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 summarise the mean response of barley yield variables to elevated CO_2 (eCO_2) and its interaction with temperature and N fertilization.

Methods

The present study quantitatively synthesized the response of barley to eCO_2 and its interaction with temperature, and Nitrogen (N). A meta-analysis procedure was used to analyse five yield variables of barley extracted from 76 articles to determine the effect size and the magnitude in relation to eCO_2 and its interaction with temperature and N.

Results

CO_2 enrichment increased biomass (23.8%), grain number (24.8%), grain yield (27.4%), and thousand-grain weight (5.6%). However, responses to eCO_2 were affected by genotype, additional stress, and experimental conditions. In comparison, genotype "*Anakin*" shows the highest response of biomass (47.1%), while "*Genebank accessions*" had a higher grain number (46.1%) and grain yield (57.1%) under eCO_2. The maximal enhancement of barley yield was observed when plants grow under a combination of eCO_2 and higher nitrogen fertilizer (>100 kg ha^{-1}). Nevertheless, biomass (-12%), and grain yield (-17%) responses were lower when eCO_2 is combined with high temperature (>25 °C). It was further noted the response of barley yield to eCO_2 was higher in the growth chamber than in other CO_2 exposure methods. Moreover, comparing pot-rooted versus field-rooted barley plants, a higher response of biomass and grain yield was observed for pot-rooted plants.

Conclusions

Overall, results suggest that the maximal barley production under eCO_2 will be obtained in combination with high nitrogen fertilizer and optimal temperature (21-25 °C).

Introduction

Evidence indicates that atmospheric carbon dioxide (CO_2) concentration increased globally, from 280 ppm in the pre-industrial period to about 410 ppm in 2019 and it might increase to 550 ppm by 2050 (NOAA, 2020). CO_2 is the most important anthropogenic greenhouse gas (GHG) and it represented 72% of overall anthropogenic GHG emissions in 2018. The changes in CO_2 concentration and other GHG emissions are expected to increase air temperature by 2.5 to 4.5 °C at the end of the 21st century (IPCC, 2018). 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, 2019; United

Nations, 2011). Alleviating future food security challenges will need precisely estimating crop production response to the ongoing increase of atmospheric CO_2, together with rising temperature, and soil fertility. The potential beneficial effect of elevated CO_2 (eCO_2) on plant growth and yield has been well documented (Ainsworth et al., 2002; Clausen et al., 2011; Curtis and Wang, 1998; Wang et al., 2013), however, the magnitude of this effect varies widely among species, genotypes, and growing conditions.

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 2019 was about 150×10^6 tonnes and barley has been cultivated in more than 100 countries worldwide (FAOSTAT, 2020). An increase in atmospheric CO_2 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 crop and wild species, Jablonski et al. (2002) documented an average increase in yield of 28% due to eCO_2. A climate chamber experiment with 700 ppm CO_2 on barley reported an increment of grain yield by 54% compared to 400 ppm (Alemayehu et al., 2014). Moreover, Manderscheid and Weigel (2006) evaluated the effects of eCO_2 using free-air carbon dioxide enrichment (FACE) at 550 ppm, and obtained yield increases of 7–15%.

The projected increase in biomass and grain yield of C3 crops due to eCO_2 is affected by certain environmental factors such as rising air temperature (Jaggard et al., 2010; Weigel et al., 1994). In general, increased temperature is primarily linked with 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; Hatfield et al., 2011). Similarly, Clausen et al. (2011) found grain yield reduction in well-watered barley of 14% compared with the same level of eCO_2 and ambient temperature, while a 53% reduction in grain yield was recorded by another study (Alemayehu et al., 2014).

Besides, the positive effect of eCO_2 on aboveground biomass and grain yield, which varied between 20 to 90% (Fangmeier et al., 1996; Fangmeier et al., 2000; Weigel et al., 1994) were modified by the influence of nitrogen fertilizer (Manderscheid et al., 2009; Thompson and Woodward, 2007). N influences plant growth mainly through seasonal variation in the total green leaf area index and the accumulated radiation absorbed (Amthor, 2001). At low N fertilizer, eCO_2 effects on the yield of barley (Fangmeier et al., 2000) and other cereals (Kim et al., 2003) are usually small. This is reinforced by findings of FACE studies with wheat and rice (Högy and Fangmeier, 2008; Kim et al., 2003). Even though the pattern of yield response to eCO_2 and its interactions with temperature and nitrogen are similar within C3 crops, distinctions are evident across species, genotypes, and growing conditions (Connor, 2002).

Previous meta-analytic studies on C3 crops, such as wheat, rice, and soybean, have provided insights into the extent of the effects of eCO_2 on yield variables (Ainsworth, 2008; Broberg et al., 2019; Feng et al., 2008). However, despite its importance, the effect of eCO_2 and its interaction with temperature and N fertilizer on barley production has not been quantitatively reviewed using meta-analysis. The objectives of the current meta-analysis are therefore two-fold (1) to synthesize and summarise the mean response of barley yield variables to eCO_2, temperature, and N fertilization and, (2) to determine whether different CO_2 exposure methods, rooting conditions, genotypes, or different stress treatments significantly alter the mean response of barley to eCO_2.

Materials And Methods

Database development

Peer-reviewed primary literature focusing on barley yield responses to eCO_2, temperature, and N were searched on Scopus, Science Direct, and Google Scholar. The following keywords were used to search the literatures in various combinations "barley", "elevated CO_2", "interaction", "interactive effects", "high temperature", "warming" and "N fertilizer". The search was intended to be comprehensive, including all relevant studies that were published between 1991 and 2020. The final database covered a total of 76 articles out of which 36 were on the response of barley to eCO_2, 22 on the interaction of eCO_2 with temperature, and 18 on the interaction of eCO_2 with N. To minimize biases the following four inclusion criteria were applied for including studies in the database: (1) the ambient CO_2 level has to be $\leq$ 450 ppm (intended to represent the past and the near future concentration) and the eCO_2 has to be $\geq$ 451 ppm (representing the CO_2 concentration after 2050); (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 CO_2 exposure technique is specified.

To test the interaction effect of eCO_2 with temperature and nitrogen, we extracted data from studies that included CO_2, temperature, and nitrogen treatments over the entire experimental period. Observations were considered independent within individual studies, if measurements were taken on different CO_2 concentration levels, genotypes, or combinations with various environmental stress factors following previous meta-analysis studies (Ainsworth et al., 2002; Gurevitch and Hedges, 1999). For experiments involving additional stress factors, such as O_3 and drought, the mean values of the control group were used. The final database included studies on the responses of barley aboveground biomass, grain number, thousand-grain weight (TGW), grain yield, and harvest index (HI). For each variable, response means and sample size were recorded from the treatment and control groups for each observation.

