treatments at the beginning of the daytime regime by an automated surface dripping system. At the early stages of growth (seedling stage), excess water was drained from the pots. Watering was reduced stepwise, when plants in a given treatment started ripening, ZS 90, and watering was ended at maturity, ZS 99. The growth stage was determined in the control treatments. The amount of water supplied was sufficient to avoid water limitation during growth under ambient conditions. Relative humidity was constant at 55/70 % (day/night) for all treatments. At growth day 27, about ZS 15-17, all plants were treated prophylactically against aphids with Confidor WG 70 (Bayer A/S). To avoid any unintended chamber specific effects the treatments were rotated between chambers once a week. When chamber rotations took place, conditions in all chambers were set to ambient, and the batches of plants were moved to their new chamber, and the corresponding treatment applied again. The chamber rotation was accomplished within one hour (all inclusive). Concurrent with the chamber rotation all tables were rotated within the treatments according to a scheme, so that any table/pot received a new position in the chamber (e.g. pots facing the outer rim were moved to the center etc.).

Further, the positions of the accessions were identical between treatments. The rotation between chambers was ended 68 days after sowing to avoid plant damage, when moving the wheeled tables through the chamber doors.

2.3 Treatments

The barley accessions were cultivated under four climatic scenarios referred to as basic treatments. The basic treatments were: 1) ambient (amb), mimicking south Scandinavian summer conditions with 19/12°C (day/night) and CO_2 concentration at 400ppm; 2) constantly elevated temperature (eTmp) with +5°C day/night; 3) constantly elevated CO_2 (eCO_2) with +300ppm; 4) combined constantly elevated temperature and CO_2 (eTmp&eCO_2). The eTmp and eCO_2 were set close to those projected by IPPC for the Nordic region at the end of the 21st century (Collins *et al*., 2013).

The heatwave treatments were superimposed to the basic treatments (then designated amb+H, eTem+H, eCO_2+H, eTmp&eCO_2+H) as constant hot temperature 33/28°C (day/night) for 10 days and applied individually to the accessions around anthesis. When half of the plants of a given accession had reached ZS 49 (first awns visible), one of the pots was moved to the heatwave treatment. The CO_2 concentration in the heatwave treatment followed the climatic scenarios and was 400ppm for amb+H and eTem+H and 700ppm for eCO_2+H, eTmp&eCO_2+H. Throughout the heatwave treatment, watering was applied in a volume of 4.4 L m^{-2} day^{-1} as in the basic treatments. After the heatwave treatment the pot was transferred back to its original basic treatment. The experimental setup is shown in Fig. 1.

2.4 Data collection and analyses

Plants were harvested individually and dried for a minimum of three weeks (20°C, continuous high air flow, 55% relative humidity). After threshing, grain yield (g plant^{-1}) and aboveground vegetative biomass (g plant^{-1}) were sized. Harvest index (HI; grain yield proportional to total aboveground biomass, %) was calculated from grain yield and aboveground biomass. Stability measures over the eight treatments were calculated by the static environmental variance (S^2; Roemer, 1917) and the dynamic Wricke's ecovalence (W^2; Wricke, 1962) according to

$$S^2_i = \sum (R_{ij} - m_i)^2 / (e - 1) \quad [1]$$

$$W^2_i = \sum (R_{ij} - m_i - m_j + m)^2 \quad [2]$$

where R_{ij} is the observed yield of the accession i in the treatment j, m_i is mean yield of the accession across treatments, e is number of environments, m is the average of all m_i termed the grand mean. To the raw data a mixed effects model with randomized accession and pot effects was applied to verify treatment effects, of eTmp, eCO_2, H, and their interactions. Random interactions between accession and treatments eTmp, eCO_2 and H were investigated and rendered insignificant prior to analysis of treatment effects. To investigate potential impact of the individual accessions, a derived mixed effects model with fixed effects of accessions instead of random was constructed, including fixed effects of accessions and interaction effects between accessions and the eTmp, eCO_2 and H treatments. The pot effect was initially investigated through Maximum Likelihood estimation, which considered potential within-pot-competition effects. After establishing a positive within-pot correlation, the analysis was carried out with standard software for mixed effects models. This model formula and parameter estimates are described in detail in the Supplementary material. Furthermore, accessions were grouped into landraces, old and modern cultivars, and the mixed effects model with random pot effect and accessions replaced with the grouping was analyzed. A similar model was applied to above ground vegetative biomass, and analyzed. Presented parameters (see supplementary material) were constructed with the REML procedure. Estimates, confidence intervals and p-values in for ratios Table 2 and ratio comparisons for relative heatwave effects were constructed through simulation. Significance levels are p<0.001:***; p<0.01:**; p<0.05:*. All modelling and correlation analysis was carried out using the software package R, version 3.2.3 (R Core Team, 2015).

3. Results

3.1 Experimental levels of temperature, CO_2 and humidity

The levels of temperature, CO_2 and humidity applied in RERAF throughout plant cultivation were according to set points (Supplementary Table S1), except for the ambient CO_2 treatment. Here the averaged value reached 452.71ppm (±33.53) around 50ppm higher than set value. The RERAF facility lacks the mechanism to absorb CO_2, hence plant and especially soil respiration have potentially caused the higher values. The hypothesis on respiration being the responsible factor was supported by the overshoots of the set-point value being most prominent within the first hours of the day and during the night regime (data not shown).

