Effects of elevated atmospheric CO₂ and its interaction with temperature and nitrogen on yield of barley ( Hordeum vulgare L.): a meta-analysis

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Abstract
Aims The general aim of this meta-analysis is to synthesize and summarize the mean response of barley yield variables to elevated CO₂ (eCO₂) and how temperature and nitrogen (N) affect the CO₂-induced yield responses of barley.
Methods A meta-analysis procedure was used to analyze five yield variables of barley extracted from 22 studies to determine the effect size and the magnitude concerning eCO₂ and its interaction with temperature and N.
Results CO₂ enrichment increased aboveground biomass (23.8%), grain number (24.8%), and grain yield (27.4%). The magnitude of the responses to eCO₂ was affected by genotype, temperature, nitrogen, and CO₂ exposure methods. Genotype “Anakin” shows the highest CO₂ response of aboveground biomass (47.1%), while “Bambina” had the highest grain number (58.4%). Grain yield response was observed to be higher for genotypes “Alexis” (38.1%) and “Atem” (33.7%) under eCO₂. The increase of aboveground biomass and grain yield was higher when plants were grown under eCO₂ in combination with higher N (151–200 kg ha⁻¹). The interaction between eCO₂ and three different temperature levels was analyzed to identify the impacts on barley yield components. The results revealed that the CO₂-induced increase in grain number and grain yield was higher in combination with a temperature level of 21–25 °C as compared to lower levels (< 15 and 16–20 °C). The response of barley yield to eCO₂ was higher in growth chambers than in other CO₂ exposure methods. Moreover, a higher response of aboveground biomass and grain yield to eCO₂ was observed for pot-grown plants compared to field-grown.

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Conclusions  Overall, results suggest that the maximal barley production under eCO₂ will be obtained in combination with high N fertilizer and temperature levels (21–25 °C).

Keywords  Climate change · Systematic review · Global change · Hordeum vulgare L · Yield variables

Introduction  One of the most important challenges of the twenty-first century is to find solutions to the problems caused by global climate change. Alleviating future food security challenges will need to estimate crop production response to the ongoing increase of atmospheric carbon dioxide (CO₂), together with rising temperature, and soil fertility. Evidence indicates that atmospheric CO₂ concentration increased globally, from 280 ppm in the pre-industrial period to about 419 ppm in 2021 and it might increase to 550 ppm by 2050 (IPCC 2021). CO₂ is the most important anthropogenic greenhouse gas (GHG) and it represented 74% of overall anthropogenic GHG emissions in 2018 (IPCC 2021). The changes in CO₂ concentration and other GHG emissions are expected to increase air temperature by 2.5 to 4.8 °C at the end of the twenty-first century (IPCC 2021). These environmental changes will have a substantial effect on crop growth and food supply in the future. At the same time, the total global food production has to increase by 25 to 70% within the next 40 years, to meet the food demand for the projected increase in the global population (Fróna et al. 2019; United Nations 2011). As the raw material for plant photosynthesis, an increase in CO₂ concentration will inevitably affect the growth and development of plants. An increase in atmospheric CO₂ generally exerts beneficial effects on plant biomass by increasing net photosynthesis by 30 to 50% and reducing photorespiration (Drake et al. 1997; Poorter and Navas 2003; Schapendonk et al. 2000). This has been studied for cereals including barley, wheat, rice, oat, and rye (Conroyac et al. 1994; Kimball et al. 2002; Long et al. 2006). For instance, in a meta-analysis comprising 79 crops and wild species, Jablonski et al. (2002) documented an increase in yield of 28% averaged across crops and wild species due to elevated CO₂ (eCO₂). A climate chamber experiment with 700 ppm CO₂ on barley reported an increment of grain yield by 54% compared to 400 ppm (Alemayehu et al. 2014), while 47% enhancement of grain yield averaged across two genotypes was reported by Schmid et al. (2016) under eCO₂ level of 550 ppm. Moreover, Manderscheid and Weigel (2006) evaluated the effects of eCO₂ on barley using Free-air CO₂ enrichment (FACE) at 550 ppm, and obtained yield increases of 7 and 15% under the combination of eCO₂ with low and high N supply respectively.