The putative factors likely to affect the response to eCO_2 of barley yield variables were further partitioned into several categories, such as CO_2 exposure methods (growth chamber, greenhouse, open-top chamber, and Free-air CO_2 enrichment), CO_2 treatment levels (451-550, 551-650, 651-750 ppm), air temperature level (<15, 15-20, 21-25, >25 °C), N fertilizer level (0-50, 51-100, 101-150, 151-200, >200 kg ha^{-1}), rooting conditions (pot and field), and genotypes (Table 1).

Meta-analysis

Meta-analysis commonly describes the extent of an experimental treatment mean ($\bar{y}_T$) relative to the control treatment mean ($\bar{y}_C$) (Ainsworth et al., 2002). To calculate the magnitude of CO_2, temperature and N treatment effect on the selected variables, we used, as the effect size, the log response ratio (expressed as mean yield ratio), the natural log of the ratio of the mean yield of the experimental to the control group. The log-transformation can make the data better approximate the normal distribution, reduce skenwness and make nonl-inear relationships more linear. For each of the three variables, we calculated the natural logarithm of the ratio of the mean response of the experimental treatment ($\bar{y}_T$) to the mean response of the control treatment ($\bar{y}_C$) as, $r = \ln(\bar{y}_T/\bar{y}_C)$ and its a 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 class 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. Means of different categorical variables were considered significantly different from each other if their 95% confidence intervals (CI) did not overlap (Ainsworth et al., 2002; 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 l*me4*.

Table 1

Summary of barley genotypes included in the meta-analysis

Genotypes	Genotype description
Genebank accession	Collection of genotypes
Alexis	Two-row German malting barley cultivar, heat tolerant
Arena	Two-row Australian modern spring barley cultivar, powdery mildew tolerant
Anakin	Modern spring barley cultivar
Atem	European modern spring cultivar, drought tolerant
Aura	Spring malting barley cultivar, disease-tolerant
Gairdner	Australian malting barley, moderately tolerant to powdery mildew
Gammer-Dansk	Old landrace
Scarlett	Two-row German spring malting barley
Spring_cultivars	A group of spring cultivars
Theresa	Winter barley cultivar

Results

CO_2 effect on barley yield variables

Across all the 76 studies, a significant enhancement of most of the measured yield variables was observed at elevated eCO_2 levels (i.e., 451-750 ppm) relative to aCO_2 ($\leq$ 450 ppm). On average, 23.8% [CI: 18.0–27.8%] CO_2-induced enhancement of aboveground biomass of barley was observed compared to barley plants grown under aCO_2 (Figure 1). Besides, grain yield was 27.4% [CI: 18.5–36.2%] higher under eCO_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 eCO_2 (Figure 1). Furthermore, the response of barley yield varied with eCO_2 concentration level such that the response of aboveground biomass (28.7%) was the highest under the eCO_2 concentration level of 551-650 ppm relative to 451-550 ppm. Also, the responses of grain yield, grain number, TGW, and HI were all significantly higher under the highest eCO_2 concentration level (651-750 ppm) relative to all the lower levels (Table 2 and Figure 2).

Table 2

Between-group heterogeneity (QB) for eCO_2 effect size across different categorical variables

Variables	No. of studies	Genotype	CO_2-tretment level	CO_2-exposure technique	Rooting condition	Stress	
						N	Temperature
AGB	58	23.4***	22.5***	14.3***	21.9***	21.5***	16.8***
GN	34	15.6***	22.4**	23.5*	20.4***	18.6**	14.7**
GY	54	29.2**	14.3^{ns}	22.8^{ns}	26.9***	24.5***	20.7*
TGW	44	4.7***	$5.7n^{s}$	1.0^{ns}	4.8^{ns}	15.6^{ns}	-6.2^{ns}
HI	44	1.9^{ns}	2.3*	4.6^{ns}	1.8^{ns}	5.4^{ns}	-

AGB: aboveground biomass, GN: grain number: GY: grain yield, TGW: thousand-grain weight. Significance level: P< 0.001 (***), P< 0.01 (**), P< 0.05 (*) and not-significant (ns).

Interactive effect of eCO_2 with N fertilization and temperature treatments

Although only a few studies reported the interactive effects of CO_2 with N or temperature, the response of barley yield variables to eCO_2 was significantly affected by both N fertilizer and temperature treatements (Table 2). The highest responses of aboveground biomass (31% [CI: 26-39%]), TGW (13% [CI: 8-16%]), and HI (20.4% [CI: 15.2-24.2%]) to eCO_2 were observed under the N level of 151-200 kg ha^{-1}, relative to lower N levels. Besides, an enhancement of grain yield by 24.5% [CI: 19.1-30%] and grain number by 31.7% [CI: 27.5-36.9%] were recorded for eCO_2 combined with an N level of 101-150 kg ha^{-1}. There was no significant difference in the response of barley yield variables to eCO_2 between plants grown under N levels of 0-50 kg ha^{-1} and 51-100 kg ha^{-1} (Figure 3). On the other hand, the highest enhancement of aboveground biomass by 28.4% [CI: 20.7-34.4%], grain yield by 28% [CI: 22-32%], grain number by 36.4% [CI: 29-41%], and TGW by 11% [CI: 5.6-16%] were observed for the combination of eCO_2 with a temperature level of 21-25 °C (Figure 4). However, the response of aboveground biomass and grain yield declined by -12% [CI: -18-(-5)%] and -17% [CI: -23-(-10)%], respectively, when eCO_2 was combined with a high-temperature level (>25 °C). The response of TGW was unaffected by variation in eCO_2 under the othertemperature levels (Figure 4).

Genotypic variation

Barley genotypes had a statistically significant effect on the response of aboveground biomass, grain number, and grain yield across all eCO_2 treatment levels (Table 2). The genotypes showed an increase in aboveground biomass, averaged across eCO_2 treatments, of 14.7 to 47.1%. The highest increase in aboveground biomass of 47.1% [CI: 38.7-53.5%] was observed for genotype "*Anakin*" followed by "*Genebank accessions*" (46.5% [CI: 38.1-51.3%]) and "*Scarlett*" (33.5% [CI: 29.7-38%]). By contrast, the genotype "*Theresa*" showed the lowest increase in aboveground biomass of 14.7% [CI: 6.3-23.1%] under eCO_2. The highest increase in grain number of 46.1% [CI: 38.3-52.7%] and grain yield of 57.1% [CI: 43.6-64.5%] were observed for "*Genebank accessions*". The lowest effect of eCO_2 on the response of grain number of 9% [CI: 3-14%] and grain yield od 10.8% [CI: 6.2-16%] was observed for "*Theresa*". The responses of TGW and harvest index to eCO_2 did not differ among the nine genotypes (Figure 5)