3.2 Effects of the basic climate treatments

Comparing the elevated CO_2 and temperature treatments with ambient conditions (Table 2), the effect of eCO_2 was found to increase overall grain yield by about 26%, while eTmp decreased overall grain yield by 43%. When the single factors were combined in eTmp&eCO_2 treatment, grain yield decreased by about 18%. Interestingly, the effect of the combined factors seemed to be additive with a non-significant interaction (p=0.25). Total aboveground vegetative biomass was also increased (35%) by eCO_2, whereas eTmp caused a moderate decrease of almost 5%. In the two-factor eTmp&eCO_2 treatment the aboveground vegetative biomass increased 20%. The effects of eCO_2 and eTmp were not additive for aboveground vegetative biomass (p=0.03); thus, the effect of the two individual factors combined could not be predicted from the effect of the individual factors. The treatment effects on grain yield and aboveground vegetative biomass were reflected in the Harvest Index (HI), which was significantly reduced in the two treatments with eTmp, while eCO_2 had no effect on HI. Hence, increase in grain yield and aboveground vegetative biomass was proportionally similar to the that in the amb treatment. The modelled production parameter estimates for the accessions are presented in Table 2. The basic treatments resemble the set up in our previous study that also included the same accessions (Ingvordsen *et al*., 2015a), and Pearsons correlation coefficient on grain yield between the previous and present experiments was high (74-82 %, p<0.001).

The accessions reached the transfer-stage (ZS 49) earliest in the two-factor eTmp&eCO_2 treatment, on average 45.5 days after sowing, 5 days earlier than in the ambient treatment (Supplementary Fig. S1).

3.3 Effects of the heatwave

All 22 accessions survived the 10-day heatwave applied around anthesis (due to faulty watering in the eTmp+H treatment of cultivar Drost P., data for this accession and treatment were excluded from the measured results). From the modelled estimates in Table 2, average grain yield was found to decrease 52%, when comparing the future eTmp&eCO_2+H scenario with the basic amb scenario, indicating severe production loss under future conditions (p<0.0001). The relative production loss caused by the heatwave is not significantly different in the future and ambient scenario (p=0.71). The relative effect of the heatwave was independent of the basic treatment in all scenarios, with p>0.13. On the basis of the similar relative decrease caused by the superimposed heatwave, we estimated the relative effect on overall grain yield as a 39% decrease. Given the similar relative effect of the superimposed heatwave, the highest grain yield was found in the treatment of eCO_2+H at 5.23g plant^{-1}, pooling all accessions (Table 2). The production of aboveground vegetative biomass was in all basic treatments increased by heatwave exposure, however not significantly for eTmp (Table 2). As the heatwave decreased yield and increased aboveground vegetative biomass in all basic treatments, HI was decreased accordingly suggesting change in allocation from grain to vegetative biomass (Table 2).

3.4 Accession specific effects

The days for the individual accession to reach the transfer-state at ZS 49 was influenced by the basic treatments. The first accession to reach ZS 49 and being transferred to the heatwave was the old Swedish cultivar ‘Mari’ grown under eTmp, and the last accession was the landrace ‘Griechische’, transferred 35 days later, also grown under eTmp (Supplementary Fig. S1). The modern Danish cultivar 'Sebastian' and the landraces 'Solenbyg' and 'Grenoble I' spanned only 2-5 days in reaching ZS 49 over all four of the basic treatments, demonstrating stable rate of development. Early accessions, reaching the transfer-state first under all basic treatments, were two modern Norwegian cultivars, 'Arve' and 'Brage', two old Swedish cultivars, 'Brio' and 'Mari' and the landraces 'Bjørne' and 'Kushteki' (Supplementary Fig. S1).

The analysis showed that in our experimental setup heatwave effects were not significantly dependent on the barley accession (p=0.08). However, the negative grain yield effects by the heatwave treatments varied among the 22 accessions and ranged from 32% to 54% reduction in the amb+H and from 55% to 72% reduction in the eTmp&eCO$_2$+H treatments (Fig. 2). Some accessions like the landraces, Königsberg and Vilm, and the Danish modern cultivar Alliot seemed to be substantially more affected by the eTmp&eCO$_2$+H treatment than the amb+H treatment. In contrast, the old Swedish cultivar Mari and the modern Danish cultivar Anakin showed stronger decrease in grain yield under the amb+H treatment than under the eTmp&eCO$_2$+H treatment, showing potential to resist heatwaves under future climate conditions. As expected, the analysis revealed that the group of modern cultivars yielded significantly higher than the group of landraces (p<0.0001), but they did not produce more aboveground vegetative biomass compared to the landraces.

The different responses in grain yield of the set of accessions over the eight applied treatments revealed a static environmental variance, S^2, ranging from 1.80 to 9.35, where lower values indicate static stability to environmental changes (Table 1). According to S^2, the landrace 'Oslo' and the French cultivar 'Prestige' were identified as most stable over all applied treatments. In addition, 'Prestige' holds the seventh highest mean grain yield across treatments, whereas 'Oslo' ranked 20th in mean yield.

Wricke's ecovalence, W^2, for grain yield ranged from 2.37 to 23.32 over the eight treatments, where a high ecovalence indicates larger fluctuation across the treatments compared to the other accessions. The modern Danish cultivar 'Evergreen' had the second highest mean grain yield over the eight treatments, however, a considerable decrease in grain yield under eTmp most likely caused 'Evergreen' to be identified as an accession responding differently from the majority, and ranking only 20th out of the 22 for W^2. Low values of W^2 were presented by the landraces 'Kushteki' and 'Moscou' and the cultivar 'Arve' released in Norway.

Calculating S^2 and W^2 separately over the four basic treatments and the four +H treatments showed that the accessions were either stable over the basic treatments or over the +H treatments (Supplementary Fig. S2). The only exceptions were the landrace 'Oslo' and the Danish cultivar 'Alf', as they showed stable grain yield according to S^2 under both the four basic treatments and the four heatwave treatments. However, both accessions were among the bottom three accessions for mean grain yield. No correlation between grain yield in the treatments with and without heatwave could be found for either S^2 (p=0.16) or W^2 (p=0.08). The lack of correlation between treatments with and without heatwave suggests that the underlying mechanisms causing stability to a heatwave and to eTmp and eCO_2 are not the same.