The projected increase in biomass and grain yield of C3 crops due to eCO₂ is affected by certain environmental factors such as rising air temperature and nitrogen (N) (Jaggard et al. 2010; Weigel et al. 1994). Despite a good response of C3 crops production to eCO₂ at near-optimal temperature (18–23 °C), the impact may be countered by rising temperature by 2–4 °C (Ainsworth 2008; Peng et al. 2004; Lobell and Field 2007; Tao et al. 2008). Accordingly, Dieleman et al. (2012) and Wang et al. (2012) have highlighted the relevance of the interactive impacts of eCO₂ and temperature on rice yield, but no particular meta-analysis addressing barley has been undertaken. In general, increased temperature is primarily linked with higher evapotranspiration, acceleration of plant development, and consequently shortening of developmental phases, leading to early maturation and decreased yields (Barnabás et al. 2008; Cox et al. 2000; Hansen et al. 2000; Högy et al. 2013; Mangelsen et al. 2011; Vara Prasad et al. 2002). Studies on six major crops including barley have indicated that increasing the seasonal average temperature by 1 °C results in a significant grain yield reduction by 4 to 10% (Barnabás et al. 2008; Hatsfield et al. 2011). Clausen et al. (2011) found a grain yield reduction of barley by 14% under eCO₂ and elevated temperature (+3 °C) in comparison with the same level of eCO₂ and ambient temperature. A 53% reduction in grain yield of barley was recorded by another study due to elevated temperature in combination with eCO₂ (Alemayehu et al. 2014).

Elevated CO₂ typically leads to a marked increase of biomass in well-fertilized plants (Bowes 1996), this response is modified when the N fertilization is suboptimal. Among the various environmental factors, N availability can have a significant impact on crop biomass and yield formation in response to eCO₂ (Stitt and Krapp 1999; Kimball et al. 2002). Several studies have revealed CO₂ and N interactions, and it
is widely assumed that N deficiency acts as a growth inhibitory factor, potentially decreasing the relative response to eCO₂ (Ainsworth and Long 2005). In general, studies address biomass accumulation under eCO₂ and variable N supply levels across cereal production (Reich et al. 2006). According to Ziska and Bunce (2007), there is now enough evidence to suggest that crop yield stimulation by eCO₂ is dependent on N availability. For example, this has been shown for barley (Kleemola et al. 1994) and wheat (Wolf 1996) and in chamber studies. However, some recent studies with rice that examined crop responses under FACE conditions and low N availability reported similar yield stimulation by eCO₂ as under sufficient N supply (Kim et al. 2003, Liu et al. 2008; Yang et al. 2009). There are still uncertainties whether this holds true also for other crops under field conditions.

Even though the pattern of yield response to eCO₂ and its interactions with temperature and N are similar within C3 crops, distinctions are evident across species, genotypes, and growing conditions (Connor 2002). The yield response of crops to eCO₂ is widely affected by enclosure systems and rooting conditions. Open-top chambers (OTC) have been widely used in eCO₂ field experiments but also questioned since they alter the micro-climate of the plants and thus may modify the magnitude of crop responses (Schimel 2006). Comparison of conditions in OTCs to the open field show that temperatures and vapor pressure deficits are higher inside chambers and airflow is altered in the plant canopy (Ziska and Bunce 2007). The use of OTCs will also reduce transmission of solar radiation and shift the ratio between diffuse and total radiation (Rawson 1995). FACE systems have been developed to create a less artificial experimental setup compared to enclosure systems like OTCs. On the other hand, FACE systems have the drawback of not being able to reach strongly elevated concentrations for eCO₂ treatments and possibly less stable concentration levels that may lead to underestimation of plant eCO₂ responses (Leakey et al. 2009). However, eCO₂ concentrations are often lower in FACE (e.g., 550 ppm) as compared to OTCs or climate chambers (> 600 ppm). It is not clear whether OTCs or FACE studies showed larger effects of elevated CO₂ on crop biomass and yield than studies performed in greenhouses or growth chambers. Plants in both greenhouse and climate chambers should be subject to edge effects like those in OTCs (Long et al. 2004). Furthermore, it is questionable whether results from experiments with plants grown in pots can be comparable to field conditions since the response to eCO₂ might be reduced due to the restricted rooting volume and the pot size (Loladze 2014; Högy and Fangmeier 2008). Field-grown wheat had similar or lower responses to eCO₂ than plants grown in a pot (Wang et al. 2013). This contradicts the premise that restricted root development, nutrient, and water supply in pot studies leads to a decrease in photosynthesis and, as a result, a reduction in plant responsiveness to eCO₂ (Arp 1991; Curtis and Wang 1998).

