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Decreased wheat grain yield stimulation by free air CO_2 enrichment under N deficiency is strongly related to decreased radiation use efficiency enhancement

Markus Dier[a,c], Jan Sickora[a], Martin Erbs[b], Hans-Joachim Weigel[a], Christian Zörb[c], Remy Manderscheid[a,*]

[a] *Thünen Institute of Biodiversity, Bundesallee 50, D-38116 Braunschweig, Germany*
[b] *Deutsche Agrarforschungsallianz (DAFA), German Agricultural Research Alliance, c/o Thünen Institute, Braunschweig, Germany*
[c] *Institute of Crop Science, Quality of Plant Products, University of Hohenheim, Emil-Wolff-Str. 25, D-70599 Stuttgart, Germany*

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ABSTRACT

Uncertainty still exists about the extent and mechanisms of yield stimulation by elevated atmospheric CO_2 (e[CO_2]) in wheat. Particularly, data of the e[CO_2] effect under severe N deficiency from field experiments are scarce. To investigate the interaction of e[CO_2] and N fertilization on important variables that determine grain yield and are often used in crop simulation models, e.g. radiation absorption by the canopy (AR), radiation use efficiency (RUE) and specific leaf N weight (SLNW), a two-year Free Air CO_2 Enrichment (FACE) experiment was conducted with two [CO_2] (393 and 600 ppm) and three N levels (severe N deficiency (Nd) with 40 (1st year) and 35 kg N ha^{-1} (2nd year); adequate N supply with 180 (1st year) and 200 kg N ha^{-1} (2nd year); and excess N supply with 320 kg N ha^{-1} (1st and 2nd year).

Final aboveground biomass ranged from 816 to 2012 g m^{-2} and grain yield from 417 to 973 g m^{-2}. e[CO_2] increased aboveground biomass by 13, 18 and 14% and grain yield by 10, 17 and 17% under Nd, Nad and Nex, respectively. Yield stimulation was primarily due to enhanced grain number. With increasing N supply, peak values of green area index were increased under e[CO_2] by 4 up to 22%, while AR was unaffected. RUE was increased by both rising SLNW, which depended on N supply, and e[CO_2] and the RUE increase was larger under Nad (+20%) and Nex (+18%) than under Nd (+6%). SLNW was decreased by e[CO_2] and this decrease was very similar among N levels (~ −6%). However, if leaf area index was included as covariable, then a e[CO_2] induced decrease of SLNW was only found under Nd.

The present study demonstrates that yield stimulation by e[CO_2] is smaller under severe N deficiency compared to high N supply in wheat. In contrast to the results of another FACE study, this decrease was not due to reduced AR but reduced RUE, which might be attributed to both restrictions on source activity, i.e. photosynthetic capacity and sink size, i.e. ear growth.

1. Introduction

Atmospheric CO_2 concentration is continuing to rise from current 400 up to 730–1020 ppm by the end of this century (IPCC, 2013). Elevated CO_2 concentration (e[CO_2]) will increase air temperature and thus possibly the frequency and severity of weather extremes that could reduce future crop yields (IPCC, 2013). On the other hand, e[CO_2] increases photosynthesis in C_3 plants (Ainsworth and Long, 2005) and reduces stomatal conductance in C_3 and C_4 plants (Ainsworth and Rogers, 2007; Wang et al., 2013), which often lead to stimulation of biomass production and grain yield (Ainsworth and Long, 2005; Manderscheid et al., 2014).

Wheat is the third most important crop in terms of global production and its range of cultivation plays a key role for food security (Shewry and Hey, 2015). Crop models predict that growth stimulation of C_3 crops by e[CO_2] will compensate for yield losses due to rising air temperature up to 2 °C, but the extent of this compensation might be different depending on the region and its related agricultural conditions such as N fertilizer availability (Rosenzweig et al., 2014). Therefore, uncertainty still exists about the extent of wheat yield stimulation by future e[CO_2]. Free Air CO_2 Enrichment (FACE) experiments can help to overcome this uncertainty and were conducted with wheat in

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* Corresponding author.
E-mail address: remy.manderscheid@thuenen.de (R. Manderscheid).