4. Discussion

4.1 Response to the single-factor basic treatments

Our results support the generally observed trend of decreased grain yield in response to eTmp and increased grain yield under eCO_2 (Morison and Lawlor, 1999; Bokszczanin and Fragkostefanakis, 2013) with the observed 26% increased grain yield by eCO_2 and the 43% decreased grain yield by eTmp for the 22 barley accessions in this study. However, the magnitude of the observed trend varies between studies. From a FACE experiment Manderscheid *et al*. (2009) observed eCO_2 at 550ppm to increase grain yield by 9-18% for the barley accession 'Theresa'. A 2°C temperature increase in the soil (4 cm depth) under field conditions caused a 4% yield decrease in the barley accession 'Quench' (Högy *et al*., 2013). In a phytotron study on four barley accessions ('Gl. Dansk', 'Lazuli', 'Anakin' and 'Barke') overall grain yield was increased by 57% when exposed to eCO_2 at 700ppm, whilst grain yield was decreased by 27% under +5°C eTmp (Clausen *et al*., 2011). The differences may result from variation in several factors such as crop species, level, timing and length of exposure to eTmp and eCO_2.

4.2 Response to the combined-factor basic treatment

Only few experimental studies have addressed effects of combined eTmp and eCO_2 treatments on grain yield and biomass. In rice, the combination of eTmp and eCO_2 at levels predicted for the end of the 20th century (+4°C and +200 to 300ppm CO_2) has been reported to affect grain yield negatively (Ziska *et al*., 1997). A modelling study of rice, wheat and soybean also reported decreased grain yield from the combined eTmp and eCO_2 (Long *et al*., 2006). Our results on barley support these earlier findings from other crops, which bodes ominously for the production in a future climate, where CO_2 and temperature will increase concerted. For grain yield we found that the effect of these two individual factors was additive and this additivity could predict the response in their combined treatment. This finding is in contrast to previous findings in a larger dataset including 138 barley accessions (Ingvordsen *et al*., 2015a). However, interaction between factors might still be present, but significance may not be detected due to the smaller set of 22 accessions. In contrast, for vegetative biomass the effect of the individual factors was not additive, when compared to the combined treatment, as also found by Ingvordsen *et al*. (2015a). The incongruence in identified additive effect of single factor treatments between the two studies can also reflect the variation in genotypic responses in the two sets of accessions. In any case, it is crucial to screen diverse sets of numerous cultivars to help fill the knowledge gap on genotype effect, information of value for breeding and in modelling studies.

4.3 Level, timing and frequency of the superimposed heatwave

A heatwave is an extreme event where timing, intensity and length are difficult to predict and therefore it is challenging to include such extreme events in the forecast for the cropping season and in choice of cultivar (Ben-Ari *et al*., 2016). In Southern Scandinavia (Denmark) a heatwave is today defined as when average of maximum temperatures registered over three consecutive days exceed 28°C (DMI, 2014). No information could be found describing most likely timing, temperature regime and length of future heatwaves in this northern region. In southern Europe, model prediction of future heatwaves forecasts that by the end of this century heatwaves will occur with a frequency between 1.7 and 2.3 times per growing season, last between 11 and 17 days, and be up to 3°C warmer than previous heatwaves (Meehl & Tabaldi, 2004). Hence the applied heatwave in the present study is +5°C warmer and 7 days longer than the current Nordic definition, and likely represents a realistic future extreme temperature event. The timing with the heatwave striking at ZS49 (first awns visible) targeted the sensitive stages of pollen development, anthesis and ovule formation (Sakata *et al*., 2000; Hakala *et al*., 2012; Gourdji *et al*., 2013) and had increased effect on yield. A study in maize, identified 13% decreased yield under a 3-day heatwave of +6°C applied at early reproductive stage (silking), but no decrease in yield when applied at early vegetative stage (Siebers *et al*., 2017). Heat tolerance around flowering has been identified as a key trait to improve the European primary production of wheat in the future climate (Stratonovitch and Semenov, 2015).

4.4 Response in grain yield to the superimposed heatwave

The heatwave superimposed in the most realistic future climate treatment, eTmp&eCO_2, halved the grain yield (52%) when compared to production in the climate of today (amb). Halving the eatable harvest is a considerable impact potentially leading to insufficient food supply. Interestingly, the results showed consistent relative decrease in grain yield on all basic treatments, in response to heatwave exposure. With the consistent relative heatwave response in all four basic treatments, the differences found in final grain yield and aboveground biomass after superimposed heatwave were caused by the basic treatments, i.e. the already present increases in temperature and CO_2. One can speculate if the superimposed heatwave was so severe that it caused physiological processes to operate at an absolute minimum during its duration, and therefore affected all basic treatments relatively uniformly. Counter to that speculation Fitzgerald *et al*., (2016) identified eCO_2 to ameliorate the effect of an 8-day naturally occurring heatwave in a semi-arid environment with temperature >35°C (FACE experimental setup). The eCO_2 increased the yield by 17-40% during the heatwave in a modern and an old wheat cultivar respectively. However, due to the heatwave occurring naturally, there are no data for the yield at ambient temperature. A study by Bencze *et al*. (2004) superimposing a less extreme heatwave, supports our suggestion that the final grain yield is determined by the basic treatment. Bencze *et al*. (2004) cultivated three wheat cultivars at 375ppm and 750ppm CO_2 and superimposed a heat event consisting of a temperature increase 8 hours a day for 15 days around grain filling at maximum 35°C in contrast to ambient temperature at maximum 24°C. The highest grain yield post heatwave exposure was identified in the accessions exposed to the high CO_2 concentration (Bencze *et al*., 2004) as observed in our study (Table 2).