Barley (Hordeum vulgare L.) is one of the most important and extensively cultivated cereal crops worldwide for human nutrition and as animal feed. The production of barley in 2020 was about 150×10⁶ tonnes and it has been cultivated in more than 100 countries worldwide (FAOSTAT 2020). However, despite its importance, the effect of eCO₂ and its interaction with temperature and N fertilizer on barley production has not been quantitatively reviewed using meta-analysis techniques. Previous meta-analytic studies on C3 crops, such as wheat, rice, and soybean, have provided insights into the extent of the effects of eCO₂ on yield variables such as aboveground biomass, grain yield, grain number, thousand-grain weight, and harvest index (Ainsworth 2008; Broberg et al. 2019; Feng et al. 2008). The rationale for a meta-analysis is that, by combining the samples of the individual studies, the overall sample size is increased, thereby improving the statistical power of the analysis as well as the precision of the estimates of treatment effects. Several studies have investigated the effects of eCO₂ and their interactions with temperature and N on barley (e.g., Weigel and Manderscheid 2012; Manderscheid et al. 2009; Fangmeier et al. 2000). However, inconsistency in the findings and estimation of the effects in individual studies was noticed. For the first time to our knowledge, the response of barley to eCO₂ and its interaction with temperature and N as well as the effect of growing condition (CO₂ exposure methods, rooting volume) or genotype is quantitatively reviewed. The objectives of the present meta-analysis are therefore two-fold (1) to synthesize and summarize the mean response of barley yield variables (i.e. aboveground biomass, grain yield, grain number, thousand-grain weight, and harvest index) to eCO₂, temperature, N fertilization, and their interactions, and (2) to determine whether...
different CO₂ exposure methods, rooting conditions, or genotypes significantly alter the mean response of barley to eCO₂.

Materials and Methods

Database development

Peer-reviewed primary literature focusing on barley yield responses to eCO₂, temperature, and N were searched on Scopus, Science Direct, and Google Scholar. The search strings used to search the literature on the search engines are presented in Appendix 1. The search was intended to be comprehensive, including all relevant studies that were published between 1991 and 2020. The response of five yield variables (aboveground biomass, grain number, grain yield, thousand-grain weight, and harvest index) of barley were included in the database as well as in the search strings. The following four inclusion criteria were applied for including studies in the database: (1) the ambient CO₂ (aCO₂) level had to be ≤450 ppm (intended to represent the past and the near future concentration) and the eCO₂ has to be ≥451 ppm (representing CO₂ concentration in the future); (2) at least one of the selected yield variables is evaluated; (3) the response means, and sample sizes (n) are reported directly in the text, table or can be indirectly derived from figures, and (4) the CO₂ exposure technique is specified. Publication bias was checked by looking at the symmetry in a funnel plot (Appendix 2, Fig. 9). The final database covered a total of 22 studies that included CO₂, temperature, and N treatments over the entire experimental period (Fig. 1). Out of the 22 studies, 84 observations were extracted and analyzed. From these 84 observations, 42 was on the response of barley to eCO₂ as a single factor, 18 on the interaction of eCO₂ with temperature, and 34 on the interaction of eCO₂ with N. Observations were considered as independent within studies, if measurements were taken on different CO₂ concentration levels, genotypes, or combinations with N and temperature following previous meta-analysis studies (Ainsworth et al. 2002; Gurevitch and Hedges 1999).

To test the interaction effect of eCO₂ with temperature and N, we extracted data only from studies that included CO₂, temperature, and N treatments. For experiments involving additional environmental factors, such as O₃ and drought, the mean of the controls group was used. For each response variable, means and sample size were recorded from the treatment and control groups for each observation. The response of barley yield variables to eCO₂ might be affected by different moderators, thus the data were grouped into several groups, such as CO₂ fumigation methods (growth chamber, GC; greenhouse, GH; open-top chamber, OTC; and Free-air CO₂ enrichment, FACE), CO₂ levels (451–550, 551–650, and 651–720 ppm), air temperature levels (<15, 15–20, and 21–25 °C), N fertilizer levels (0–50, 51–100, 101–150, and 151-200 kg ha⁻¹), growing conditions (pot-grown and field-grown), and genotypes. Sixteen genotypes were found in several studies, and they were used for the analysis of the CO₂ effects on the response of barley yield variables (Table 1). However, in addition to these 16 genotypes, a group of spring cultivars and accessions were used for the overall non-genotype-based analysis. For the analysis of all categorical variables including the interaction of eCO₂ with temperature and N, averaged eCO₂ was used across all levels.