CO_2 exposure methods and rooting conditions

The responses of barley yield (except for TGW) to eCO_2 were significantly affected by the four CO_2 exposure methods (Table 2). Aboveground biomass increased by 38% [CI: 26.9-47.7%] in the GC, 21.1% [CI: 16.7-26.3%] in OTC, and 12% [CI: 6-17%] in FACE under eCO_2 compared to aCO_2 (Figure 6). The highest increase in barley grain yield under eCO_2 (49.8% [CI: 40.1-55.1%]) was observed for the plants grown in the GC. In contrast, barley plants that were grown under OTC had only a 9% [CI: 3-14%] higher harvest index, while the response declined by -5.2% [CI: -10.3-0%] under OTC (Figure 6). Barley yield response was also significantly affected by rooting conditions. Higher responses of aboveground biomass (31% [CI: 26-36%]), grain number (30% [CI: 23-35%]), and grain yield (41% [CI: 34-47%]) were obtained for the plants grown in pots. However, the responses of TGW and harvest index of barley were not affected by rooting conditions (Table 2 and Figure 7).

Discussion

Responses of barley yield components to atmospheric CO_2 enrichment

This quantitative review synthesises the literature on barley yield as a function of eCO_2, temperature, and N fertilizer tretaments and provides insights into contemporary paradigms. The rise in atmospheric CO_2 causes mostly positive effects on 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 eCO_2 is similar to other reported estimates (Manderscheid et al., 2014; Thompson and Woodward, 1994; Weigel and Manderscheid, 2012). The aboveground biomass and yield showed similar patterns of increase with increasing level of eCO_2. Plants grown under a CO_2 treatment level of 551-650 ppm showed the highest response in aboveground biomass (28.7%) compared to lower CO_2 concentrations (450-550 ppm). Other studies have also reported a significant increase in aboveground biomass in barley of 38% and 24% at 550 and 650 ppm, respectively (Fangmeier et al., 2000; Weigel et al., 1994). On the other hand, a maximum increase of about 70 to 110% in aboveground biomass of two barley genotypes was reported under a eCO_2 concentration of 500 ppm (Weigel et al., 1994). FACE experiments with wheat and several crop types also reported about 12% enhancement in aboveground biomass under eCO_2 (Ainsworth and McGrath, 2010; Kimball et al., 2002; Weigel and Manderscheid, 2012). Similarly, a positive effect of eCO_2 on aboveground biomass of 37% in soybean (Ainsworth et al., 2002), 10% in ryegrass (Weigel and Manderscheid, 2012), and 21% in oilseed rape (Högy et al., 2010a) have been observed. A meta-analytic study of 79 crop and wild species also documented an average enhancement of biomass by 28% across all species due to eCO_2 (Jablonski et al., 2002).

Likewise, a positive effect of eCO_2 was recorded for grain yield (27.4%) averaged across all the studies, mainly due to the significant and positive effect of eCO_2 on grain number (27.4%). These results support findings from other studies on barley, that have reported an increase in grain yield induced by eCO_2 (Fangmeier et al., 2000; Högy et al., 2009; Weigel et al., 1994). Similarly, studies with other C3 crops, for instance, wheat (Högy et al., 2010b), soybean (Ainsworth et al., 2002), and oilseed rape (Högy et al., 2010a) have also noted significant increases in grain yield due to CO_2 enrichment of 10, 24, and 18%, respectively. In agreement with the findings from other studies, the response of TGW was not affected by eCO_2, which reflects its lower market value (Schmid et al., 2016; Weigel et al., 1994). Comparing the response of harvest index under different eCO_2 levels, the highest increase was observed for plants grown under the highest concentration level of 651-750 ppm. However, the response of harvest index of barley was not affected across all the CO_2 levels, similar to findings of other studies (Fangmeier et al., 1996; Palta and Ludwig, 2000).

The interactive effect of eCO_2, N fertilizer, and temperature

Aboveground biomass and grain yield responses were lower when eCO_2 was combined with low N level (<50 kg ha^{-1}) than with higher N levels. Nevertheless, the important interactive effects of N with eCO_2 have only rarely been studied. High positive effects of eCO_2 on the response of aboveground biomass (31%) and harvest index (20.4%) were observed under the higher N level (151-200 kg ha^{-1}). Accordingly, barley plants fertilized with 140 kg ha^{-1} N had 13% more aboveground biomass than plants fertilized with 80 kg ha^{-1} under eCO_2 (Fangmeier et al., 2000). In addition, a significant decrease in grain yield of cereal crops of between 10 and 22% was recorded under a combination of eCO_2 and 50 kg ha^{-1} N compared to 100 kg ha^{-1} N (Manderscheid et al., 2009). The response of harvest index to eCO_2 also slightly decreases under low N fertilizer (Fangmeier et al., 1996). The CO_2 enrichment effect on biomass and grain yield of barley and other cereals is negative when N accessibility is condensed compared with when it is not in accord with findings of other studies.

Even though eCO_2 had a positive effect on the yield production of barley, the effect was low under high temperatures (>25 °C). High temperature had negative impacts on aboveground biomass and grain yield compared with optimal temperatures (Högy et al., 2019; Usui et al., 2014; Wheeler et al., 1996). Consequently, aboveground biomass and grain yield decreased by -12% and -17%, respectively, when eCO_2 was combined with high temperatures (>25 °C). This might be due to the shorter duration of crop growth and development under high temperatures, and the perturbation of processes related to carbon assimilation (Stone, 2001). TGW and harvest index were not affected by the interaction of eCO_2 with temperature but TGW can decrease significantly with eCO_2 at high temperatures (Alemayehu et al., 2014; Högy et al., 2013).

Variation in the response of barley yield to eCO_2

Genotypic variation

The significant effect of genotype on barley yield response to eCO_2 was might be related to the varietal character of genotypes. The modern genotypes had higher aboveground biomass. Thus, the modern spring barley genotype "*Anakin*" had 47.1% more aboveground biomass under eCO_2 than the other genotypes. The genotype "*Genebank accessions*" had the highest grain number (46.1%) and its grain yield increased by 57.1% under eCO_2. Other studies have similarly found modern barley genotypes to higher responses than old ones (15-34%) under CO_2 enrichment (Alemayehu et al., 2014; Plessl et al., 2005; Schmid et al., 2016). Similarly, a stronger positive effect of eCO_2 on grain yield was observed for the modern genotype "*Maurit*" (released in 2004) than for old genotypes released between 1952 and 1996 (Franzaring et al., 2013). This suggests breeding for the exploitation of eCO_2 might enhance future crop production. The lowest response to eCO_2 was recorded for the genotype "*Gammel Dansk*",consistent with findings of other CO_2 enrichment studies (Clausen et al., 2011).