4.5 Response in biomass to the superimposed heatwave

The aboveground vegetative biomass was increased by the heatwave at all basic treatments, whereas grain yield decreased, hence, the allocation between vegetative biomass and grain changed, as was observed in the HI (Table 2). Considering the disruptive effect the heatwave had on flowering, with less grain formed, it is likely that grains were not filled making resources available for vegetative biomass. Allocation from reproductive biomass to vegetative biomass was also identified by Batts *et al*. (1998) in one of two wheat cultivars exposed to a temperature gradient. As plants from the basic eTemp treatment came from an environment with elevated temperature before heatwave exposure, plants from the amb and eCO_2 treatments experienced the highest temperature increases of +14°C (eTmp and eTmp&eCO_2 +9°C) when transferred to the heatwave, and also showed the largest gain in vegetative biomass suggesting temperature to be the dominant factor for the shift in allocation. Numerous plant processes are involved in the allocation of resources to organs, and HI is a good indicator for shifts in resource allocation. In addition, HI has been shown to have a high heritability (Hay, 1995) and therefore, grain production under future climate conditions could benefit from identification of genotypes with stable and high HI in a variable climate. With an apparent future increase in aboveground vegetative biomass, its functionality should be explored (Ghaly and Alkoaik, 2010).

4.6 Genetic resources for future resilient cultivars

Our analysis of 22 spring barley accessions showed that heatwave effects did not appear to be significantly dependent on accession. One can only speculate if an accession specific response would have shown if the applied heatwave had been less extreme, or if other accessions e.g. accessions adapted to warm drought prone environments had been included.

The recorded complexity in the response patterns to applied treatments (Fig. 2) will not simplify the task for plant breeders. Various studies have represented CO_2-responsivenes as a potential breeding target that has not previously been exploited (Manderscheid and Weigel, 1997; Ziska *et al*., 2004; Franzaring *et al*., 2013). In the present study, the heatwave response was independent of the basic treatment, and consequently the higher grain yield from eCO_2 continuously lead to the highest grain yield being produced under eCO_2+H suggesting that CO_2-responsivenes is beneficial in a future climate with higher occurrence of heatwaves. Correlating CO_2-responsiveness (increased grain yield under eCO_2) with yield in the eTmp&eCO_2+H scenario in the present study was though non-significant.

The optimal climate resilient cultivar is high yielding in environments with climate stresses over its life cycle. Yet, among accessions in the present study, stability and high grain yield were rarely characteristics of the same accession. Stability over treatments were combined with low yield in the eTmp&eCO_2+H treatment, and poor stability combined with high yield in the eTmp&eCO_2+H treatment. Accessions that were stable and/or high yielding in the eTmp&eCO_2+H treatment are potential candidates in breeding programs aiming at diminishing climate caused losses in production, especially if the desired traits can be easily exploited using marker assisted selection (Ingvordsen *et al*., 2015b).

5. Conclusion

Translation of findings from studies of environmental effects under artificial conditions to actual field conditions needs to be carefully considered. Environmental factors like light, water, nutrients and temperature conditions are much more variable under field conditions and plants are exposed to a verity of beneficial and pathogenic microorganism and will possible influence the magnitude of the findings. However, manipulating temperature and mimicking heatwaves under field conditions is only partly possible so far (Kimball et al., 2007; Bruhn et al., 2013). Therefore results from studies using controlled growth conditions are sometime the best option to gain knowledge about future climate change related effect on crop production, and relative differences between temperature associated treatments. .

Under future climate conditions decreased summer precipitation is projected for southern Scandinavia (IPCC, 2007). In the present study water allocation was identical in all treatments and pots. However, in the treatments of eTmp and under heatwave conditions increased vapor pressure deficit has despite equal relative humidity changed evapotranspiration conditions from those of the ambient treatment. Therefore, reported effects of the treatments with eTmp can be concerted responses to heat and water availability. From today's climate to a climate with a 10-day heatwave superimposed to IPCC's worst case scenario around year 2100, we measured an immense 52% decrease in grain yield over all 22 accessions. Modern accessions were highest yielding and effects of the superimposed heatwave did not depend significantly on accession. With a similar relative yield decrease from the superimposed heatwave in the four basic treatments, final grain yield was predominantly determined by the basic treatments.

The 52% decrease in grain yield strongly emphasize that future temperature extremes exert a great threat to crop production systems and stress the need to continuously identify genotypic variation for breeding future climate resilient cultivars. Together with new better cultivars also diversified cropping systems and management should be prioritized to feed the future world population.

Acknowledgements

We would like to thank all the hands that helped during cultivation, harvest, threshing and measuring, Allan Murphy and Esben Højrup for technical assistance in RERAF. We also thank Air Liquide Danmark A/S for generously supply of the CO_2 used in this experiment.

Funding

This work was supported by the Nordic Council of Ministers (NordForsk) through funding of the network 'Sustainable primary production in a changing climate','COBRA' (Core Organic II) and the FTP project 'Climate Change Effects on Plant Health'.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at *xxxx*

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Table 1. The tested barley accessions with mean yield and stability across all treatments; ambient, elevated temperature, elevated CO_2, elevated temperature and elevated CO_2 in combination and all four treatments +/-heatwave. Modern cultivar (mCV), old cultivar (oCV), landrace (LR), genebank number (NGB), environmental variance (S^2) and Wricke's ecovalence (W^2). The accessions are sorted after the mean grain yield across the eight treatments (m_i), and numbers in brackets are the ranking based on their stability indices. *Values for Drost P. based on seven of the eight treatments (eTemp+H excluded due to faulty watering).