Meta-analysis

Meta-analysis commonly describes the extent of an experimental treatment mean (yₑ) relative to the control treatment mean (yᶜ) (Ainsworth et al. 2002). The log response ratio (mean yield of the experimental to the control group) was used as the effect size to calculate the magnitude of CO₂, and its interaction with temperature and N treatment on the selected yield variables of barley. The log transformation can make the data better approximate to the normal distribution, reduce skewness, and make non-linear relationships linear. For each treatment (eCO₂, eCO₂ with temperature, and N), we calculated the natural logarithm of the ratio as, r = yₑ/yᶜ and its percentage change from the control ((r-1)×100). Thus, the expected mean percentage change is positive for r > 1 but negative for r < 1. Linear mixed models were fitted, assuming that differences among studies within a treatment combination are due to both sampling error and random variation. As variance or related parameters were not reported in several studies, unweighted analyses were performed for all the variables. However, resampling and bootstrapping techniques were used to obtain the confidence intervals of the mean effect.
size (Gurevitch and Hedges 1999). For each categorical variable, between-group heterogeneity (QB) was examined. The significance of the mean differences from categorical variables was tested (Gurevitch and Hedges 1999). All the analyses were performed in R statistical software (R Core Team 2019). The linear mixed model was fitted using the R library lme4.

Results

CO₂ effect on barley yield variables

Across all the 42 observations out of 22 studies, a significant enhancement in most of the measured yield components was observed at eCO₂ levels (i.e., 451–720 ppm) relative to aCO₂ (≤450 ppm). Aboveground biomass of barley was increased by 23.8% [CI: 18.0–27.8%] under eCO₂ compared to barley plants grown under aCO₂. Grain yield was increased by 27.4% [CI: 18.5–36.2%], mainly due to higher grain number (24.8% [CI: 17.7–31.9%]) and thousand-grain weight (5.6% [CI: 3.5–8.1%]), however, the response of harvest index was not affected by eCO₂ (Fig. 2). The response of barley yield components varied with eCO₂ concentration levels (Fig. 3). For instance, the highest percent enhancement of aboveground biomass (28.7%) was observed under the eCO₂ concentration level of 551–650 ppm (Fig. 3). Under 451–550 ppm, aboveground biomass was increased by x%. Due to data limitations, the response of aboveground biomass was not evaluated under the highest eCO₂ level (651–720 ppm). Significantly higher positive responses of grain yield, grain

Fig. 1 PRISMA flow diagram for studies selection
number, harvest index, and thousand-grain weight were observed under the highest eCO2 concentration level (651–720 ppm) relative to all the lower levels (Table 2 and Fig. 3).

Interaction of eCO2 with N fertilization and temperature treatments

The response of barley yield components to eCO2 was significantly affected by N fertilizer and temperature treatments (Table 2). The results from the interaction of eCO2 with N showed an increase of yield components with increasing N level except for thousand-grain weight and harvest index. The highest responses of aboveground biomass (57.4% [CI: 54–62%]) and grain yield (58.7% [CI: 55–63%]) to eCO2 were observed under the N level of 151–200 kg ha\(^{-1}\), relative to lower N levels (Fig. 4). Grain number was increased by 28.8% due to eCO2 under the application of 51–100 kg ha\(^{-1}\) N, which is not significantly different from the response under N level (151–200 kg ha\(^{-1}\)) as shown in Fig. 4. The response of thousand-grain weight and harvest index to eCO2 were not significantly different between the N levels.

In comparison, aboveground biomass was increased, under the combination of eCO2 with 15–20 °C (38.5% [CI: 34–43%]) compared to temperature levels <15 and 21–25 °C (Fig. 5). On the other
hand, we observed a mixed trend in the response of barley yield components to eCO2 in combination with different temperature levels. Grain number (36.4% [CI: 29–41.4%]), and grain yield (59.7% [CI: 54–63%]) were higher when eCO2 combined with the higher temperature level of 21–25 °C compared to the lower levels (Fig. 5). Due to lack of data, the interaction of temperature higher than 25 °C with eCO2 was not evaluated in the present study.