However, modern gentotypes do not necessarily always perform better than new ones at higher CO_2 levels. For example, the aboveground biomass of an older wheat genotype (52%) can increase more than that of a new genotype (39%) in response to increasing CO_2 (Hay and Gilbert, 2001). Furthermore, older wheat genotypes can have higher grain yield than newer genotypes under certain experimental conditions (Franzaring et al., 2013). The responses of harvest index and TGW to eCO_2 did not differ among the nine study barley genotypes but TGW can vary widely among other barley genotypes (Weigel et al., 1994). For example, a climate chamber experiment with old and new malt barley genotypes recorded higher TGW for the modern genotype "*Bambina*" (Schmid et al., 2016). A review of the harvest index of cereals found that modern genotypes had a significantly higher harvest index than older ones (HAY, 1995). Other trials with barley, oat, and oilseed rape have also shown that plant genotypes react differentially to climate change (Clausen et al., 2011; Fangmeier et al., 2000; Johannessen et al., 2005).

Experimental conditions

The response of crop yield to CO_2 enrichment scan be significantly altered by CO_2 exposure methods. But the effect of CO_2 exposure methods can vary with several factors, including yield variable andcrop species. Thus, enhancement of grain yield at eCO_2 can be lower under FACE experiments than under enclosure methods (Long et al. 2006). Similarly, aboveground biomass yield can be greater under FACE experiments thanunder the OTC or growth chamber (Tubiello et al., 2007). But rice yield can behigher for plants grown in OTCs than with FACE (Broberg et al., 2019). Our meta-analysis shows that the responses of aboveground biomass and grain yield in barley increased by 38 and 50%, respectively, when plants were grown in growth chambers, than when they were grown in FACE or OTC, in accord with earlier studies (Long et al., 2006). Similar results have been reported in meta-analyses of rice (Wang et al., 2015) and wheat (Wang et al., 2013). However, another meta-analysis of wheat noted no significant difference between FACE and OTC experiments with respect to the response of grain yield to eCO_2 (Feng et al., 2008). Nonetheless, no study seems to have directly compared the response to different CO_2 exposure methods of the same genotype grown under identical soil, environmental condition, and cultivation practice.

The effect of rooting condition on the response of barley yield to eCO_2 varies with other factors, suc has yield variable and crop species. The aboveground biomass (31.3%), grain number (30%), and grain yield (41.3%) significantly increased for barley grown in a pot rather than under field conditions. However, the responses of TGW and harvest index were insentive to the rooting condition. In sagreement with our findings, previous meta-analyses have also reported higher yield responses of pot-rooted wheat plants under eCO_2 compared to field-rooted plants (Taub and Wang, 2008; Wang et al., 2013). But other studies have also reportedsimilar responses of grain yield to eCO_2 for field-grown and pot-grown wheat plants (Feng et al., 2008). Lastly, a significant decline in TGW in wheat of up to 3% in OTC experiments can occur due to limited rooting volume (Ainsworth, 2008).

Conclusions

This meta-analysis quantified the effect of eCO_2 as a single factor and its interaction with N and temperature on barley production. A strong positive effect of eCO_2 was observed for aboveground biomass, grain yield, and grain number. However, the responses of aboveground biomass, grain number, and grain yield to eCO_2 were lower under limited N fertilizer (<50 kg ha^{-1}) or higher temperature (>25 °C). In general, the magnitude of the CO_2-induced effect on barley grain yield will depend on the future atmospheric CO_2 concentration and agronomic practices such as genotype choice, and growing conditions. Modern barley genotypes "*Anakin*" had higher aboveground biomass under eCO_2 than older ones, with "*Genebank accessions*" having the highest grain yield and grain number response to eCO_2. Uncertainties remain, however, regarding the responses to environmental stress of yield variables,mainly aboveground biomass, grain number, and grain yield e . Field experiments that better characterize the responses of barley and its interaction with additional stressors to eCO_2 can help reduce uncertainties due to climate change in estimating future food production.

Declarations

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Conflict of interest:

The authors have no conflict of interest.

Availability of data and material:

Data obtained for the current study is available.

Code availability:

Software application code is available.

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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Figures