Accessions name	**NGB / Breeder**	**Culton type**	**Sub type**	**Country of origin / Country of breeding**	**Year of release**	m_i	S^2	W^2
Bjørne	NGB9326	LR	6	unknown		6.25	6.19(18)	5.23(6)
Evergreen	Nordic Seed A/S Plant Breeding	mCV	2	Denmark	2010	6.19	9.35(22)	17.46(21)
Brio	NGB9327	oCV	6	Sweden	1924	6.13	6.04(16)	5.93(9)
Brage	Graminor Plant Breeding	mCV	6	Norway	2010	5.97	5.15(8)	5.89(8)
Anakin	Sejet Plant Breeding I/S	mCV	2	Denmark	2006	5.91	5.83(12)	5.09(5)
Solenbyg	NGB13402	LR	6	Norway		5.90	7.38(19)	8.41(14)
Prestige	NGB16750	mCV	2	France	2000	5.88	2.68(2)	9.00(15)
Kushteki	NGB6288	LR	6	Afghanistan		5.87	5.48(10)	2.37(1)
Moscou	NGB9482	LR	2	unknown		5.83	5.93(14)	4.00(3)
Drost P.*	NGB6281	oCV	2	Denmark	1951	5.81	4.90(7)	7.30(13)
Alliot	NGB16757	mCV	2	Denmark	1999	5.73	4.42(6)	15.03(19)
Sebastian	Sejet Plant Breeding I/S	mCV	2	Denmark	2002	5.72	3.89(4)	5.98(10)
Griechische	NGB9333	LR	6	Greece		5.56	5.57(11)	4.11(4)
Arve	NGB11311	mCV	6	Norway	1990	5.36	5.90(13)	3.72(2)
Grenoble I	NGB9378	LR	6	France		4.63	8.67(21)	23.32(22)
Edvin	Boreal Plant Breeding	mCV	6	Finland	2008	4.54	7.95(20)	11.76(17)
Vilm	NGB9435	LR	2	Germany		4.21	5.98(15)	5.34(7)
Anita	NGB15250	oCV	6	Norway	1962	4.20	6.15(17)	7.27(12)
Mari	NGB1491	oCV	2	Sweden	1960	4.12	5.36(9)	12.03(18)

Oslo	NGB9315	LR	6	Norway		4.09	1.80(1)	10.25(16)
Königsberg	NGB9310	LR	6	unknown		3.65	3.12(3)	16.71(20)
Alf	NGB4707	mCV	2	Denmark	1978	3.41	4.20(5)	6.32(11)

Table 2. Model estimates for grain yield, aboveground vegetative biomass and harvest index (HI) for the 22 barley accessions with 95% standard confidence intervals, when cultivated under ambient (amb), elevated levels of temperature (eTmp) and CO_2 (eCO_2) as single factors or in combination ($eTmp\&eCO_2$) and with (+H) and without a 10-day heatwave around anthesis. The *p*-values indicate the difference to the production parameter under ambient conditions (amb). $***p < 0.001$; $**p < 0.01$; $*p < 0.05$. Difference in % is relative to ambient conditions (amb).

Treatment	**Grain yield (g plant^{-1})**	**Difference in %**	**Aboveground vegetative biomass (g plant^{-1})**	**Difference in %**	**HI (%)**	**Difference in %**
amb	7.16±0.51	-	8.33±0.86	-	45.31±2.51	-
eTmp	4.06±0.51***	-43.3 (±5.6)	7.94±0.86	-4.6 (±7.7)	35.76±2.53 ***	-21.1 (±4.9)
eCO_2	9.00±0.51***	25.8 (±7.3)	11.21±0.86***	34.7 (±9.,9)	45.31±2.51	0
$eTmp\&eCO_2$	5.90±0.51***	-17.5 (±8.1)	9.99±0.86***	20.1 (±10.2)	35.75±2.51 ***	-21.1 (±4.9)
amb+H	4.51±0.51***	-37.0 (±6.7)	10.27±0.86***	23.4 (±9.1)	27.50±2.53 ***	-39.3 (±4.7)
eTmp+H	2.70±0.53***	-62.3 (±6.6)	8.11±0.86	-2.6 (±9.0)	23.66±2.53 ***	-47.8 (±4.7)
eCO_2+H	5.23±0.51***	-26.9 (±6.9)	14.33±0.86***	72.3 (±14.1)	27.50±2.53 ***	-39.3 (±4.7)
$eTmp\&eCO_2$+H	3.42±0.51***	-52.2 (±6.5)	11.34±0.86***	36.3 (±9.9)	23.66±2.53 ***	-47.8 (±4.7)