### Genotypic variation

Barley genotypes had a significantly different response of yield components to eCO2 (Table 2 and Fig. 6). Comparing 13 genotypes on the response of aboveground biomass, the highest increase by 47.1% [CI: 43–51%] was observed for genotype “Anakin”, while the lowest was observed for “Harrington” (2.7% [CI: -1–6%]) under eCO2 (Fig. 6). The grain yield response was only available for 6 genotypes, out of them “Alexis” showed the highest grain yield by 38.1% [CI: 32–43%], while the lowest response was observed for genotype “Gairdner”. The response of grain number by 58.1% [CI: 32–43%] was the highest for the “Bambina”, while harvest index response was the highest for genotype “Golden_Promise” under eCO2 (29.2 [CI: 24–33%]) (Fig. 6).

### CO2 exposure methods and rooting conditions

The responses of barley yield to eCO2 were significantly affected by the four CO2 exposure methods except for thousand-grain weight (Table 2). The percent of aboveground biomass enhancement under eCO2 was higher when plants were grown in GH (34.9% [CI: 30–39%]) followed by GC (29.3% [CI: 24–33%]) as shown in Fig. 7. On the other hand, the highest increase in barley grain number (41.8% [CI: 37–45%]) and grain yield (31.8% [CI: 26–37.3%]) under eCO2 were observed for the plants grown in the GC. In contrast, barley plants that were grown under FACE had a significantly negative response of grain number, harvest index, and thousand-grain weight (Fig. 7). On the other hand, comparing yield variable response of barley plants grown in pots and on-field conditions, higher responses were observed for plants grown in pots except for harvest index.

**Fig. 3** Relative percentage change in barley yield response to three levels of CO2 treatment (451–550, 551–650, 651–720 ppm) analyzed out of 42 observations on the response of yield variables/parameter to eCO2. Due to a lack of data, the response of aboveground biomass to the highest level of CO2 concentration was not evaluated. The symbols represent the percentage change (±95% CI) in response relative to the corresponding control. TGW: thousand-grain weight; HI: harvest index; GY: grain yield; GN: grain number; AGB: aboveground biomass.

**Table 2** Relative percentage change between-group heterogeneity (QB) for eCO2 effect size across different categorical variables

| Variables | No. of studies | No. of observations | Genotype | CO2 levels | CO2-exposure techniques | Rooting conditions | N | Temperature |
|-----------|----------------|---------------------|----------|------------|-------------------------|-------------------|---|-------------|
| TGW       | 8              | 44                  | 0.93 ns  | 4.4 ns     | 1.0 ns                  | 4.5 ns            | -0.8 ns | 6.2 ns      |
| HI        | 9              | 52                  | 10.5*    | 3.2*       | 4.6*                    | 12.1*             | -0.7 ns | 1.35 ns     |
| GY        | 11             | 46                  | 22.9**   | 21.2**     | 22.8*                   | 21.1***           | 29.9*** | 31.6*       |
| GN        | 12             | 40                  | 25.7***  | 17.5***    | 23.5***                 | 30.8***           | 15.9**  | 21.5**      |
| AGB       | 17             | 78                  | 22.9***  | 22.3***    | 23.5***                 | 22.2***           | 30.9*** | 27.3***     |

TGW: thousand-grain weight; HI: harvest index; GN: grain number; GY: grain yield; and AGB: aboveground biomass. Significance level: P < 0.001 (***) , P < 0.01 (**), P < 0.05 (*) and not-significant (ns)
Higher responses of aboveground biomass (29.8\% [CI: 25–34\%]), grain number (38.3\% [CI: 35–42\%]), and grain yield (25.3\% [CI: 21.1–29.2\%]) under eCO2 were obtained for the plants grown in pots. However, the response of harvest index of barley was significantly higher for plants grown on field conditions compared to pot-grown plants (Table 2 and Fig. 8).