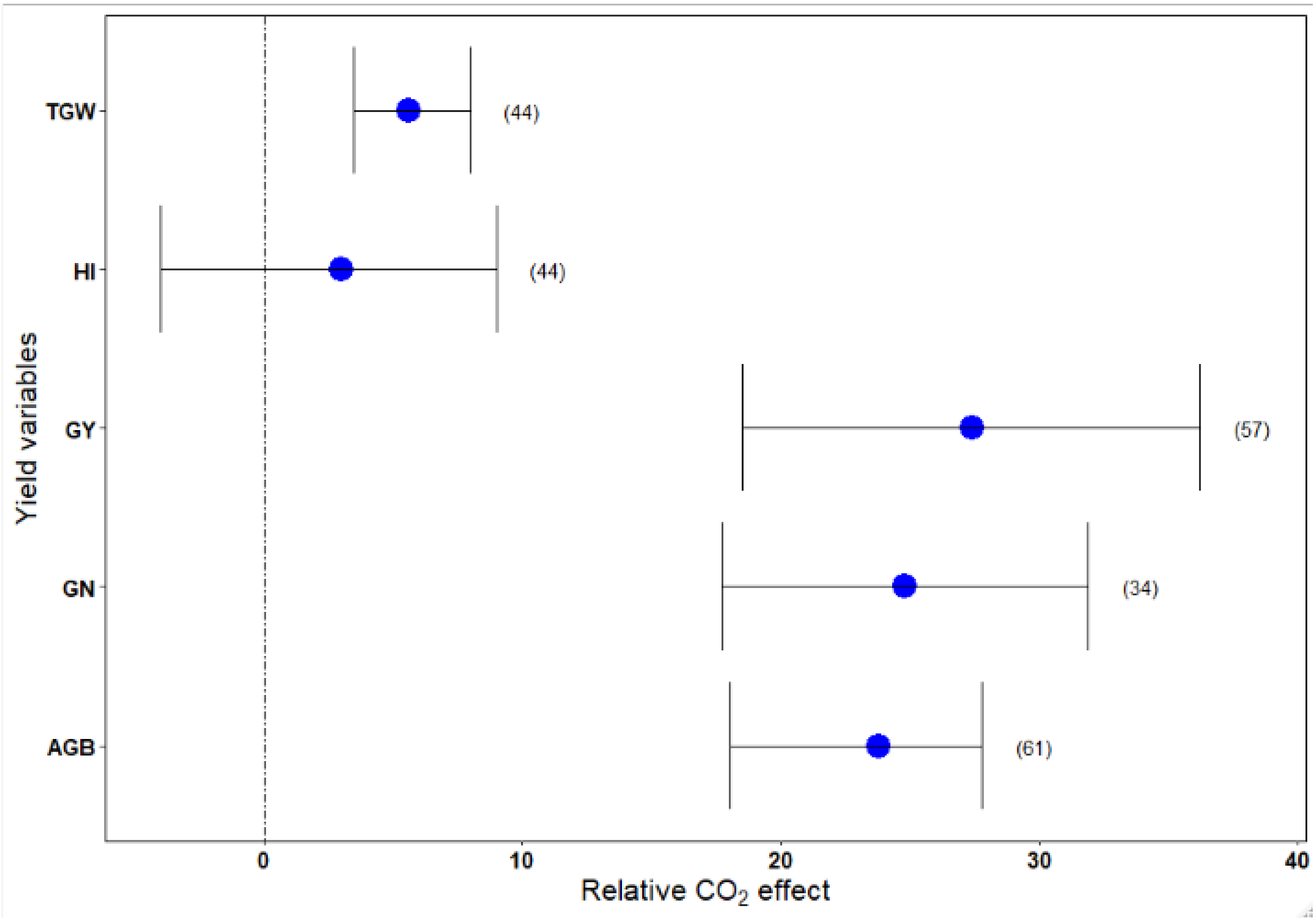

Figure 1

Relative percentage change in barley yield response to eCO2. The symbols represent the percentage change (± 95% CI) in response relative to the corresponding control. The sample size is given in parenthesiss. AGB, aboveground biomass; GN, grain number; GY, grain yield; HI, harvest index; TGW, thousand-grain weight.

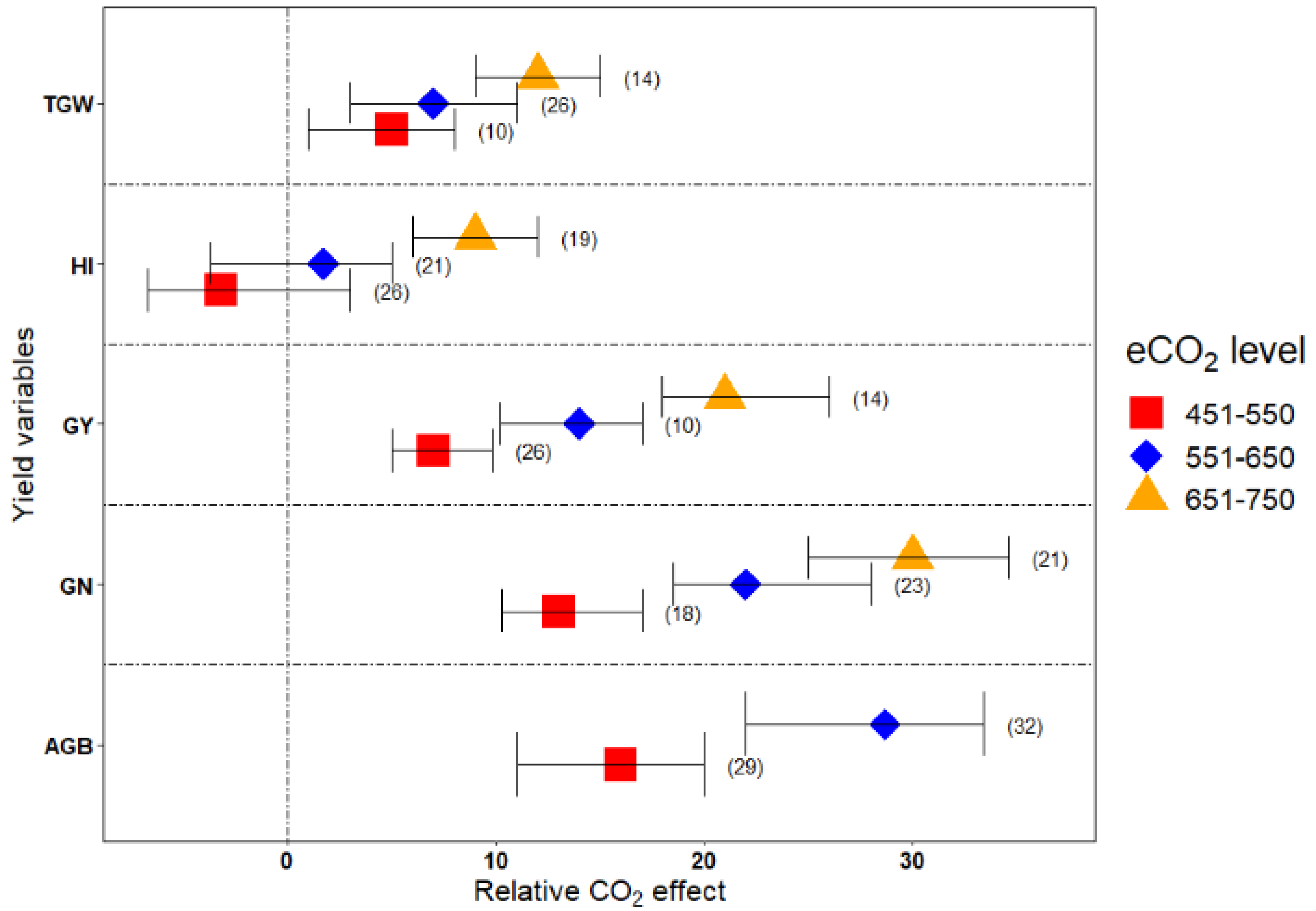

Figure 2

Relative percentage change in barley yield response to three levels of CO2 treatment (451–550, 551–650, 651-750 ppm). The symbols represent the percentage change (± 95% CI) in response relative to the corresponding control. The numbers of observations are given in parentheses. AGB, aboveground biomass; GN, grain number; GY, grain yield; HI, harvest index; TGW, thousand-grain weight.