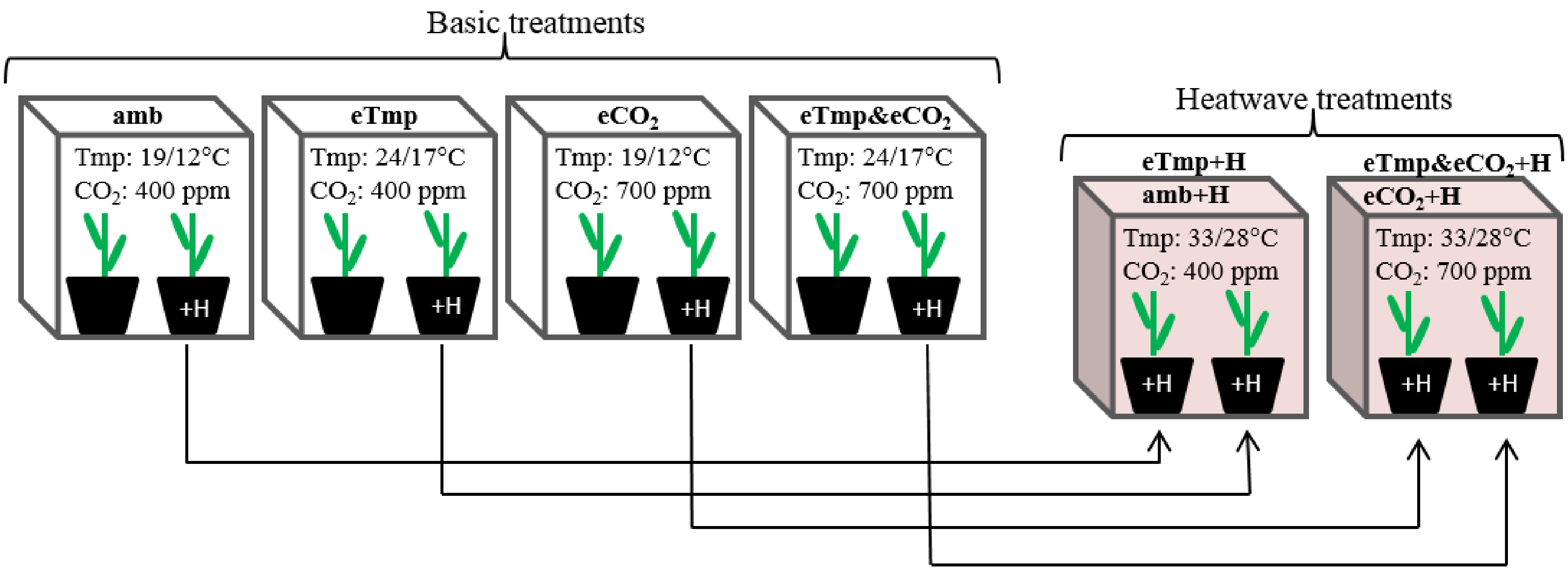

Fig. 1. Schematic overview of the four climatic scenarios and the superimposed 10-day heatwave treatment, illustrated for one accession. For the basic treatments it was one treatment per chamber and during heatwave treatments, two basic treatments in each of the heatwave chambers. amb: ambient conditions, eCO_2: elevated CO_2, eTmp: elevated temperature, eTmp&eCO_2: elevated temperature and elevated CO_2 in combination, +H: heatwave superimposed to basic treatment. For each accession one pot in the basic treatment was transferred to the heatwave treatment as indicated with arrows.

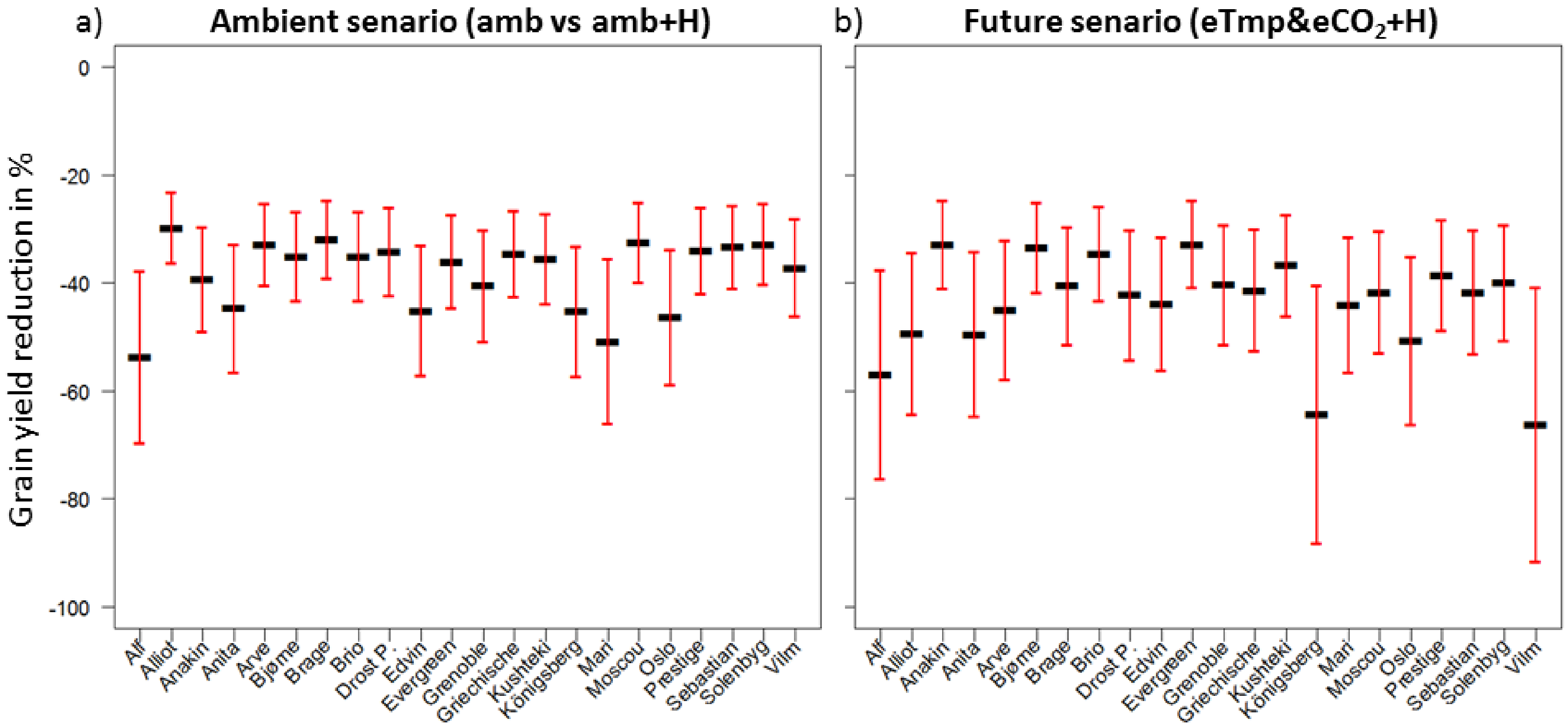

Fig. 2. Reduction in grain yield of 22 barley accessions after a 10-day heatwave superimposed around flowering to plants grown under climatic conditions corresponding to (a) ambient conditions (amb) or (b) futur senario with elevated temperature and CO_2 (eTmp&eCO_2).

Supplemental

Table A.1. Set point and experimental levels of temperature, atmospheric concentration of CO_2 ([CO_2]) and humidity ±standard deviations in the six chambers; four chambers mimicking basic treatments and two chambers mimicking basic treatments with a superimposed heatwave (+H).