Discussion

Responses of barley yield to eCO2 and the interaction with N and temperature

A meta-analysis technique was used to quantitatively review and synthesize the literature on barley yield as a function of eCO2, and its interaction with temperature, and N fertilizer treatments. The rise in atmospheric CO2 causes mostly an increase of the total biomass of C3 plants such as barley, by stimulating net photosynthesis and reducing photorespiration (Drake et al. 1997; Mitterbauer et al. 2017; Schapendonk et al. 2000). The average increase in aboveground biomass by 23.8\% under eCO2 in this study is in line with previous meta-analysis studies on C3 crops (Ainsworth 2008; Wang et al. 2013). Similarly, a meta-analytic study of 79 crop and wild species also documented an average enhancement of biomass by 28.2\% across all species due to eCO2 (Jablonski et al. 2002). In the present study, the aboveground biomass and grain yield showed similar patterns of increase with increasing levels of eCO2. Plants grown under an eCO2 level of 551–650 ppm showed the highest response in aboveground biomass compared to lower eCO2 concentrations (450–550 ppm). In the present study, grain yield and grain number were significantly increased under eCO2 (651–720 ppm). Consequently, harvest index response was significantly increased under the highest eCO2 (651–720 ppm), however,
no significant variation was observed for lower eCO₂ levels. A higher harvest index under eCO₂ implies that a relatively higher proportion of assimilated carbon is allocated to the grains. Ainsworth et al. (2002) reported a higher percentage of stimulation on aboveground biomass and grain yield at the highest eCO₂ level (600–699 ppm) in rice. Also, Kimball et al. (2001) reported an increase in the grain yield of wheat under eCO₂. The present study’s findings also revealed an association with an increase in grain yield due to a larger increase in grain number rather than thousand-grain weight. As a result, the response of barley yield to eCO₂ has largely been driven by an increase in grain number. This result is similar to findings reported in other studies on C3 plants (Wilcox and Makowski 2013; Knox et al. 2016). Furthermore, increased grain yields have been linked to a higher number of tillers and grains per spike rather than an increase in the number of spikes or grain size in wheat and barley (Bourgault et al. 2013; Pleijel and Högy 2015; Amthor 2001; Wang et al. 2013). The additional carbon assimilates produced by eCO₂ levels may ensure the development of flowers and grains (Deng and Woodward 1998). However, the effect of eCO₂ on individual grain weight varied, with increases (Van Oijen et al. 1999; Li et al. 2001), decreases (Rawson 1995; Batts et al. 1997; Van Oijen et al. 1999; Heagle et al. 2000), and no change (Heagle et al. 2000; Pleijel et al. 2000).

The CO₂-derived “fertilization” effect may differ/may be different under different growth conditions such as nitrogen and temperature levels (Aranjuelo et al. 2011). It has been shown that the eCO₂ effect on total biomass and grain yield of barley decreases if the N availability is reduced (Wang et al. 2015). In line with a previous meta-analysis study on rice (Wang et al. 2015), we observed a reduction of grain yield response to eCO₂ under limited N fertilizer (0–50 kg ha⁻¹). In the present study, the highest CO₂-induced increase of aboveground biomass and grain yield was observed under the higher N level (151–200 kg ha⁻¹). In comparison, the response grain number showed a larger response to eCO₂ with 101–150 kg ha⁻¹ N. In addition, the percentage increase in grain yield at eCO₂ with a combination of higher N level was related to the percentage increase...
in grain number, demonstrating a positive relationship. Low N fertilization limited N concentration in vegetative plant parts, limiting any increase in grain number and, consequently, grain yield response to eCO2 is reduced (Kim et al. 2003). Limitation in N fertilizer may also cause more pronounced acclimation of photosynthesis to eCO2, which can limit total biomass increases at eCO2 (Suter et al. 2001; Ainsworth et al. 2003). Because eCO2 has a significant effect on crop N uptake and concentration in biomass, crop production’s response to elevated CO2 is highly dependent on the availability of nutrient resources (Leakey et al. 2012). In our meta-analysis, low N input constrained barley yield in response to eCO2 as compared to high N input. This decrease is most likely due to the direct relationship between N availability and growth parameters such as grain number throughout the growing season (Mitchell et al. 1993; Kim et al. 2001, 2003).