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Arizona (Kimball et al., 2002), Australia (Tausz-Posch et al., 2012), China (Kou et al., 2007; Ma et al., 2007; Lam et al., 2012; Han et al., 2015; Cai et al., 2016) and Germany (Högy et al., 2009; Weigel and Manderscheid, 2012). However, comprehensive growth data from such studies, especially those on the interactions between e[CO_2] and N fertilization, are still scarce (Rosenzweig et al., 2014; Vanuytrecht and Thorburn, 2017).

Grain yield (Y) can be described as a function of three factors describing fundamental processes: (i) absorbed photosynthetic active radiation (PAR) accumulated over the growing season (AR), (ii) conversion efficiency of AR to biomass (radiation use efficiency: RUE) and (iii) share of produced biomass allocated to the grains (harvest index: HI):

$$Y = AR * RUE * HI \tag{1}$$

AR is determined by the size and evolution of the green area index (GAI), the sum of the green surfaces of leaves, stems and ears. RUE increases with rising light-saturated net photosynthetic rate in a curvelinear manner (Sinclair and Horie, 1989) and both variables depend on both the leaf biochemical composition such as level and activity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) and the internal structure of the leaf. Easily determinable proxies for the variables describing the leaf biochemical composition and internal structure are green leaf N concentration, leaf mass per unit leaf area (specific leaf weight) and their composite variable leaf N mass per unit leaf area (specific leaf N weight). Increase in soil N availability stimulates crop growth primarily by increasing the size and duration of GAI and thus AR (Garcia et al., 1988; Jamieson et al., 2000). RUE is not influenced over a broad range of leaf and soil N levels, but declines sharply when these N levels become very low (Sinclair and Horie, 1989). Effects of e[CO_2] are expressed primarily through effects on RUE via influencing the activity of RuBisCO (Long, 1991; Jamieson et al., 2000).

Variation in grain yield due to e[CO_2] is primarily due to variation in grain number (Högy et al., 2009; Cai et al., 2016), but some studies also found e[CO_2] effects on individual grain weight (Fernando et al., 2014; Tausz-Posch et al., 2015). Grain number is strongly associated with growth between flag leaf emergence and anthesis (Bindraban et al., 1998), the period in which radiation supply (Fischer, 1975) and e[CO_2] (Fischer and Aguilarm, 1976) have their greatest influence on grain number.

CO_2 enrichment studies with chambers (Sionit et al., 1981; Wolf, 1996) and FACE (Kimball et al., 2002; Weigel and Manderscheid, 2012) showed that growth stimulation of wheat by e[CO_2] declined when N supply decreased. Kimball et al. (2002) reported for the Arizona FACE study, the only previous FACE study that had a severe N deficiency treatment, that the grain yield increase under e[CO_2] was only half as much under severe N deficiency compared to ample N supply. Nevertheless, FACE studies showed similar biomass and grain yield increases under e[CO_2] in plants grown under low and high N supply (Ma et al., 2007; Han et al., 2015). In the two-year FACE study of Weigel and Manderscheid (2012) lower grain yield stimulation under moderate N deficiency as compared to adequate N supply was only observed in one year.