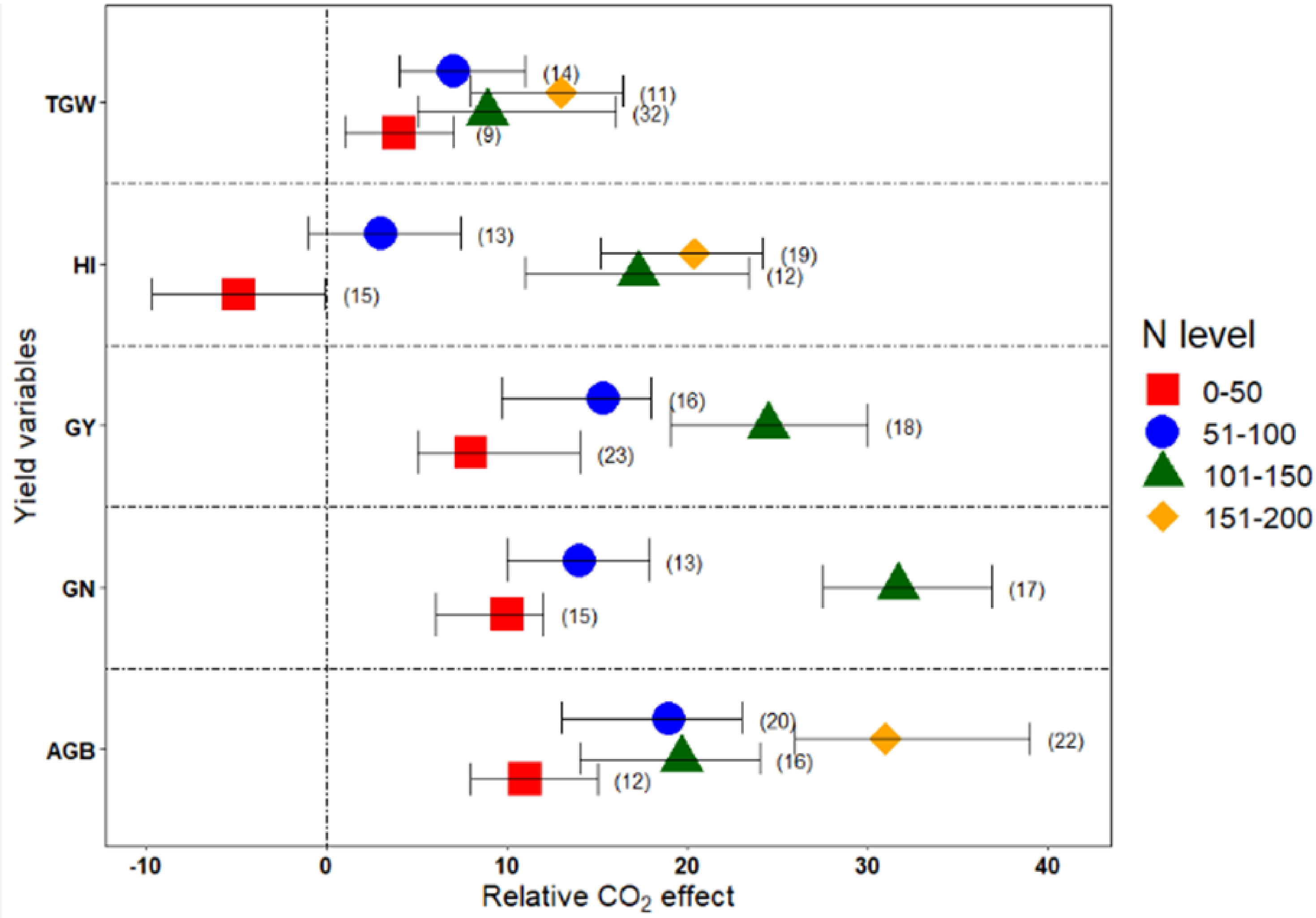

Figure 3

Relative percentage change in barley yield response to eCO2 under four different N fertilization treatments. The four levels of N were 0-50, 51-100, 101-150, 151-200 kg ha-1. The symbols represent the percentage change (± 95% CI) in response relative to the corresponding control. The sample size is given in parenthesiss. AGB, aboveground biomass; HI, harvest index; TGW, thousand-grain weight.

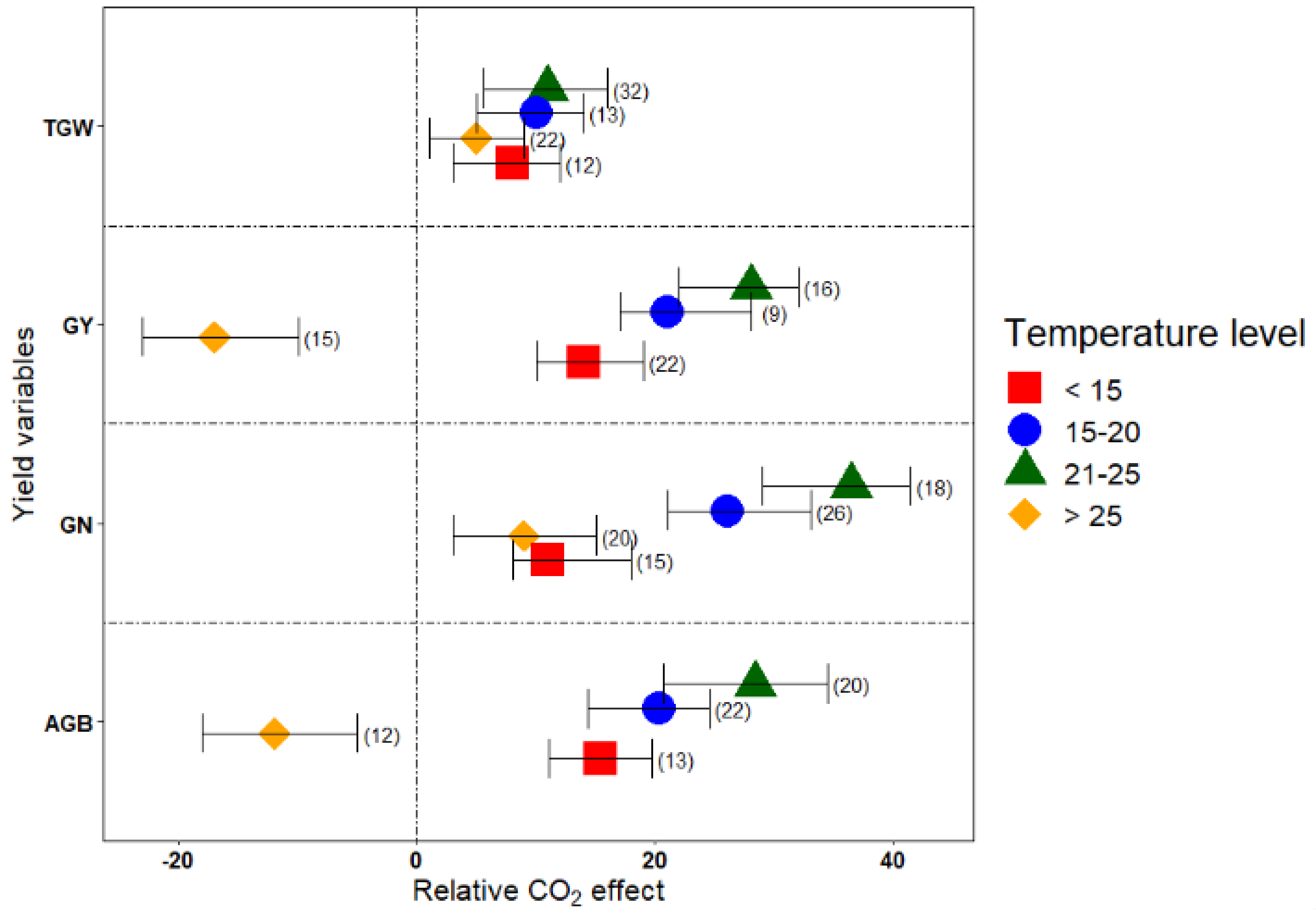

Figure 4

Relative percentage change in barley yield response to eCO2 under four different temperature treatements. The four temperature levels were <15, 15-20, 21-25, >25 °C. The symbols represent the percentage change (± 95% CI) in response relative to the corresponding control. The sample size given in parenthesis. AGB, aboveground biomass; GN, grain number; GY, grain yield; TGW, thousand-grain weight.