On the other hand, the temperature is also one of the most determinant factors of crops development rates and yield (Wang et al. 2015). Higher temperatures result in accelerated crop development, and thus a shorter growing period, resulting in lower grain yield (Hatfield and Prueger 2015). We found a significant interaction between eCO2 and temperature on barley yield variables. In comparison, better enhancement of aboveground biomass was observed under the combination of eCO2 and temperature level (15–20 °C). Moreover, grain yield and grain number were also increased under the interaction of eCO2 and temperature level (21–25 °C)), which disagrees with previous studies (Wang et al. 2015; Hatfield and Prueger 2015). Due to lack of data, the interactive effect of eCO2 with a temperature higher than 25 °C is missing in the present study. Nevertheless, the significantly higher number of grains observed in the present study might be responsible for higher grain yield under the combination of eCO2 and higher temperature (21–25 °C). In contrast to our study, Wang et al. (2015) reported that under eCO2 an increase of temperature by 1 °C may lead to a decrease in rice yield by 9.4% at temperature levels of 24–26 °C. In addition, Amthor (2001) reviewed the effects of eCO2 on wheat and found that increasing temperatures by 5 °C from the ambient level (12.7 °C) may offset the positive effects of eCO2. However, he mentioned also that eCO2 can counteract the negative effects of higher temperatures, which may partially explain the increase in grain yield and grain number due to eCO2 in combination with higher temperature levels in the present study.

Variation in the response of barley yield to eCO2

Genotypic variation

The identification of consistent genotypic variability in the response to eCO2 is a prerequisite to using this information in breeding programs. Barley yield variable responses to eCO2 were different among barley genotypes, which might be related to the varietal character of genotypes. In the present study modern spring barley genotype “Anakin” had more aboveground biomass under eCO2, followed by the old landrace “Gammel_Dansk”, “Bambina” and “Aura”, while “Iranis” showed the lowest response. The genotype “Bambina”, a mid-maturing spring cultivar, had the highest grain number followed by early maturing and high yielding genotype “Golden Promise” at eCO2. However, grain yield and harvest

Fig. 8 Relative percentage change in barley yield response to eCO2 under two different rooting conditions (field-grown and pot-grown). The symbols represent the percentage changes (±95% CI) in response relative to the corresponding controls. TGW: thousand-grain weight; HI: harvest index; GY: grain yield; GN: grain number; AGB: aboveground biomass
index response were higher for “Alexis”, a heat-tolerant, two-rowed German genotype, and “Atem”, a drought-tolerant European modern spring genotype. Genetic variability on the response of total biomass and grain yield to eCO₂ was reported in previous studies on wheat (Ziska et al. 2004) and rice (Wang et al. 2015). Modern genotypes do not necessarily always perform better than old ones at higher CO₂ levels. For example, the aboveground biomass of an older wheat genotype can increase more than that of a modern genotype in response to increasing CO₂ (Hay and Gilbert 2001). In contrast to the present findings, previous studies in soybean (Bishop et al. 2015) and common bean (Bunce 2008) could not detect differences between the cultivars tested in their response to eCO₂ for grain yield and other yield variables evaluated. The response of thousand-grain weight to eCO₂ did not differ among the barley genotypes in the present study. However, previous studies have found a variety of genotypes response of thousand-grain weight under eCO₂ (Weigel et al. 1994). The findings from the present meta-analysis suggest breeding for the exploitation of eCO₂ might enhance future crop production. Previous studies have suggested that there is very little evidence that breeders have inadvertently selected for increased CO₂ responsiveness, and indeed several studies have suggested the opposite, that older genotypes are more responsive to eCO₂ than modern genotypes (Ainsworth et al. 2008; Leakey and Lau 2012; Ziska et al. 2012).

**Experimental conditions**

The estimation of the response of barley yield to eCO₂ can be significantly affected by CO₂ exposure methods. Previous studies reported an enhancement of aboveground biomass and grain yield at eCO₂ is lower under FACE experiments than other enclosure methods (Long et al. 2006; Tubiello et al. 2007). In addition, a meta-analysis study by Broberg et al. (2019) recorded a higher wheat yield for plants grown in OTCs than with FACE. The present meta-analysis shows that plants grown in GC had relatively higher aboveground biomass and grain yield due to eCO₂ than those plants grown under FACE or OTC, which is in line with an earlier study (Long et al. 2006). Similarly, when plants were grown in GC, higher grain yield due to eCO₂ has been reported in meta-analyses of rice (Wang et al. 2015) and wheat (Wang et al. 2013). The findings from the present meta-analysis and previous studies showed that the rapid fluctuation of CO₂ concentration has lowered plant photosynthesis in FACE experiments, which resulted in a lower accumulation of biomass and grain yield (Holtum and Winter, 2003). However, another meta-analysis of wheat noted no significant difference between FACE and OTC experiments concerning the response of grain yield to eCO₂ (Feng et al. 2008). Nonetheless, no study seems to have directly compared the response of barley yield variables to different CO₂ exposure methods of the same genotype grown under identical soil, environmental condition, and cultivation practice.