	Temperature (day/night)		**[CO_2]** (constant)		**Humidity** (day/night)	
	Set point	Experimental	Set point	Experimental	Set point	Experimental
Ambient	19/12°C	18.36±2.18/13.02±2.48	400 ppm	451.54±40.65	55/70	56.55±4.53/67.43±5.41
eTmp	24/17°C	22.97±2.18/18.20±2.45	400 ppm	459.72±40.85	55/70	56.64±4.61/67.25±5.43
eCO_2	19/12°C	18.22±2.23/13.04±2.45	700 ppm	700.27±23.18	55/70	56.63±4.65/67.51±5.38
eTmp & eCO_2	24/17°C	23.05±2.24/18.08±2.44	700 ppm	693.89±23.76	55/70	56.66±4.69/67.32±5.42
+H	33/28°C	32.41±2.63/28.01±2.52	400 ppm	446.88±19.09	55/70	56.47±4.41/67.59±5.24
+H & eCO_2	33/28°C	32.42±2.52/28.02±2.50	700 ppm	703.14±21.00	55/70	56.43±4.55/67.55±5.20

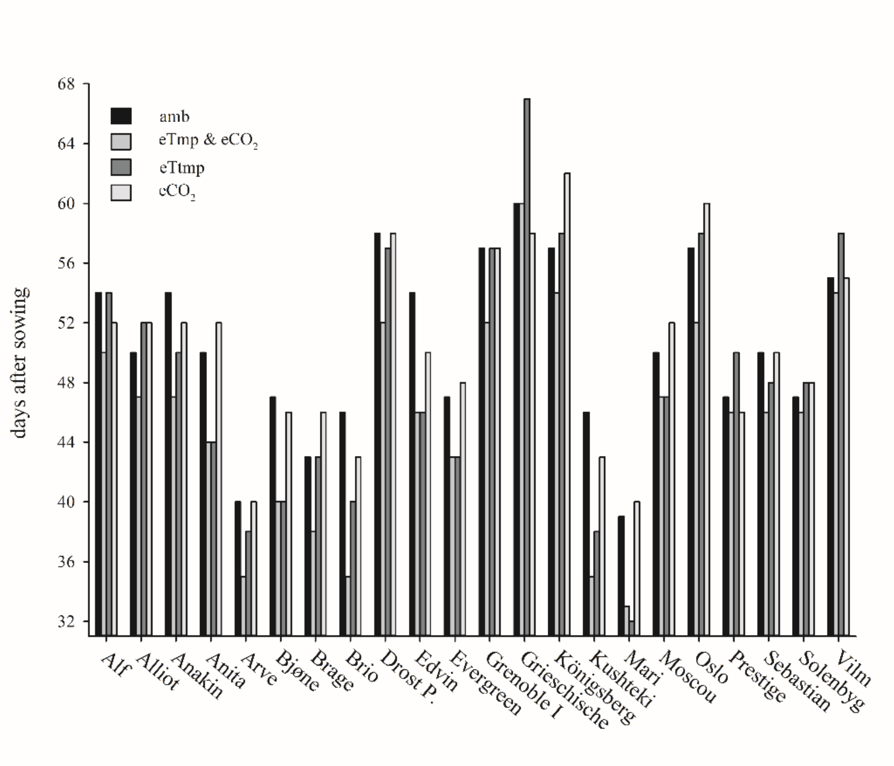

Fig. A.1. Number of growing days before transfer to the heatwave treatment. An accession was transferred when four of eight plants reached Zadoks growth stage 49. Ambient conditions: amb, elevated CO_2: eCO_2, elevated temperature: eTmp and elevated CO_2 and temperature in combination: eTmp & eCO_2.