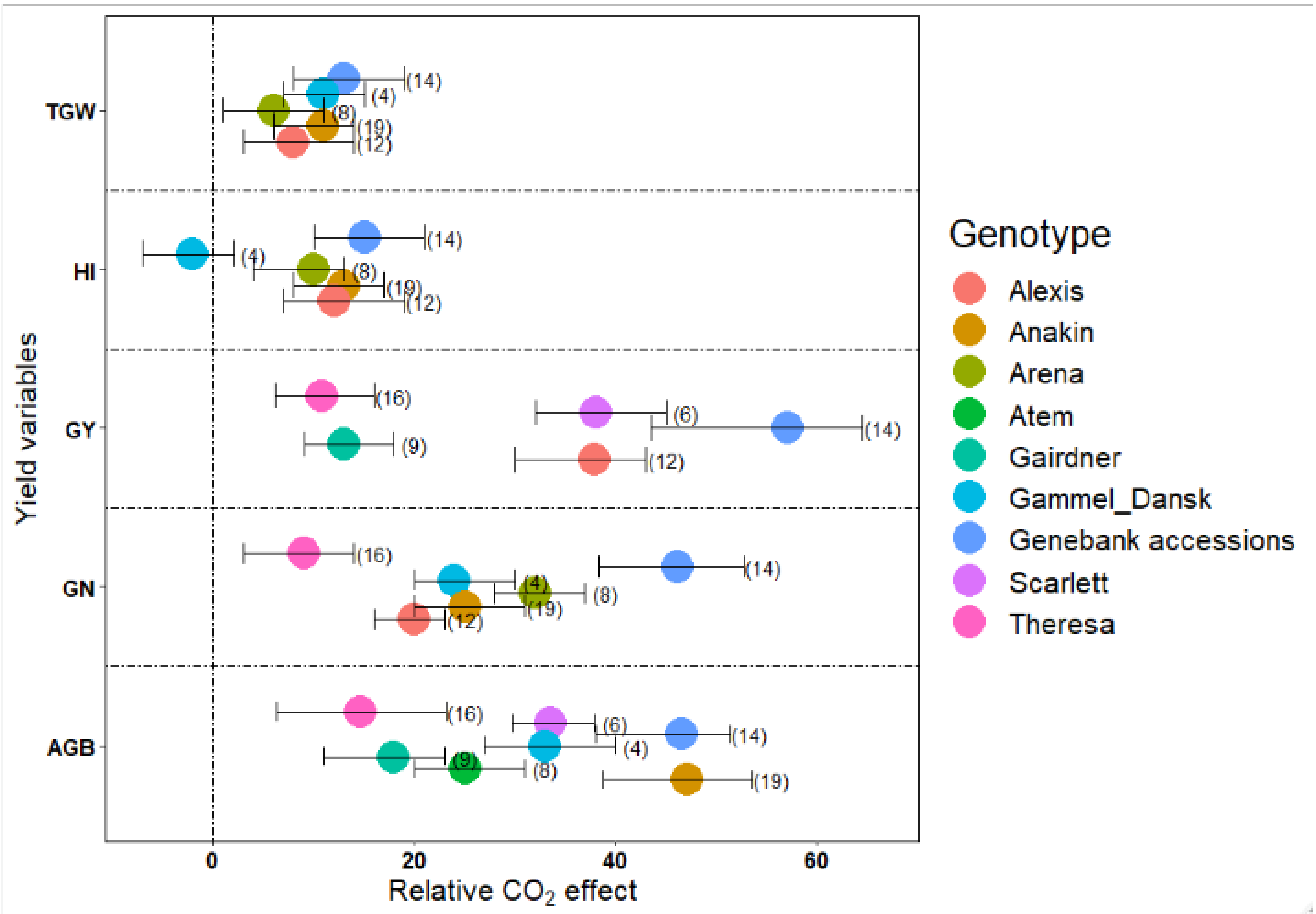

Figure 5

Relative percentage change in yield response to eCO2 for nine different barley genotypes. The symbols represent the percentage change (± 95% CI) in response relative to the corresponding control. The sample size is given in parenthesis. AGB, aboveground biomass; GN, grain number; GY, grain yield; HI, harvest index; TGW, thousand-grain weight.