The effect of growth conditions on the response of barley yield to eCO₂ varies between yield variables (Wang et al. 2015; Broberg et al. 2019). In the present study, the response of aboveground biomass, grain number, and grain yield were significantly higher for pot-grown barley rather than under field grown. This disagrees with the hypothesis that restricted root growth in pot experiments leads to a down-regulation of photosynthesis and consequently diminishes the response of plants to eCO₂ (Arp 1991; Curtis and Wang 1998). In the present meta-analysis, the restricted rooting volume for pot-grown plants did not have a major impact on the eCO₂ stimulation of aboveground biomass and the number of grains in barley. One possible reason for the apparent discrepancy may be that all the results from pot-grown plants in the present meta-analysis derived from GC studies, which showed much larger responses to eCO₂ than FACE conditions. In agreement with our findings, previous meta-analyses have also reported higher aboveground biomass and grain yield responses of pot-grown wheat plants under eCO₂ as compared to field-grown plants (Taub and Wang 2008; Wang et al. 2013). In contrast, other studies have reported non-significant variation in responses of grain yield to eCO₂ for pot-grown and field-grown wheat plants (Feng et al. 2008). However, the responses of harvest index to eCO₂ were higher for field-grown plants in the present study, which disagrees with the previous study on rice (Ziska and Bunce 2000).
Conclusions

This meta-analysis quantified the effect of eCO₂ as a single factor and its interaction with N and temperature on barley production. A strong positive effect of eCO₂ was observed for aboveground biomass, grain yield, and grain number. However, the responses of aboveground biomass, grain number, and grain yield to eCO₂ were lower under limited N fertilizer (<50 kg ha⁻¹). In general, the magnitude of the CO₂-induced effect on barley grain yield will depend on the future atmospheric CO₂ concentration and agronomic practices such as genotype choice, and growing conditions. The existence of genetic variation in barley response to eCO₂ is needed to breed barley to the future atmospheric environment. Modern barley genotype “Anakin” had higher aboveground biomass under eCO₂ than older ones, whereas “Alexis” and “Atem” showed higher grain yield and harvest index. Grain number was relatively higher due to eCO₂ for genotype “Bambina”. Uncertainties remain, however, regarding the responses to environmental conditions (temperature, N) of barley yield parameters, mainly aboveground biomass, grain number, and grain yield were significantly affected. The positive effect of eCO₂ was observed to be higher in combination with high N (150–200 kg ha⁻¹) and temperature levels (21–25 °C). In the present meta-analysis, some other important interactions, which potentially affect crop production such as the interaction of eCO₂ with drought and O₃, were not quantified. In addition, there is a lack of data that compares the effect of different exposure methods and rooting conditions side by side on barley yield response to eCO₂. Field experiments that better characterize the responses of barley and its interaction with additional factors to eCO₂ can help reduce uncertainties due to climate change in estimating future food production. Such studies might be used for summarizing and drawing conclusions on estimating food production in the future.

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Author Contributions M.G. and P.H. conceived and designed the study; data collection was made by M.G. M.G and W.A.M participated in the analysis of the data; M.G. wrote the paper with substantial input from P.H. B.H and W.A.M.

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Data availability Data obtained for the present study is available.

Code availability Software application code is available.

Declarations

Conflict of interest The authors have no conflict of interest.

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Appendix 1

Literature search strings for the meta-analysis review were used in various databases.

Scopus, Science Direct, and Google Scholar were used to search the literature using the below search strings.

“climate change” [title] [tiab] [key] AND (“barley yield” [title] OR “yield variables” [title] OR “yield components” [title] OR “elevated CO₂” [title], OR “carbon dioxide and temperature” [title] OR “carbon dioxide and nitrogen” [title] OR “elevated CO₂” [title] OR (“temperature” OR “nitrogen” AND (“aboveground biomass” OR “grain yield” OR “grain number” OR “thousand-grain weight” OR “harvest index”)) [title] OR meta-analysis [title] OR “meta analysis” [title] OR “systematic review” [title] OR “systematic-review” [tiab] OR “quantitative review” [tiab]).
Appendix 2

Fig. 9 Funnel plot of sample size against the log response ratio of the mean response of the experimental treatment (Yt) to the mean response of the control treatment (Yc) to identify a possible publication bias. AGB: aboveground biomass; GY: grain yield; GN: grain number and TGW: thousand-grain weight

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