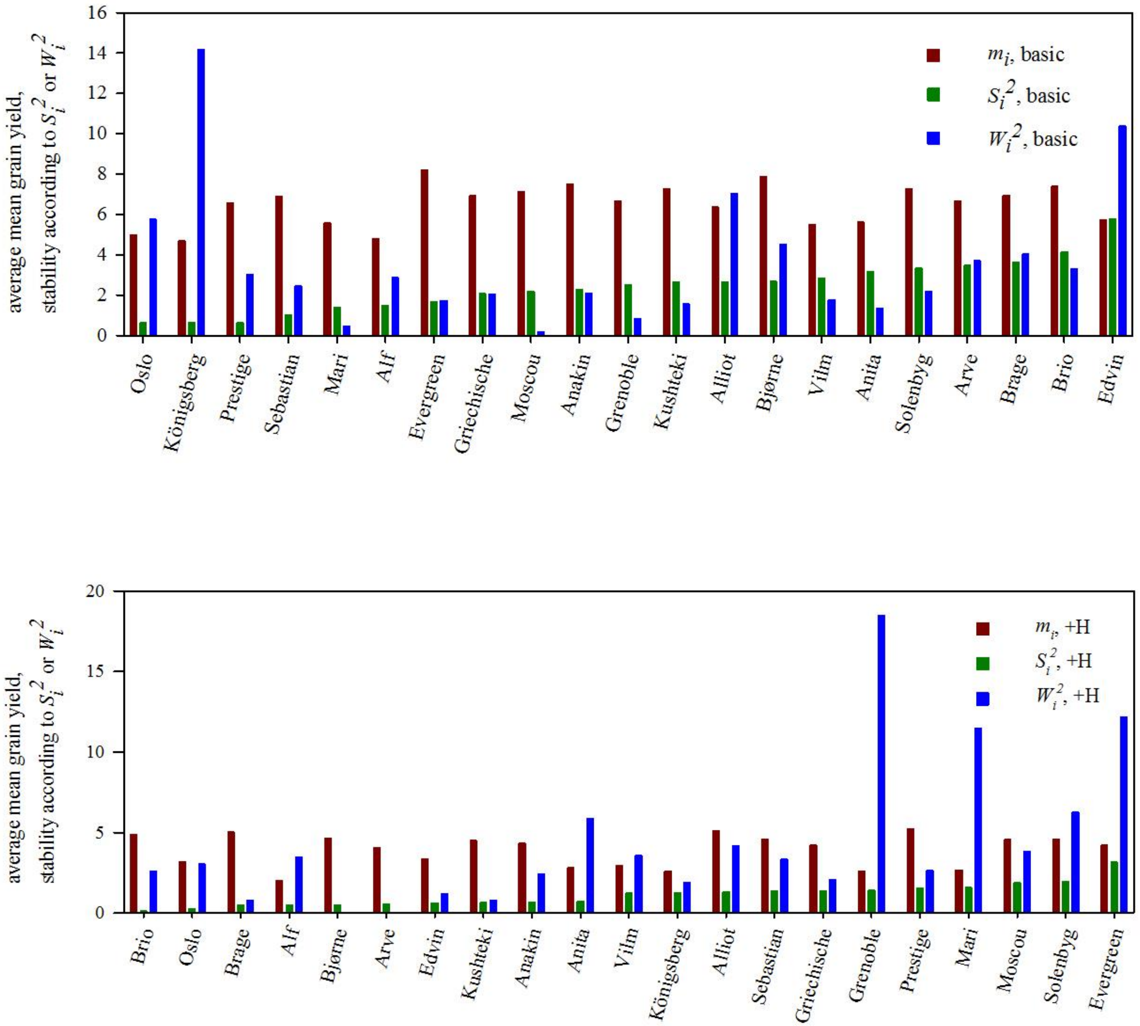

Fig. A.2. Environmental variance (S_i^2), Wricke's ecovalence (W_i^2) and mean grain yield across either the four basic treatments (top) or four basic+Heatwave (+H) treatments (bottom). Pearson's correlation of S_i^2 between the basic and basic+H treatments was -0.335 with p-value at 0.135. Drost P. not included, as watering in the eTemp+H treatment was defective.

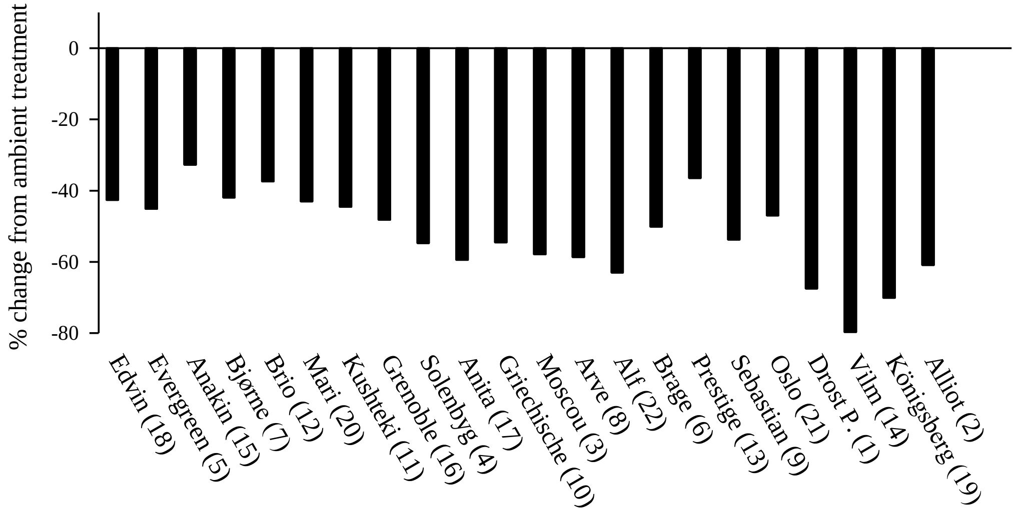

Fig. A.3. Change (%) in grain yield of the 22 spring barley accessions exposed to ambient climate treatment of 19/12°C (day/night) and 400ppm CO_2 and no heatwave exposure and the future climate scenario with elevated temperature (24/17°C) and elevated CO_2 (700ppm) in combination and a superimposed 10-day heatwave around flowering. In brackets is the rank (1: highest, 22: lowest) according to grain yield under basic ambient conditions.

Model description

The model used for generating estimates for Table 2 is of the form

$$Y_i = \alpha + \beta_T + \beta_{CO2} + \beta_H + \beta_{T:CO2} + \beta_{T:H} + \beta_{CO2:H} + Z_{ACC|POT} + \varepsilon_i, \qquad (1)$$

Where the response Y is one of Grain Yield, Biomass or Harvest Index. The treatment types elevated Temperature (T) and elevated CO_2 (CO_2) together with the superimposed Heatwave (H) enters into the parameters according to the treatment of the *i*'th observation and presence of heatwave or not. Z denotes randomized effects of Accessions and Pots, nested within Accessions. Absence of treatment refers to the ambient conditions. Thus, if observation *i* has been subject to elevated Temperature but no Heatwave and no elevated CO_2, the model for observation *i* is

$$Y_i = \alpha + \beta_T + Z_{ACC|POT} + \varepsilon_i,$$

While an observation *i* that has been subject to both elevated Temperature and a superimposed Heatwave, but not elevated CO_2, has the model

$$Y_i = \alpha + \beta_T + \beta_H + \beta_{T:H} + Z_{ACC|POT} + \varepsilon_i.$$

The estimated difference between these two scenarios is thus described by the parameter sum $\beta_H + \beta_{T:H}$.

Parameters estimates in the basic model (1) is listed in Table A.2. below for all three response types.

Table A.2. Parameter estimates in the random effects model (1), for responses Grain Yield (GrY), Biomass (BiM) and Harvest Index (HI) and SD for estimates.

	GrY			**BiM**			**HI**		
	estimate	sd	p	estimate	Sd	p	estimate	sd	p
$\boldsymbol{\alpha}$	7.16	0.26	<0.0001***	8.33	0.44	<0.0001***	45.31	1.28	<0.0001***
$\boldsymbol{\beta_{CO2}}$	1.84	0.23	<0.0001***	2.88	0.33	<0.0001***	-	-	NS
$\boldsymbol{\beta_T}$	-3.10	0.23	<0.0001***	-0.39	0.33	0.25	-9.56	1.23	<0.0001***
$\boldsymbol{\beta_H}$	-2.65	0.28	<0.0001***	1.93	0.33	<0.0001***	-17.81	1.24	<0.0001***
$\boldsymbol{\beta_{CO2:T}}$	-	-	NS	-0.83	0.38	0.03*	-	-	NS
$\boldsymbol{\beta_{CO2:H}}$	-1.12	0.32	0.0006***	1.18	0.38	0.002**	-	-	NS
$\boldsymbol{\beta_{T:H}}$	1.29	0.32	0.0001***	-1.77	0.38	<0.0001***	5.72	1.75	0.001**