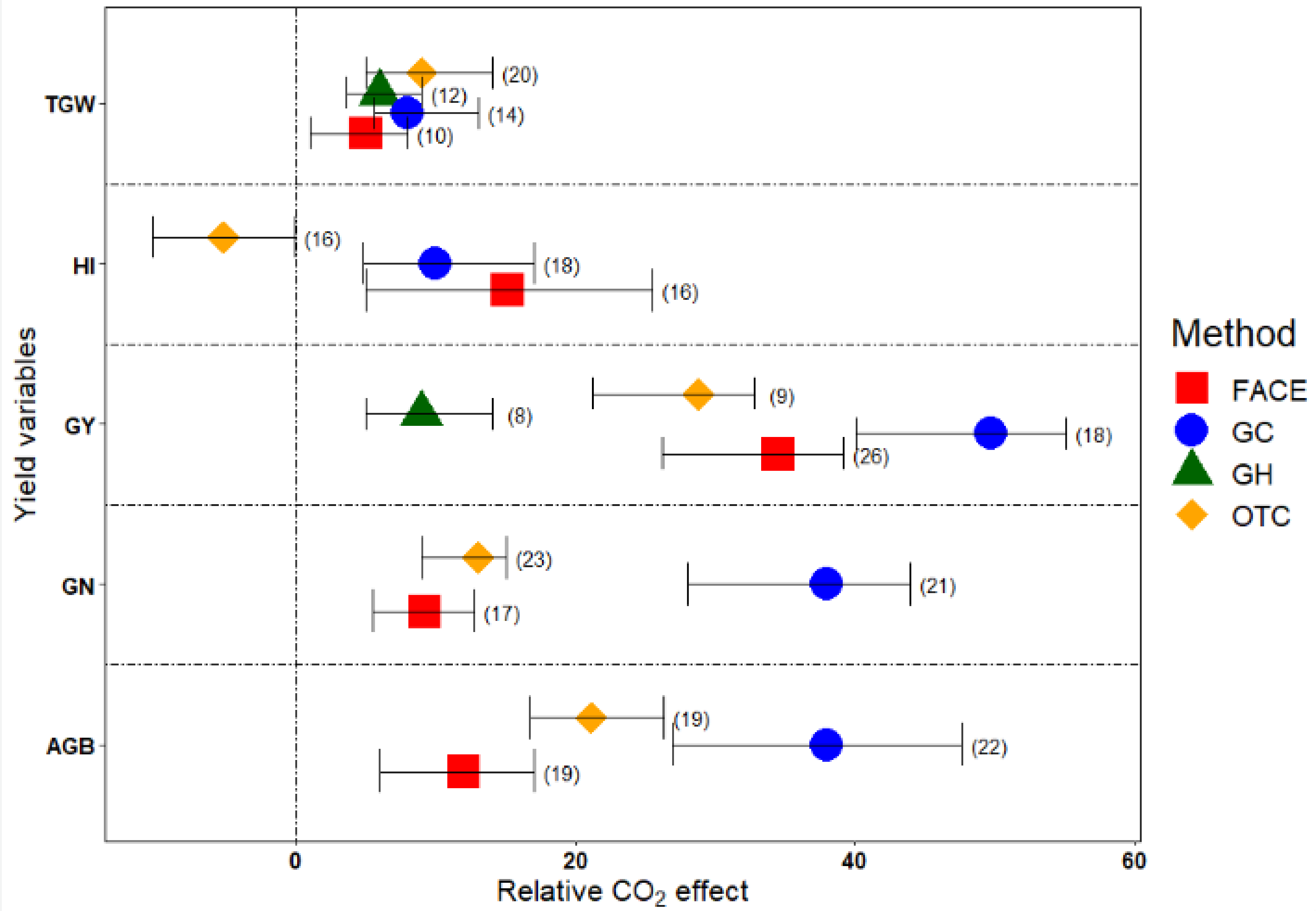

Figure 6

Relative percentage change in barley yield response to eCO2 under fourdifferent CO2 exposure methods. The four exposure methods were free-air CO2 enrichment (FACE), growth chambers (GC), greenhouses (GH), open-top chambers (OTC). The symbols represent the percentage change (± 95% CI) in response relative to the corresponding control. The sample size is given in parenthesiss. AGB, aboveground biomass; GN, grain number; GY, grain yield; HI, harvest index; TGW, thousand-grain weight.

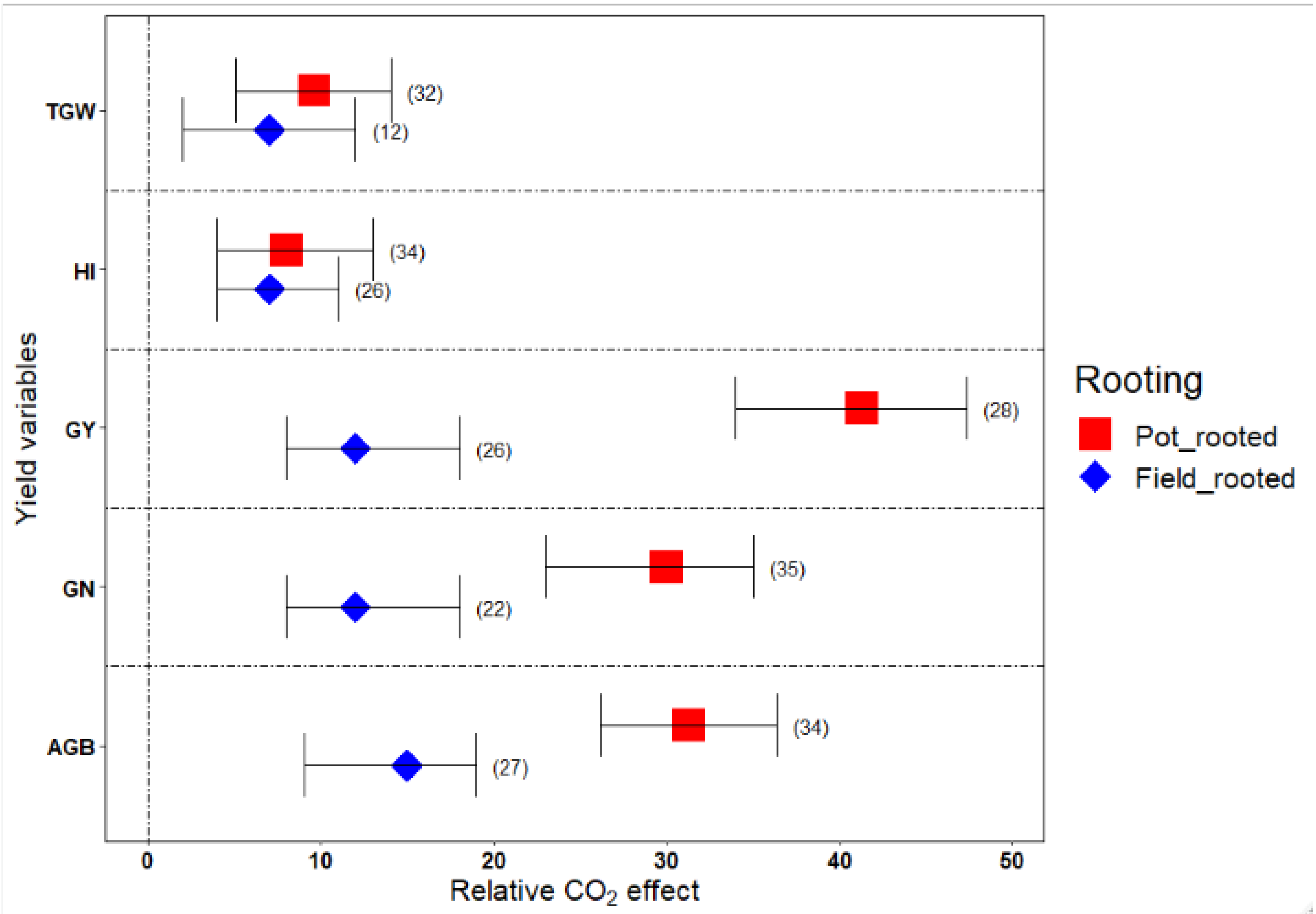

Figure 7

Relative percentage change in barley yield response to eCO2 under two different rooting conditions (Field rooted and Pot rooted). The symbols represent the percentage changes (± 95% CI) in response relative to the corresponding controls. The sample sizeis given in parenthesis. AGB, aboveground biomass; GN, grain number; GY, grain yield; HI, harvest index; TGW, thousand-grain weight.

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