While AR, RUE and harvest index are important parameters used in many crop models, only little experimental data from FACE experiments related to these parameters exists (Vanuytrecht et al., 2012), which might be responsible for the poor representation of CO_2 x N interactions in crop growth models (Rosenzweig et al., 2014; Vanuytrecht and Thorburn, 2017). According to Jamieson et al. (2000), the smaller grain yield stimulation of e[CO_2] under severe N deficiency in the Arizona FACE experiment was due to reduced AR because of accelerated canopy senescence under e[CO_2]. Moreover, in the same experiment e[CO_2] reduced leaf N concentration by up to -25% (Kimball et al., 2002) under severe N deficiency when leaf N levels were low (Sinclair et al., 2000), but there was hardly any reduction of leaf N concentration by e[CO_2] under ample N supply (Kimball et al., 2002). Based on these findings, it was concluded that photosynthetic capacity is primarily reduced by e[CO_2] under very low N availability (Rubio-Asensio and Bloom, 2016), which might result in smaller stimulation of RUE by e[CO_2] under such N levels compared to high N supply. However, there is no field study available for wheat that has investigated in wheat the CO_2 x N interaction on RUE. Because limited N fertilizer levels are affordable in many developing countries, investigating e[CO_2] effects on yield formation under severe N deficiency is of overall importantance to provide more accurate predictions of future global food security.

In the present study a two-year FACE experiment was conducted with winter wheat (*Triticum aestivum* L.) under irrigated agriculture to avoid interactive effects with water stress supplied with three levels (severe deficiency, adequate, excess) of N fertilizer. The main objective was to analyze how e[CO_2] influences growth and yield formation under a broad range of N fertilizer levels, and in particular whether and to what extent growth and yield stimulation by e[CO_2] is lower under severe N deficiency compared to high N supply. Moreover, the specific question was addressed: is lower grain yield stimulation by e[CO_2] under severe N deficiency associated with (i) decreased AR under e[CO_2] due to accelerated canopy senescence or (ii) reduced RUE stimulation by e[CO_2] compared to high N supply due to a strong decrease of leaf N concentration?

2. Material and methods

2.1. Study site and experimental design

The experiment was conducted on a field site (52°18′N, 10°26′E, 79 m.a.s.l.) at the Thünen-Institute in Braunschweig, Germany in 2014 and 2015. The soil profile has a depth of about 60 cm (30 cm Ap, 15 cm Al, 15 cm Bt, and > 60–70 cm CII) and the lower layers are almost pure sand. The soil in the plough horizon (0–40 cm) is a luvisol of loamy sand texture (69% sand, 24% silt and 7% clay) with a pH of 6.88, and a carbon and nitrogen (N) content of 1.00% and 0.09%, respectively. Soil N levels at the beginning of the main growing season (mid-March) were 14.2 and 22.4 kg N ha^{-1}. The lower (−1.5 MPa soil water tension) and upper limit (0.01 MPa soil water tension) of plant available soil water are a volumetric soil water content of 5 and 23%, respectively. The soil water amount in the 0–40 cm soil profile at the beginning of the main growing season was 92 mm. Altogether, the soil has low to intermediate fertility with a shallow rooting zone.

Winter wheat (*Triticum aestivum* L. variety “Batis”) was grown at ambient [CO_2] and e[CO_2] in circular plots (diameter 20 m), in which three N subplots (3 m × 5 m) were randomly established. Overall the experiment consisted of six different CO_2 x N treatments that were replicated three times. The CO_2 and N treatments had the same position on the field site in 2014 and 2015.

2.2. CO_2 enrichment

CO_2 enrichment was carried out with a Free Air CO_2 Enrichment (FACE) system with blowers constructed according to the Brookhaven National Laboratory design (Lewin et al., 1992). CO_2 enrichment started from the four leaf stage on March 31 in 2014 and the three leaf stage on March 12 in 2015. CO_2 enrichment took place during the day and was interrupted when wind speed exceeded 6 m s^{-1} or air temperature fell below 5 °C. The 1 min average [CO_2] in the e[CO_2] plots was within 600 ppm ± 10% for 95.6% of the operation time in 2014 and 95.7% for the one in 2015. During the CO_2 enrichment period, average [CO_2] in the ambient plots was 394 in 2014 and 392 ppm in 2015.

2.3. Crop management

Winter wheat was sown with a density of 380 kernels per m^{-2} on October 29 in 2014 and on November 4 in 2015. Crop management measures were performed according to local farm practice with